Universidad de Oviedo

Programa de Doctorado en Biogeociencias

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El oso pardo (*Ursus arctos*) en la Cordillera Cantábrica como ejemplo de la coexistencia entre humanos y grandes carnívoros en ambientes humanizados

Brown bear (*Ursus arctos*) in the Cantabrian Mountains as an example of the coexistence between humans and large carnivores in human-dominated landscapes

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RESUMEN (en español)

Ampliar el conocimiento sobre la ecología de los grandes carnívoros, así como sobre los conflictos que plantean sus interacciones con los humanos, es de vital importancia para promover su conservación y una coexistencia sostenible, especialmente en ambientes muy humanizados. Dada la recuperación de muchas poblaciones y la colonización de nuevos territorios, las interacciones de estas especies con las actividades humanas podrían aumentar, lo que pone en riesgo la sostenibilidad de sus poblaciones.

El objetivo principal de esta tesis es estudiar la ecología de la población de oso pardo de la Cordillera Cantábrica y la influencia que tiene sobre ella un ambiente altamente humanizado. Los resultados que se presentan en esta tesis sirven a su vez como base para hacer recomendaciones de gestión y conservación de la especie, exponiendo amenazas y situaciones que pueden afectar su viabilidad. Con este propósito, esta tesis se compone de los siguientes capítulos:

En el Capítulo 1 se abordan las preferencias de hábitat de esta población, además de su expansión. En la Cordillera Cantábrica, los osos prefieren zonas de bosque de gran altitud y pendiente, bastante inaccesibles para el humano. En el área occidental de Asturias estas zonas ya están ocupadas por el oso, por lo que su aumento y dispersión a territorios cercanos les pondría más en contacto con las personas. Las infraestructuras que separan las dos subpoblaciones son un gran impedimento para la dispersión pero la mejora de la conectividad podría favorecer su expansión a zonas del oriente de Asturias, donde la especie todavía dispondría de hábitats favorables no ocupados.

En el Capítulo 2 se aborda la selección de hábitat de los diferentes grupos de oso durante la reproducción, ya que el infanticidio es una importante causa de mortalidad de las crías. Aunque en esta población las hembras también recurran a la poligamia para reducir la posibilidad de un infanticidio, seleccionar zonas que no solapen con las de reproducción también puede ser una ventaja. Pero dada el área de distribución restringida y la disponibilidad limitada de hábitat para los osos de la Cordillera Cantábrica las zonas utilizadas por las hembras con crías en la Cordillera Cantábrica solapan con las zonas de reproducción.

En el Capítulo 3 se estudian los cambios en el comportamiento en función de la distancia a infraestructuras humanas. Nuestros hallazgos sugieren que el patrón general de los osos de evitar a los humanos se adapta al paisaje modificado por el hombre en el que habitan. Los principales cambios en los comportamientos de alerta reflejan las relaciones de dominancia y patrones de evitación entre los diferentes tipos de oso en cada época del año. Esto sugiere que los osos pueden haber elegido previamente zonas donde el efecto de las actividades humanas es menor, o una adaptación del comportamiento de los osos a la presencia humana.

En el Capítulo 4 se analizan los patrones espacio-temporales de aparición de conflictos, específicamente los daños producidos por el oso a ganado, cultivos y colmenas. Conocer las causas y pudiendo prever dónde y cuándo es más probable que ocurran conflictos es de vital importancia para enfocar los esfuerzos de prevención adecuadamente. Así, en este capítulo se pone de manifiesto la necesidad de estudios particulares, ya que los conflictos dependen mucho de cada población y su comportamiento, así como de los usos del suelo, las condiciones climáticas e incluso las particularidades de cada unidad territorial.

En conclusión, esta tesis proporciona resultados que deberían ser utilizados para diseñar estrategias de conservación mejoradas para promover la persistencia a largo plazo de los osos pardos de la Cordillera Cantábrica. Además, los nuevos conocimientos y la mejor comprensión de los resultados obtenidos en esta tesis deberían ser de interés para otras especies, contextos de gestión y áreas de estudio en las que la coexistencia entre humanos y grandes carnívoros es importante para la conservación.

RESUMEN (en Inglés)

Increasing knowledge about large carnivore's ecology, as well as about the conflicts posed by their interactions with humans, is of vital importance in promoting their conservation and sustainable coexistence, especially in highly human-dominated landscapes. Given the recovery of many populations and the colonization of new territories, the interactions between these species and human activities could increase, putting at risk the sustainability of their populations.

The main objective of this thesis is to study ecology of the brown bear population in the Cantabrian Mountains and the influence that a highly human-dominated landscape has on it. The results presented in this thesis serve in turn as a basis for making management and conservation recommendations for the species, exposing threats and situations that can affect its viability. To this end, this thesis consists of the following chapters:

Chapter 1 addresses the habitat preferences of this population, as well as its expansion. In the Cantabrian Mountains, bears prefer high altitude and sloping forests, quite inaccessible to humans. In the western area of Asturias these territories are already occupied by the bear, so their increase and dispersion to nearby territories would put them in more contact with people. The infrastructures that separate the two subpopulations are a great barrier to dispersion but the improvement of connectivity could favour its expansion to areas in the east of Asturias, where the species would still have favourable habitats that are not occupied.

Chapter 2 deals with habitat selection for different groups of bears during reproduction, since infanticide is an important cause of mortality of the cubs. Although females in this population also use polygamy to reduce the possibility of infanticide, selecting areas that do not overlap with breeding areas can also be an advantage. However, given the restricted distribution area and the limited availability of habitat for bears in the Cantabrian Mountains, the areas used by females with cubs in the Cantabrian Mountains overlap with the breeding areas.

In Chapter 3, changes in behaviour as a function of distance from human infrastructure are studied. Our findings suggest that the general pattern of bears avoiding humans is adapted to the human-modified landscape in which they live. The main changes in avoidance behaviours reflect the dominance relationships and avoidance patterns among different bear types in each season. This suggests that bears may have previously chosen areas where the effect of human activities is lower, or an adaptation of bear behaviour to human presence.

Chapter 4 discusses spatial and temporal patterns of conflict occurrence, specifically bear damage to livestock, crops and beehives. Knowing the causes and being able to predict where and when conflicts are most likely to occur is vital to focus prevention efforts appropriately. Thus, this chapter highlights the need for particular studies, since conflicts are highly dependent on each population and its behavior, as well as on land uses, climate conditions and even the particularities of each territorial unit.

In conclusion, this thesis provides results that should be used to design improved conservation strategies to promote the long-term persistence of Cantabrian brown bears. Furthermore, the new knowledge and better understanding of the results obtained in this thesis should be of interest to other species, management contexts and study areas where coexistence between humans and large carnivores is important for conservation.

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ÍNDICE

“The greatest threat to our planet is the

belief that someone else will save it”

Robert Swan

INTRODUCCIÓN GENERAL

La importancia de los grandes carnívoros

Se consideran como grandes carnívoros aquellas especies de gran tamaño, con amplios territorios y gran capacidad de desplazamiento, altos requerimientos energéticos y bajas tasas de reproducción y densidad de población (Carbone et al., 1999). Son especies icónicas, pero a la vez en precario estado de conservación. Además, son clave en el mantenimiento del equilibrio ecológico de los hábitats en los que residen (Ripple et al., 2014).

Al encontrarse en la cima de la cadena alimentaria, controlan interacciones entre todos los niveles tróficos (Miller et al., 2001). Regulan la densidad y la calidad de las poblaciones de sus presas, reduciendo la presión herbívora que impide la regeneración de la vegetación (Bowyer et al., 2005) y, al alimentarse de los individuos más débiles y accesibles, también la prevalencia de enfermedades infecciosas que pueden incluso transmitirse al ganado doméstico (Packer et al., 2003; Tanner et al., 2019). A su vez, reducen la abundancia de mesocarnívoros como zorros, garduñas o tejones, lo que se deriva a su vez en un reajuste de la distribución de ungulados y otros herbívoros más pequeños (Estes et al., 2011; Suraci et al., 2016). Algunos de estos grandes carnívoros, como los osos, debido a su condición omnívora, actúan también como dispersores de semillas (Koike et al., 2008; Lalleroni et al., 2017).

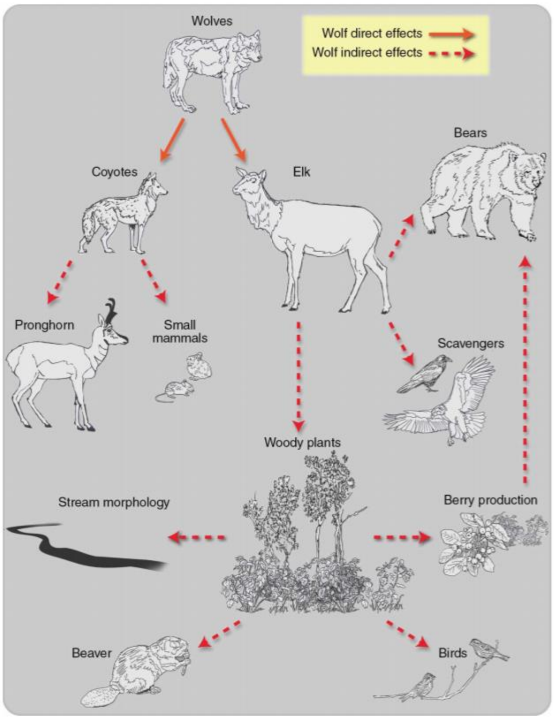


Figura 1. Diagrama conceptual que muestra los efectos directos (líneas continuas) e indirectos (líneas discontinuas) de la reintroducción del lobo gris en el ecosistema de Yellowstone, Estados Unidos. Imagen obtenida de Ripple et al. (2014).

Además, al ser especies tan carismáticas y llamativas (especies "bandera") y tener unos requerimientos de hábitats tan grandes y a veces específicos, sirven como "paraguas" para la conservación de otras especies que se incluyen en su mismo hábitat y que pueden no llamar tanto la atención (Gittleman et al., 2001; Linnell et al., 2000). Incluso influyen en la productividad neta de los ecosistemas, así como en los ciclos del carbono y de nutrientes (Ripple et al., 2014; Schmitz et al., 2010; Wilmers and Schmitz, 2016). Aportan también grandes beneficios económicos asociados al turismo de naturaleza (Richardson and Loomis, 2009).

Pero todo ello no niega que los grandes carnívoros también produzcan conflictos que se derivan de su presencia en zonas dominadas por el ser humano, a menudo asociados a amenazas a la propiedad o a la seguridad de las personas (Kleiven et al., 2004; Muhly and Musiani, 2009). Debido a ello, los potenciales beneficios ligados a estas especies han sido en general subestimados por la sociedad, que les ha perseguido durante siglos debido a estos conflictos (Ripple et al., 2014).

Estado de las poblaciones y amenazas

En los últimos dos siglos muchas de las poblaciones de grandes carnívoros se han visto mermadas hasta rozar la extinción, especialmente debido a su persecución (Woodroffe, 2000). Actualmente, gracias a una legislación más protectora y tolerante que aboga por la recuperación y el mantenimiento de sus poblaciones, y la implementación de importantes acciones de conservación y manejo, su precaria situación está revirtiendo (Chapron et al., 2014; Linnell et al., 2001).

Pero estas especies todavía se enfrentan a múltiples, y generalmente concurrentes, amenazas que ponen en riesgo su supervivencia. Ahora que se están recuperando y recolonizando antiguos territorios, muchas zonas se han desacostumbrado a su presencia tras tantos años de ausencia, lo que catapulta la percepción de riesgo y aviva aún más el miedo hacia estos animales (Linnell et al., 1996; Löe and Röskaft, 2019). Además, muchas de las zonas de distribución de estos animales se caracterizan por una alta densidad humana, actividades como la agricultura o la ganadería muy extendidas y una red de transporte bastante densa, todo ello en creciente expansión, lo que fomenta la aparición de conflictos (Chapron et al., 2014).

Por ello, y aunque muchas de estas especies están ya protegidas por la ley, todavía se permite la caza de determinado número de individuos en algunas zonas (Treves, 2009). Además, la caza ilegal o el envenenamiento se siguen utilizando para evitar los conflictos e incluso con fines comerciales, lo que dificulta en gran medida su conservación (Challender and Macmillan, 2014; Liberg et al., 2012; Pohja-mykrä and Kurki, 2014). A su vez, la pérdida, degradación y fragmentación del hábitat promovida cada vez más por el crecimiento de las poblaciones humanas compromete la viabilidad de los grandes carnívoros (Crooks et al., 2011). Y la reducción y el deterioro de las poblaciones de sus presas, que sufren amenazas similares y de las que dependen para subsistir, agrava más aún su situación (Wolf and Ripple, 2016).

El cambio climático también afecta a sus hábitats y recursos tróficos. Variaciones en la floración y fructificación requieren grandes cambios en la dinámica anual de millones de especies, influyendo en su comportamiento, desplazando sus patrones estacionales e incluso privándoles de su alimento (Bellard et al., 2012; Penteriani et al., 2019). Responder a estos cambios requiere una gran capacidad de adaptación, pero la gran velocidad a la que se están produciendo reduce inmensamente las posibilidades de adaptarse y sobrevivir para muchas especies, lo que afecta a la estructura de los ecosistemas (Walther et al., 2002). Además, las poblaciones de pequeño tamaño y aisladas, especialmente las localizadas en entornos altamente humanizados, son especialmente vulnerables y menos capaces de responder a las perturbaciones (Lande, 1988).

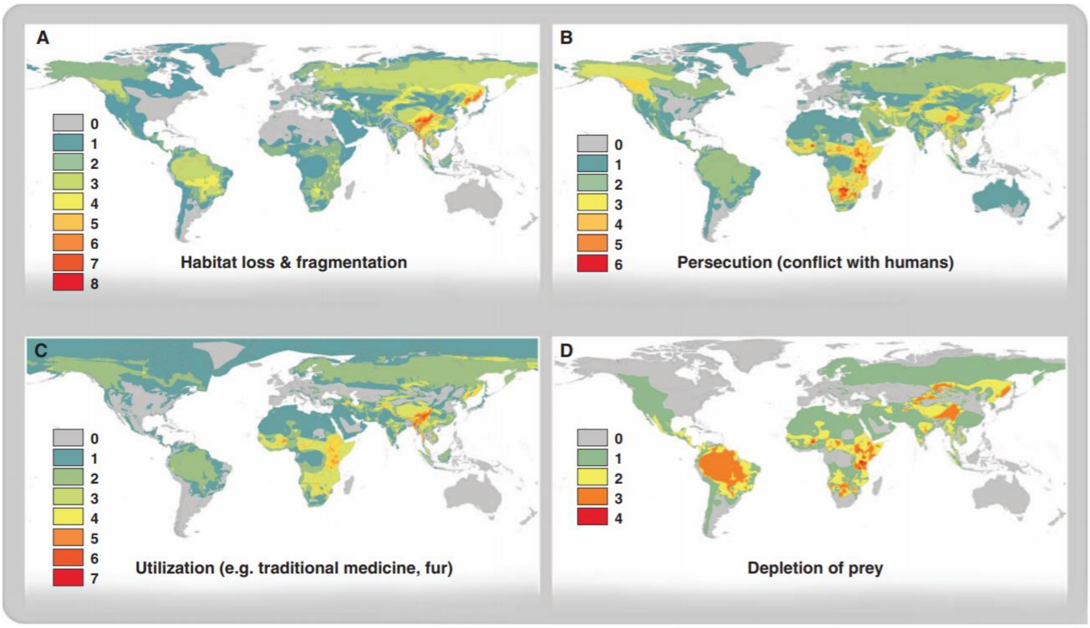


Figura 2. Mapas que muestran el solapamiento espacial de las áreas de distribución de las especies de grandes carnívoros por categoría de amenaza para: (A) la pérdida y fragmentación del hábitat, (B) la persecución, (C) la utilización (e.g. medicina tradicional, pieles) y (D) el agotamiento de las presas. El número de especies de grandes carnívoros afectados por cada amenaza específica se muestra en la leyenda de cada mapa. Obtenida de Ripple et al. (2014).

La presencia y actividad humana puede influir también sobre el comportamiento de los animales, alterando su distribución y uso del espacio, patrones de actividad, hábitos alimenticios, e incluso su reproducción o el cuidado de las crías, reduciendo su ratio de supervivencia (Ciuti et al., 2012; Oriol-Cotterill et al., 2015; Smith et al., 2017; Tuomainen and Candolin, 2011). Incluso el turismo de observación de naturaleza puede tener efectos negativos sobre los individuos, especialmente si no está regulado de manera adecuada, causando estrés e influyendo en su comportamiento natural en sus zonas de distribución (Higham and Shelton, 2011; Vincenzo Penteriani et al., 2017).

Coexistencia y conservación

La presencia de los grandes carnívoros en zonas humanizadas siempre ha llevado ligada la aparición de conflictos. La dieta rica en proteínas de estas especies y sus grandes áreas de distribución los sitúan en competencia directa con los humanos, que tienen necesidades similares (Treves and Karanth, 2003). Los daños a ganado son la principal fuente de conflictos con los carnívoros en la mayor parte del mundo, generando pérdidas económicas considerables (Bautista et al., 2019). Los ataques a personas también son un problema que genera preocupación, especialmente con el aumento de las actividades al aire libre, ya que los encuentros inesperados con uno de estos animales pueden acabar en tragedia (Penteriani et al., 2016). Pero tanto la vulnerabilidad de los grandes carnívoros ante la extinción como su capacidad de estructurar y mantener el funcionamiento de los ecosistemas hacen de su conservación una prioridad (Ripple et al., 2014).

Facilitar la coexistencia con los grandes carnívoros es uno de los principales objetivos, y también desafíos, de los planes de gestión y conservación, especialmente después de la recuperación de estas especies en muchas partes del mundo y la creciente ocupación del territorio por parte de los humanos. Pero la viabilidad de sus poblaciones depende mucho de su capacidad de adaptación a los ambientes altamente humanizados (Støen et al., 2015), lo que se puede promover aplicando las estrategias adecuadas que permitan su coexistencia con las poblaciones humanas y además no perjudiquen su desarrollo (Mace, 2014).

El apoyo de la opinión pública y su cooperación son cruciales para el éxito de estas acciones (Kleiven et al., 2004). Lograr una conservación efectiva depende en gran medida de la capacidad de traducir el valor global de los carnívoros en beneficios tangibles lo suficientemente grandes como para impulsar la conservación a nivel local, promoviendo medidas colaborativas y la aceptación pública de la gestión de la vida silvestre (Dickman et al., 2011). Por ello, los programas de conservación incluyen medidas de mitigación de conflictos (ej. vallado eléctrico, protección del ganado) y compensaciones económicas por daños y pérdidas, destinadas a mejorar el punto de vista de los más afectados (Nyhus et al., 2003). Estas acciones deben basarse en una mejor comprensión de la ecología y el comportamiento de los carnívoros, así como en el conocimiento acumulado y las experiencias locales sobre los conflictos (Shivik, 2006; Treves and Karanth, 2003).

Caso práctico: el oso pardo en la Cordillera Cantábrica

Actualmente la Península Ibérica alberga dos de las poblaciones de oso pardo europeas que se encuentran en mayor peligro de extinción: la pirenaica y la cantábrica. Esta última está dividida en dos subpoblaciones, localizadas la mayor de ellas en la zona occidental de la Cordillera Cantábrica y la otra en la zona oriental. Esta población, al igual que ha ocurrido en gran parte de Europa, se está recuperando en los últimos años (Gonzalez et al., 2016), pasando de unos 74 individuos en los años 90 a más de 250 en 2014 (Pérez et al., 2014). Gracias a su evolución positiva, ambas subpoblaciones se encuentran ahora ligeramente conectadas después de un completo aislamiento durante años, aunque el flujo es prácticamente unidireccional, de la subpoblación occidental hacia la oriental (Pérez et al., 2010). Aunque la densidad de población en la Cordillera Cantábrica es en general baja, los pueblos están dispersos por todo el territorio, conectados por una red de transportes bastante extensa. Además, la amplia distribución de actividades ligadas a la presencia humana como la ganadería y la agricultura intensifican la fragmentación de los hábitats naturales (García et al., 2005).

Como ocurre con otros carnívoros, la población de osos de la Cordillera genera conflictos con las actividades humanas con las que comparte territorio (ej. daños a ganado, colmenas, árboles frutales), lo que no ayuda a mejorar la opinión pública, especialmente en el medio rural. Por ello la caza furtiva y otras causas humanas de mortalidad siguen siendo una amenaza para el oso en España, junto con la invasión de sus hábitats naturales (expansión de la red de carreteras, incremento del turismo de montaña), la baja diversidad genética y la pérdida de conectividad entre poblaciones debida generalmente a la fragmentación del hábitat (Pérez et al., 2010; Wiegand et al., 1998). Aun así, el oso es una especie apreciada en la Cordillera Cantábrica, ya que atrae bastante turismo de naturaleza (Penteriani et al., 2017) y las pérdidas económicas que produce son menores que, por ejemplo, las del lobo (Fernández-Gil et al., 2016). Además, el sector ganadero, que es el más afectado por la presencia de grandes carnívoros, no se ve muy perjudicado por la presencia de osos debido al reducido consumo de carne en su dieta en comparación con otras poblaciones (Bojarska and Selva, 2012). En cambio, la apicultura es el sector que sufre mayores pérdidas derivadas de la presencia del oso (Bautista et al., 2017).

Aunque la población de osos pardos de la Cordillera Cantábrica haya aumentado considerablemente en estas dos últimas décadas, el estado actual de la población no garantiza todavía su viabilidad y el efecto que las actividades humanas tienen sobre ella no ha sido estudiado a fondo. Las principales motivaciones de esta tesis han sido producir nueva información científica enfocada esencialmente a promover y facilitar la coexistencia del oso y el hombre en un espacio altamente humanizado como la Cordillera Cantábrica, y ayudar a la correcta gestión de la especie con fines de conservación.

Objetivos

Esta tesis forma parte de un proyecto más amplio cuyo objetivo principal es el de producir nueva información científica, a la vez que actualizar la ya disponible, sobre la ecología y el comportamiento de la población de oso pardo de la Cordillera Cantábrica. Centrándonos en el efecto que un entorno altamente humanizado puede tener sobre esta población, así como en el estudio y la mitigación de los conflictos entre osos y humanos, se pretende conseguir una mejora en la gestión y la conservación de esta población, así como mejorar la coexistencia con el ser humano y desarrollar y aportar a la comunidad científica nuevas metodologías aplicables a otras poblaciones de grandes carnívoros.

El objetivo principal de esta tesis es el de aumentar el conocimiento sobre aspectos básicos de la población de oso pardo de la Cordillera Cantábrica, su estado actual y perspectivas de futuro. En ella se exploran cuatro pilares fundamentales: (1) las características del hábitat de la población y sus posibles áreas de expansión, así como (2) la selección de hábitat de los diferentes grupos de oso en época de reproducción (hembras con crías de primer año, de segundo año y zonas de reproducción), (3) los posibles cambios en el comportamiento en función de la proximidad a diferentes infraestructuras humanas y (4) los patrones espacio-temporales que pueden afectar la aparición de daños a ganado, colmenas y cultivos.

Cada uno de los cuatro capítulos en los que se ha divido este trabajo se corresponde con un artículo científico publicado o en fase avanzada de publicación. Cada uno de ellos persigue diferentes objetivos específicos:

CAPÍTULO 1. El objetivo principal de este capítulo es el de encontrar y caracterizar las áreas potenciales de expansión del oso pardo en la provincia de Asturias. Para ello, analizamos primero las variables que definen los hábitats que prefiere el oso pardo cantábrico a pequeña y gran escala, señalando las áreas que cumplen estas condiciones y que por tanto son favorables para la presencia de la especie. Gracias a esto, localizamos las áreas favorables que todavía no tienen presencia de oso, y que consecuentemente, es probable que sean ocupadas si la expansión de la población continúa.

CAPÍTULO 2. El principal propósito de este capítulo es comprobar si las áreas utilizadas por las osas con crías más propensas a sufrir un infanticidio difieren de las elegidas por otros grupos de osos como estrategia para evitar el infanticidio. Para ello, se comparan a diferentes escalas la estructura y composición del paisaje, así como la presencia humana, de las zonas utilizadas por estas hembras durante los primeros meses después de la salida de la osera con las áreas frecuentadas por osas con crías del año anterior, sujetas a un menor riesgo de infanticidio, y las zonas de reproducción, donde hay mayor riesgo debido a la presencia de machos adultos.

CAPÍTULO 3. El objetivo esencial de este capítulo es comprobar si el comportamiento del oso pardo en la Codillera Cantábrica se ve influido por la actividad humana de su entorno. Se analiza en primer lugar la relación entre los diferentes comportamientos del oso y la distancia a diferentes infraestructuras humanas (pueblos, carreteras asfaltadas, caminos y puntos de observación de osos) y tipos del hábitat (bosque, matorral, pradera y cultivos). En segundo lugar, se explora si la cercanía a estas infraestructuras y hábitats deriva en la aparición o la duración de comportamientos de alerta y si esto influye en el resto de comportamientos.

CAPÍTULO 4. El principal objetivo de este capítulo es el de analizar qué patrones espacio-temporales pueden explicar la aparición de daños de oso a ganado, colmenas y cultivos en los tres núcleos de oso pardo localizados en España (Cantábrico occidental, Cantábrico oriental y Pirenaico). Para ello, se estudia el número de daños producidos a cada tipo de actividad humana en función del año y la temporada, de la población y de la provincia donde ocurren. Finalmente, se analiza si la aparición de los diferentes tipos de daños se puede explicar en función de diferentes indicadores de productividad y clima.

CAPÍTULO 1

Identifying potential areas of expansion for the endangered brown bear (Ursus arctos) population in the Cantabrian Mountains (NW Spain).

PloS one, 14 (1), e0209972.

ABSTRACT

Many large carnivore populations are expanding into human-modified landscapes and the subsequent increase in coexistence between humans and large carnivores may intensify various types of conflicts. A proactive management approach is critical to successful mitigation of such conflicts. The Cantabrian Mountains in Northern Spain are home to the last remaining native brown bear (*Ursus arctos*) population of the Iberian Peninsula, which is also amongst the most severely threatened European populations, with an important core group residing in the province of Asturias. There are indications that this small population is demographically expanding its range. The identification of the potential areas of brown bear range expansion is crucial to facilitate proactive conservation and management strategies towards promoting a further recovery of this small and isolated population. Here, we used a presence-only based maximum entropy (MaxEnt) approach to model habitat suitability and identify the areas in the Asturian portion of the Cantabrian Mountains that are likely to be occupied in the future by this endangered brown bear population following its range expansion. We used different spatial scales to identify brown bear range suitability according to different environmental, topographic, climatic and human impact variables. Our models mainly show that: (1) 4977 km^2 are still available as suitable areas for bear range expansion, which represents nearly half of the territory of Asturias; (2) most of the suitable areas in the western part of the province are already occupied (77% of identified areas, 2820 km^2), 41.4% of them occurring inside protected areas, which leaves relatively limited good areas for further expansion in this part of the province, although there might be more suitable areas in surrounding provinces; and (3) in the eastern sector of the Asturian Cantabrian Mountains, 62% (2155 km^2) of the land was classified as suitable, and this part of the province hosts 44.3% of the total area identified as suitable areas for range expansion. Our results further highlight the importance of increasing: (a) the connectivity between the currently occupied western part of Asturias and the areas of potential range expansion in the eastern parts of the province; and (b) the protection of the eastern sector of the Cantabrian Mountains, where most of the future population expansion may be expected.

INTRODUCTION

As a consequence of the implementation of major conservation and management actions (Linnell et al., 2001; Treves and Karanth, 2003), many large carnivore populations are expanding into human-modified landscapes (Breitenmoser, 1998; Chapron et al., 2014; Kaczensky P, Chapron G, von Arx M, Huber D, Andrén H, 2013; Pyare et al., 2004; Zedrosser et al., 2011), which may provoke an increase in several types of conflicts, e.g., livestock predation, crop damage and, more rarely, attacks on humans (Athreya et al., 2013; Penteriani et al., 2016; Stahl et al., 2001). Predicting potential range expansion areas is an important step towards proactive management strategies minimizing conflict, thereby enhancing large carnivore population viability (Ericksson and Dalerum, 2018; Kaartinen et al., 2009; Treves et al., 2004). This is particularly important for small and isolated populations that are confined as a result of the expansion of humans and habitat degradation, and for which spatial expansion is therefore essential for their conservation. Different habitat suitability models, like maximum entropy models (Merow et al., 2013; Phillips et al., 2017, 2006), are nowadays commonly used for exploring the availability of favourable habitats and the likely spatial distribution of population expansions, as well as the environmental factors determining them (Jedrzejewski et al., 2008; Jerina et al., 2003; Muntifering et al., 2006; Rondinini et al., 2005). Since reliable absence data is frequently difficult to obtain, these models are usually based on species presence-only occurrence data such as maximum entropy models. In human-dominated landscapes, where fragmentation and loss of good habitat, primarily large patches of continuous forest with little human encroachment (Huck et al., 2010; Mateo-Sánchez et al., 2016; Mateo Sánchez et al., 2013), is continually arising, these models have become very popular in carnivore population studies and conservation (Kuemmerle et al., 2011; Schadt et al., 2002; Swanepoel et al., 2013; Whiteman et al., 2017), given the abovementioned difficulty in obtaining absence data (Bassi et al., 2015). Further, a key ingredient of these models is the spatial scale considered. While large-scale spatial models are useful for understanding broad population patterns and processes related to the distribution of a species, high-resolution models offer information on specific niche requirements of locally adapted populations (Martin et al., 2012, 2010). Thus, combining different spatial scales provides the opportunity to address and improve our knowledge about the relationships between species and the environment by providing more accurate predictions on species distributions (Mateo-Sánchez et al., 2016; Mateo Sánchez et al., 2013).

The brown bear *Ursus arctos* is one of the most widespread large carnivores in the world, occupying different countries in North America, Europe and the north of Asia (http://www.iucnredlist.org/details/41688/0). Brown bears were historically persecuted and nearly eliminated from much of Western Europe in the 20th century in order to avoid conflicts and as a result of hunting (Zedrosser et al., 2011). The effects of direct persecution were aggravated by other threats like habitat loss and fragmentation due to the expansion of the human population, which conflicts with the large spatial requirements of this species (Swenson et al., 2000).

Northern Spain is home to the last two isolated populations of brown bear in south-western Europe, which have been protected for more than 30 years. The main population, which is estimated to consist of approximately 200 individuals (95% CI: 183 – 278; (Pérez et al., 2014)) only, inhabits the Cantabrian Mountains (NW Spain) and is divided into two tenuously connected subpopulations (Gonzalez et al., 2016), with most of the population inhabiting the western sector of the Cantabrian Mountains belonging to the province of Asturias (hereafter referred to as "Asturias"). Previous studies have shown that both subpopulations are increasing in number and range, especially in the western region (Gonzalez et al., 2016; Martínez Cano et al., 2016; Palomero et al., 2007; Pérez et al., 2014, 2010). This current positive trend may cause re-colonisations of areas where bears have disappeared and/or the occupation of new ones (Chapron et al., 2014).

The small number of bears, their complete isolation and the limited connectivity between the two subpopulations make the study of the range expansion of this population particularly interesting. In addition, as its expansion might increase conflicts with human populations and activities (i.e. livestock predations, crop and apiary damages, attacks on humans), the identification of potential new colonization areas is of great importance for supporting conservation management actions. Here, by using maximum entropy models, we aim to identify the potential range expansion areas of Cantabrian brown bears. We have specifically: (1) identified suitable areas for bears at a coarse scale (5 x 5 km); (2) explored, at a finer scale (1 x 1 km), the best areas highlighted in the previous model; and (3) evaluated which environmental variables determine habitat suitability for this population on both scales.

METHODS

Study area

Asturias is one of the four regions of north-western Spain still inhabited by brown bears. The region is characterised by an oceanic climate with mild temperatures and high humidity, with annual mean temperatures ranging from 14 ºC on the coast, to 2-3 ºC on the highest points of the mountains (http://www.worldclim.org/). Asturias comprises 10,602 km^2 with more than a million inhabitants distributed both in big cities and small towns from the coast to the Cantabrian Mountains. Population density is ca. 100 inhabitants/km^2 (Instituto Nacional de Estadística http://www.ine.es/jaxiT3/Datos.htm?t=2886) and road density is 47.4 km/100 km^2 (http://www.seap.minhap.gob.es/index.html). Elevation ranges from 0 to 2648 m a.s.l. (http://www.sadei.es/). The Cantabrian Mountains are principally covered by forests of chestnut (*Castanea sativa*), oak (*Quercus petraea*, *Q. robur*, *Q. pyrenaica* and *Q. ilex*) and beech (*Fagus sylvatica*), alternating with pastures and brushwood, and subalpine matorral above 1700 m (Martínez Cano et al., 2016; V. Penteriani et al., 2017b).

Bear occurrence data

We used a database of brown bear occurrences within Asturias that consists of geolocalized direct observations; indirect signs of the presence of the species (i.e., footprints, hair and scats); and damage records caused by bears to livestock, beehives, crops, and human activities and infrastructures. The database covers observations from 1995 to 2016 and has been compiled by the regional government of Asturias (Supplementary Figure S.1). Observation data came from several sources, primarily: (a) systematic direct bear observations by regional government field staff (the Patrulla Oso, i.e., the Bear Patrol, and all the guards of the Principado), as well as by the Brown Bear Foundation (FOP, Fundación Oso Pardo), the Asturian Foundation for the Conservation of Wildlife (FAPAS, Fondo para la Protección de los Animales Salvajes) and personal observations of the authors; and (b) camera traps that were randomly located by the FAPAS and Bear Team during the last twenty years, mainly in forested areas where bears are less visible. Any indirect observations, i.e. tracks, signs and damages, were done by trained personnel. We removed observations with obviously erroneous or doubtful spatial locations (e.g., incomplete coordinates or poorly georeferenced observations).

Definition of utilized brown bear range and identification of potential expansion areas

We evaluated the potential areas of bear expansion by using two different spatial scales (Mateo-Sánchez et al., 2016). We first defined a coarse scale of 5 x 5 km (25 km^2), which is approximately the average size of Spanish brown bear home ranges (Martin et al., 2012; Naves et al., 2003; V. Penteriani et al., 2017b). For this coarse scale, we opted to model the suitability for distribution range rather than for occurrence (Ericksson and Dalerum, 2018), to obtain a primary and more general distribution of the favourable habitat for the species. Therefore, we first defined the distribution range of Asturian brown bears as pixels with 3 or more years of presence. We binarily classified the model into suitable and unsuitable areas. Within areas identified as suitable range from the coarse scale model, we then considered a model with a finer scale of 1 x 1 km to enable identification of suitable areas for brown bears within their area. For this scale, we therefore used raw observations as model input so that the model describes suitability for bear presence within areas that are regarded as within their suitable range.

Environmental variables

We used 25 layers related to human infrastructures, vegetation and geomorphology as predictors in our habitat suitability models (Supplementary Table S.1). Climatic variables came from the WorldClim 2.0 database (http://www.worldclim.org/) and were described by Hijmans et al., (2005). We used a discrete land cover layer available from the Cartografía Temática Ambiental del Principado de Asturias 1989-1998 (1:50,000), which we converted into percentage area within each pixel. We discarded any land cover class that did not possess at least 1% mean occurrence. We used each of the remaining classes as separate layers for our models, where each layer describes the relative abundance of a particular class. We also utilized the total number of land cover classes per pixel as well as the Shannon index of relative occurrences. We employed a Normalized Difference Vegetation Index (NDVI) as an index of greenness, which was provided by the Instituto de Recursos Naturales y Ordenación del Territorio (INDUROT). We used a digital elevation model from MDT200. From this model we derived elevation and mean aspect of the slopes. We obtained human population density from the Sociedad Asturiana de Estudios Económicos e Industriales (http://www.sadei.es/es/portal.do) and highway, road and footpath density as well as river density from geophysical layers maintained by the Principado of Asturias.

In case of a spatial correlation > 0.7 (Pearson coefficient) between two layers we only retained the layer that we regarded as most relevant for bear biology. For instance, we removed all climatic variables except seasonal variability in precipitation, since they were all correlated with elevation which is more ecologically relevant for bears (Kobler and Adamic, 2000; Posillico et al., 2004).

We retained 19 uncorrelated variables: % shrublands, % gorse, % heath, % fern % forests, % pastures, % planted forest, % planted conifer forest % cliffs, mean value per pixel of the Shannon index of land cover heterogeneity and the normalized difference vegetation index, number of land cover classes, elevation, slope, precipitation seasonality, river, human population, highway, road and footpath density. All the variables were projected to the same reference system (ETRS89 / ETRS-UTM29) and scaled to a 5 x 5 and a 1 x 1 km resolution. For the final modelling, we removed any cells which had less than 50% of its area within the limits of the study region in each scale (most of these cells occurred along the coast) and we included all the variables mentioned above.

Modelling with MaxEnt

We used the software MaxEnt version 3.4.1 (Phillips et al., 2017) called from the statistical environment R (R. Core Team, 2018) version 3.3.3 using the packages dismo version 1.0-12 (Hijmans et al., 2017) and ENMeval version 0.2. (Muscarella et al., 2014). Because of the limited number of observations in eastern Asturias, which could have been partly due to observer bias, we only trained models on data from east of the A-66 and AS-1 highways (Fig 1). These roads appear to function as partial physical barriers for the dispersal of brown bears between west and east subpopulations (Gonzalez et al., 2016; Mateo-Sánchez et al., 2016). With this restriction, we retained 4878 bear locations which were clustered into 99 5 x 5 km pixels of bear range that were used as training locations for the coarse scale model, and 1091 1 x 1 km pixels within the suitable bear range which contained observations that were used for the finer scale model. For each scale, we utilized the centre coordinate of each cell, which was either classed as bear home range (coarse scale) or that contained a bear observation (finer scale), as occurrence data. We used 500 iterations, a convergence threshold of 10^{-5} and values from all cells in the west section of Asturias to build our first two models. Then, for both scales, we projected the model output onto the whole of Asturias once an optimal model structure had been selected (see below) using values from the eastern section of Asturias for the coarse scale and identified suitable range in the eastern part for the finer scale as background points.

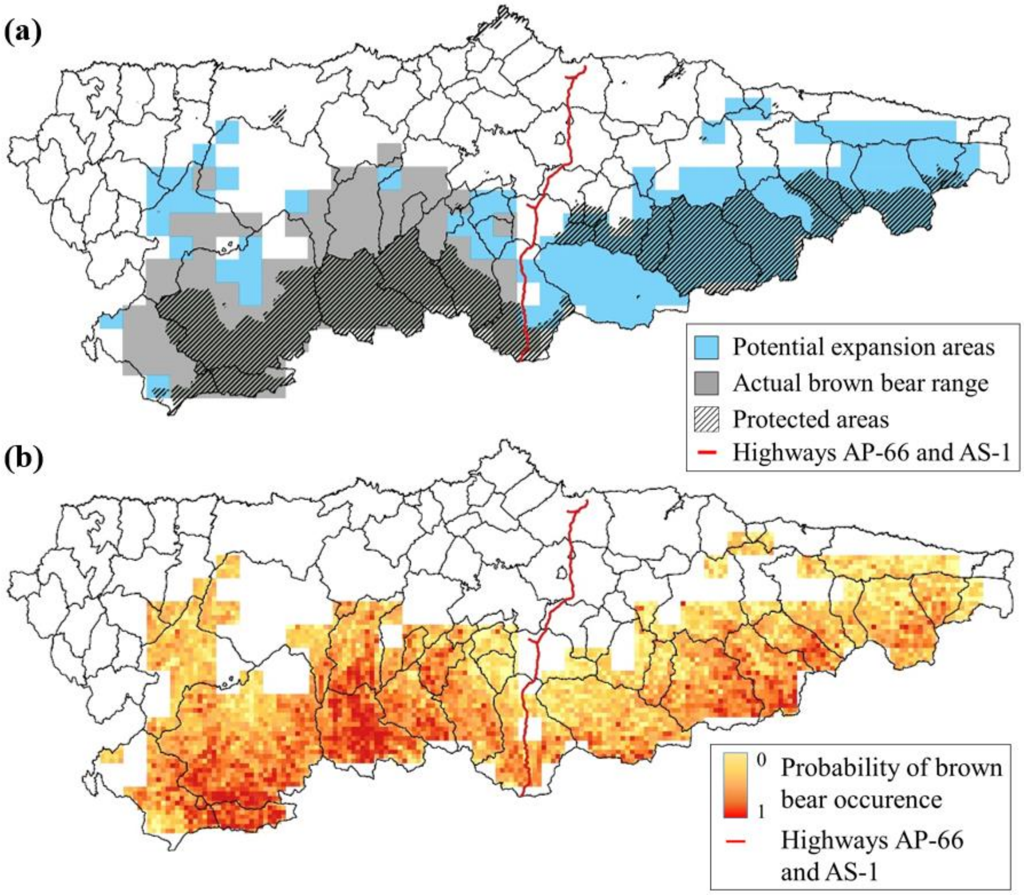


Figure 1. Coarse and fine scale models. Binary classification of a coarse (5 x 5 km) MaxEnt model broadly identifying suitable range areas, including favourable areas that are part of the current bear range, as well as protected areas (a); and model output from the fine scale (1 x 1 km) MaxEnt model identifying the probability of bear occurrence within the identified suitable bear range in the coarse model (b).

Selecting and evaluating the models

MaxEnt associates the presence data to environmental values using 5 different feature types (linear, quadratic, product, threshold and hinge), which represent different types of parameterizations. These feature types represent different transformations of the covariates, allowing the modelling of potential complex relationships between the variables and preventing overfitting (Elith et al., 2011). The mean of each feature has to be close (within some error limits) to the empirical average over the presence locations (Phillips and Dudík, 2008). The software also controls over-fitting using a regularization parameter which penalizes variables with low contribution to the model. Although machine learning algorithms such as the one used in MaxEnt generally favour more complex model solutions than likelihood based algorithms, overfitting can still be problematic since models essentially parameterize random spatial noise (Warren and Seifert, 2011). Hence, to identify an optimal model structure we evaluated candidate models with all types of feature combinations, each run over a set of regularization multipliers ranging from 0 to 10 (Supplementary Figure S.2. (13)). Each model included the same set of 19 uncorrelated environmental variables. We identified the best combination of feature types and regularization multiplier using Akaike's Information Criterion corrected for small sample sizes (AIC_c) (Akaike, 1974). We calculated the AIC_c values from the raw model output where the sum of the log transformed raw values were treated as equivalent to model likelihood (Warren and Seifert, 2011). Although potentially at odds with machine learning philosophy, AIC values have been shown to be an efficient and reliable method for identifying optimal levels of model complexity in MaxEnt applications. Following (Burnham, K. P., & Anderson, 2002), we regarded models within 2 AIC_c units of each other as having equivalent empirical support. Of these models, we selected the model containing the least number of parameters, and if two models had the same number of parameters we chose the model with the lowest number of feature types. We regard this quantitative method of model selection beneficial, since it provides objective and rigidly defined criteria for evaluating the numerous alternative models associated with any given MaxEnt exercise.

To evaluate model performance we first used the AUC (Area Under a Receiver Operating Characteristic –ROC– Curve) value (Fielding and Bell, 1997), which indicates how efficiently a model differentiates between occurrence and background locations. AUC values from 0.7 to 1 generally suggest that the model has adequate predictive ability (Araújo et al., 2005). Second, we calculated three model performance metrics based on cross validation using a checkerboard method to separate our occurrence data into training and testing (45): AUC_{test} (ability of testing locations to distinguish between background and presence locations), AUC_{diff} (difference in the ability to distinguish between presence and background locations between training and test data (Warren and Seifert, 2011) and OR_{min} (proportion of test locations with a value below the lowest value of training locations (Muscarella et al., 2014).

Evaluating variable contributions

To evaluate the relative contribution of each environmental variable to the models we used a jacknife procedure and a heuristic method provided by MaxEnt. The jacknife test shows the gain in AUC value of each variable when used in isolation and the lack of gain when removed from the full set of variables (Supplementary Figure S.3). The heuristic method calculates the percent contribution of each variable as the proportional contribution to the model training gain for every iteration of the model fitting process (Phillips et al., 2006).

Presentation of model output

For both models we used the complementary log-log (cloglog) format as model output, as it has an intuitive interpretation and is monotonically related to other potential output formats (Phillips et al., 2017). This format allows interpreting model output as a probability of occurrence. However, as we were interested in suitable areas for bear range in our coarse scale model, and not necessarily the relative suitability within identified range, we have presented the coarse scale model as a binary classification, which broadly identifies favourable bear range. For this purpose we used the 10 percentile training presence in the cloglog values as a threshold for suitable bear range. This threshold selects the value above which 90% of the training locations are correctly classified, and is one of the most common thresholds used in MaxEnt habitat suitability model (Young et al., 2011). However, we have presented the unclassed cloglog output of our coarse scale model in Supplementary Figure S.4. For the fine scale we maintained the cloglog values in order to represent habitat suitability for bear occurrence.

Identification of potential bear expansion areas and evaluation of the suitability of used range and expansion areas

For the coarse scale, cells classed as suitable but which were not part of the identified distribution range were regarded as potential expansion areas. To evaluate whether Asturian brown bears have expanded their range incrementally out of an initial core area (Supplementary Figure S.5), we calculated the NODF nestedess index as an index of spatial nestedness over time (Almeida Neto et al., 2008). This value describes the extent to which cells included in the range of a given year also form part of the range in subsequent years (Ericksson and Dalerum, 2018), which can be regarded as a temporal analogue to spatial nestedness (Ulrich et al., 2009). Following Ericksson and Dalerum (2018) we calculated the nestedness on annually identified pixels recognized as suitable range. The index value ranges from 100, indicating complete nestedness, to 0, indicating an anti-nested pattern. To evaluate if our observed values differed from random expectations we compared our nestedness index to values derived from 999 null models constrained to retain the original marginal sums. We only conducted this analysis on the coarse scale, as we do not regard absences of observations within pixels in the finer scale to be especially informative.

We evaluated whether suitability at the fine scale differed between the used range and the potential range expansion areas using a linear model. We used the log transformed raw model output as a response variable, and a 3 level factor as a predictor. This factor consisted of the classes obtained from the coarse model “used range” (suitable areas already occupied by bears), “expansion areas west” (unoccupied areas west of highways A-66 and A-S1) and “expansion areas east” (unoccupied areas east of highways A-66 and AS-1). We opted to separate the expansion areas in eastern and western Asturias because we suspect there may be observation bias in the eastern part, which may have underestimated the used range. We also added up to 7th order polynomials of the spatial coordinates to the model predictors to account for spatial autocorrelation. We selected this level of complexity for eliminating spatial autocorrelation by selectively adding polynomial complexity until we could not detect further autocorrelation using Moran’s I values calculated on the residuals (Moran, 1950). For our data set, a polynomial approach was more efficient in removing spatial autocorrelation than approaches directly defining spatial autocorrelation in the model correlation matrix (Pinheiro and Bates, 2000) or approaches using spatial eigenvectors as predictors (Borcard and Legendre, 2002). To explore pairwise differences between the classes we used least square means with a Tukey correction for multiple comparison (Lenth, 2016; Tukey, 1949).

RESULTS

Maxent model selection and evaluation

The optimal coarse scale model identified by the AICc values included linear features, a regularization multiplier of 10, and discarded 12 variables of the whole set because of their limited contribution (Supplementary Table S.2). The fine scale model included linear, quadratic, product and threshold features with a regularization multiplier of 0, and included all the selected variables with the minimum contribution being 0.6. Table 1 shows the different values of the evaluation metrics (see Methods) for the five candidate models for each of the coarse and fine scales with the highest empirical support. The best models at each scale had mean AUC values of 0.782 and 0.7368 respectively, showing adequate predictive ability. However, several models of both coarse and fine scale were regarded as having equal empirical support (Table 1). More complex models generally showed clear signs of over fitting, whereas less complex models lost predictive abilities (Supplementary Figure S.2). The 10 percentile method yielded a threshold of 0.359 in cloglog values, which we used to defined suitable areas for bear range in the coarse scale.

Model	Feature types[a]	Regularization multiplier	Full AUC	Mean AUC	AUC diff	OR min	AICc	Δ AICc	Nparam
oarse scale	L	10	0.795	0.782	0.010	0.031	1004	0	8
	L, Q, T	10	0.796	0.782	0.012	0.020	1005	0.20	9
	L, Q	10	0.796	0.782	0.012	0.020	1005	0.21	9
	L	7	0.796	0.786	0.011	0.031	1006	1.29	9
	L, Q, H	7	0.800	0.787	0.014	0.010	1006	2.14	12
Fine scale	L, Q, P, T	0	0.844	0.768	0.098	0.198	62041	0	299
	L, Q, H, P, T	0	0.844	0.769	0.085	0.177	62041	0	299
	L, Q, T	0	0.842	0.766	0.099	0.191	62119	78.41	292
	L, Q, H, T	0	0.842	0.768	0.085	0.182	62119	78.41	292
	L, Q, P, T	0.5	0.842	0.772	0.089	0.177	62161	119.88	272

[a] Feature types: L – linear, Q – quadratic, H – hinge, P – product, T – threshold

Table 1. Evaluation metrics of the 5 candidate models with the highest empirical support at a coarse scale (5 x 5 km, a) and a fine scale (1 x 1 km, b), built to evaluate the suitability for brown bear range (coarse scale) and brown bear occurrence within suitable range (fine scale) within Asturias.

Maxent variable contribution

The two variables that contributed the most to the coarse scale model (5 x 5 km) were altitude and slope (Table 2), which were confirmed both using the jacknife tests and the heuristic evaluations (Supplementary Figure S.3 and Supplementary Table S.2). Both had a positive effect on the suitability for bear distribution (Supplementary Figure S.6). Some variables of human impact (i.e., highways and footpaths) contributed modestly to this model with a negative influence on habitat suitability for bears (Supplementary Figure S.5). Noteworthy is that several variables had no influence on the coarse scale model. These included precipitation seasonality, human population density, NDVI, pastures, cliffs, conifer plantations, rivers, shrubland, land cover classes and roads. The finer scale model (1 x 1 km) was most influenced by percentage of forest cover, precipitation seasonality and human population density (Table 2), with forest cover and precipitation seasonality being positively associated and human population density negatively associated with probability of bear presence (Supplementary Figure S.7). As with the coarse scale model, the variable contributions were confirmed by both the jacknife tests and the heuristic evaluations (Supplementary Figure S.3 and Supplementary Table S.2).

Model	Variable	Percentage contribution
Coarse scale	Elevation	37.3
	Slope	34.4
	Fern	14.4
	Gorse	4.2
	Highways	3.1
Fine scale	Forest	24.3
	Precipitation seasonality	11.5
	Human density	10
	Slope	9.7
	Gorse	8.1

Table 2. The five most influential variables for coarse (5 x 5 km resolution) and fine scale (1 x 1 km resolution) MaxEnt models describing the probability of bear range and bear occurrence in Asturias, respectively. The percentage values are based on a heuristic method that estimates the proportional contribution of each variable to the model training gain for every iteration during model fitting.

Predicted range distribution and potential expansion areas

Brown bears occupy a total of 2430 km^2 in Asturias. Most bear territory was identified in the south western part of the province, and our coarse scale model confirmed that most suitable areas are in the southern parts of the province (Fig 1a). The NODF nestdeness value characterizing the type of spatial expansion of brown bears in Asturias was marginally less nested than random expectations ($NODF_{obs} = 18.42$, $NODF_{exp} = 18.70 \pm 0.136$, $z = -1.97$, $p = 0.05$). This suggests that the expansion has not been caused by annual range expansions in which individuals have settled in neighbouring areas, but rather that they have dispersed in different directions and hence moving the utilized range over time.

Our coarse scale model identified 4977 km^2 as suitable bear range, which represents close to half of the territory of Asturias (Fig 1a). However, most of the suitable areas in the western part of the province were already occupied (77% of identified areas, 2820 km^2), 41.4% of them occurring inside protected areas (Fig 1a). This leaves relatively limited good areas for further expansion in this part of the province, although there might be more suitable areas in surrounding provinces. In the eastern part of the Asturias, however, 62% (2155 km^2) of the land was classified as suitable, and this part of the province boasted 44.3% of the total areas identified as suitable bear range. Forty-one percent of all expansion areas (suitable areas outside the current bear range) were identified in protected areas (Fig 1a).

Our finer scale model identified the most favourable areas in the southwestern part of the range (Fig 1b). In line with this observation, there were significant differences in suitability between the used areas and the unused areas in the western and eastern parts of the province

($F_{2,2} = 821.8$, $p < 0.001$), with the utilised areas having significantly higher suitability than the unused areas both in the west ($t = 26.7$, $df = 1$, $p < 0.001$) and in the east of Asturias ($t = 26.8$, $df = 1$, $p < 0.001$). The areas in eastern Asturias had, however, higher suitability than the unused areas in the western part of the province ($t = 26.8$, $df = 1$, $p < 0.001$) (Fig 2).

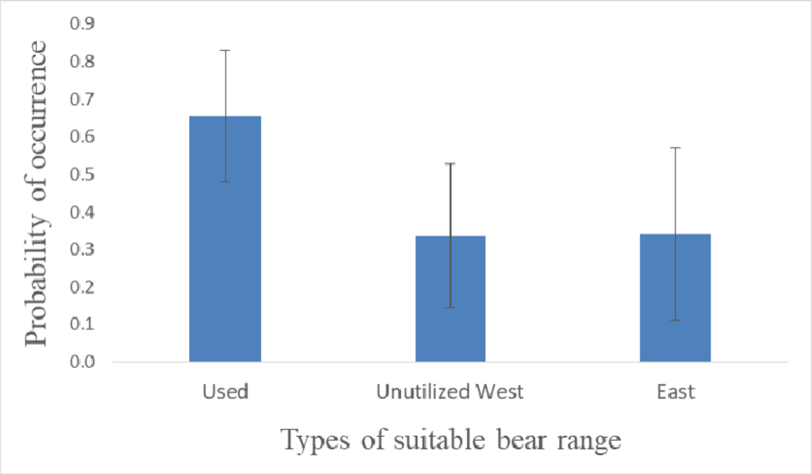


Figure 2. Probability of bear occurrence in 1 x 1 km cells inside the area identified as suitable bear range by a coarser (5 x 5 km) model, in utilised areas in western Asturias, unutilised areas in western Asturias, and eastern Asturias.

DISCUSSION

Our study highlights that (a) a large portion of the Cantabrian Mountains belonging to Asturias is potentially suitable as bear range and (b) only most of the suitable western areas of the province have already been occupied. In fact, according to our coarse scale model, more than 75% of the favourable areas of western Asturias have records of brown bear presence. Because dispersal out of this area seems to be limited (Gonzalez et al., 2016; Martínez Cano et al., 2016; Pérez et al., 2010), if the population continues to expand as previously projected (Pérez et al., 2014) it may either experience a local density increase or bears will expand into areas relatively far from the core of the population. Anecdotal information suggests that bears have already moved out of the most favourable areas and most of the observations made in cells outside of our classed bear range have been recorded in recent years.

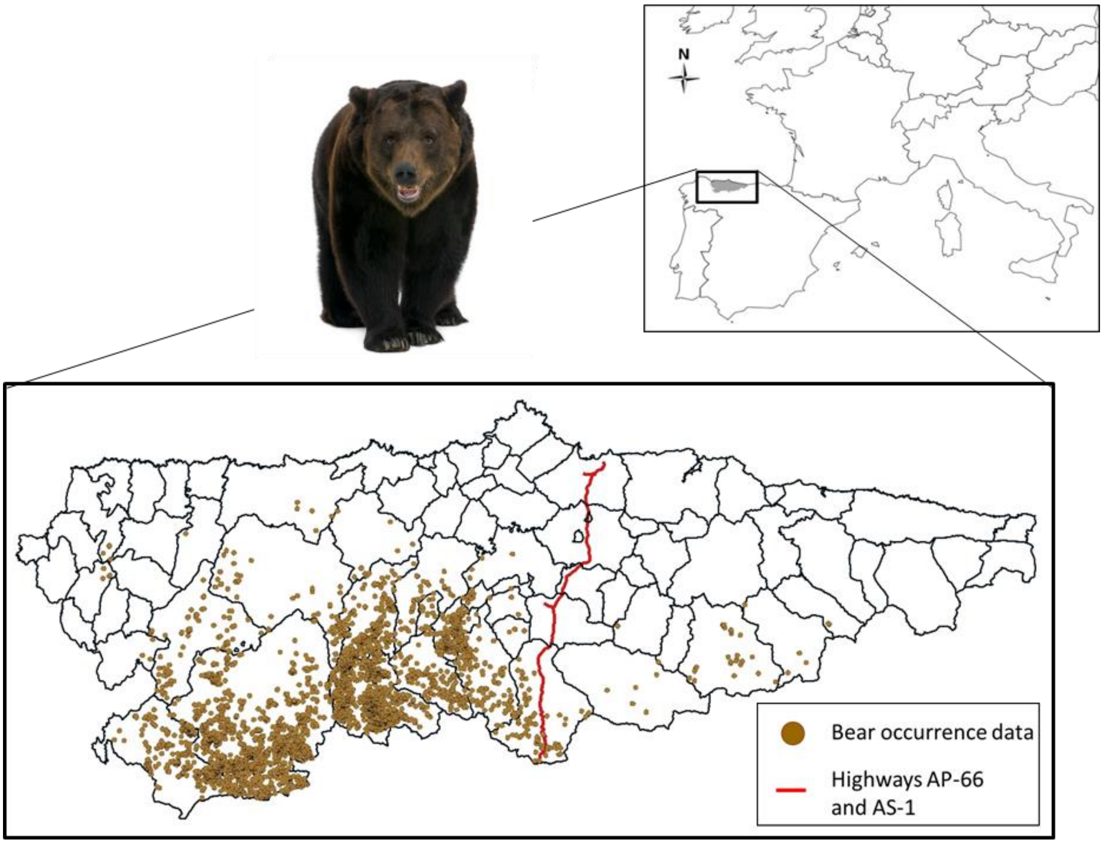
Despite the consistent positive trend in the population size of the western subpopulation of the Cantabrian brown bear, the eastern subpopulation has had a substantially smaller population increase (Martínez Cano et al., 2016). Although we cannot rule out that at least part of this lesser increase may be caused by observer bias, the stark contrast in population growth between the western and eastern subpopulations suggests high mortality rates in the eastern subpopulation and/or a relatively limited dispersal of bears out of western Asturias. Indeed, some previous studies have suggested a narrow connection between the two subpopulations (Mateo-Sánchez et al., 2014; Pérez et al., 2010). Additionally, prior studies hypothesised a prevalence of low quality food-items in the eastern sector of the Cantabrian Mountains (Naves et al., 2006, 2003).

Our results also highlight the importance of using different scales to model habitat suitability. Indeed, the most important environmental variables differed between the coarser- and finer-scale models. This difference may be related to the relative influence of landscape features depending on the scale. While a broader spatial scale yields a general environmental description for the entire species distribution (even among different populations), a finer spatial scale is more related to local requirements (Martin et al., 2012). On the one hand, altitude and slope were the most influential environmental variables in the coarse spatial scale model. This agrees with previous studies on brown bear distribution patterns (Clevenger, 1995; Kobler and Adamic, 2000; Martin et al., 2012; Mateo-Sánchez et al., 2016; Mateo-Sánchez et al., 2014; Penteriani et al., 2018b, Penteriani et al., in press). Brown bears tend to appear in high and rugged areas, especially females with cubs trying to avoid infanticide. They also appear quite elusive nearby human settlements, in order to escape from disturbances produced by high human activity. Our results point to more inaccessible areas, where human density and activities are scarce, as suitable areas for the bears. Although with less influence, the coarse spatial scale model was also negatively affected by footpaths and highways. The latter has previously been negatively associated with habitat suitability for brown bears (Mateo Sánchez et al., 2013), suggesting that it may represent a limitation for brown bear dispersal.

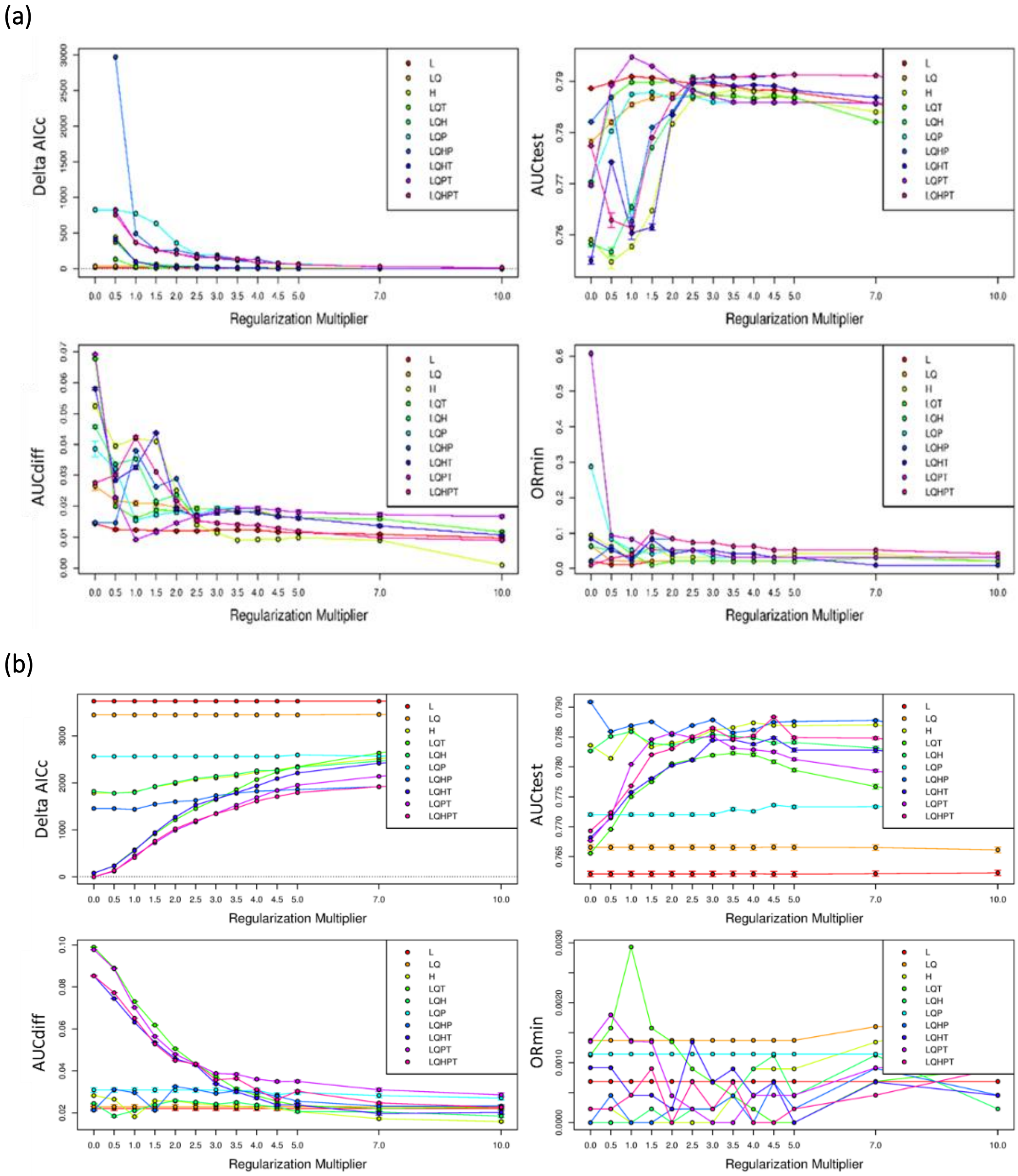
On the other hand, forest cover (positive effect) and human population density (negative effect) were the most influential variables in the fine scale model. Indeed, forest cover represents crucial food and shelter for the Cantabrian brown bear, as one of its main food resources in the Cantabrian mountains are acorns (Fernández-Gil, 2013; Naves et al., 2006; Rodríguez et al., 2007). On the other hand, human density may be related to bear avoidance of human disturbance, as proved in other studies showing that bears are more detectable further from human settlements, where human activity is greater (Clevenger et al., 1990; Mateo-Sánchez et al., 2016; Mateo Sánchez et al., 2013; Oberosler et al., 2017).

We expect that the results of our models can also be used as a practical tool for brown bear damage prevention and conflict mitigation. Indeed, knowing the areas into which the population of the Cantabrian brown bear is likely expand in the near future would allow authorities and conservation organizations to focus information campaigns and pre-emptive damage control actions on these areas. Such proactive approaches are important for successful large carnivore conservation and management (Ripple and Beschta, 2012). For Cantabrian brown bears, damages to apiaries are the main source of conflict, and damage prevention strategies have been shown to be effective to avoid them (Naves et al., 2018). We suggest that our maps of potential brown bear range expansion areas should be overlaid with spatially explicit data on apiaries to allow for the identification of high risk areas where conflicts may occur. In addition, since brown bears have disappeared from certain areas some decades ago, local communities are no longer familiar with how to coexist with this large carnivore. Thus, local information campaigns directed at inhabitants of areas of potential bear expansion and based on studies like the present one may represent a crucial strategy to prevent human-wildlife conflicts.

SUPPLEMENTARY MATERIAL

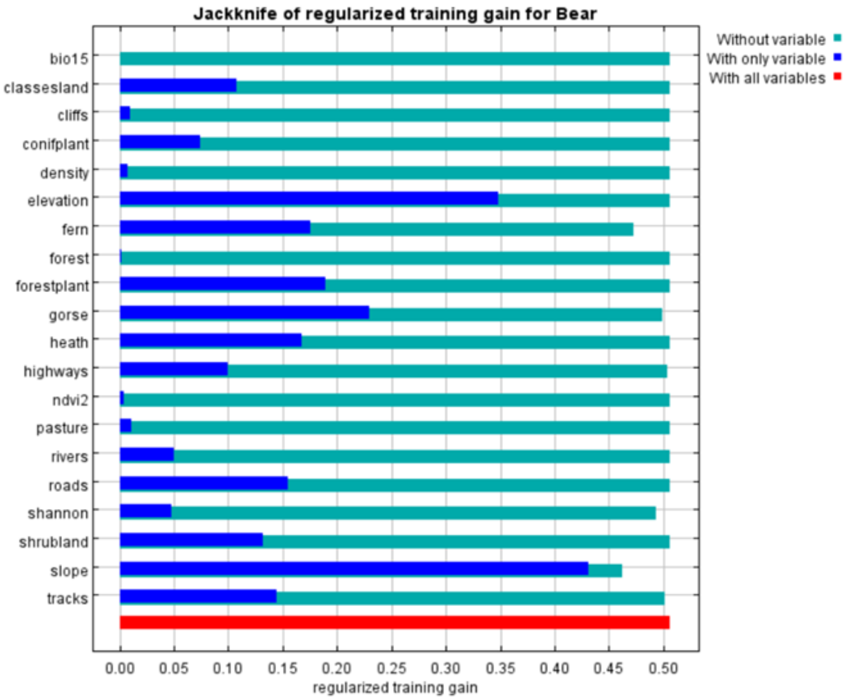


Supplementary Figure S.1. Brown bear occurrence data and location of the study area in Europe.

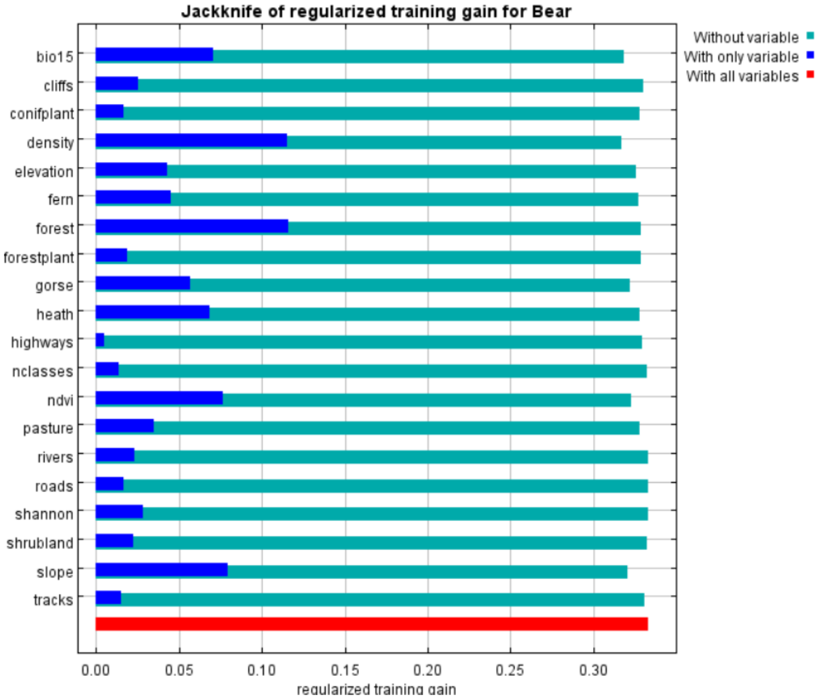


Supplementary Figure S.2. Evaluation metrics for 130 candidate models containing different levels of complexity defined by a range of five feature type combinations including linear (L), quadratic (Q), product (P), threshold (T) and hinge (H) features, each evaluated over a range of regularization multipliers ranging from 0 to 10, for (a) the coarse and (b) fine scales of the distribution of the Cantabrian brown bear in Asturias. Evaluation metrics include delta AICc, which is the difference in AICc (Akaikes Information Criterion corrected for small sample sizes, calculated as the sum of the log transformed raw output penalized by the number of model parameters), AUC test, which is the AUC (area Under the receiving operator characteristics Curve) score for the testing data set, AUC diff, which is the difference in AUC scores between the training and testing data sets, and OR min, which is a threshold dependent statistic corresponds to the proportion of testing localities that have Maxent output values lower than the value associated with the training locality with the lowest value.

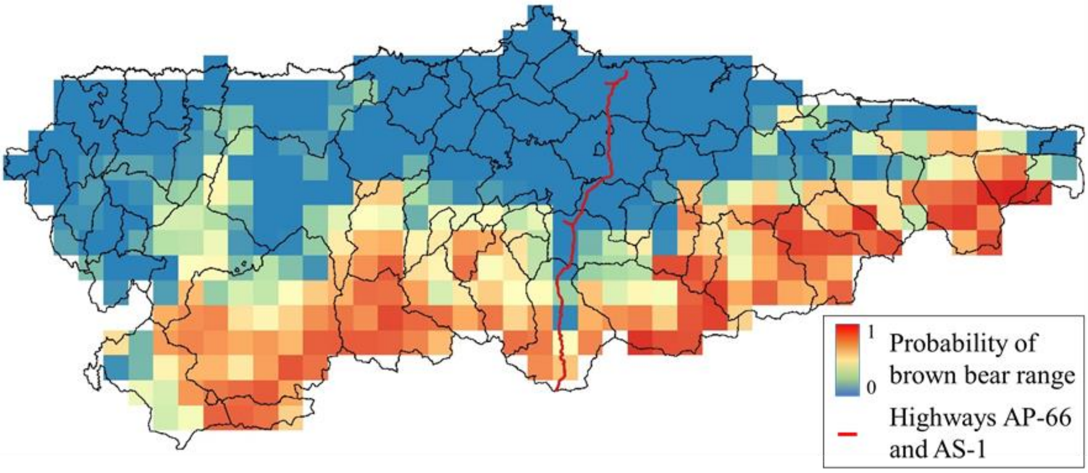
(a)



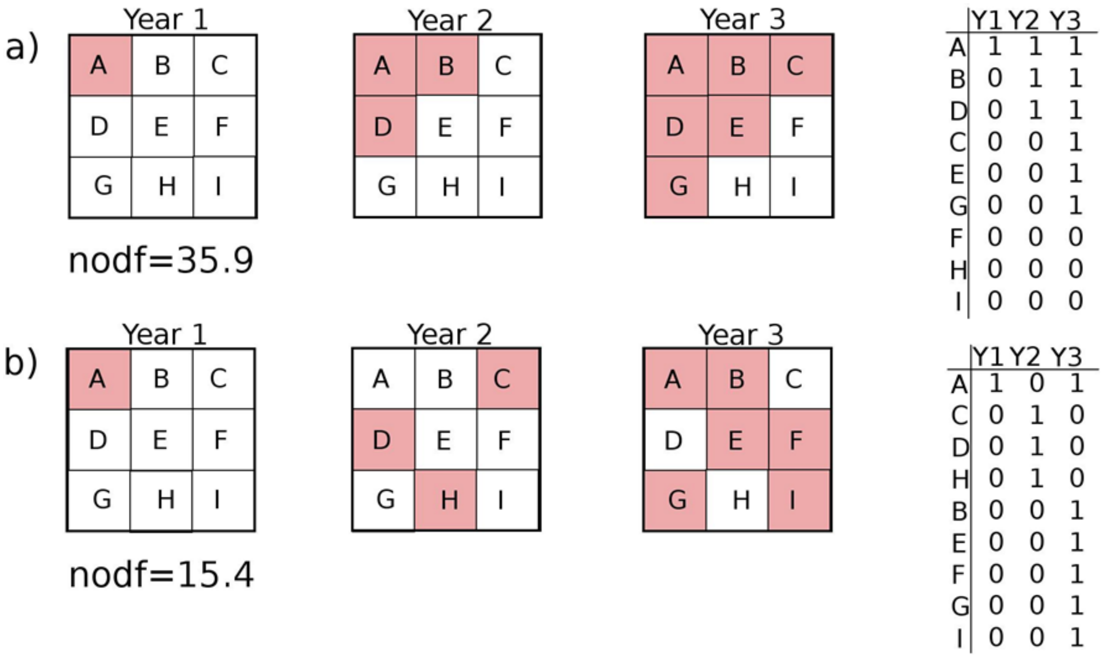
(b)



Supplementary Figure S.3. Jacknife evaluations of variable contributions to the (a) coarse and (b) fine scale models. The variables with the highest gain when used in isolation are slope for the coarse scale (a) and forest cover foir the fine scale model (b). These variables therefore seem to have provided the most useful information by themselves for each scale. The variables that decreased the gain most when omitted, and thus possessed the greatest amount of information not present in the other variables, were slope for the coarse scale (a) and population density for the fine scale model (b).



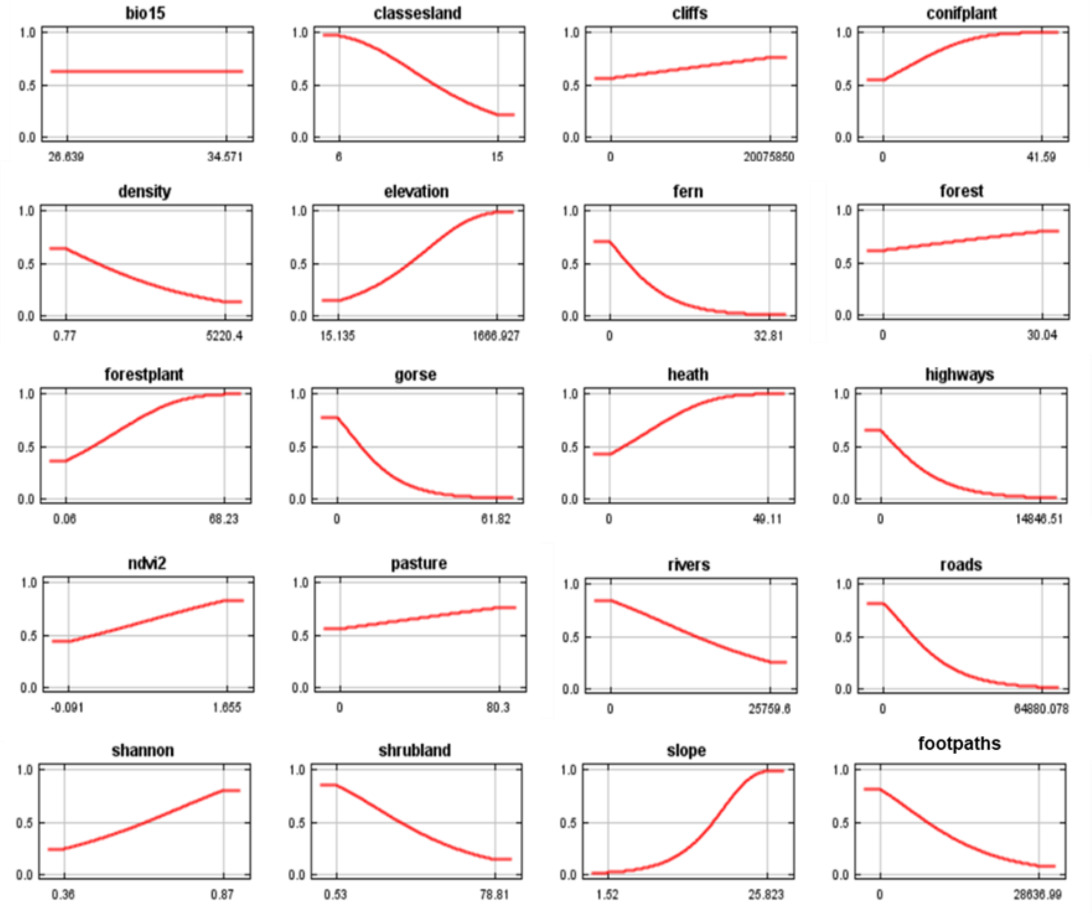
Supplementary Figure S.4. Output of the coarse scale model with a 5 x 5 km resolution. The map presents a clog-log transformation of the raw MaxEnt output, which can be interpreted as a probability of brown bear range occurrence.



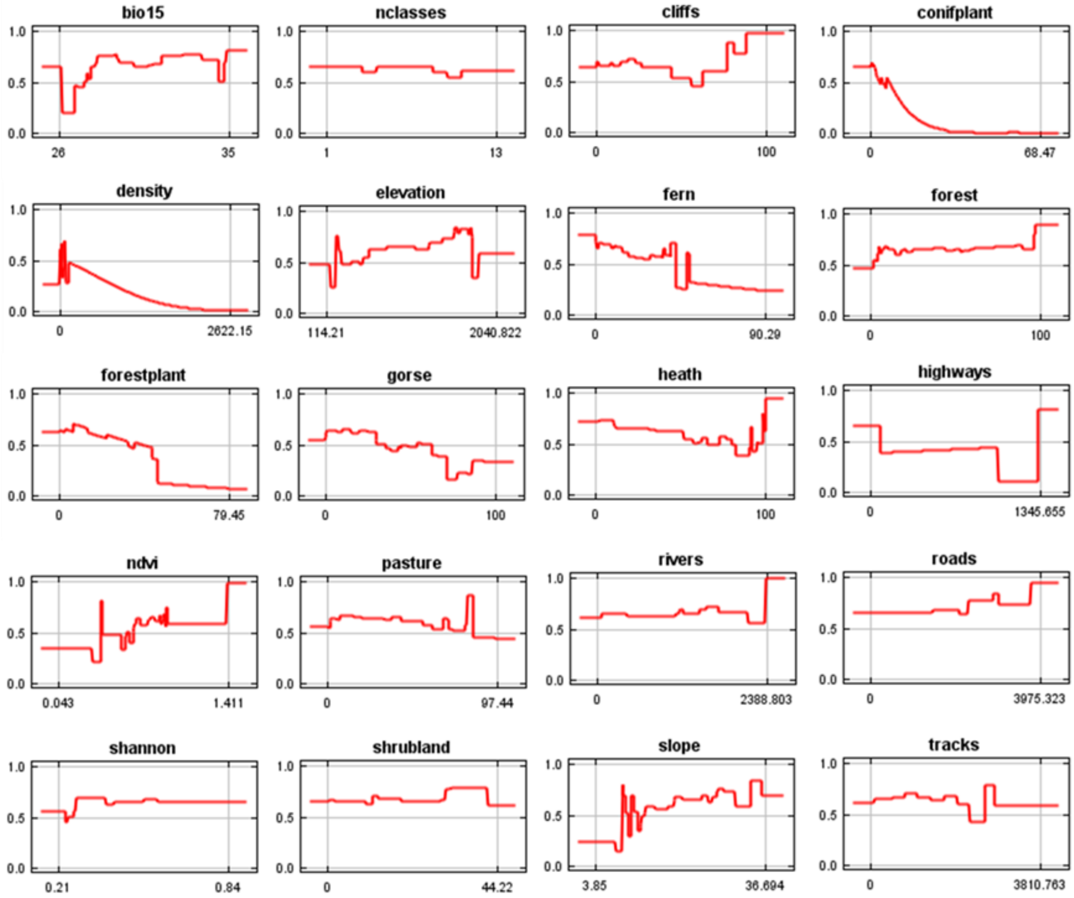
	Y1	Y2	Y3
A	1	1	1
B	0	1	1
D	0	1	1
C	0	0	1
E	0	0	1
G	0	0	1
F	0	0	0
H	0	0	0
I	0	0	0

	Y1	Y2	Y3
A	1	0	1
C	0	1	0
D	0	1	0
H	0	1	0
B	0	0	1
E	0	0	1
F	0	0	1
G	0	0	1
I	0	0	1

Supplementary Figure S.5. Schematic examples of incremental range expansion (a) out of an initial core area as well as (b) a patchy range expansion were no area is occupied two consecutive years, their nestedness values as well as the association matrices used to calculate nestedness.



Supplementary Figure S.6. Associations between predicted suitability estimated from the coarse scale model each of the included environmental predictors.



Supplementary Figure S.7. Associations between predicted suitability estimated from the fine scale model each of the included environmental predictors

Name	Description	Source	Format
Highways*	Length highways	BCN200	Vector
Roads*	Length autonomic and national roads	BCN200	Vector
Footpaths*	Length footpaths	BCN200	Vector
Rivers*	Length rivers	BCN200	Vector
Elevation and slope*		MDT200	Raster
NDVI*	Normalized difference vegetation index	Instituto de Recursos Naturales y Ordenación del Territorio (INDUROT)	Raster
Land cover*	% of each class per grid: cliffs, fern, forests, gorse, heath, pastures, conifer plantations, forest plantations, fruit plantations and shrublands, nº classes and Shannon index	Cartografía Temática Ambiental del Principado de Asturias 1989-1998 (1:50000)	Vector
Human density*		SADEI nomenclator	
Bio 1	Annual Mean Temperature	Worldclim	Raster
Bio 5	Max Temperature of Warmest Month	Worldclim	Raster
Bio 6	Min Temperature of Coldest Month	Worldclim	Raster
Bio 7	Temperature Annual Range (BIO5-BIO6)	Worldclim	Raster
Bio 12	Annual Precipitation	Worldclim	Raster
Bio 15*	Precipitation Seasonality (Coefficient of Variation)	Worldclim	Raster

Supplementary Table S.1. Description, source and original format of the 25 environmental variables initially developed for the construction of the models. Variables marked with * are the ones not correlated and ultimately used in the modelling.

Model	Variable	Percentage contribution
Coarse scale	Elevation	37.3
	Slope	34.4
	Fern	14.4
	Gorse	4.2
	Highways	3.1
	Shannon index	3
	Forest plantations	2.8
	Footpaths	0.8
Fine scale	Forest	24.3
	Precipitation seasonality	11.5
	Human density	10
	Slope	9.7
	Gorse	8.1
	Heath	7
	Fern	5.7
	NDVI	4.9
	Elevation	4
	Pasture	3.5
	Cliffs	1.8
	Forest plantations	1.6
	Conifer plantations	1.5
	Rivers	1.3
	Footpaths	1.1
	Highways	1
	Shrubland	0.9
	Number of landcover classes	0.8
	Roads	0.6
	Shannon index	0.6

Supplementary Table S.2. Variable contribution to the construction of the coarse and fine scale models.

CAPÍTULO 2

Female brown bears use areas with infanticide risk in a spatially confined population

Ursus, In Press.

ABSTRACT

Areas used by female brown bears (*Ursus arctos*) with cubs-of-the-year (hereafter, FCOY) during the first months after den exit are crucial for offspring survival, primarily because of the risk of infanticide by male bears. Therefore, FCOY may allow them to avoid areas frequented by adult males during the mating season. The main aim of this study was to identify landscape features (i.e., structure, composition, and human footprint) that may differentiate the habitat use of FCOY in the small bear population of the Cantabrian Mountains (northwestern Spain) from: (a) areas frequented by females with yearlings, because older cubs are at less risk of infanticide than cubs of the year and, (b) bear mating areas, i.e., the riskiest areas for FCOY, because of the presence of adult males. During the first months after den emergence (April-June), FCOY settled in the roughest areas of the Cantabrian Mountains at most spatial scales. This settlement pattern might represent a behavioral adaptation of FCOY to reduce the risk of encounters with males during the mating season. However, FCOY also settled in similar landscapes to those used by adult bears during the mating season, which may increase the likelihood of risky encounters. Indeed, we observed a spatial overlap between observed locations of FCOY and mating areas, which may help explain the high frequency of infanticide observed in the Cantabrian Mountains. We hypothesize that the need for both shelter and food in early spring may ‘trap’ FCOY in otherwise favorable areas that overlap with mating areas. This may occur predominately in small and confined bear populations, such as the one in the Cantabrian Mountains, where a restricted range and limited habitat availability might prevent FCOY from avoiding risky areas successfully.

INTRODUCTION

Life-history theory predicts that animals display optimal levels of parental investment, with energy expenditure for offspring traded off with the effects on the probability of survival and future reproduction of the parents (Roff, 1992). In addition to the expenditure of nutrients associated with female brown bears (*Ursus arctos*) raising cubs for at least 1.5 years (males provide no parental care and thus offspring depend completely on their mothers; Dahle and Swenson, 2003; Palombit, 2015), the mothers have to take into account the risk of infanticide by adult males, because this is a major cause of death of cubs during their first months of life in some bear populations (Steyaert et al., 2012). Sexually selected infanticide is a reproductive strategy of males that can increase their fitness by killing unrelated offspring so as to bring a female into reproductive condition and, thus, increase the chance of reproducing with her (Hrdy, 1979). This form of infanticide occurs in seasonal breeders during the mating season (van Schaik and Janson, 2000). Because infanticide is costly for victimized females, several counterstrategies have evolved against it (reviewed by Steyaert et al., 2016). Among them, spatial avoidance of potentially infanticidal males is similar to predation avoidance (Agrell et al., 1998), i.e., individuals selectively use space to minimize risky encounters. Following the body of theory on predator-prey interactions and ecology of fear (Brown et al., 1999), spatial segregation from risky encounters can be attained in two main ways: (1) habitat-mediated avoidance (Fedriani et al. 2000, Sergio et al. 2007), i.e., females with offspring avoid habitats associated with a high risk of male encounters, such as those preferred by males during the mating season; and (2) distance-sensitive avoidance (Palomares et al. 1996, Durant 1998). That is, regardless of habitat types, females with offspring select sites as far away as possible from adult males, exploiting discontinuities in their distribution.

Infanticide is common in some brown bear populations, e.g., in Scandinavia (Bellemain et al. 2006, Steyaert et al. 2012) and Spain (Palomero et al., 2011, Fernández-Gil, 2013, and authors' unpublished data). Females with cubs-of-the-year (hereafter FCOY) may alter their habitat selection and avoid areas frequented by adult males during the mating season to reduce the risk of infanticide (Wielgus and Bunnell 1995, Mcloughlin et al. 2002, Rode et al. 2006). For example, individuals may select landscapes that offer shelter, possibilities of escape, and/or minimize the likelihood of risky encounters, following the patterns described in predator-prey theory (Lima and Dill, 1990). Thus, habitat selection of mother bears can be an important component of offspring survival (Steyaert et al., 2016). Indeed, after den emergence, FCOY tend to adopt a secretive and sedentary lifestyle, presumably to minimize the risk of infanticide (Dahle and Swenson 2003*b*, Martin et al. 2013, Steyaert et al. 2013).

The main aim of this study was to describe habitat use of FCOY in the areas used by FCOY during the first months after den exit in early spring, and at different spatial scales. Our multi-scale approach compares the landscape structure and composition, as well as the presence of human infrastructure, at areas used in early spring by FCOY with: (a) areas frequented by females with yearlings (hereafter FYRL); and (b) bear mating areas, defined as areas where bears were seen copulating or at least one male and one female without cubs were observed together during the primary mating period, which is April-June in the Cantabrian Mountains (Ordiz et al. 2007, Martínez Cano et al. 2016). We expected that FCOY use areas characterized by landscape components that differ from the other 'classes' of bears, mainly as a strategy to avoid infanticide, because: (1) older cubs of FYRL are at less risk of infanticide than cubs of the year (e.g., Swenson et al., 2001); and, (2) mating areas represent the riskiest areas for FCOY, because of the presence of adult males.

METHODS

Study area

We recorded bear observations in Asturias, the region inhabited by most of the Cantabrian brown bear population. The Cantabrian Mountains are one of the main mountain range systems in Spain, stretching over 300 km across the northern part of the country, running east-west parallel to the Atlantic Coast. The maximum elevation is 2648 m a.s.l. and the average elevation is around 1100 m (Naves et al. 2003, Martínez Cano et al. 2016). The oceanic climate is mild and humid throughout the year (range: 900-1900 mm; Martínez Cano et al., 2016), favoring oaks (*Quercus petraea*, *Q. pyrenaica* and *Q. rotundifolia*), beech (*Fagus sylvatica*), and chestnut (*Castanea sativa*) on north-facing slopes, whereas drier, south-facing slopes are mainly dominated by oaks (*Q. petraea* and *Q. pyrenaica*) and beech. Subalpine matorral (*Juniperus communis*, *Vaccinium uliginosum*, *V. myrtillus* and *Arctostaphylos uva-ursi*) dominates mountain areas above the treeline (~1700 m) (Martínez Cano et al., 2016). In some areas, former forests have been converted into pasture and brushwood (*Genista*, *Cytisus*, *Erica* and *Calluna*) through human activities (Naves et al., 2006, 2003). The main economic activity in brown bear range is livestock farming, followed by mining, tourism, agriculture, and timber harvesting. The human population density is <15 habitants/km^2 (http://ec.europa.eu/eurostat/statistics-explained/index.php/Population_grids), but areas surrounding the core bear range have experienced extensive urban and agriculture development, connected by a network of transport infrastructure (Mateo-Sánchez et al., 2016).

Data collection

The locations of FCOY, FYRL, and mating areas (Fig. 1) were obtained from: (1) systematic bear observations performed by personnel of (a) the Bear Team (Patrulla Oso) of the Principado de Asturias, (b) the Asturian Foundation for the Conservation of Wildlife (FAPAS, Fondo para la Protección de los Animales Salvajes); (c) the Brown Bear Foundation (FOP, Fundación Oso Pardo); and (d) the Asturian Bear Foundation (FOA, Fundación Oso de Asturias), as well as by the authors. Direct observations were performed almost daily from den exit to the end of the mating period (June), generally from sunrise to sunset; and (2) camera traps that were placed randomly by the FAPAS and Bear Team during the last twenty years, mainly in forested areas where bears are less visible (FAPAS/FIEP, 2017). The presence of the above-mentioned systematic and random observations, which have previously been applied successfully to the study of this bear population (Palomero et al. 2007, Gonzalez et al. 2016), indicate that most of the area potentially favorable to bears has been covered intensively every year (Fig. 2). The locations of FCOY, FYRL, and mating areas occupied ca. 1500 km^2, i.e., ca. 23% of the total bear range (ca. 6520 km^2) in the Asturian Cantabrian Mountains.

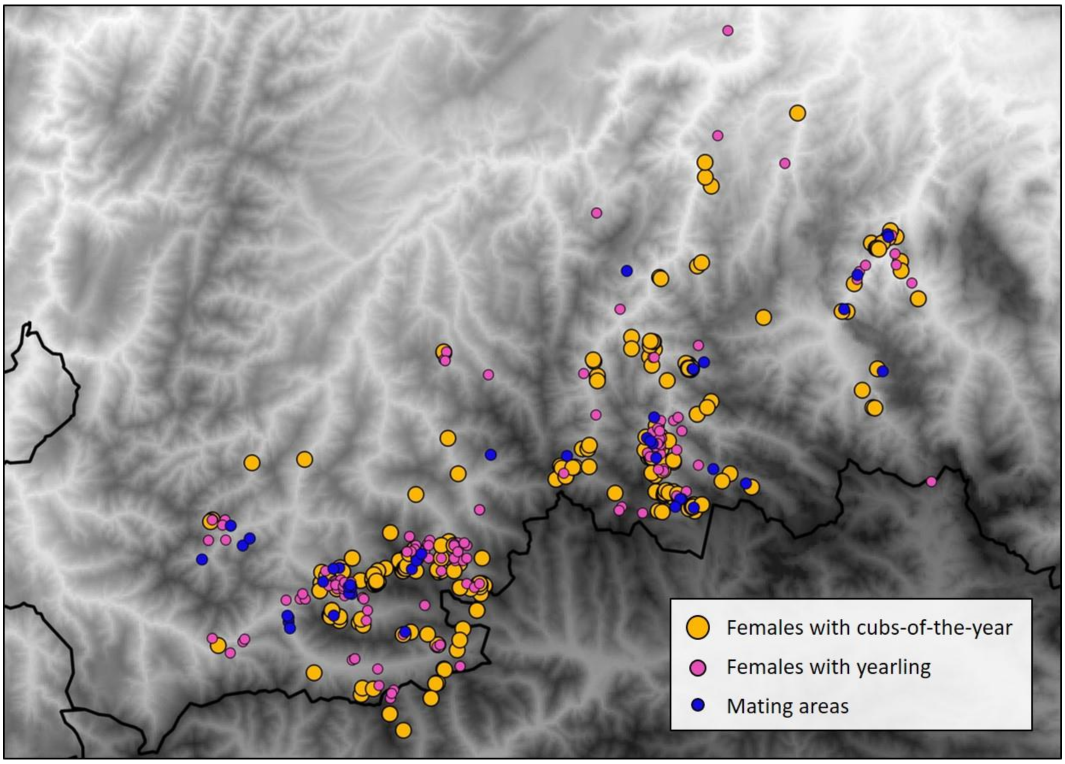


Figure 1. Spatial distribution of localizations of brown bear females with cubs (orange dots), females with yearlings (bright pink dots) and bear mating areas (blue dots) in the Cantabrian Mountains, NW Spain.

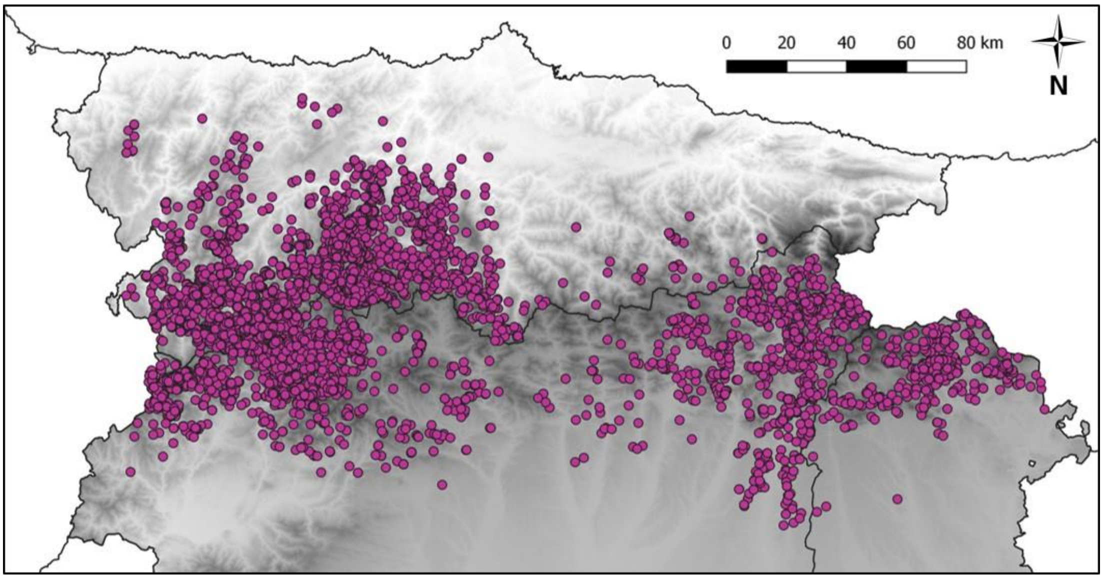


Figure 2. The spatial distribution of the sampling effort (direct observations and camera traps) for brown bear occurrence data (n = 8,784 locations) in the Cantabrian Mountains.

In April-June and from 2001 to 2016, we collected 397 locations of FCOY (assigned to 84 families), 163 locations of FYRL (assigned to 48 families), and 44 locations of bears at mating areas. The different bear families were identified on the basis of : (a) color patterns of mothers, (b) number and characteristics of cubs, and by (c) distance between observations of family groups (Ordiz et al., 2007; Penteriani et al., 2018b). This information also allowed differentiating between families observed the same day in neighboring areas. We made all observations during daytime and from distances that varied from several hundred meters to 1-1.5 km (Zarzo-Arias et al., 2018). Camera traps allowed additional information on FCOY locations, especially when they were not in open habitats.

Landscape characterization

We used a multi-scale approach of the habitat use of FCOY, considering four spatial scales, i.e., circular plots with radii of 500, 1000, 2000, and 3000 m, around each bear location. Such plots covered most of the FCOY range of movements in our study area during the first months of the year, from the abandonment of the den where they gave birth until the end of the spring-early summer (authors' unpublished data pers. obs. and Gardner et al. 2014; Ordiz et al., 2007). FCOY also have small home ranges in spring in other brown bear populations, e.g., in Scandinavia (Dahle & Swenson, 2003b; Steyaert, Swenson & Zedrosser, 2014) and in North America (Miller et al. 1997; Gardner et al. 2014; Steyaert et al. 2014), which supports our reasoning for the establishment of small spatial scales in this study.

Our multi-scale approach is also based on Johnson's (1980) conceptual framework, which assumes that animals make decisions regarding basic resources (e.g. breeding sites, cover and food) at progressively smaller scales in a hierarchical manner. The identification of the scales at which particular environmental variables influence habitat selection is crucial for understanding habitat suitability patterns as perceived by animals in complex landscapes. Indeed, what may appear important at one scale may have little relevance at another, making results scale sensitive (Ciarniello et al., 2007). In particular, habitat relationships have been shown to be highly sensitive to the scale at which predictor variables are evaluated for brown bears in the Cantabrian Mountains (Mateo Sánchez et al., 2013).

Landscape features for FCOY, FYRL, and mating areas were characterized by three categories of variables, namely landscape structure, landscape composition, and human footprint (i.e., landscape variables associated with humans) (see Table 1 for more details). Landscape GIS layers were extracted from 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).

Variable		Description
Structural variables	Altitude	Altitude of the plot centers (m a.s.l.), obtained from a raster layer of altitude of the Iberian Peninsula 'http://www.diva-gis.org' and calculated by QGIS *Point Sampling Tool*
	Slope orientation*	Eight orientations, i.e. the four cardinal directions and the intermediate points between them (intercardinal directions), calculated by the QGIS tool *Aspect* (*Terrain Analysis*) the plot centers
	Ruggedness	A variable calculated as the total length (m) of the linear development of level curves within the four different circular plots with the function *$length*
Human footprint	Paved road and dirt road length	Two variables calculated as the total length (m) of their linear development within the buffers with the function *$length*
	Distance (m) to the nearest paved road, Dirt road, human settlement (village/town), human infrastructure (e.g. industrial areas, power plants, mines) and river	Five variables calculated with the *Hub Distance* function in MMQGIS

Habitat composition variables	% of vegetation patches	We reclassified the totality of landscape layers of the Principado de Asturias into 16 broader classes: cliff, crops, conifer, fern, forest, fruit trees, grassland, human infrastructures, pasture, riparian forest, rocky area, shrubland, gorse, heath, villages/towns and young forest. Then, we used (a) the tool *Intersect* to extract the information of the layers for each plot and (b) the function *$area* to calculate the area occupied by each patch of habitat, which was successively converted to a %

Table 1. Structural, human, and habitat composition variables used to characterize areas used in early spring by brown bear females with cubs, females with yearlings, and mating areas for circular plots with radii of 500, 1000, 2000 and 3000 m in the Cantabrian Mountains, Spain. Variables marked with an (*) were correlated and therefore were not included in the models.

Statistical analyses

To explore the possibility that areas used in early spring by FCOY differed from the areas frequented by FYRL and mating areas, we modeled habitat plots using two generalized linear models for each spatial scale, assuming a logistic error structure. Within each spatial plot, one model analyzed areas of FCOY *vs*. FYRL and the other model, areas of FCOY *vs*. mating areas. Explanatory variables were represented by the landscape features and human infrastructures described in Table 1. We tested for multicollinearity and removed variables with a variance inflation factor (VIF) >10. The dataset was extremely heterogeneous, i.e., many family groups had many observations, whereas many others had only one observation (range = 1-26 observations per family group). Having many family groups with only one observation precluded us from including this variable as a random factor. This is because the intra-class variance would be underestimated, and this could bias our results. As randomly selecting one observation per family group resulted in loosing less data compared to removing those family groups with only one observation, we chose the former option. This resulted in a final number of observations of 84 locations for FCOY, 48 locations of FYRL, and 44 locations of mating bears. Because of the extension of the scales (plots with radii of 500—3000 m) of our multi-scale approach and the reported small displacements (few hundreds of meters) of FCOY after den exit, we are confident that our results are not an artefact of our random subset. Indeed, most of the bear family locations were inside these plots, and using different plot sizes around diverse random subsets of locations would have essentially described the same areas. Following Crawley (2007), model simplification was performed by backward selection of variables from the full model, and models were compared using likelihood ratio tests until a minimal adequate model was obtained. All statistical analyses were performed using R 3.3.1 statistical software (R Development Core Team, 2013), and corrplot (Wei and Simko, 2016) and lme4 (Bates and Maechler, 2009) packages. Statistical significance was set at α < 0.05.

RESULTS

Our multi-scale approach showed that FCOY used cliffs more than FYRL, a pattern that was evident at 2000- and 3000-m scales (Table 2 and Supplementary Table S.1). FYRL used more riparian forests, which are located along streams at the bottom of the valleys, and were closer to human settlements than FCOY (Table 2 and Supplementary Table S.1).

We did not find differences among locations used by FCOY and mating bears at the 1000-, 2000- and 3000-m scales (Table 2). These findings suggest that the habitat use of FCOY did not generally differ from the habitat use of adult bears during the mating period.

500 m		Estimate	SE	z	P
Females with cubs vs. females with yearlings					
Deviance = 8 %	Intercept	-0.59	0.19	-3.08	0.002
	Distance to village/town	-0.47	0.26	-1.80	0.07
	% riparian forest	0.68	0.22	3.14	0.002
Females with cubs vs. mating areas					
Deviance = 14 %	Intercept	0.76	0.22	-3.47	<0.001
	% fern	0.52	0.24	-2.22	0.03
	% riparian forest	0.58	0.26	-2.23	0.03
	% pasture	-0.67	0.26	-2.63	0.009
	% rocky	-0.67	0.33	-2.01	0.04

1000 m		Estimate	SE	z	P
Females with cubs vs. females with yearlings					
Deviance = 11 %	Intercept	-0.63	0.20	-3.20	0.001
	Ruggedness	-0.49	0.22	-2.30	0.021
	Distance to dirt road	0.60	0.20	3.04	0.002
	% riparian forest	0.45	0.21	2.18	0.03
Females with cubs vs. mating areas					
No significant differences					

2000 m		Estimate	SE	z	P
Females with cubs vs. females with yearlings					
Deviance = 11 %	Intercept	-0.65	0.20	-3.24	0.001
	% cliffs	-0.47	0.27	-1.75	0.08
	Dirt road length	0.39	0.21	1.84	0.07
	Distance to village/town	-0.58	0.24	-2.43	0.015

	% riparian forest	0.65	0.23	2.82	0.005
Females with cubs vs. mating areas					
No significant differences					

3000 m		Estimate	SE	z	P
Females with cubs vs. females with yearlings					
Deviance = 8 %	Intercept	-0.68	0.21	-3.29	0.001
	Distance to village/town	-0.47	0.22	-2.14	0.03
	% cliffs	-0.44	0.26	-1.71	0.09
	% grassland	-0.56	0.30	-1.87	0.06
	% riparian forest	0.51	0.23	2.23	0.03
Females with cubs vs. mating areas					
No significant differences					

Table 2. Linear models fitted by maximum likelihood showing landscape and human features that differentiate early (April-June) observed locations of female brown bears with cubs from (A) observed locations of females with yearlings, and (B) bear mating areas in the Cantabrian Mountains, Spain. All bear locations were from the same April-June period.

DISCUSSION

Maternal care strategies in brown bears include reducing movements (i.e., small home ranges) during the mating season, displaying more diurnal behavior, and spatial segregation from adult bears when females are accompanied by cubs of the year. Such strategies have been observed in several populations, both in Europe and North America (Ordiz et al., 2007; Steyaert et al., 2012 and references therein). Our study documented that, during the first few months after den emergence when bear cubs are most vulnerable, FCOY settled in potentially safe areas, like cliffs, more than did FYRL, which may provide shelter from both conspecifics and from human activities. Preference for quite inaccessible areas is likely a behavioral adaptation of FCOY to both reduce infanticide risk and survive in human-modified landscapes. However, in Scandinavia, successful mothers also selected for areas in relative close proximity to human habitations, which were avoided by adult males, showing that human footprint (i.e., landscape variables associated with humans) can locally act as protective shield for FCOY (Steyaert et al., 2016).

At the largest spatial scales, FCOY settled in landscapes with similar characteristics as areas used by males during the mating season. FCOY generally move short distances in early spring, i.e., during our study period, and are more active during the day than adult bears (authors' unpublished data and Ordiz et al., 2007), which likely represent strategies to avoid encounters with other bears (authors' pers. obs. and Fernández-Gil et al., 2006). However, similar habitat use by FCOY and males during the mating season, which might result in similar habitat use, may have increased the likelihood of infanticidal encounters. In fact, between 2013 and 2016, 15 1 km x 1 km survey blocks contained both locations of FCOY (n total = 75 squares) and mating areas (n total = 23 squares) within the study area (authors' unpublished data). Thus, 20% of FCOY locations and 65.2% of mating areas located during the last 4 years occurred within the same 1-km^2 areas.

These observations provide some evidence that, in some cases, the FCOY choices for shelter and food in early spring may 'trap' them in areas where they also overlap with mating bears, which is contrary to distance-sensitive avoidance (Penteriani et al., 2018a). Evolutionary traps arise when individuals make maladaptive choices based on apparently reliable environmental cues, which ensnare individuals in situations or places that reduce their lifetime fitness or survival (Schlaepfer et al., 2002). The type of evolutionary trap we propose is different, because classical evolutionary traps are habitat types of lower fitness return that are preferred to other habitat types with higher fitness return, whereas we propose here that an individual may be constrained to use habitat types that are not optimal, which does not necessarily mean that it prefers non-optimal habitat. This scenario might be more prone to occur in small and confined populations, such as the Cantabrian bear population, where limited habitat availability and a distribution range surrounded by a variety of human activities and higher human densities might prevent FCOY from successfully avoiding areas also used by other bears (Gonzalez et al., 2016, Martínez Cano et al., 2016). Indeed: (a) most of the suitable habitat in western Asturias Province is already occupied (77 % of identified potential areas of bear expansion; Zarzo-Arias et al., 2019) and (b) the core bear range shows extensive urban and agriculture development, with a road density for the study area of ca. 47 km/100 km^2 (http://www.seap.minhap.gob.es/index.html); see also (Penteriani et al., 2017).

Even if FCOY alter their activity times to avoid male bears (Fernández-Gil et al., 2006), a phenomenon known as temporal segregation (Fedriani et al., 1999), restricted habitat availability in a human-modified landscape and the presence of males searching for reproductive opportunities (Ordiz et al., 2007) may promote encounters among bears during the mating season, which can in turn lead to infanticide events. In bear populations confined to areas with high human encroachment, FCOY habitat-mediated avoidance may only occur at small spatial scales, e.g., in the surroundings of the den after it is abandoned in early spring. Because habitat use by FCOY did not differ from habitat use by adult bears at the largest landscape scales during the mating period, further studies should elucidate the possibility that scale-dependent differences exist regarding infanticide avoidance.

The combination of the restricted range and size of the Cantabrian bear population, the documented cases of infanticide, and the potential consequences of habitat use of FCOY overlapping with adult males in mating areas may have an overall, important impact on the bear population dynamics in the Cantabrian Mountains, where suitable bear habitats seem to be limited by human encroachment (Naves et al., 2003). Therefore, future direct monitoring of space use, movements, and rhythms of activity of both FCOY and adult bears will be crucial to understand the development of this bear population and, consequently, to plan effective conservation strategies preserving the positive trends observed recently (Pérez et al. 2014, Gonzalez et al. 2016, Martínez Cano et al. 2016). For the time being, proactive conservation of rugged terrain is an important management recommendation, as it is certainly used by FCOY, especially when such places are close to human settlements and outdoor human activities (e.g., ski resorts, hiking, and climbing areas), which are a potential source of disturbance and may cause displacement of FCOY from these sensitive areas.

SUPPLEMENTARY MATERIAL

	Significant variables	Mean	SD	min - max	Mean	SD	min - max
500 m		Females with cubs of the year			Females with yearlings		
	% riparian forests	0.8	1.7	0 - 10.6	2.1	2.9	0 - 11.6
	Distance to villages (m)	375.8	116.9	133.2 - 494.2	34.7	69.3	25.7 - 430.6
		Females with cubs of the year			Mating areas		
	% fern	0.5	1.8	0 -10.0	1.5	3.8	0 - 13.1
	% riparian forests	0.8	1.7	0 - 10.6	2.1	3.8	0 - 14.6
	% pasture	13.6	17.5	0 - 68.2	10.0	17.0	0 - 44.3
	% rocky	3.3	5.8	0 - 24.6	1.1	5.4	0 - 11.7
1000 m		Females with cubs of the year			Females with yearlings		
	Ruggedness (total length in m of the linear development of level curves)	17.9	2.6	11.9 - 28.8	17.1	2.9	8.8 - 10.7
	Distance to dirt roads (m)	130.7	264.3	1.3 - 908.9	312.2	339.3	0.4 - 942.4
	% riparian forests	1.0	1.4	0 - 6.4	1.7	1.5	0 - 7.5
		Females with cubs of the year			Mating areas		
	NONE	-			-		
2000 m		Females with cubs of the year			Females with yearlings		
	% cliffs	4.2	5.2	0 - 32.8	3.2	3.5	0 - 12
	Dirt road length	1.9	2.6	0 - 10.5	2.6	2.6	0 - 8
	Distance to village/town	688.5	644.1	0-1992.4	499.8	640.4	0-1578.1
	% riparian forest	0.9	0.8	0 - 4	1.3	0.8	0 - 5.3
		Females with cubs of the year			Mating areas		

	NONE	-			-		
3000 m		**Females with cubs of the year**			**Females with yearlings**		
	% cliffs	3.9	4.7	0 - 24.5	2.8	3.3	0 - 16.9
	% riparian forests	0.9	0.5	0 - 3	1.2	0.5	0 - 3.5
	% grasslands	1.0	1.3	0 - 5.2	0.5	0.6	0 - 2.3
	Distance human settlements	598.7	1003.9	0 - 2877.5	301.6	1000.3	0 - 2506.1
		Females with cubs of the year			**Mating areas**		
	NONE	-			-		

Supplementary Table S.1. Values (mean ± SD, min, max) of the significant parameters (see Table 2) that characterized the comparisons between areas used in early spring by female brown bears with cubs and (1) females with yearlings, and (2) bear mating areas in the Cantabrian Mountains, Spain.

CAPÍTULO 3

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

Global Ecology and Conservation, 16, e00499.

ABSTRACT

Large carnivores are recolonizing parts of their historical range in Europe, a heavily modified human landscape. This calls for an improvement of our knowledge on how large carnivores manage to coexist with humans, and on the effects that human activity has on large carnivore behaviour, especially in areas where carnivore populations are still endangered. Brown bears *Ursus arctos* have been shown to be sensitive to the presence of people and their activities. Thus, bear conservation and management should take into account potential behavioural alterations related to living in human-modified landscapes. We studied the behaviour of brown bears in the Cantabrian Mountains, NW Spain, where an endangered population thrives in a human-modified landscape. We analysed bear observations video-recorded over a 10-year period to try to identify human and landscape elements that could influence bear behaviour. Neither the occurrence nor the duration of vigilance behaviour in Cantabrian bears seemed to be influenced by the proximity of human infrastructures and activity. Our findings suggest that the general pattern of human avoidance by bears is adapted to the human-modified landscape they inhabit. Bears generally avoid people, but close presence of human infrastructures or activity did not seem to trigger an increased bear behavioural response. Coexistence between large carnivores and humans in human-modified landscapes is possible, even when human encroachment is high, provided that carnivores are not heavily persecuted and direct interactions are avoided. Further research should also document the potential existence of other responses to human presence and activity, e.g., hunting, traffic noise, and measuring stress levels with physiological indicators.

INTRODUCTION

Large carnivores are recolonizing parts of their historical range in Europe (Chapron et al., 2014), in so-called human-modified landscapes (Kuijper et al., 2016), i.e. areas characterised by a widespread presence of people and infrastructures. This phenomenon is thus bringing wild animal populations closer to humans, in areas where habitats are fragmented and encroached on by towns, villages, roads, and a variety of human activities (Lowry et al., 2012; Venter et al., 2016; Watson et al., 2015).

Theoretically, the close coexistence of large carnivores and humans could produce human-driven disturbances that can affect species behaviour (Gaynor et al., 2018; Geffroy et al., 2015). Disturbance can alter space use and distribution (Hebblewhite et al., 2005; Leblond et al., 2013), food habits (Newsome et al., 2016; Valeix et al., 2012), and fitness-related behaviours like mating or nursing cubs (Ditchkoff et al., 2006; Frid and Dill, 2002; Higham and Shelton, 2011), potentially reducing survival rates (Basille et al., 2013; Shannon et al., 2017). Human disturbances can also be perceived by animals in a similar way to predation risk (Frid and Dill, 2002). Even apex predators display anti-predator behaviour in response to human presence (Clinchy et al., 2016; Ordiz et al., 2011; Parco Naturale Adamello e Brenta, 2007).

Studying animal behaviour is often the first approach to determine wildlife reactions to human-induced environmental changes and species' capacity to adapt to areas where animals and humans have to coexist (Tuomainen and Candolin, 2011). Animal behaviour can be a good indicator of the stress levels triggered by humans and can inform conservation and management of typically endangered species such as large carnivores (Dimitri and Longland, 2018). Moreover, the current expansion of these species in human-modified landscapes demands an improvement of our knowledge on how large carnivores manage to coexist with humans (Carter and Linnell, 2016), and what potential effects human presence and activities may have on their behaviour (Carter et al., 2012; Carter and Linnell, 2016; Elfström et al., 2014; Penteriani et al., in press). This is particularly important in areas with increasing but still endangered populations (Treves and Karanth, 2003; Ordiz et al., 2013a) .

Brown bears *Ursus arctos* are sensitive to human presence and activity (e.g., Ordiz *et al.*, 2011). Bears change activity patterns to avoid encounters with people by becoming more nocturnal (Blankenheim, 2018; Clevenger et al., 1990; Swenson et al., 2000; Tattoni et al., 2015), being less detectable when closer to human settlements (Oberosler et al., 2017), and avoiding roads (Bischof et al., 2017; Skuban et al., 2017), for instance. Besides, the brown bear is one of the most targeted species by wildlife tourism (Vincenzo Penteriani et al., 2017). Sharing the landscape with humans may be costly (Cooper and Frederick, 2007), and thus bear conservation and management strategies should take into account potential behavioural alterations related to living in human-modified landscapes, so as to favour the effectiveness of conservation practices (Treves and Karanth, 2003).

Brown bears in the Cantabrian Mountains (NW Spain) represent an example of an endangered large carnivore population in human-modified landscapes. It is a native bear population, which was never reinforced with relocations, officially protected since 1973. Most of their range is characterised by high human population densities (Penteriani et al., in press), extensive agricultural livestock activities and urban development, connected by a diffuse network of transport infrastructures (Lamamy et al., 2019; Mateo-Sánchez et al., 2016; Penteriani et al., in press), which have determined a reduction of continuous suitable habitat for this species (Martínez Cano *et al.*, 2016). As a consequence, human activities and presence in the Cantabrian Mountains have the potential to cause stress to bears and, therefore, alter their behaviour. Additionally, brown bear viewing is nowadays a common practice in the Cantabrian Mountains (Penteriani et al., 2017; Ruiz-Villar et al., 2019). Generally, the places where brown bear viewing occurs (Penteriani et al., 2017; Ruiz-Villar et al., 2019) are not controlled or managed by local authorities and frequently appear randomly in the area inhabited by bears, e.g., when a female with cubs settles in a given place or several individuals congregate during hyperphagia (Ruiz-Villar et al., 2019)Such viewing spots can be close to bears, and thus bear viewing has the potential to negatively influence their behaviour. All of these factors might negatively impact the present positive trend of this endangered population, which is about 220 bears (Pérez et al., 2014).

We studied bear behaviour by analysing video recordings of direct observations during a 10-year period. In particular, we explored whether brown bear behaviours may be influenced in a human-modified landscape. We first analysed the time bears dedicated to different behaviours, namely walking, feeding, nursing and resting, in relation to the human features of the landscape they inhabit. Second, we studied whether human infrastructures may cause the appearance of vigilance/alert behaviour and influence its duration, and if that vigilance behaviour is affecting brown bear behaviour. As individual behaviour is the results of the complex interaction between internal (e.g. age) and external factors (natural habitat characteristics and season), we accounted for these effects when studying brown bear behaviour in human-modified landscapes. We hypothesised that, if brown bears are negatively influenced by the presence of humans, they should modify their behaviours, becoming especially vigilant when in closer proximity to people and/or human infrastructures. However, if brown bears have adapted their behaviour to human presence, we should not find any difference in their behaviours as a function of the distance to human infrastructures.

METHODS

Study area

Brown bear videos were recorded in the western sector of the Cantabrian Mountains (Fig. 1), which includes the west of Asturias and north of León Autonomous Provinces. The Cantabrian Mountains run parallel to the Atlantic coast of northern Spain and exhibit a mild and humid climate throughout the year (900-1900 mm, average total precipitation; Martínez Cano *et al.*, 2016). Average elevation is around 1100 m (Martínez Cano et al., 2016; Naves et al., 2003). The main tree species are oaks (*Quercus petraea, Q. pyrenaica* and *Q. rotundifolia*), beech (*Fagus sylvatica*) and chestnut (*Castanea sativa*). Subalpine shrubland (*Juniperus communis, Vaccinium uliginosum, V. myrtillus* and *Arctostaphylos uva-ursi*) dominates mountain areas above the treeline (~1700 m; Martínez Cano *et al.*, 2016). In some areas, former forests have been converted into pasture and brushwood (*Genista, Cytisus, Erica* and *Calluna*) through human activities (Naves et al., 2006, 2003). The main economic activities throughout the bear's range include livestock farming, mining, tourism, agriculture, and timber harvesting, with a generally low human population density (Blanco-Fontao et al., 2011). Surrounding areas have experienced extensive urban and agricultural development, and are fragmented by a network of main transport infrastructures (Mateo-Sánchez et al., 2016).

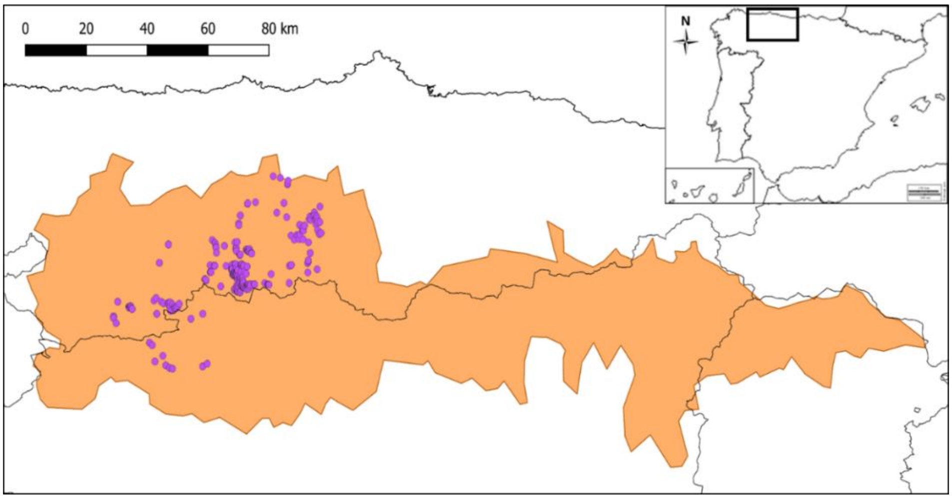


Figure 1. The locations of the 3,132 videos (78.5 hours in total) of different brown bear behaviours associated with 167 adults, 42 subadults and 112 females with cubs, within the species distribution (orange shape) in the Cantabrian Mountains.

Behavioural analyses

Brown bears were recorded with the digiscoping technique (a telescope with a digital camera) over a period of 10 years, from 2008 to 2017. All the observations were done at a safe distance from bears (from several hundreds of meters to > 1km) to avoid influencing bear behaviours. We assigned bear behaviours following ethograms established in other studies (Perdue, 2016), setting up 10 different classes: (1) feeding; (2) walking; (3) resting; (4) vigilance; (5) territorial marking; (6) conspecific aggression; (7) females nursing cubs; (8) mating; (9) social interaction; and (10) other behaviour (see Table 1). In particular, we focused on vigilance behaviour, which was taken as a response of individuals to human disturbances. We considered that bears were exhibiting vigilance behaviour when they were: (1) sniffing the air; (2) exploring their surroundings by intensively looking around; and (3) focusing attention in a given direction.

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

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

We measured the time bears spent on each behaviour with the free software BORIS (http://www.boris.unito.it/pages/download.html), which allows quantifying the time dedicated to behaviours previously defined in an ethogram (Friard and Gamba, 2016).

Specific characteristics of individuals, such as fur marks, colour and body morphology, allowed identification of some individuals during video recordings and over the years (Fagen and

Fagen, 1996; Higashide et al., 2012). When possible, individuals were assigned to one of three bear age or sex related categories (hereafter, bear class), i.e., adult, subadult and female with cubs. Beyond the fact that it was not possible to observe bears during the night, we consider that diurnal observations are best to detect bear reactions to humans because that is the time when humans are usually active, and there is greater potential for bear and human overlap. Each video was also classified seasonally, on the basis of the main bear cycle in the Cantabrian Mountains (Martínez Cano *et al.*, 2016), including 'winter', when most bears, but not all, hibernate (January to mid-April), 'spring-early summer', when the mating season occur, (mid-April to June) and 'late summer and autumn', which includes the hyperphagia period when bears store fat for the next winter (July to December). In the Cantabrian Mountains, not all bears hibernate every year and hibernation may be relatively short (author's personal observations and Nores *et al.*, 2010), and thus some bear observations (n= 90) were also recorded in winter.

Environmental variables

The location of each video-recorded bear was used to analyse the characteristics of the human and natural environment surrounding bear behaviour (Fig. 1) by using QGIS 3.0.2 (Quantum GIS Development Team, 2015). Bears generally moved only a short distance during the observations and the position of the bear when it was first observed and video-recorded was considered the location corresponding to each video.

For each video location, we measured human disturbance (i.e. human presence and activities) as the minimum bear distances to: (1) paved roads; (2) unpaved roads and trails; and (3) urban settlements. To obtain the minimum distance to roads and trails we used the transportation network information from CNIG (http://centrodedescargas.cnig.es), whereas for urban settlements we used the Base Topográfica Nacional BTN100. We also included a variable related to brown bear viewing activities, calculating the minimum distance from one of the six most common bear viewing points located in the Cantabrian Mountains to the location of the video.

Additionally, we evaluated natural habitat characteristics around bears by estimating the following parameters: (1) altitude; bear minimum distance to (2) forests; (3) shrubland; (4) natural open areas (grasslands and pastures) and (5) crops. Minimum distances to natural landscape variables were calculated using the Mapa Forestal de España MFE50 (http://www.mapama.gob.es). However, as the minimum distance to crops was highly correlated to urban settlements and trails, whereas altitude was so to roads (Pearson correlation coefficients > 0.6), we did not include minimum distance to crops and altitude in our statistical models.

Statistical analysis

To study brown bear behaviours in a human-modified landscape, we first explored the association between the duration of the recorded behaviours (i.e., walking, feeding, nursing and resting) and the environmental variables, season and bear class. In order to make behaviours recorded during different times comparable between them, we divided the time of each observed behaviour by the duration of the recorded video. As individual behaviours are intrinsically correlated, i.e. when a bear is walking is not resting, we constructed four separate covariance matrices with the dyads of walking and feeding, walking and resting, resting and feeding, and nursing and feeding. We run four separate bivariate models to quantify estimates of variance and covariance components between dyads of the behavioural traits considered (Doncaster and Davey, 2007). In these models, the explanatory variables were the environmental variables, season and bear class. In all models, year and individual identity were included as random factors. In order to test the significance of a covariance, we compared the models with and without the covariance set to 0 using a log-likelihood ratio test.

Second, to study whether human infrastructures may cause the appearance of vigilance/alert behaviour and also influence its duration, we built two separate generalized linear mixed-effects models (GLMMs). In the first model, we analysed the appearance of the vigilance behaviour (binomial variable: 0 = no vigilance behaviour showed by the individual; 1 = appearance of a vigilant behaviour) in relation to the presence of humans and their activities. To take into account that brown bear behaviour also depends on other external and internal factors, we also included natural habitat features (forest, open habitat and shrubland), individual characteristics (i.e. bear class) and season. While the presence of humans and natural landscape characteristics were included as covariates, those related with individual characteristics and the variables related with time were included as factors. We then built a second general linear mixed-effect model to test whether the time bears spent alert (vigilance behaviour duration being normally distributed) depended on the proximity of different human structures (human settlements, roads, trails and bear tourism viewing points). Again, we included natural habitat landscape characteristics (forest, open habitat and shrubland), bear class and season. In these two models, we account for the intrinsic annual variability and for the fact that vigilance behaviour is more likely to last longer as the time recorded increases by including year as a random factor and the duration of the video as an offset, respectively. The offset is a structural predictor, whose coefficient is assumed to have the value 1; thus, the values of the offset are simply added to the linear predictor of the target (Bates and Sarkar, 2006). We selected the best models using the Akaike's Information Criterion, considering models with ΔAIC values lower than 2 as competitive. For each set of models, we employed model averaging on the 95% confidence set to derive relative importance values (RIV) and parameter coefficients of each variable using the full-model averaging approach (Burnham, K. P., & Anderson, 2002).

Finally, by returning to the bivariate analysis of variance explained above, we study whether brown bear behaviour (i.e., walking, feeding, nursing and resting) was influenced by the time individuals spend in alert behaviour. In this case, we analysed the covariance matrices described above against time alert behaviour, bear class and season as alternative explanatory variables.

All statistical analyses were performed using R 3.4.1 statistical software (R Core Team, 2013), using the MuMIn package (Barton, 2018) with lme4 package (Bates and Sarkar, 2006) and ASReml-R for bivariate models (Butler et al., 2009).

RESULTS

We analysed 3132 videos, including 78.5 hours of observed brown bear behaviours, of 167 adult bears, 42 subadults and 112 females with cubs (Supplementary Table S.2).

Non-alert behaviours

Feeding was the behaviour in which bears spent more time (54% of the total amount of time recorded) (Supplementary Table S.1). Together with subadults in 'late summer and autumn' (Supplementary Table S.2), females with cubs were the bear group that spent more time feeding in all seasons (especially during 'spring-early summer': 5.45 ± 7.62 min, range = 0–47.5 min). Looking at the mean distance to human structures among bear classes (Supplementary Table S.3), adults were further away from urban settlements during 'spring-early summer' and 'late summer and autumn' than females with cubs or subadults (see also Fig. 2). Incorporating the covariance of behaviour explained a significant proportion of variance compared with models in which covariance was not included (Supplementary Table S.4 and S.5). Regarding the covariance between dyads of behaviour and environmental factors, we found that only the dyad between feeding and nursing was associated with human variables (Supplementary Table S.5). Specifically, we found a negative covariation between feeding and nursing associated with human settlements and a positive covariation with viewpoints. These results suggest that individuals tend to change from feeding and nursing to the other of these two behaviours as they get closer to urban settlements. In addition, our analyses suggest that around viewpoints, individuals were more often feeding and nursing.

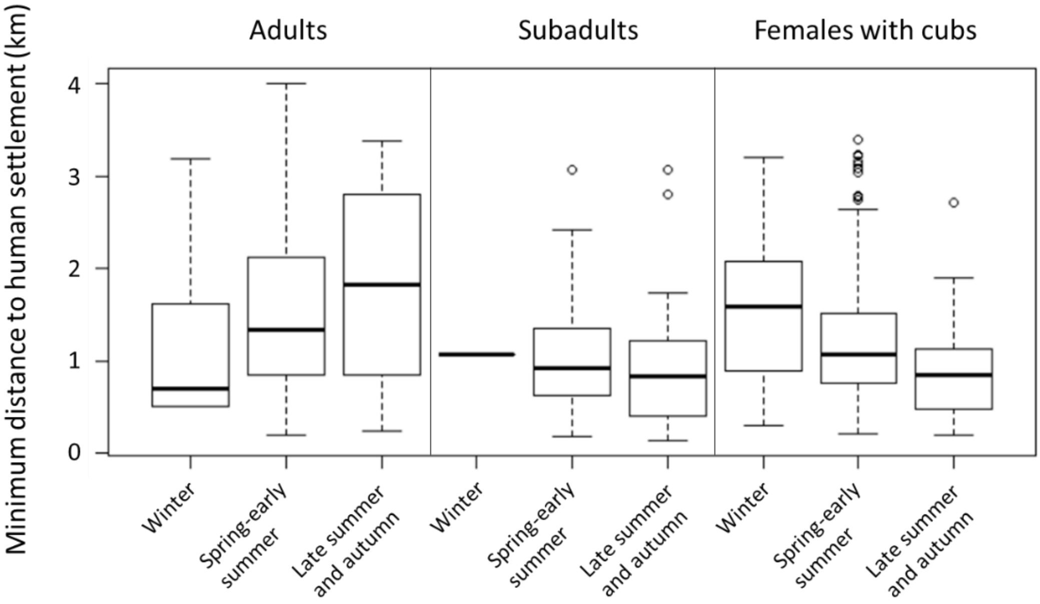


Figure 2. Distribution of the minimum distance (km) to human settlements (town and villages) of all brown bear observations among the different bear classes (adults, subadults and females with cubs) in each season (‘winter’, ‘spring-early summer’ and ‘late summer and autumn’).

Appearance of vigilance behaviour and its duration

We found that the appearance of vigilant behaviours was related to bear class and video duration (all RIV = 1; Table 2). In particular, the appearance of vigilance behaviour was less likely in adult bears than in subadults and females with cubs. The appearance of vigilance behaviour was never strongly related to any of the human elements or natural habitat variables (although their RIV values were above 0.56) (Table 3), suggesting that the appearance of vigilance behaviour was neither related to the natural habitat variables where bears inhabit.

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

Table 2. Model averaged coefficients and relative importance values (RIV) for vigilance appearance in relation to the human environment, habitat composition and individual characteristics (i.e., bear class). Vigilance appearance is a binary variable indicating whether there is any vigilance behaviour recorded (1) or not (0).

DEPENDENT VARIABLE	COMPETING MODELS	df	AIC	ΔAIC	Weight	R²
Vigilance appearance	BearClass + Forest + OpenHabitat + Shrubland + Duration	7	681.75	0	0.05	0.1292167
	BearClass + Season + Forest + OpenHabitat + HumanSettlement + Duration	9	682.13	0.38	0.04	0.1349776
	BearClass + Forest + OpenHabitat + HumanSettlement + Shrubland + Duration	8	682.15	0.41	0.04	0.1352757
	BearClass + Season + Forest + OpenHabitat + Shrubland + Duration	9	682.33	0.59	0.03	0.1338969
	BearClass + Forest + OpenHabitat + HumanSettlement + Shrubland + Trail + Duration	9	682.38	0.64	0.03	0.1370742
	BearClass + Season + Forest + OpenHabitat + HumanSettlement + Shrubland + Duration	10	682.71	0.96	0.03	0.1395005
	BearClass + Forest + OpenHabitat + HumanSettlement + Duration	7	683	1.25	0.02	0.1272648
	BearClass + Season + Forest + OpenHabitat + Duration	8	683.08	1.33	0.02	0.1258817
	BearClass + Season + Forest + OpenHabitat + HumanSettlement + Trail + Duration	10	683.15	1.4	0.02	0.1361518
	BearClass + Forest + OpenHabitat + Shrubland + Trail + Duration	8	683.21	1.47	0.02	0.1287212
	BearClass + Season + Forest + OpenHabitat + HumanSettlement + Shrubland + Trail + Duration	11	683.35	1.61	0.02	0.1416621
Vigilance duration	Season + Duration	5	5262.13	0	0.06	0.0721443
	Season + Viewing point + Duration	6	5262.69	0.55	0.04	0.07451133
	Season + HumanSettlement + Duration	6	5263.69	1.56	0.03	0.0732944
	Season + Forest + Duration	6	5263.89	1.76	0.02	0.07280913
	Season + Shrubland + Duration	6	5264.01	1.88	0.02	0.07179663
	Season + OpenHabitat + Duration	6	5264.12	1.99	0.02	0.07237139
	Season + Road + Duration	6	5264.13	1.99	0.02	0.07232507

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

The duration of vigilance behaviour was related to the season and the video duration (Table 4). The amount of time bears appeared vigilant mostly differed among seasons (Table 3), spending less time in vigilance during 'late summer and autumn' than in the other periods. Among all combinations of behavioural types explored, we found that alert duration was negatively associated with the covariance of multiple dyads of behaviour (Supplementary Table S.4). Specifically, we found that alert duration was negatively associated with the covariance of feeding-resting, feeding-walking and nursing-feeding (Supplementary Table S.4). This suggests that as alert duration increased, individuals choose to follow one or another behaviour. Conversely, in situations where alert duration was minimal, individuals were more likely to display both behaviours.

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

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

DISCUSSION

Our results show that neither the appearance nor the duration of vigilance behaviour in Cantabrian brown bears seemed to be influenced by the closeness of any of the human structures and activities that we took into account in this study, i.e., roads, trails, urban settlements, and viewing points. Populations of bears and other carnivores that have been facing human persecution for centuries are more elusive, e.g., more crepuscular and nocturnal, than their counterparts inhabiting remoter areas (Ordiz et al., 2011; Zedrosser et al., 2011). Bears that have coexisted with humans for many generations seem to have adapted their behaviour to human presence and activities, especially if they cannot easily hide from humans (Skuban et al., 2018), and none of the habitat or human variables that we analysed seemed to increase or decrease the time that bears spent alert.

Human activities can trigger detectable behavioural changes in brown bears. In northern Europe, where bears are hunted, bears become even more nocturnal when hunting season starts (Ordiz et al., 2012) and after encounters with people in the forest (Ordiz et al., 2013b). Bears also seek more concealed daybeds following seasonal increases in human activity levels (Ordiz et al. 2011). However, the flight responses of experimentally approached bears were not dependent on the densities of human populations and roads inside the bears' home ranges, or the distances from the bears to roads and settlements when encountered (Moen et al., in press). Consistency in bear behavioural responses regardless of proximity to human infrastructures, both in our study and in northern Europe, likely reflects the fact that bears living in human-modified landscapes have developed a solid pattern of human avoidance. Most bears move away after a direct encounter with a person, both in Fennoscandia (Moen *et al.*, in press; Ordiz *et al.*, 2013b), where bears are hunted, and in Spain (authors' personal observations), where they are legally protected. However, behavioural responses of bears do not seem to be dependent on the mere presence of human infrastructures in generally encroached landscapes, and this applies to both hunted (e.g., Fennoscandia) and non-hunted (e.g., Spain) bear populations.

Season seemed to have some effects on brown bear behaviour. That is, bears spend less time alert during 'late summer and autumn', when they focus on feeding prior to hibernation and cubs are no longer at risk of infanticide (Eva Bellemain et al., 2006; Steyaert et al., 2013). Bears also appeared closer to human settlements in this period, probably due to the high availability of attractive food resources like fruit trees or crops (Libal et al., 2011; Skuban et al., 2018). During the 'spring-early summer' period, when the need to protect offspring is crucial due to the high risk of infanticide, females with cubs spend more time on vigilance behaviours compared to other seasons (Supplementary Table S.4). Then, alert behaviours of females with cubs may reflect the potential risk driven by males rather than by humans and their activities. Adult males and single females are often the most elusive bear classes, using areas further away from human settlements (Elfström et al., 2014; Smith et al., 2005). However, females with cubs may use proximity to human presence as a shield strategy (Skuban et al., 2018; Steyaert et al., 2016), and subadult bears also use areas closer to people, which are generally avoided by adult bears (Nellemann et al., 2007). Our results confirm this general pattern (Fig. 2), which reflects the interface between intraspecific avoidance of the most vulnerable bear classes (Eva Bellemain et al., 2006; Steyaert et al., 2016, 2013) and varying tolerance or adaptation of different bear classes to human presence (Elfström et al., 2014; Nellemann et al., 2007). Indeed, even if levels of vigilance are not generally high, a few individuals may conserve high alertness due to the individual variations in brown bears' behaviours (Milleret et al., 2018).

In the Cantabrian Mountains, brown bear mortality associated with roads is rare and illegal poaching, the most common driver of human-induced bear deaths (Palomero et al., 2007), may have declined in recent decades, resulting in the positive trends exhibited by this population (Gonzalez et al., 2016). Lower rates of human-induced mortality in recent times might have improved bear-to-human tolerance, as may have happened in other populations where bears are not persecuted (Smith et al., 2005). A previous study in the Cantabrian range documented that bear behaviour associated with vigilance was not different inside and outside natural parks (Naves, 2016), which perhaps might have been different if there were areas where bears were hunted and areas where they were fully protected.

Brown bears have largely coexisted with humans in Europe, including northern Spain (Clevenger et al., 1987), where the bear population is increasing (Gonzalez et al., 2016). If the positive trend persists, brown bears would have to expand into even more encroached landscapes, although suitable areas are still available in the Cantabrian Mountains (Zarzo-Arias et al., 2019). Human activities and infrastructure do not seem to provoke acute behavioural responses in the brown bears of the Cantabrian Mountains, but physiological reactions of bears to human presence, i.e., stress responses, should also be investigated, because they do not necessarily need to manifest visible behavioural changes and can have a cost on disturbed animals (Støen et al., 2015).

Certain levels of tolerance from both humans and large carnivores, which are reflected in behavioural patterns, seem crucial to facilitate persistence and eventual recovery of bears and other carnivores in human-modified landscapes, even where human encroachment is high, but management agencies must ensure that direct interactions between human and animals are not likely to occur. For instance, some authors have proposed that good brown bear tourism practices and the minimization of human-bear conflicts can improve and enhance the conservation of this species (Herrero et al., 2005; Vincenzo Penteriani et al., 2017; Smith et al., 2005). Finding that bears tended to change from feeding and nursing to the other of these behaviours as they were closer to urban settlements may suggest bear awareness, whereas finding that bears more often feed and nurse near viewpoints (Supplementary Table S.5) likely reflects the fact that these points are located where it is easiest to see bears. This highlights that effective management of bear viewing is necessary to ensure that tourists do not interact with bears (Vincenzo Penteriani et al., 2017), and the same concern should apply in general to other human activities in areas that are inhabited by large carnivores, thus avoiding any potential change in carnivore behaviour.

Finally, it is noteworthy that the goodness of fit (R^2) of our models was usually quite low, which is understandable because of underfitting, i.e., other important variables might not be in the models. Evidently, not all the external factors acting on the recorded individuals might have been recorded, and we also lack of information on what bears may have experienced just before our recording, as well as on the health state of individuals and on their behavioural traits (e.g., shy *vs*. bold individuals).

CONCLUSIONS

Our results suggest that the general pattern of human avoidance by bears is adapted to the human-modified landscape they inhabit. Bears generally avoid people, but close presence of human infrastructures or activity did not seem to trigger an increased bear behavioural response. Coexistence between large carnivores and humans in human-modified landscapes is possible, even when human encroachment is high, provided that carnivores are not heavily persecuted and direct interactions are avoided. Further research should also document the potential existence of other responses to human presence, e.g., hunting, traffic noise, and measuring stress levels with physiological indicators.

SUPPLEMENTARY MATERIAL

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

Supplementary Table S.1. Total time dedicated and percentage of each behaviour by each bear class (adults, subadults and females with cubs) in each season to the different behaviours included in the ethogram.

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

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

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

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

Supplementary Table S.2. Mean, standard deviation (SD), minimum (Min) and maximum (Max) duration (in sec) of all the brown bear behaviours during the three seasons ((‘winter’, ‘spring-early summer’ and ‘late summer and autumn’) of the bear cycle (see text for more details) for adults (A), subadults (B) and females with cubs (C).

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

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

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

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

Supplementary Table S.3. Mean, standard deviation (SD), minimum (min) and maximum (max) distance (in meters) to human structures and habitats during the three seasons ((‘winter’, ‘spring-early summer’ and ‘late summer and autumn’) for adults (A), subadults (B) and females with cubs (C).

	Variable	Estimate	df	Wald	P
Feeding-resting	Intercept		2	639.66	<0.001
Sig cov: p=0.001	Stress duration	-0.234 ± 0.023	1	96.99	**<0.001**

	Age		2	8.66	<0.001
	Adult	0			
	Subadult	0.059 ± 0.018			
	Female with cubs	0.053 ± 0.012			
	Season		2	24.01	0.013
	Winter	0			
	Spring-early summer	-0.049 ± 0.016			
	Late summer and autumn	-0.049 ± 0.019			
Resting-walking	Intercept		2	108.203	<0.001
Sig cov: p=0.854	Stress duration	-0.031 ± 0.023	1	1.657	0.198
	Age		2	3.087	0.213
	Adult	0			
	Subadult	-0.023 ± 0.018			
	Female with cubs	-0.020 ± 0.012			
	Season		2	7.842	0.01982
	Winter	0			
	Spring-early summer	-0.048 ± 0.017			
	Late summer and autumn	-0.041 ± 0.019			
Feeding-walking	Intercept		1	721.01	<0.001
Sig cov: p=0.002	Stress duration	-0.256 ± 0.025	2	96.35	**<0.001**
	Age		2	15.35	<0.001
	Adult	0			
	Subadult	0.060 ± 0.022			
	Female with cubs	0.052 ± 0.015			
	Season		2	6.72	0.034
	Winter				
	Spring-early summer	-0.005 ± 0.019			
	Late summer and autumn	0.031 ± 0.022			
Nursing-feeding	Intercept		1	676.30	<0.001
Sig cov: p=0.060	Stress duration	-0.110 ± 0.017	2	40.13	**<0.001**
	Age		2	75.47	<0.001
	Adult	0			
	Subadult	0.031 ± 0.013			
	Female with cubs	0.074 ± 0.008			
	Season		2	5.15	0.075
	Winter				
	Spring-early summer	0.024 ± 0.011			
	Late summer and autumn	0.012 ± 0.013			

Supplementary Table S.4. Association between the covariance of different behaviours and duration of stress response for brown bears in the Cantabrian Mountains (see 2. Methods for details on the models).

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

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

Population	-0.000005231529 ± 0.000006411933	1	5.93	**0.015**
Viewpoint	0.000001871871 ± 0.000001094458	1	10.05	**0.002**
Forest	-0.000006007738 ± 0.00004929487	1	0.4	0.526
Open area	0.000000125456 ± 0.000005432183	1	0.06	0.809
Shrub	-0.000008901726 ± 0.00002111216	1	2.81	0.094
Age		2	51.84	**<0.001**
Adult	0			
Subadult	0.0187464 ± 0.01376408			
Female with cubs	0.06531672 ± 0.009159461			
Season		2	5.67	0.059
Winter	0			
Spring-early summer	0.025342 ± 0.01249231			
Late summer and autumn	0.01041436 ± 0.01449922			

Supplementary Table S.5. Association between the covariance of different behaviours and environmental variables for brown bears in the Cantabrian Mountains (see Methods for details on the models).

CAPÍTULO 4

Seasonality, local resources and environmental factors drive patterns of brown bear damages: implications for management

ABSTRACT

The coexistence of humans and large carnivores is a major challenge for conservation and management, especially in human-modified landscapes. The ongoing recovery of some large carnivore populations is good conservation news, but it also brings about increased levels of conflict with humans. Compensation payments and preventive measures are used worldwide as part of conservation programs with the aim of reducing such conflicts and improving public attitude towards large carnivores. However, understanding the drivers triggering conflicts is a conservation priority which helps prevent and reduce damages. Here, we have analysed the spatio-temporal patterns of brown bear *Ursus arctos* damages to apiaries, crops and livestock in the two small, isolated and endangered bear populations in northern Spain. Damages varied among years, seasons and bear populations, and seemed to mainly depend on the local availability of natural food items, weather conditions and the availability of apiaries and livestock. Fluctuating availability of food items may explain the frequency of damages, which is yet another call to apply preventive measures in carnivore attacks to human property in seasons and years when food availability is lower than usual. Understanding and preventing damage is in turn essential to mitigate conflicts where humans and large carnivores share the same landscape.

INTRODUCTION

Coexistence with people is a major challenge for large carnivore conservation (Treves and Karanth, 2003), which is key to preserving the ecological balance of ecosystems (Ordiz et al., 2013a). In human-modified landscapes, where human populations and activities are extensive, conflicts with wildlife are also widespread (Zimmermann et al., 2010). Over time, human populations have grown exponentially, increasing encroachment on natural habitats and facilitating the occurrence of conflicts with wildlife. In turn, conflicts trigger the persecution of large carnivores to diminish livestock or agricultural losses (St John et al., 2012), resulting in a massive reduction of carnivore populations (Ripple et al., 2014; Treves, 2009). Despite their persecution, large carnivore populations have been recovering in recent decades mostly due to great conservation efforts (e.g., protective legislation, reintroductions), allowing the partial recolonization of former ranges (Chapron et al., 2014). Nevertheless, in places where people have become unfamiliar with the presence of large carnivores, husbandry practices have relaxed and preventive measures have been abandoned (Bautista et al., 2019). In this context, the return of large carnivores can increase damages to human property, and in recolonization areas damage prevention is often implemented only after problems emerge (Marsden et al., 2017).

Positive public attitude towards large carnivores is key to successfully achieving population recovery (Bautista et al., 2019). Hence, most conservation programs include compensation payments and the instauration of preventive measures, which are a fundamental step to deal with damages and reduce their occurrence (Nyhus et al., 2005; Rigg et al., 2011). Nowadays, the growth of large carnivore populations is harming tolerance towards them, as people believe that population increases are directly linked to an increased risk of damage (Eriksson et al., 2015). But many factors can affect the occurrence and the frequency of these damages (Majić Skrbinšek and Krofel, 2014). Increasing damage could be due to the availability of potential sources of conflict (Molinari et al., 2014) or periodic decreases in natural food availability (Gunther et al., 2004), and/or may be caused by just a few individuals (Bereczky et al., 2011; Swan et al., 2017). Understanding the basal and more recurrent causes behind large carnivore damage patterns is crucial in order to manage conflicts properly and it can improve the effectiveness of existing preventive strategies (Jerina et al., 2015; Majić Skrbinšek and Krofel, 2014). Some countries thus far have tried to assess this matter for several species (e.g., Jerina et al., 2015; Molinari et al., 2014; Patterson et al., 2004; Sangay and Vernes, 2008; Treves et al., 2004; Wilson et al., 2005), which has been proved to be useful in conflict management. However, most of them have been confined to the spatial scale, identifying general hot-spots on which to focus, leaving aside temporal variation in conflicts and the effect of scarce natural food resources. But, as stated by

Baruch-Mordo (2007), weather-related variables can be the most important predictors of conflict occurrence.

Brown bears *Ursus arctos* are currently the most common large carnivores in Europe, yet some populations remain critically endangered (Chapron et al., 2014). As they frequently inhabit human-modified landscapes, bears often resort to anthropogenic food feeding on crops, livestock and beehives (Bautista et al., 2017). In Spain, there are two isolated and critically endangered brown bear populations located in mountainous areas in the north. The first one, between France and Spain, has been reinforced by translocations of bears from Slovenia since 1996 due to its critical and imminent risk of extinction (Gonzalez et al., 2016; Quenette et al., 2001; Swenson et al., 2011). The other bear population inhabits the Cantabrian Mountains, where two subpopulations are slightly interconnected (Gonzalez et al., 2016; Lamamy et al., 2019; Zarzo-Arias et al., 2019). Within their range, the bears coexist with several human activities, which may be attractive to them. For example, beekeeping is widespread, and bears in the Cantabrian Mountains cause the highest number of damages to apiaries in Europe (Bautista et al., 2017). In the Pyrenees, damages to livestock are more common than to apiaries, and bears mostly attack sheep (Elosegi, 2010).

In this long-term study, with up to two decades of data in two of the study areas, we first analysed the spatio-temporal patterns of claims of brown bear damages in the three bear nuclei located in Spain (Pyrenean, and western and eastern Cantabrian). Second, we focused on a number of potential drivers that might trigger human-bear conflicts. The following main hypotheses have guided this exploration. First, we hypothesized that the patterns of brown bear damages differ at two different temporal scales, namely seasonal and yearly scales. For example, we might expect to find the greatest number of damages occurring during summer and fall, during the so-called hyperphagia period, as bears need to achieve minimum fat reserves before hibernation. In addition, we expected the frequency of damages to vary among years, which may be explained by different factors (e.g., peaks of damages occurring in years when the availability of natural food was lower, and the size of brown bear populations in Spain has increased over the last years, yet at different rates for each nuclei). Accordingly, as human activities vary locally and the number of bears differs among populations, we hypothesized that the observed temporal patterns of brown bear damages will also change over space. We accounted for this potential spatial variation in bear damage patterns, considering both the number and type of damages, at each bear nuclei (i.e. western Cantabrian, eastern Cantabrian and Pyrenean), in each administrative province (i.e. Asturias, León, Palencia and Lleida), and treating separately each Cantabrian subpopulation (western and eastern). Then, we hypothesized that the causes of damages would also depend on its type, the latter thus affecting the observed spatio-temporal patterns of damages. Finally, we tested whether the number of each type of damages depended on availability of natural food resources. We expected that different climatic factors and productivity indicators would be the best features to predict when the different types of bear damages may occur.

METHODS

Study area

Our study area comprises two mountainous systems in the north of Spain, the Cantabrian Mountains (Asturias, León and Palencia provinces) and the Pyrenees (Lleida province) (Fig. 1).

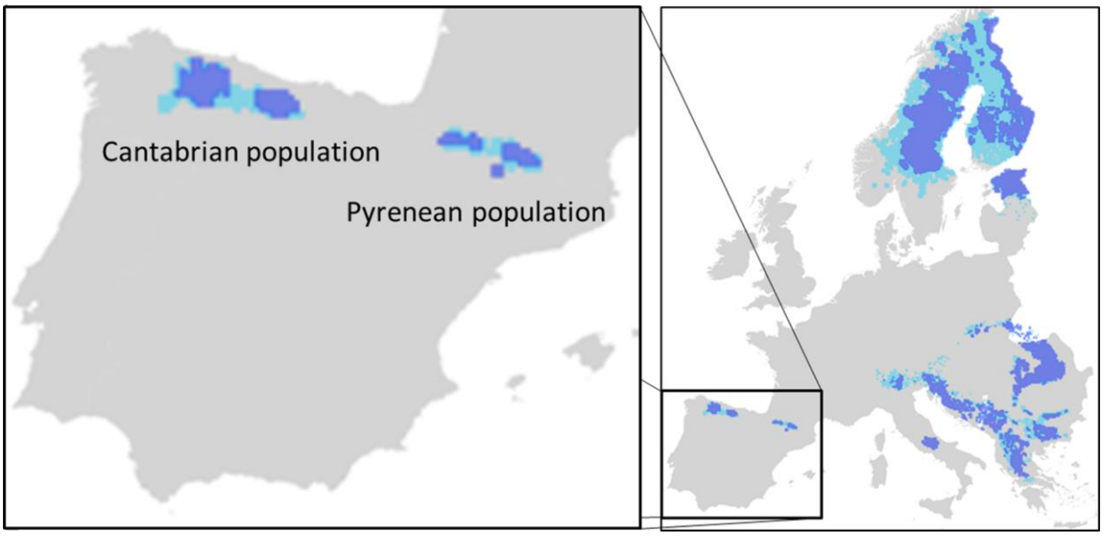


Figure 1. Distribution of the brown bear in Europe and focus populations of this study (extracted from https://www.lcie.org/Large-carnivores/Brown-bear).

In the Cantabrian Mountains elevation reaches up to 2,648 m a.s.l. (Martínez Cano et al., 2016) and the mountain range has an Atlantic climate, characterized by mild winters and rainy summers (Pato and Obeso, 2012). Forests of oak (*Quercus petraea*, *Quercus pyrenaica* and *Quercus robur*), beech (*Fagus sylvatica*), chestnut (*Castanea sativa*) and white birch (*Betula pubescens*) are dominant, alternating with pastures and brushwoods and subalpine scrubs (Penteriani et al., 2019; Zarzo-Arias et al., 2019). The average population density is ca. 4.9 inhabitants/km^2 for the eastern Cantabrian subpopulation and 10.9 inhabitants/km^2 in the western area, with a large road network (Lamamy et al., 2019). The most common human activities are livestock farming, mining, tourism, agriculture, and timber harvesting (Fernández-Gil et al., 2006).

In the Pyrenees elevation extends from 500 to 3,404 m a.s.l. and the range is characterised by a climate varying from Oceanic to Mediterranean (Martin et al., 2012). Beech and silver fir (*Abies alba*), oak, hazel (*Corylus avellana*), and gall oak (*Quercus cerrioides*) are dominant. At higher eleveations common birch (*Betula pendula*) stands out together with black pine (*Pinus uncinata*) and scots pine (*Pinus sylvestris*) on southern slopes, with alpine meadows on top. Average population density is ca. 5 inhabitants/km^2 and road density is low (1 km/km^2). The main human activities are forestry with associated road building, cow and sheep farming and, during summer and autumn, recreational tourism (e.g., hiking, hunting or fishing) and mushroom picking (Martin et al., 2012).

Damage and bear occurrence data

Due to the difficulties in data collection for the French part of the brown bear population of the Pyrenees, we were only able to include the damages recorded in the Spanish Pyrenees in our analyses. Damage claims data for each of the provinces included was available for different periods: in Asturias from 1997 to 2017 and in León and Palencia from 2008 to 2017, for the Cantabrian population; and in Lleida from 1998 to 2017, for the Pyrenean population.

The data included: (1) damage location (UTM); (2) day of the damage occurrence; and (3) type of damage, i.e., beehives, crops (more than 95% fruit trees as apple or hazel) or livestock (i.e. cow, sheep, goats and horse). We separated the damage data into three different groups: (1) Pyrenees, (2) west-Cantabrian and (3) east-Cantabrian. For each year, we also grouped the damages by phenological bear season, as defined by Martínez Cano et al. (2016): (1) hibernation (January to mid-April), with some bears remaining active during most of the winter (Nores et al., 2010; Zarzo-Arias et al., 2018), (2) mating (mid-April to June) and (3) hyperphagia (July to December).

In order to test the potential influence of the size of each bear population on the amount of damage, we also took into consideration an annual estimation of the number of bears for each nucleus. For the Cantabrian population, we used the yearly number of females with cubs for each Cantabrian subpopulation as a proxy of population size (Ordiz et al., 2007), whereas for the Pyrenean population the total number of bears was available.

Productivity and climate indicators

To assess availability of natural food resources for bears, we used several annual indicators of productivity. First, we collected annual productivity data of fruit tree crops (apple-tree, cherry and hazel) either rainfed (kg/ha) or scattered (kg/tree) for each province available from the Ministry of Agriculture, Fisheries and Food (http://www.mapama.org/). We used the variable when information was complete for more than 3 years in each bear nuclei.

We also included productivity for the most common soft and hard mast items appearing in the diet of both Cantabrian and Pyrenean brown bears (Elosegi, 2010; Naves et al., 2006; Rodríguez et al., 2007): acorn, chestnut, blueberry, cherry (*Prunus spp.*) and beechnut. For each species, we selected the most limiting climate factor (temperature or precipitation) according to the available literature. For acorns, we used September rainfall, as heavy rainfall makes acorns fall while too little rainfall impedes growth (García-Mozo et al., 2012), and spring rainfall, which also reduces acorn productivity in dry springs (Alejano et al., 2008). For chestnuts, August mean temperature positively related to higher productivity (Afif-Khouri et al., 2011). For blueberries, low winter mean temperature (December-March) favours higher fruit production (Nestby et al., 2010). For beeches we used June-July mean temperature of the previous year as warm conditions determine productivity the following year (Müller-Haubold et al., 2013). Finally, for *Prunus*, November-February minimum temperatures, if they are low, reduce fructification success (Caprio and Quamme, 2011).

Additionally, as climate indicators, we considered the mean per year of five variables: temperature, precipitation, North Atlantic Oscillation index (NAO), Normalized Difference Vegetation Index (NDVI), and sun radiation. We included temperature, precipitation and NAO values for the previous year because plants might react with a certain delay to climate, and for temperature we added averaged mean values from April to August because they represent the key season for fruit tree growth (Koenig & Knops, 2000). Finally, we included total precipitation of the summer period (June-September) as a drought indicator, representing a high risk for forest productivity (Müller-Haubold et al., 2013; Zimmermann et al., 2015).

Temperature, precipitation and sun radiation information were collected from the Territorial Delegation of the Agencia Estatal de Meteorología (AEMET, i.e., the Spanish state agency responsible for weather data). Specifically, for the western bear subpopulation in the Cantabrian Mountains we used climatic data from the Genestoso station (1170 m a.s.l.) and sun radiation data from Oviedo (Asturias). For the eastern Cantabrian subpopulation, we used climatic data from the Boca de Huérgano station (1104 m a.s.l.) and sun radiation data from

Virgen del Camino (León); and for the Pyrenean population we used climatic data from the Canfranc station (1160 m a.s.l.) and sun radiation data from Lleida. NAO index data was extracted from https://www.cpc.ncep.noaa.gov/. We downloaded NDVI layers from http://ivfl-info.boku.ac.at/, extracting mean annual values for each of the three bear nuclei.

Statistical analysis

First, to explore the spatio-temporal patterns of brown bear damages, we built two models: the first one included the observations collected from 2008 to 2017 in all studied bear nuclei, so as to have the same number of years recorded and avoid unbalanced data; the second model compared the west Cantabrian subpopulation with the Pyrenean population, using data from 1997 to 2017. The number of damage events was the response variable, and year, season, the interaction between them, bear nuclei, number of brown bears in each bear nuclei, and type of damage and its interaction with year were included as potential explanatory variables. However, as the number of brown bears was correlated with the variable year in each bear nuclei (VIF = 15.67 west Cantabrian, 6.84 east Cantabrian and 5.63 Pyrenean) we removed it from the models. Our response variable was discrete, thus we ran generalized linear models (GLM) with negative binomial error distribution. We compared all possible candidate models and selected the most parsimonious one using the Akaike method (Burnham and Anderson, 2002).

We also performed two sets of additional GLMs including bear damage number and type as explanatory variables with multinomial and binomial error distribution between (1) Provinces and (2) the two Cantabrian subpopulations, respectively.

Finally, to test whether bear damages depended on natural food availability, we built separate Principal Component Analyses (PCAs) for each bear damage type recorded in each bear nuclei. We scaled the variables by their standard deviations, with prior logarithmic transformation of habitat variables, and removed missing values. We grouped the variables into two sets: one with productivity indicators, i.e., annual productivity per province for different trees (rainfed or scattered apple, cherry, and hazel) and climate indicators limiting bear food productivity (acorn, chestnut, blueberry, beech, and *Prunus*). And the other set only with climatic indicators, i.e., NAO index, NAO of the previous year, sun radiation, NDVI, annual mean temperature, mean temperature from April to August, previous year mean temperature, previous year mean temperature from April to August, annual precipitation, previous year total precipitation and summer precipitation. Following Kaiser's criterion we applied a varimax rotation with Kaiser normalization to the retained components (McGarigal et al., 2000) in order to maximize the variance of the components' loadings, facilitating the interpretation of the PCA as it associated each variable with one or a few components. Following Kaiser's criterion (Kaiser, 1958), we only retained the components with eigenvalues > 1 and in each component we only considered the variables with an influence greater than 0.4 (either negative or positive).

All analysis were performed in R 3.5.1 statistical software (R Core Team, 2013), using the packages MASS (Ripley et al., 2013), lme4 (Bates and Sarkar, 2006), nnet (Ripley et al., 2016) and MuMIn (Barton, 2018).

RESULTS

The type of damages varied in the different bear nuclei (Supplementary Table S.1) over the different seasons (Fig. 2). Damages to beehives were the most common in the Cantabrian bear subpopulations, especially during the hyperphagia season. Damages to crops and livestock also increased remarkably during hyperphagia compared to the mating season. In the Pyrenean bear population, cow and sheep farming was the most damaged activity during both mating and hyperphagia, while apiaries were damaged more often during hyperphagia than in the mating season (Supplementary Table S.1), and no damages to crops were reported.

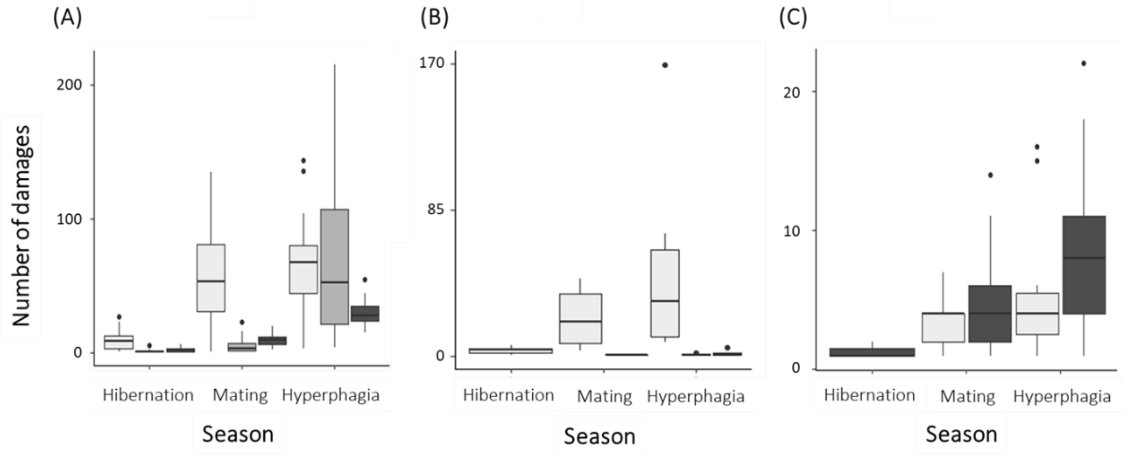


Figure 2. Amount of damage by type produced in each season (hibernation, mating and hyperphagia) during the periods: (A) 1997-2017 in the western Cantabrian brown bear subpopulation; (B) 2008-2017 in the eastern Cantabrian subpopulation; and (C) 1997-2017 in the Pyrenees. Beehives = light grey, crop = grey and livestock = dark grey. Note that the scale of the Y axis is different for each study area.

The number of damage events (all types together) varied at the different spatio-temporal scales considered. Damages varied (A) across seasons (Supplementary Table S.2, Supplementary Table S.3), with the largest number of claims occurring during hyperphagia and the lowest during hibernation (Fig. 2), and (B) among years, with a positive trend in all bear nuclei (Fig. 3). We also found that the number of damages varied across study areas (Supplementary Table S.4), with the highest number of damages occurring in the western Cantabrian subpopulation (Fig. 3). The number of damages also varied at the province level (Supplementary Table S.5), being more numerous in Asturias than in León, Palencia and Lleida.

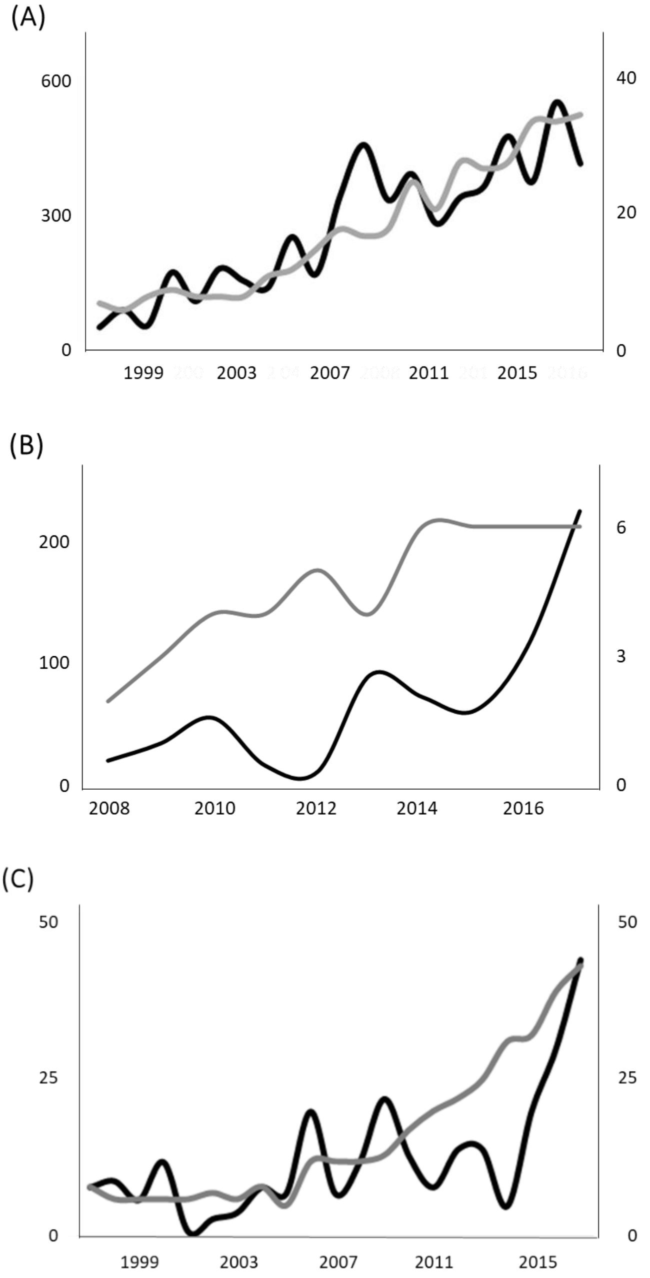
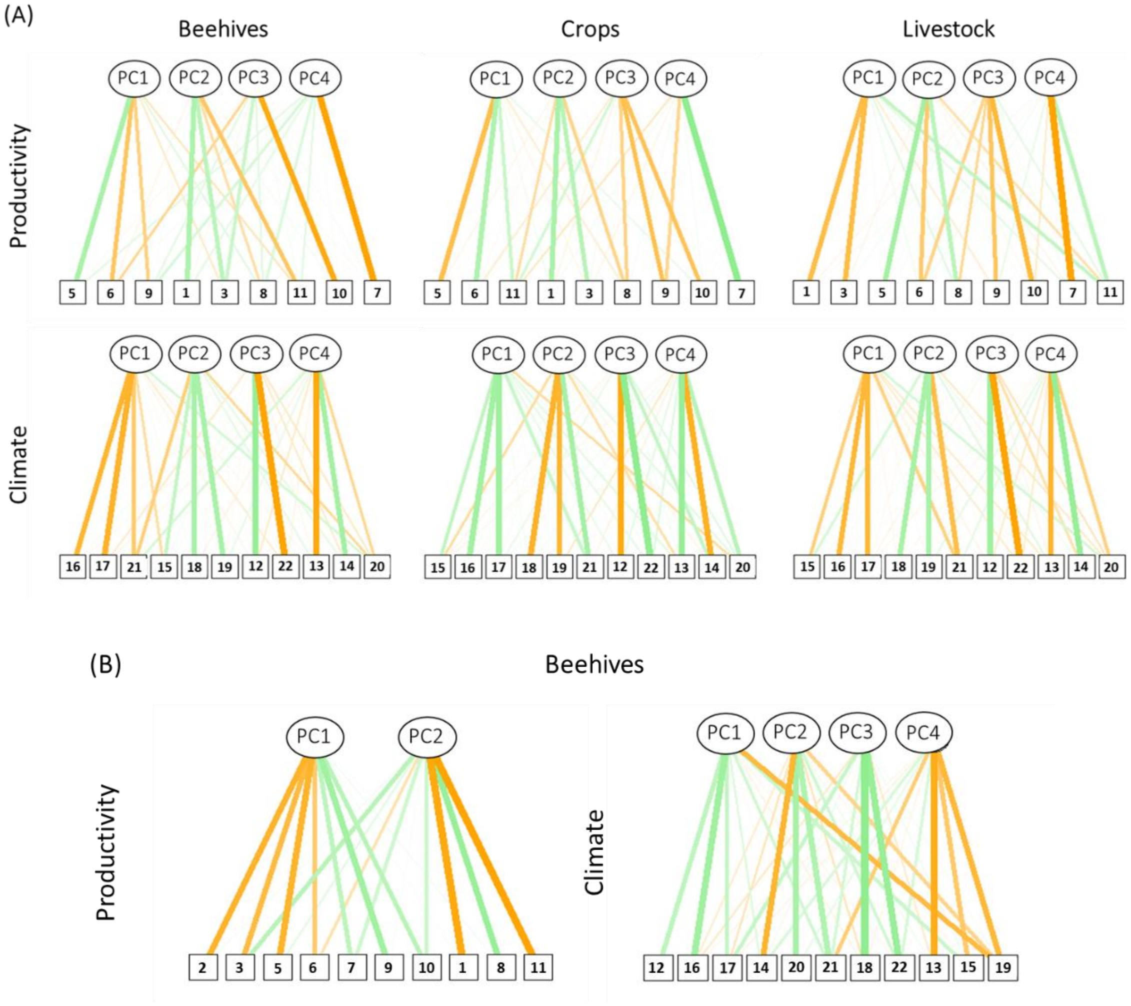


Figure 3. Evolution of the total number of damages (black line) and the size (grey line) of the three brown bear nuclei: (A) western Cantabrian subpopulation (1997-2017), (B) eastern Cantabrian subpopulation (2008-2017) and (C) Pyrenean population (1997-2017). The left vertical axis reflects the number of damages, while the right vertical axis shows the number of females with cubs for A and B and the total number of bears in C.

The variation in the number of different types of damages across populations was related with some local factors (Supplementary Table S.6). In the western Cantabrian subpopulation (Fig. 4A): (1) a decrease in mean temperature was related to an increase in the number of damages to apiaries and livestock, and a decrease in the number of damages to crops; (2) the number of damages to beehives rose when the yearly productivity of cultivated apple-trees was high; (3) the number of damages to livestock increased in years characterised by a low productivity of hazel and cherry; and (4) the number of damages to crops increased when acorn and apple productivity was low. In the eastern Cantabrian subpopulation (Fig. 4B), the number of damages to beehives was related to high mean annual temperatures and to low productivity of fleshy fruits. Finally, in the Pyrenees (Fig. 4C), the number of damages to livestock was related to high temperatures, whereas the number of damages to apiaries was associated with low temperatures (similar to what occurred in the western Cantabrian subpopulation) and a low NAO index. In terms of productivity, low productivity of fleshy fruits and acorns were linked to an increase in the number of damages to beehives and livestock, but attacks on livestock were also positively related to hazel productivity.



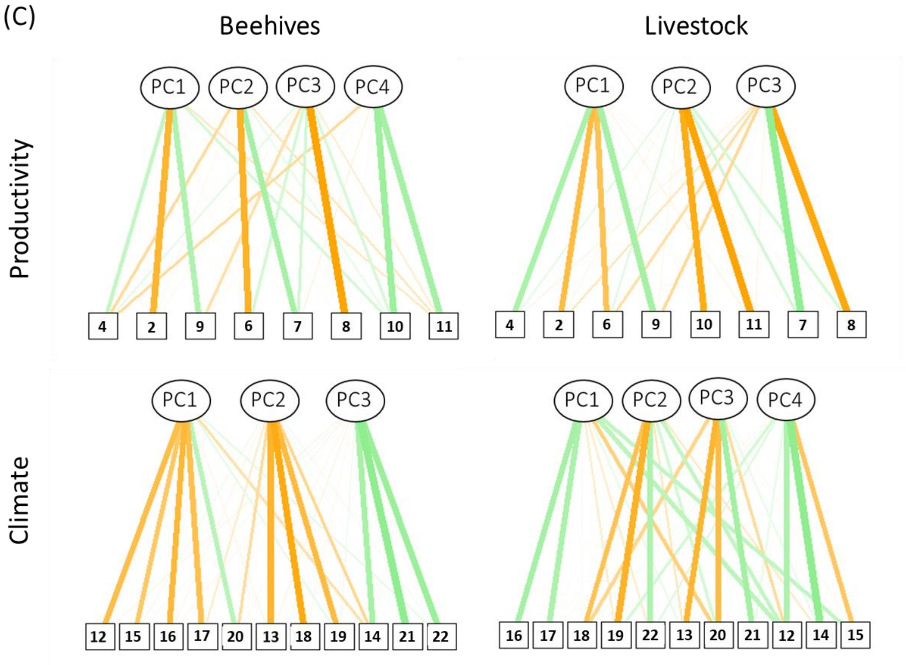


Figure 4. Correlations between varimax rotated variables and the principal components selected (with an eigenvalue > 1) in: the (A) western and (B) eastern Cantabrian subpopulations, and (C) the Pyrenean population, explained by productivity (upper panels) and climatic (lower panels) indicators. Green lines correspond to positive correlations, while orange lines denote negative correlations. The thickest lines represent high loading values. Productivity indicators: (1) scattered cherry, (2) rainfed cherry, (3) scattered hazel, (4) rainfed hazel, (5) rainfed apple-tree, (6) September precipitation (acorn), (7) spring precipitation (acorn), (8) mean temperature August (chestnut), (9) mean winter temperature (blueberry), (10) mean temperature previous June-July (beech), (11) minimum temperature Nov-Feb (prunus); climatic indicators: (12) annual NAO, (13) previous year NAO, (14) sun radiation, (15) NDVI, (16) mean annual temperature, (17) mean temperature April-August, (18) mean temperature previous year, (19) mean temperature April-August previous year, (20) annual precipitation, (21) precipitation previous year and (22) summer precipitation.

DISCUSSION

Patterns of negative interactions between brown bears and human activities, such as damages, are complex, as many factors and their combination may motivate bears to exploit anthropogenic resources. Such complexity, however, should not prevent us from trying to identify the main drivers and their effect at different spatio-temporal scales, determining brown bear interest in anthropogenic resources. This represents a necessary first step to predict and prevent conflicts. We found that the number of damage events has increased over the years, which may be at least partially related to the observed general increase in the number of bears in all the bear nuclei that we considered in our study, together with other year-related factors (e.g., productivity of natural food resources). In fact, the increase in the number of damages has indeed varied in parallel with the increase in bear numbers. This helps explain the differences among bear subpopulations in the Cantabrian mountains, the western Cantabrian subpopulation with more than 200 bears in 2014 (Pérez et al., 2014) presenting the greatest number of damages. This trend is in line with the one reported by Jerina et al. (2015), who found that the size of the population influences the number of damages in Slovenia (but see Bautista et al., 2017). By only using data from the Lleida province, the Pyrenean population (the smallest bear nucleus with 46 bears in 2017; S. Palazón, personal communication), showed the lowest number of damages. However, if we take into account damages occurring in France, we can see that bears from the smallest population are responsible of way more livestock damages than any of the Cantabrian subpopulations (Bautista et al., 2017), mostly due to the differences in husbandry methods. Further, we found that the number of damages mainly showed seasonal differences, with the fewest damages during winter, when most bears are hibernating, and the highest during the hyperphagia period, when bears intensely seek food because they must put on fat in order to successfully hibernate.

The most common type of bear attack in each subpopulation seemed to be related to the availability of different resources (Supplementary Table S.5). Apiaries were the most harmed item in the Cantabrian Mountains, where environmental conditions surrounding them can increase the probability of damages (Fernández-Gil et al., 2016; Naves et al., 2018), followed by crops and livestock. The latter was the least affected by damages, maybe because Cantabrian bears are predominantly vegetarian (Bojarska and Selva, 2012; Naves et al., 2006; Rodríguez et al., 2007). Furthermore, damages to crops in the eastern Cantabrian Mountains were very scarce, in an area where agricultural activities are nowadays nearly absent (www.atlas.itacyl.es). In contrast, attacks to livestock were the most reported damage in the Pyrenees, which continues to fuel conflict and challenges the recovery of this bear population (e.g., Enserink and Vogel, 2006). The primary cause of the differences between these two bear populations may reflect differences in land use and livestock raising. Beekeeping is much more common in the Cantabrian Mountains than in the Pyrenees and livestock is mostly bovine, while in the Pyrenees sheep are more common and more prone to suffer a bear attack (www.mapa.gob.es). Furthermore, the virtual absence of wolves and bears for a long time in the Pyrenees has led to the abandonment of traditional husbandry practices, prevention measures, and vigilance (Bautista et al., 2019; Elosegi, 2010).

Damages caused by large carnivores are typically a main driver of the attitudes of local people towards them; e.g., Glikman et al. (2019) for another critically endangered population of

European brown bear. Therefore, preventing damage is a major task in many areas (e.g., Majić Skrbinšek and Krofel, 2014). Indeed, damages and the ensuing retaliation, such as the legal and illegal removal of carnivores, have a major impact on large carnivore population dynamics, which are exceedingly more positive if conflict is low than if it intensifies. For instance, the availability of free-ranging sheep is the main reason why large carnivores are very controversial in Norway, while much larger numbers of individuals from the same population thrive in Sweden, where there are no free-ranging sheep (see Swenson and Andrén, 2005). Indeed, bears in the French Pyrenees and in Norway showed the highest damage ratio in Europe (Bautista et al., 2017), and both preyed primarily on free-ranging sheep.

It is also worth mentioning that in the Pyrenees, damages to livestock might also be more common because of the different diet (Supplementary Fig. S.1) of released bears coming from Slovenia, where they also have access to carrion supplementary feeding sites (Graf et al., 2018). Furthermore, these past years some reintroduced bears, like Goiat (https://piroslife.cat/en/a-device-is-activated-with-the-aim-to-chase-away-the-goiat-bear-and-change-its-behaviour/), have stood out for their strong predator behavior. This might support the possibility that increased damages could also be due to a marked predatory behavior of just a few individuals, which makes them problematic bears prone to attack livestock (Bereczky et al., 2011; Majić Skrbinšek and Krofel, 2014; Swan et al., 2017).

Additionally, we observed that each type of damage may be related to diverse local environmental factors affecting natural food availability. Indeed, beehives and livestock damages were more abundant in the western Cantabrian subpopulation when both mean annual temperatures and temperatures from April to August were lower, which have the potential to affect pollination and decrease fruit production success (Sanzol and Herrero, 2001) and hard mast crop size (Koenig and Knops, 2000) in hyperphagia. In addition, during the years in which fruit tree (i.e., apples or cherries) productivity was better, we detected an increase in the damages to apiaries. One possibility is that bears, by approaching human settlements looking for fruits, are also closer to apiaries, which may expose beehives to a greater risk of a bear attack. On the other hand, other types of damages occurred more often when there was low availability of food resources. For example, damages to crops increased: (a) when there was low acorn productivity, which is a key food resource for bears during hyperphagia (Supplementary Fig. S.2) when most of these damages occurred; and (b) in years with a low productivity of apples, which are consumed more frequently during hyperphagia, after fleshy fruit production is over (Naves et al., 2006). Damages to livestock were also related to the low availability of cherries and hazelnuts, two important resources during mating and hyperphagia, respectively. In turn, in the east of the

Cantabrian Mountains, increasing damages to beehives were linked to high annual temperatures, contrary to what happens in the other subpopulations. This can drive more pollination activity (Sanzol and Herrero, 2001) and, thus, more honey production that might lure bears, but these differences could be due to other factors not considered in our study and dependent of the area and specific management of beehives. Lastly, in the Pyrenees both low annual temperatures and, more specifically, temperatures from April to August, drove an increase in apiary damages. As in the Cantabrian Mountains, low annual temperatures may reduce fruit and mast availability. These damages also rose with low NAO values, which generally denote low vegetation productivity (Gonsamo et al., 2016).

As an omnivorous species, brown bears have the ability to shift from one source of food to another depending on their fluctuating availability (Kozakai et al., 2011; Rodríguez et al., 2007). We have found that reduced availability of natural food may lead bears to use foods related with human activities, as stated for other bear populations (Jerina et al., 2015; Lewis et al., 2015). In turn, this triggers conflict with humans, which harms public attitude towards bear conservation (Bautista et al., 2019; Eriksson et al., 2015). This is a particularly serious threat for carnivore conservation where human encroachment is high, as is the case for the small and isolated populations of brown bears in northern Spain. Our results suggesting that years with lower availability of natural food can trigger increasing damages by brown bears to beehives and/or livestock, depending on availability, are yet another reason to assert that preventive measures for both beehives (e.g., Naves et al., 2018) and livestock (e.g., Ordiz et al., 2017) are crucial to reduce conflict and thus favour human-large carnivore coexistence. Particularly in the Pyrenees, the eventual recovery of this critically endangered bear population does not look promising if conflict levels are not mitigated.

Finally, it is important to highlight here that the data used in this study corresponds to claims gathered by each administration responsible for bear management, whereas it has been impossible to evaluate the correspondence between claims and all possible bear damages, e.g. the factors that could influence damages (type of livestock, scavenging of already dead animals, difficulty to locate damage remains). Also, it is important to emphasize that there might be other economic and social factors, such as availability of livestock or beehives, husbandry methods and preventive measures, that might affect the occurrence of a damage and that have not been considered in our analyses. Furthermore, there is a big lack of natural food availability data in our study areas, thus a better monitoring of these factors would help to improve the study of damage patterns and their prevention in the future.

SUPPLEMENTARY MATERIAL

BEAR NUCLEI	Hibernation			Mating			Hypeprhagia		
	Beehives	Crops	Livestock	Beehives	Crops	Livestock	Beehives	Crops	Livestock
West Cantabrian	185	11	41	1306	87	203	1612	1446	640
East Cantabrian	27	0	0	222	0	2	459	5	11
Pyrenean	0	0	4	30	0	97	61	0	154

PROVINCE	Hibernation			Mating			Hyperphagia		
	Beehives	Crops	Livestock	Beehives	Crops	Livestock	Beehives	Crops	Livestock
Asturias	136	9	25	786	70	124	786	1159	367
León	27	0	7	223	6	29	431	67	86
Palencia	10	0	0	98	0	0	272	1	4
Lleida	0	0	1	21	0	60	50	0	60

Supplementary Table S.1. Number of damages produced to beehives, crops and livestock during the different bear cycle seasons in (A) each bear nuclei and (B) each different province that hosted bears from 2008 to 2017.

(A)

Intercept	Type of damage	Year	Season	Bear nucleus	Type of damage*Year	Season *Year	df	logLik	AICc	ΔAICc	weight
2.609	**+**	**0.2853**	**+**	**+**			**9**	**-591.453**	**1202.1**	**0**	**0.725**
2.609	+	0.1147	+	+		+	11	-590.648	1205.1	2.98	0.164
2.602	+	0.2391	+	+	+		11	-591.212	1206.2	4.11	0.093
2.604	+	0.08842	+	+	+	+	13	-590.493	1209.5	7.38	0.018
2.537	+		+	+			8	-600.379	1217.7	15.6	0
2.093		0.2198	+	+			7	-618.775	1252.3	50.18	0
2.089		0.1372	+	+		+	9	-618.63	1256.5	54.36	0
2.063			+	+			6	-622.948	1258.4	56.34	0
4.349	+	0.3163		+			7	-641.376	1297.5	95.38	0
4.335	+	0.2668		+	+		9	-641.218	1301.6	99.53	0

(B)

EXPLANATORY VARIABLE	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	2.609	0.17477	14.928	< 2e-16 ***
Mating	1.72806	0.19657	8.791	< 2e-16 ***
Hyperphagia	2.50223	0.19389	12.906	< 2e-16 ***
Crops	-1.12753	0.19309	-5.839	5.24E-09 ***
Livestock	-1.33689	0.15437	-8.66	< 2e-16 ***
Eastern Cantabrian subpopulation	-1.6956	0.17033	-9.955	< 2e-16 ***
Pyrenean population	-2.16691	0.19002	-11.403	< 2e-16 ***
Year	0.28527	0.06665	4.28	1.87E-05 ***

R-squared = 0.7023

Supplementary Table S.2. Comparison of the first ten generalised linear models explaining the number of damages produced by bears in the Cantabrian Mountains and the Pyrenees (2008-2017) (A). Models are ranked from the lowest (best model) to the highest AIC value. Positive cells show when a categorical variable was included in the model.

(A)

Intercept	Type of damage	Year	Season	Bear nucleus	Type of damage*Year	Season *Year	df	logLik	AICc	ΔAICc	weight
1.943	**+**	**0.3287**	**+**	**+**	**+**		**10**	**-805.94**	**1632.9**	**0**	**0.849**
1.947	+	0.3045	+	+	+	+	12	-805.491	1636.4	3.54	0.144
1.946	+	0.3119	+	+			8	-813.156	1643	10.07	0.006
1.954	+	0.2676	+	+		+	10	-813.091	1647.2	14.3	0.001
2.016	+		+	+			7	-827.13	1668.8	35.87	0
1.624		0.3151	+	+			6	-835.535	1683.5	50.55	0
1.621		0.3344	+	+		+	8	-835.431	1687.5	54.62	0
1.696			+	+			5	-847.766	1705.8	72.9	0
2.06	+	0.2848	+		+		9	-850.193	1719.2	86.32	0
2.062	+	0.2698	+		+	+	11	-850.13	1723.5	90.59	0

(B)

EXPLANATORY VARIABLE	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	-0.0110	30.06431	-3.654	0.000258 ***
Mating	1.57	0.16198	9.711	< 2e-16 ***
Hyperphagia	2.46	0.15972	15.426	< 2e-16 ***
Pyrenean population	-1.58	0.13362	-11.812	< 2e-16 ***
Crops	-0.0127	51.69493	-2.46	0.013895
Livestock	0.603	40.43563	1.492	0.135806 *
Year	0.0557	0.01497	3.72	0.000199 ***
Crops*Year	0.0629	0.02574	2.443	0.014558 *
Livestock*Year	-0.0305	0.02014	-1.513	0.130243

R-squared = 0.6888

(A)

Supplementary Table S.3. Comparison of the first ten generalised linear models explaining the number of damages produced by bears in the western Cantabrian subpopulation and the Pyrenees (1997-2017) (A). Models are ranked from the lowest (best model) to the highest AIC value. Positive cells show when a categorical variable was included in the model. No competing model had a ΔAICc < 2, compared to the best model, which is highlighted in bold. The coefficients for the variables included in the best model are summarized below (B).

Intercept	Type of damage	Number of damages	df	logLik	AICc	ΔAICc	weight
9.417	**+**	**-0.06859**	**5**	**-10.917**	**33.2**	**0**	**1**
1.651		-0.02787	3	-22.453	51.4	18.25	0
-0.3567			2	-34.552	73.4	40.19	0
-3.208e-16	+		4	-33.756	76.4	43.21	0

(B)

EXPLANATORY VARIABLE	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	9.417	2.875	3.276	0.00105**
Number of damages	-0.069	0.020	-3.511	0.00045***
Crops	-6.973	2.659	-2.623	0.00873**
Livestock	-7.599	2.514	-3.022	0.00251**

R-squared = 0.6042

Supplementary Table S.4. Comparison of the competing models ranked from lowest (best model) to highest AICc value for the binomial analysis between Cantabrian subpopulations (2008-2017) (A). Positive cells show when a categorical variable was included in the model. No competing model had a ΔAICc < 2, compared to the best model, which is highlighted in bold. The coefficients for the variables included in the best model are summarized below (B).

(A)

Intercept	Type of damage	Number of damages	df	logLik	AICc	ΔAICc	weight
+	**+**	**+**	**12**	**-65.242**	**158.6**	**0**	**1**
+		+	6	-88.704	190.4	31.84	0
+	+		9	-111.018	242.3	83.73	0
+			3	-119.176	244.6	86.05	0

(B)

PROVINCE	EXPLANATORY VARIABLE	Estimate	Std. Error	z value	Pr(>|z|)
LEÓN	Intercept	5.448	1.625	3.3521	0.00080 ***
	Crops	-7.225	2.727	-2.65	0.00805 ***
	Livestock	-8.233	2.631	-3.129	0.00176 ***
	Number of damages	-0.087	0.024	-3.66	0.00025 ***
	Year	5.448	1.625	3.3521	0.00080 ***
PALENCIA	Intercept	5.888	1.668	3.5298	0.00042 ***
	Crops	-9.837	2.983	-3.297	0.00098 ***
	Livestock	-10.001	2.768	-3.614	0.00030 ***
	Number of damages	-0.107	0.027	-3.968	0.00007 ***
	Year	5.888	1.668	3.5298	0.00042 ***
LLEIDA	Intercept	6.474	1.667	3.884	0.00010 ***
	Crops	-18.487	0.049	-374.5	0.00000 ***
	Livestock	-9.362	2.76	-3.392	0.00069 ***
	Number of damages	-0.164	0.035	-4.65	0.00000 ***
	Year	6.474	1.667	3.884	0.00010 ***

PseudoR2 McFadden = 0.452561

Supplementary Table S.5. Comparison of the competing models ranked from lowest (best model) to highest AICc value for the multinomial analysis among the four different provinces that are home to brown bears in Spain (A). Positive cells show when a categorical variable was included in the model. No competing model had a ΔAICc < 2, compared to the best model, which is highlighted in bold. The coefficients for the variables included in the best model are summarized below (B).

(A)

BEEHIVES

	Component	% variance	Variable	Effect
PRODUCTIVITY n=2944	PC1	25.6%	Rainfed apple-tree	+
	PC2	20.5%	Scattered cherry	+
			Minimum temperature Nov-Feb (Prunus)	-
	PC3	15.4%	Mean temperature previous June-July (beech)	-
	PC4	11.8%	Spring precipitation (acorn)	-
	TOTAL	**73.3%**		
CLIMATIC n=3103	PC1	33.6%	Mean temperature Apr-Aug	-
			Mean annual temperature	-
	PC2	21.5%	Mean temperature previous year	+
			Mean temperature Apr-Aug previous year	+
	PC3	13.2%	Summer precipitation	-
			Annual NAO	+
	PC4	10.5%	Previous year NAO	-
			Sun radiation	+
	TOTAL	**78.8%**		

CROPS

	Component	% variance	Variable	Effect
PRODUCTIVITY n=1494	PC1	28.5%	September precipitation (acorn)	+
			Rainfed apple-tree	-
	PC2	19.5%	Scattered cherry	+
			Scattered hazel	+
	PC3	16.6%	Mean winter temperature (blueberry)	-
			Mean temperature previous June-July (beech)	-
	PC4	11.5%	Spring precipitation (acorn)	+
	TOTAL	**76.1%**		
CLIMATIC n=1544	PC1	37.4%	Mean temperature Apr-Aug	+
			Mean annual temperature	+
	PC2	21.9%	Mean temperature previous year	-
			Precipitation previous year	+
			Mean temperature Apr-Aug previous year	-
	PC3	12.5%	Summer precipitation	+
			Annual NAO	-
	PC4	11.1%	Previous year NAO	-
			Sun radiation	+
	TOTAL	**82.9%**		

LIVESTOCK				
	Component	**% variance**	**Variable**	**Effect**
PROCUTIVITY n=840	PC1	24.3%	Scattered hazel	-
			Scattered cherry	-
	PC2	23.2%	Rainfed apple-tree	+
	PC3	13.8%	Mean temperature previous June-July (beech)	-
			Mean winter temperature (blueberry)	-
	PC4	12.1%	Spring precipitation (acorn)	-
	TOTAL	**73.4%**		
CLIMATIC n=884	PC1	36.1%	Mean temperature Apr-Aug	-
			Mean annual temperature	-
	PC2	19.7%	Mean temperature previous year	+
			Mean temperature Apr-Aug previous year	+
	PC3	12.9%	Summer precipitation	-
			Annual NAO	+
	PC4	10.6%	Sun radiation	+
			Previous year NAO	-
	TOTAL	**79.3%**		

(B)

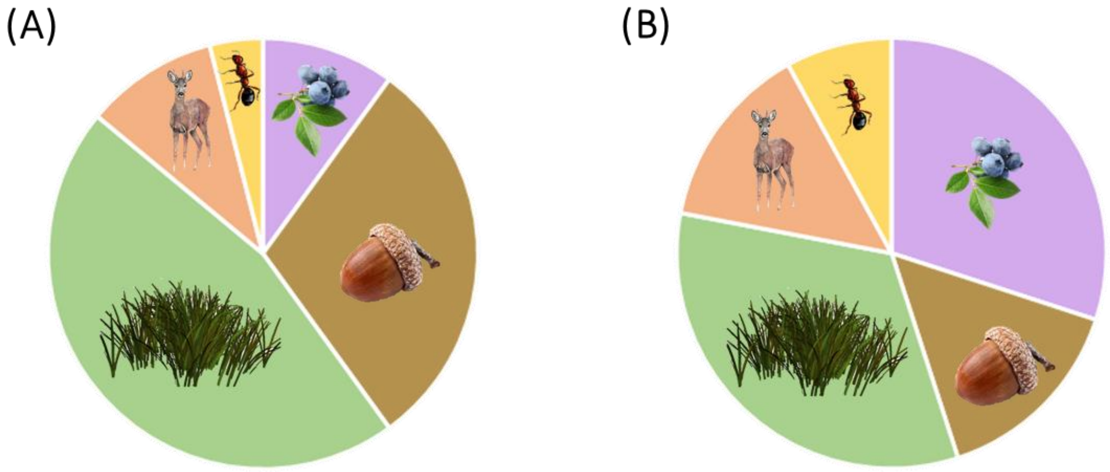
BEEHIVES				
	Component	**% variance**	**Variable**	**Effect**
PRODUCTIVITY n=711	PC1	43.7%	Rainfed cherry	-
			Mean winter temperature (blueberry)	+
			Rainfed apple-tree	-
	PC2	31.6%	Minimum temperature Nov-Feb (Prunus)	-
			Scattered cherry	-
			Mean temperature August (chestnut)	+
	TOTAL	**75.3%**		
CLIMATIC n=711	PC1	41.3%	Mean annual temperature	+
	PC2	16.9%	Sun radiation	-
			Annual precipitation	+
	PC3	15.40%	Mean temperature previous year	+
			Summer precipitation	+
	PC4	10.80%	Previous year NAO	-
	TOTAL	**84.4%**		

(C)

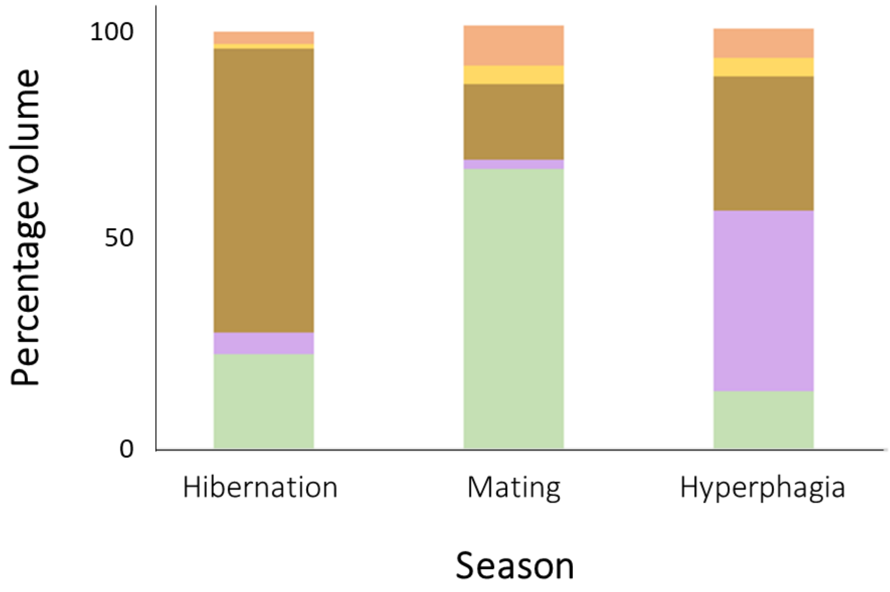
BEEHIVES				
	Component	**% variance**	**Variable**	**Effect**
PRODUCTIVITY n=76	PC1	30.8%	Rainfed cherry	-
			Mean winter temperature (blueberry)	+
	PC2	23.9%	September precipitation (acorn)	-
			Spring precipitation (acorn)	+
	PC3	21.7%	Mean temperature August (chestnut)	-
	PC4	13.3%	Mean temperature previous June-July (beech)	+
			Minimum temperature Nov-Feb (Prunus)	+
	TOTAL	**89.7%**		
CLIMATIC n=54	PC1	38.6%	Mean annual temperature	-
			Annual NAO	-
			Mean temperature Apr-Aug	-
	PC2	25.7%	Mean temperature previous year	-
			Previous year NAO	-
			Mean temperature Apr-Aug previous year	-
	PC3	17.3%	Precipitation previous year	+
			Summer precipitation	+
			Sun radiation	+
	TOTAL	**81.6%**		

LIVESTOCK				
	Component	**% variance**	**Variable**	**Effect**
PRODUCTIVITY n=213	PC1	31.6%	Mean winter temperature (blueberry)	+
			Rainfed hazel	+
			Rainfed cherry	-
			September precipitation (acorn)	-
	PC2	21.1%	Minimum temperature Nov-Feb (Prunus)	-
			Mean temperature previous June-July (beech)	-
	PC3	18.8%	Spring precipitation (acorn)	+
			Mean temperature August (chestnut)	-
	TOTAL	**71.5%**		
CLIMATIC n=138	PC1	36.5%	Mean annual temperature	+
			Mean temperature Apr-Aug	+
	PC2	21.7%	Mean temperature Apr-Aug previous year	-
			Summer precipitation	+
	PC3	16.2%	Precipitation previous year	+
			Previous year NAO	-
	PC4	9.5%	Sun radiation	+
			NDVI	-
	TOTAL	**83.9%**		

Supplementary Table S.6. Most contributing variables (varimax loadings < -0.4 and > 0.4) with their effect in the components of the Principal Component Analyses with an eigenvalue > 1 and percentage of variance explained for each type of damage abundant in each bear nucleus (A: western Cantabrian subpopulation from 1997 to 2017; B: eastern Cantabrian subpopulation from 2008 to 2017; C: Pyrenean population from 1998 to 2017), for both productivity and climatic sets of indicators.



Supplementary Figure S.1. Percentage of hard mast, fruits and berries, insects, mammals and herbs in the brown bear diet for the (A) Cantabrian population and (B) Pyrenean population extracted from FAPAS, 2017. Extracted from FAPAS, 2017.



Supplementary Figure S.2. From bottom to top, mean seasonal percentage volume of herbs, fleshy fruits, hard mast, insects and vertebrates (same colours as in **Figure S.1**) consumed by brown bears in the Cantabrian Mountains from 1974 to 2004 (extracted from Naves et al., 2006).

DISCUSIÓN GENERAL

La presente tesis se centra en producir nueva información científica enfocada esencialmente en promover y facilitar la coexistencia entre humanos y osos pardos en un espacio altamente humanizado como es la Cordillera Cantábrica, y ayudar a la correcta gestión de la especie con fines de conservación. Con este objetivo, he desarrollado mi trabajo desde tres puntos de vista fundamentales: selección de hábitat, comportamiento y conflictos con las actividades humanas. Desde el punto de vista de la selección de hábitat, en el capítulo uno se identifican las zonas preferidas por el oso, que se clasifican, atendiendo a su utilización, en zonas ocupadas por el oso en la actualidad y en aquellas a las que se prevé su expansión en el futuro. Así, se señalan las áreas prioritarias en las que focalizar medidas de manejo y conservación de la especie y sus conflictos derivados en cada caso. En el capítulo dos también se aborda este aspecto, explorando las zonas utilizadas por las diferentes clases de oso en época de reproducción. Los resultados evidencian el solapamiento entre las áreas utilizadas por las hembras con crías de primer año y los adultos reproductores, favoreciendo la aparición de infanticidios. El capítulo tres se centra en el estudio de la adaptación de esta población de oso a la presencia humana en términos de comportamiento, estableciendo las bases para su coexistencia con las poblaciones humanas. Finalmente, en el capítulo cuatro, se consideran los tres núcleos de oso pardo de la Península Ibérica (cantábrico occidental, cantábrico oriental y pirenaico) con el objeto de determinar las diferencias en la aparición de daños, tanto locales como derivadas de diferente disponibilidad de alimento y condiciones climáticas. Este estudio expone la complejidad de los patrones de aparición de daños, y su dependencia tanto de las condiciones ambientales y de la disponibilidad de recursos tróficos, como de la gestión de las diferentes administraciones y el comportamiento de las poblaciones humanas en cada núcleo. En general, los resultados de esta tesis, que se discuten a continuación, pretenden mejorar nuestro conocimiento y mejor entendimiento de la coexistencia entre humanos y grandes carnívoros en un contexto ilustrativo, inspirando posibles investigaciones futuras y proporcionando herramientas prácticas para la conservación de esta pequeña y aislada población osera del sur de Europa.

Los capítulos uno y dos confirman la evitación de fuentes de perturbación derivadas de la actividad humana por parte del oso pardo (Martin et al., 2010; Mateo-Sánchez et al., 2016; Oberosler et al., 2017). A su vez, definen las áreas más propicias para la especie, que se caracterizan por gran altitud y pendiente, así como por la cobertura de bosque, que representa áreas clave de alimentación y refugio (Kobler and Adamic, 2000; Moe et al., 2007; Posillico et al., 2004). Sin embargo, de este hecho se deriva una trampa para las hembras con crías de primer año, que se reproducen en áreas muy concretas donde encuentran disponibilidad tanto de refugio como de alimento. En la zona occidental, y dado que los individuos adultos también tratan de evitar las perturbaciones humanas (Elfström et al., 2014; Smith et al., 2005), las zonas donde se localizan estas hembras son similares a las zonas de reproducción, lo que, junto a la mayor densidad de osos, incrementa la probabilidad de un encuentro con un macho en celo, y, por lo tanto, las posibilidades de que ocurra un infanticidio (Gonzalez et al. 2016, Martínez Cano et al. 2016). Por ello, la conservación proactiva de los terrenos escarpados, especialmente durante la primavera, es una recomendación de gestión importante. La aplicación de medidas como el cierre de los accesos y caminos cercanos a las zonas donde se detectan hembras con crías, especialmente cuando dichos lugares son frecuentados por actividades de ocio como el senderismo o la escalada, pueden reducir las perturbaciones y evitar el desplazamiento de estas hembras. Además, este tipo de estudios pueden ayudar a detectar trampas evolutivas y/o ecológicas (selección de un determinado comportamiento o hábitat de baja calidad, que repercute en su supervivencia o productividad, pese a tener a su disposición otras opciones adecuadas) que podrían estar perjudicando a las poblaciones y limitando la eficacia de los esfuerzos de conservación (Penteriani et al., 2018a).

En cambio, en la zona oriental existen todavía grandes extensiones de áreas favorables en el Principado de Asturias en las que apenas se han localizado osos, y en las que hay gran disponibilidad de refugios (García et al., 2007). Estas zonas no han sido colonizadas todavía debido a la combinación del pequeño tamaño de la subpoblación oriental, su menor tasa de crecimiento y tamaño de camada con respecto a la occidental, además de a su menor diversidad genética (Palomero et al., 2007; Penteriani et al., 2018b), ya que las condiciones del hábitat no parecen ser suficientes para explicar sus diferencias con respecto a la subpoblación occidental (Lamamy et al., 2019). El mayor crecimiento de la subpoblación de mayor tamaño y su dispersión, evidenciada por la localización de observaciones fuera de las zonas óptimas en los últimos años, podrían potenciar la recuperación de la subpoblación oriental y la ocupación de estos territorios favorables. Pero la reducida conectividad entre ambas subpoblaciones, que limita el flujo de individuos, retrasan la colonización de estas áreas (Mateo-Sánchez et al., 2014; Pérez et al., 2010). Otra problemática añadida podría ser la menor calidad de alimentos naturales en este sector, sugerida por Naves et al. (2006, 2003), que fomentaría el aprovechamiento de recursos antrópicos por parte de los osos en caso de expansión y, por tanto, la aparición de conflictos. Pero la falta de datos cuantitativos sobre esta posibilidad hace que la falta de alimento sea una especulación, por lo que son necesarios futuros estudios al respecto. Estos resultados sirven como herramienta para la prevención y mitigación de potenciales conflictos, así como para desarrollar campañas de información, al identificar las zonas prioritarias donde se puede producir un aumento en la densidad de osos, o en las que está actualmente ausente pero a las que se prevé su expansión. Además, el futuro monitoreo directo del uso del espacio, movimientos y ritmos de actividad de las hembras con crías, los individuos dispersantes y los demás grupos de osos será crucial para entender el desarrollo y las dinámicas de esta población.

A pesar de todo, al haber convivido tantos años con la presencia humana, los osos han podido adaptarse y habituarse a las perturbaciones que se derivan de ella, por ejemplo, seleccionando los lugares donde su impacto es menor. En consecuencia, como se demuestra en el capítulo tres, la aparición de signos de alerta en el comportamiento de esta población refleja principalmente las relaciones de dominancia y patrones de evitación entre los diferentes tipos de oso en cada época del año, pero no se incrementan en función de la proximidad a las principales infraestructuras humanas. Además, las hembras con crías grabadas se localizaron a menudo (y después de haber abandonado el área cercana a la osera de reproducción) más cerca de algunas infraestructuras humanas como los pueblos durante las épocas con mayor riesgo de infanticidio, lo que se puede interpretar, como ocurre en otras poblaciones (Skuban et al., 2018; Steyaert et al., 2016), como una ventaja adaptativa al utilizar como zonas de mayor protección aquellas más próximas a perturbaciones humanas, ya que son generalmente evitadas por los individuos adultos solitarios. Estos resultados son de especial interés para el turismo, ya que demuestran que los puntos de observación de osos no desencadenan una respuesta de estrés visible a nivel de comportamiento en los osos, por localizarse a una distancia suficiente como para no influirles negativamente. Aun así, monitorizar y promover las buenas prácticas en estos lugares para eliminar las posibles interacciones de los turistas con los osos es de gran importancia para evitar cambios en su comportamiento (Penteriani et al., 2017). Investigar la respuesta de estrés a nivel fisiológico ante la presencia humana es el siguiente paso necesario, ya que el estrés puede no verse reflejado a nivel de comportamiento, pero tener otras consecuencias para los animales (Støen et al., 2015). Además, evitar la mortalidad por causa antrópica de manera efectiva, a la vez que reducir las interacciones que potencialmente podrían influir negativamente en el estrés y el comportamiento de estos animales, es crucial para la persistencia y recuperación de los osos y otros carnívoros en ambientes humanizados. Futuras investigaciones deberían focalizarse en la existencia de respuestas a diferentes actividades derivadas de la presencia humana, como puede ser la caza, el tráfico o el turismo de montaña, además de tener en cuenta patrones temporales de evitación de estas perturbaciones.

Como se ha mencionado anteriormente, la localización de las zonas potencialmente conflictivas (zonas de expansión del oso, así como en las que se predice un aumento de su densidad de población), es crucial para favorecer la coexistencia. Pero no sólo es necesario localizar las áreas donde podría habitar el oso, si no también definir las variables que determinan que se produzcan conflictos. Como se evidencia en el capítulo cuatro, el número de daños varía acorde a la época del año y al tamaño de la población en la Cordillera, y en otras poblaciones (Jerina et al., 2015), aunque no siempre ocurre así (Bautista et al., 2017). Las diferencias en la gestión del territorio de las distintas administraciones, junto con la disponibilidad de recursos antrópicos y los diferentes métodos de cría y protección del ganado y otras actividades (e.g. cercados, pastores eléctricos, perros guardianes), tienen una influencia importante en el número de daños que se producen en cada lugar. A su vez, el haber compartido siempre territorio con estos animales favorece que las poblaciones humanas de la Cordillera Cantábrica hayan mantenido el uso de medidas preventivas. En cambio, en zonas donde los osos desaparecieron, pero donde recientemente se han vuelto a reintroducir, se han abandonado este tipo de prácticas. Como consecuencia, en estas áreas la recuperación de las poblaciones de oso está produciendo un gran aumento en la cantidad de conflictos (e.g. Francia o Noruega (Bautista et al., 2019, 2017)). En la Cordillera Cantábrica la apicultura es la principal actividad dañada por el oso, siendo más atractiva ya que esta población se caracteriza por su escaso consumo de carne (Bojarska and Selva, 2012; Naves et al., 2006; Rodríguez et al., 2007) y además, el ganado predominante (vacuno) es menos accesible, mientras que en los pirineos los ataques se producen sobre todo al ganado ovino.

Una reducida disponibilidad de alimentos naturales comunes en la dieta del oso en momentos puntuales puede promover el consumo de alimentos de origen antrópico y la aparición de daños a ganado, colmenas o cultivos, como ocurre en otras poblaciones (Jerina et al., 2015; Lewis et al., 2015). Las condiciones climáticas de cada lugar afectan de manera diferente a cada tipo de daño, lo que puede deberse tanto a las características específicas del área como a diferencias en la gestión, o incluso a la capacidad del oso de cambiar de fuente de alimento dependiendo de su disponibilidad (Kozakai et al., 2011; Rodríguez et al., 2007). Además, el cambio climático tiene la capacidad de alterar la distribución de sus recursos tróficos, provocando desplazamientos importantes en la población con el potencial de incentivar estos conflictos, especialmente si las zonas adecuadas en el futuro se localizan a menor altitud, donde la ocupación humana es mayor (Penteriani et al., 2019). Por ello, la realización de estudios particulares detallados sobre la aparición de daños y su relación con la disponibilidad de recursos tróficos (incluyendo la mejora de su monitorización), así como el desarrollo y la aplicación de medidas de protección, son cruciales para prevenir y reducir los conflictos y favorecer así la coexistencia con éste y otros grandes carnívoros.

Para concluir, espero que los resultados obtenidos por el trabajo realizado en esta tesis puedan tener su aplicación real como importante herramienta predictiva con implicaciones para la conservación, sugiriendo estrategias de gestión proactivas y a múltiples niveles que aborden tanto el factor humano (a través de la resolución de conflictos) como la conservación del paisaje, minimizando así los efectos negativos de la coexistencia de los osos con el ser humano. Estas estrategias son de crucial importancia especialmente cuando se trata de una población de oso pardo pequeña, aislada y en peligro como la de la Cordillera Cantábrica. Estos resultados proporcionan a su vez nueva información sobre potenciales amenazas para esta población, así como nuevas perspectivas sobre su convivencia con las personas en un ambiente tan humanizado. Y, aunque los osos son capaces de desarrollar estrategias para reducir el impacto derivado de la presencia de actividades humanas (Martin et al., 2010), las poblaciones que comparten territorio con ellos deben a su vez intentar minimizar las perturbaciones que producen en la medida de lo posible, para evitar sucesos que comprometan la viabilidad de la especie. En las montañas cantábricas, tanto la amplia experiencia como la disposición y la tolerancia de las personas en este territorio a convivir con el oso pardo incrementan las posibilidades de esta población de recuperarse y mantenerse en este hábitat, aunque la humanización del entorno sea alta (Dorresteijn et al., 2014). Los resultados de esta tesis aportan una visión de esta capacidad de coexistir entre humanos y grandes carnívoros, planteando la posibilidad de una convivencia adecuada y exitosa en el futuro. También pone de manifiesto la necesidad de combinar la investigación con la gestión, y de transmitir la información adquirida por estos medios al público en general, mejorando la percepción sobre estas especies e implicando a todas las partes en su conservación.

CONCLUSIONES

1. El estudio de la ecología de los grandes carnívoros en ambientes humanizados permite conocer la relación entre sus poblaciones y las actividades humanas y comprender mejor la vía hacia la coexistencia para desarrollar las medidas de gestión y conservación óptimas.
2. Los osos pardos de la Cordillera Cantábrica prefieren zonas de bosque con gran altitud y pendiente y bajo impacto humano. Esta población dispone todavía de hábitat favorable para su expansión, especialmente en la zona oriental donde actualmente se encuentra la subpoblación de menor tamaño.
3. El aumento de la conectividad entre ambas subpoblaciones es crucial para fomentar su expansión y asegurar la viabilidad de la subpoblación oriental, así como incrementar la protección de estas zonas y crear campañas de información y prevención de daños en las áreas potenciales de expansión.
4. El infanticidio es una amenaza para el oso pardo cantábrico, ya que la fragmentación del hábitat y la invasión humana de los territorios atrapa a las hembras con crías de primer año en las mismas zonas que usan los individuos adultos para la reproducción.
5. La protección y reducción de la actividad humana en las áreas donde se encuentran las hembras con crías de primer año durante la primavera puede ayudar a reducir la probabilidad de que ocurra un infanticidio, pero es necesario un mejor monitoreo de estos osos y sus patrones de actividad.
6. Los osos de la Cordillera Cantábrica han adaptado su comportamiento a la convivencia con el ser humano, mostrando las mismas pautas en los comportamientos de alerta independientemente de la cercanía a infraestructuras humanas. Futuros estudios deberían focalizarse sobre la existencia de respuestas a diferentes actividades humanas (caza, tráfico, turismo), teniendo en cuenta los niveles de estrés a nivel fisiológico y los patrones temporales de evitación de estas perturbaciones.
7. Los patrones de aparición de daños de oso son muy complejos. El número de daños producidos por el oso en la Codillera Cantábrica y en Pirineos varían en función del tipo de daño, la estación, el año, la provincia y de cambios en la productividad y las condiciones climáticas. Pero localmente otros factores económicos y sociales, como la disponibilidad de ganado o colmenas, los métodos de cría y las medidas preventivas, pueden influir en sus dinámicas.
8. Reducir la aparición de conflictos es necesario para mantener una coexistencia pacífica con las poblaciones humanas que comparten territorio con los grandes carnívoros. Para ello se deben potenciar los estudios locales sobre su aparición, incluyendo un mejor monitoreo de

la disponibilidad de alimento, con el fin de poder anticipar dónde y cuándo se puede producir un daño y aplicar las medidas preventivas de forma óptima.

9. La coexistencia entre los grandes carnívoros y los seres humanos en paisajes modificados por el ser humano es posible, siempre que los carnívoros no sean altamente perseguidos y se eviten las interacciones directas. Además, la colaboración entre la investigación, los organismos gestores y el público en general es necesaria para el correcto manejo y conservación con estas especies.

BIBLIOGRAFÍA

Afif-Khouri, E., Álvarez-Álvarez, P., Fernández-López, M.J., Oliveira-Prendes, J.A., Cámara-Obregón, A., 2011. Influence of climate, edaphic factors and tree nutrition on site index of chestnut coppice stands in north-west Spain. Forestry 84, 385–396. https://doi.org/10.1093/forestry/cpr025

Agrell, J., Wolff, J., Ylönen, H., 1998. Counter-strategies to infanticide in mammals: costs and consequences. Oikos 83, 507–517.

Akaike, H., 1974. A new look at the statistical model identification. IEEE Trans. Automat. Contr. 19, 716–723. https://doi.org/10.1109/TAC.1974.1100705

Alejano, R., Tapias, R., Fernández, M., 2008. Influence of pruning and the climatic conditions on acorn production in holm oak (Quercus ilex L.) dehesas in SW Spain. Ann. For. Sci. 65, 209.

Almeida Neto, M., Guimaraes, P., Guimaraes, P.R.J., Loyola, R.D., Ulrich, W.A., 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. Oikos 117, 1227–1239.

Araújo, M.B., Pearson, R.G., Thuiller, W., Erhard, M., 2005. Validation of species–climate impact models under climate change. Glob. Chang. Biol. 11, 1504–1513. https://doi.org/10.1111/j.1365-2486.2005.001000.x

Athreya, V., Odden, M., Linnell, J.D.C., Krishnaswamy, J., Karanth, U., 2013. Big Cats in Our Backyards: Persistence of Large Carnivores in a Human Dominated Landscape in India. PLoS One 8, 2–9. https://doi.org/10.1371/journal.pone.0057872

Barton, K., 2018. Package 'MuMIn': Multi-model inference. Available at: http://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf.

Baruch-Mordo, S., 2007. Black bear-human conflicts in Colorado: Spatiotemporal patterns and predictors. Thesis, Color. State Univ. Fort Collins, USA.

Basille, M., Van Moorter, B., Herfindal, I., Martin, J., Linnell, J.D.C., Odden, J., Andersen, R., Gaillard, J.M., 2013. Selecting Habitat to Survive: The Impact of Road Density on Survival in a Large Carnivore. PLoS One 8. https://doi.org/10.1371/journal.pone.0065493

Bassi, E., Willis, S.G., Passilongo, D., Mattioli, L., Apollonio, M., 2015. Predicting the spatial distribution of wolf (Canis lupus) breeding areas in a mountainous region of central Italy. PLoS One 10, 1–14. https://doi.org/10.1371/journal.pone.0124698

Bates, D., Maechler, M., 2009. lme4: Linear Mixed-Effects Models using S4 Classes. Version 0.999375-31.

Bates, D., Sarkar, D., 2006. The lme4 Package. Available at: http://ftp.auckland.ac.nz/software/CRAN/doc/packages/lme4.pdf.

Bautista, C., Naves, J., Revilla, E., Fernández, N., Albrecht, J., Scharf, A.K., Rigg, R., Karamanlidis, A.A., Jerina, K., Huber, D., Palazón, S., Kont, R., Ciucci, P., Groff, C., Dutsov, A., Seijas, J., Quenette, P.I., Olszańska, A., Shkvyria, M., Adamec, M., Ozolins, J., Jonozovič, M., Selva, N., 2017. Patterns and correlates of claims for brown bear damage on a continental scale. J. Appl. Ecol. 54, 282–292. https://doi.org/10.1111/1365-2664.12708

Bautista, C., Revilla, E., Naves, J., Albrecht, J., Fernández, N., Olszańska, A., Adamec, M., Berezowska-Cnota, T., Ciucci, P., Groff, C., Härkönen, S., Huber, D., Jerina, K., Jonozovič, M., Karamanlidis, A.A., Palazón, S., Quenette, P.-Y., Rigg, R., Seijas, J., Swenson, J.E., Talvi, T., Selva, N., 2019. Large carnivore damage in Europe: Analysis of compensation and prevention programs. Biol. Conserv. 235, 308–316. https://doi.org/10.1016/j.biocon.2019.04.019

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., Courchamp, F., 2012. Impacts of climate change on the future of biodiversity. Ecol. Lett. 15, 365–377. https://doi.org/10.1111/j.1461-0248.2011.01736.x

Bellemain, Eva, Swenson, J.E., Taberlet, P., 2006. Mating Strategies in Relation to Sexually Selected Infanticide in a Non-Soc. Ethology 112, 238–246.

Bellemain, E, Zedrosser, A., Manel, S., Waits, L., Swenson, J., 2006. The dilemma of female mate selection in the brown bear, a species with sexually selected infanticide. Proc. R. Soc. London B 273, 283–291.

Bereczky, L., Pop, M., Chiriac, S., 2011. Trouble-making brown bear Ursus arctos Linnaeus, 1758 (Mammalia: Carnivora)-behavioral pattern analysis of the specialized individuals. Trav. du Muséum Natl. d'Histoire Nat. Grigore Antipa 54, 541–554. https://doi.org/10.2478/v10191-011-0032-0

Bischof, R., Steyaert, S.M.J.G., Kindberg, J., 2017. Caught in the mesh: roads and their network-scale impediment to animal movement. Ecography (Cop.). 40, 1369–1380. https://doi.org/10.1111/ecog.02801

Blanco-Fontao, B., Quevedo, M., Obeso, J.R., 2011. Abandonment of traditional uses in mountain areas: Typological thinking versus hard data in the Cantabrian Mountains (NW Spain). Biodivers. Conserv. 20, 1133–1140. https://doi.org/10.1007/s10531-011-0016-1

Blankenheim, D., 2018. A camera trapping study about the seasonal habitat use and circadian activity of brown bears (Ursus arctos) regarding the human factor in northern Pindos, Greece. Master Thesis dissertation, Science in Wildlife Ecology and Wildlife Management, Institute of Wildlife Biology and Game Management (IWJ) Department for Integrative Biology and Biodiversity Research.

Bojarska, K., Selva, N., 2012. Spatial patterns in brown bear Ursus arctos diet: The role of geographical and environmental factors. Mamm. Rev. 42, 120–143. https://doi.org/10.1111/j.1365-2907.2011.00192.x

Borcard, D., Legendre, P., 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. Ecol. Modell. 153, 51–68.

Bowyer, R.T., Person, D.K., Pierce, B.M., 2005. Detecting top-down versus bottom-up regulation of ungulates by large carnivores : implications for conservation of biodiversity, in: Ray, J.C., Redford, K.H., Steneck, R.S., Berger, J. (Eds.), Large Carnivores and Conservation of Biodiversity Y. Island Press, Washington, D.C., USA., pp. 342–361.

Breitenmoser, U., 1998. Large predators in the Alps: The fall and rise of man's competitors. Biol. Conserv. 83, 279–289. https://doi.org/10.1016/S0006-3207(97)00084-0

Brown, J.S., Laundre, J.W., Gurung, M., 1999. The ecology fear: optimal foraging, game theory, and trophic interactions. J. Mammal. 80, 385–399.

Burnham, K. P., & Anderson, D.R., 2002. Model selection and multimodel inference. Springer Sci. Bus. Media.

Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, Berlin.

Butler, D., Cullis, B.R., Gilmour, A.R., Gogel, B.J., 2009. Asreml: asreml () fits the linear mixed model. R Packag. version 3.

Caprio, J.M., Quamme, H.A., 2011. Influence of weather on apricot, peach and sweet cherry production in the Okanagan Valley of British Columbia. Can. J. Plant Sci. 86, 259–267. https://doi.org/10.4141/p05-032

Carbone, C., Mace, G.M., Roberts, S.C., Macdonald, D., 1999. Energetic constraints on the diet of terrestrial carnivores. Nature 402, 286–288. https://doi.org/10.1038/46266

Carter, N.H., Linnell, J.D.C., 2016. Co-Adaptation Is Key to Coexisting with Large Carnivores. Trends Ecol. Evol. 31, 575–578. https://doi.org/10.1016/j.tree.2016.05.006

Carter, N.H., Riley, S.J., Liu, J., 2012. Utility of a psychological framework for carnivore conservation. Oryx 46, 525–535. https://doi.org/10.1017/S0030605312000245

Challender, D.W.S., Macmillan, D.C., 2014. Poaching is more than an Enforcement Problem. Conserv. Lett. 7, 484–494. https://doi.org/10.1111/conl.12082

Chapron, G., Kaczensky, P., Linnell, J.D.C., von Arx, M., Huber, D., Andren, H., Lopez-Bao, J. V., Adamec, M., Alvares, F., Anders, O., Bal iauskas, L., Balys, V., Bed, P., Bego, F., Blanco, J.C., Breitenmoser, U., Broseth, H., Bufka, L., Bunikyte, R., Ciucci, P., Dutsov, A., Engleder, T., Fuxjager, C., Groff, C., Holmala, K., Hoxha, B., Iliopoulos, Y., Ionescu, O., Jeremi, J., Jerina, K., Kluth, G., Knauer, F., Kojola, I., Kos, I., Krofel, M., Kubala, J., Kunovac, S., Kusak, J., Kutal, M., Liberg, O., Maji, A., Mannil, P., Manz, R., Marboutin, E., Marucco, F., Melovski, D., Mersini, K., Mertzanis, Y., Mys ajek, R.W., Nowak, S., Odden, J., Ozolins, J., Palomero, G., Paunovi, M., Persson, J., Poto nik, H., Quenette, P.-Y., Rauer, G., Reinhardt, I., Rigg, R., Ryser, A., Salvatori, V., Skrbin ek, T., Stojanov, A., Swenson, J.E., Szemethy, L., Trajce, A., Tsingarska-Sedefcheva, E., Va a, M., Veeroja, R., Wabakken, P., Wolfl, M., Wolfl, S., Zimmermann, F., Zlatanova, D., Boitani, L., 2014. Recovery of large carnivores in Europe’s modern human-dominated landscapes. Sience 346, 1517–1519. https://doi.org/10.1126/science.1257553

Ciarniello, L.M., Boyce, M.S., Seip, D.R., Heard, D.C., 2007. Grizzly bear habitat election is scale dependent. Ecol. Appl. 17, 1424–1440.

Ciuti, S., Northrup, J.M., Muhly, T.B., Simi, S., Musiani, M., Pitt, J.A., Boyce, M.S., 2012. Effects of Humans on Behaviour of Wildlife Exceed Those of Natural Predators in a Landscape of Fear. PLoS One 7. https://doi.org/10.1371/journal.pone.0050611

Clevenger, A., Purroy, F., Pelton, M., 1990. Movement and Activity Patterns of a European Brown Bear in the Cantabrian Mountains, Spain. Bears Their Biol. Manag. 8, 205–211.

Clevenger, A.P., 1995. El Oso en León. Univ. León, Spain.

Clevenger, A.P., Purroy, F.J., de Buruaga, M.S., Purdoy, F., de Burguaga, M.S., 1987. Status of the brown bear in the Cantabrian Mountains, Spain. Bears Their Biol. Manag. 7, 1–8.

Clinchy, M., Zanette, L.Y., Roberts, D., Suraci, J.P., Buesching, C.D., Newman, C., Macdonald, D.W., 2016. Fear of the human “super predator” far exceeds the fear of large carnivores in a model mesocarnivore. Behav. Ecol. 27, 1826–1832. https://doi.org/10.1093/beheco/arw117

Cooper, W.E., Frederick, W.G., 2007. Optimal flight initiation distance. J. Theor. Biol. 244, 59–67. https://doi.org/10.1016/j.jtbi.2006.07.011

Crawley, M., 2007. The R Book. J. Wiley, Chichester.

Crooks, K.R., Burdett, C.L., Theobald, D.M., Rondinini, C., Boitani, L., 2011. Global patterns of fragmentation and connectivity of mammalian carnivore habitat. Philos. Trans. R. Soc. B Biol.

Sci. 366, 2642–2651. https://doi.org/10.1098/rstb.2011.0120

Dahle, B., Swenson, J.E., 2003a. Factors influencing length of maternal care in brown bears (Ursus arctos) and its effect on offspring. Behav. Ecol. Sociobiol. 54, 352–358. https://doi.org/10.1007/s00265-003-0638-8

Dahle, B., Swenson, J.E., 2003b. Seasonal range size in relation to reproductive strategies in brown bears Ursus arctos. J. Anim. Ecol. 72, 660–667.

Dickman, A.J., Macdonald, E.A., Macdonald, D.W., 2011. A review of financial instruments to pay for predator conservation and encourage human – carnivore coexistence. Proc. Natl. Acad. Sci. 108, 13937–13945. https://doi.org/10.1073/pnas.1012972108

Dimitri, L.A., Longland, W.S., 2018. The Utility of Animal Behavior Studies in Natural Resource Management. Rangelands 40, 9–16. https://doi.org/10.1016/j.rala.2017.12.003

Ditchkoff, S.S., Saalfeld, S.T., Gibson, C.J., 2006. Animal behavior in urban ecosystems: Modifications due to human-induced stress. Urban Ecosyst. 9, 5–12. https://doi.org/10.1007/s11252-006-3262-3

Doncaster, C., Davey, A., 2007. Analysis of Variance and Covariance: How to Choose and Construct Models for the Life Sciences., Cambridge: Cambridge University Press. https://doi.org/10.1017/CBO9780511611377

Dorresteijn, I., Hanspach, J., Kecskés, A., Latková, H., Mezey, Z., Sugár, S., von Wehrden, H., Fischer, J., 2014. Human-carnivore coexistence in a traditional rural landscape. Landsc. Ecol. 29, 1145–1155. https://doi.org/10.1007/s10980-014-0048-5

Durant, S., 1998. Competition refuges and coexistence: an example from Serengeti carnivores. J. Anim. Ecol. 67, 370–386.

Elfström, M., Zedrosser, A., Støen, O.G., Swenson, J.E., 2014. Ultimate and proximate mechanisms underlying the occurrence of bears close to human settlements: Review and management implications. Mamm. Rev. 44, 5–18. https://doi.org/10.1111/j.1365-2907.2012.00223.x

Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E., Yates, C.J., 2011. A statistical explanation of MaxEnt for ecologists. Divers. Distrib. 17, 43–57. https://doi.org/10.1111/j.1472-4642.2010.00725.x

Elosegi, M.M., 2010. El oso pardo en los Pirineos. Lynx Edicions.

Enserink, M., Vogel, G., 2006. The carnivore comeback. Science. 314, 746–749. https://doi.org/10.1126/science.314.5800.746

Ericksson, T., Dalerum, F., 2018. Identifying areas for an expanding wolf population. Biol. Conserv. In Press.

Eriksson, A.M., Sandström, C., Ericsson, Göran, Eriksson, M., Sandstr, C., Ericsson, G, 2015. Direct experience and attitude change towards bears and wolves. Wildlife Biol. 21, 131–137. https://doi.org/10.2981/wlb.00062

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pikitch, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soulé, M.E., Virtanen, R., Wardle, D.A., 2011. Trophic Downgrading of Planet Earth. Science. 333, 301–306.

Fagen, R., Fagen, J.M., 1996. No TitleIndividual Distinctiveness in Brown Bears, Ursus arctos L.

Ethology 102, 212–226.

FAPAS/FIEP, 2017. El Oso. Pirineos y Cordillera Cantábrica. Gráficas Muñiz, Gijón, Spain.

FAPAS, 2017. El oso. Pirineos y Cordillera Cantábrica. Cuaderno de campo y conservación.

Fedriani, J., Palomares, F., Delibes, M., 1999. Niche relationships among three sympatric Mediterranean carnivores. Oecologia 121, 138–148.

Fedriani, J.M., Fuller, T.K., Sauvajot, R.M., York, E.C., 2000. Competition and intraguild predation among three sympatric carnivores. Oecologia 125, 258–270. https://doi.org/10.1007/s004420000448

Fernández-Gil, A., 2013. Comportamiento y conservación de grandes carnívoros en ambientes humanizados. Osos y Lobos en la Cordillera Cantábrica 296. https://doi.org/10.1017/CBO9781107415324.004

Fernández-Gil, A., Naves, J., Delibes, M., 2006. Courtship of brown bears Ursus arctos in northern Spain: phenology, weather, habitat and durable mating areas. Wildlife Biol. 12, 367–373. https://doi.org/10.2981/0909-6396(2006)12[367:cobbua]2.0.co;2

Fernández-Gil, A., Naves, J., Ordiz, A., Quevedo, M., Revilla, E., Delibes, M., 2016. Conflict misleads large carnivore management and conservation: Brown bears and wolves in Spain. PLoS One 11. https://doi.org/10.1371/journal.pone.0151541

Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence / absence models. Environ. Conserv. 24, 38–49. https://doi.org/10.1017/S0376892997000088

Frid, A., Dill, L., 2002. Human-caused Disturbanve Stimuli as a Form of Predation Risk. Conserv. Ecol. 6, 16.

García-Mozo, H., Dominguez-Vilchez, E., Galán, C., 2012. A model to account for variations in holm-oak (Quercus ilex subsp. ballota) acorn production in southern Spain. Ann. Agric. Environ. Med. 19.

García, D., Quevedo, M., Ramón Obeso, J., Abajo, A., 2005. Fragmentation patterns and protection of montane forest in the Cantabrian range (NW Spain). For. Ecol. Manage. 208, 29–43. https://doi.org/10.1016/j.foreco.2004.10.071

García, P., Lastra, J., Marquínez, J., Nores, C., 2007. Detailed model of shelter areas for the Cantabrian brown bear. Ecol. Inform. 2, 297–307. https://doi.org/10.1016/j.ecoinf.2007.08.003

Gardner, C.L., Pamperin, N.J., Benson, J.F., Gardner, C.L., Pamperin, N.J., Benson, J.F., 2014. Movement patterns and space use of maternal grizzly bears influence cub survival in Interior Alaska. Ursus 25, 121–138. https://doi.org/10.2192/URSUS-D-14-00015.1

Gaynor, K.M., Hojnowski, C.E., Carter, N.H., Brashares, J.S., 2018. The influence of human disturbance on wildlife nocturnality. Science. 360, 1232–1235. https://doi.org/10.1126/science.aar7121

Geffroy, B., Samia, D.S.M., Bessa, E., Blumstein, D.T., 2015. How Nature-Based Tourism Might Increase Prey Vulnerability to Predators. Trends Ecol. Evol. 30, 755–765. https://doi.org/10.1016/j.tree.2015.09.010

Gittleman, J.L., Funk, S.M., Macdonald, D.W., Wayne, R.K., 2001. Carnivore conservation. Cambridge Univ. Press, Cambridge.

Glikman, J.A., Ciucci, P., Marino, A., Davis, E.O., Bath, A.J., Boitani, L., 2019. Local attitudes toward Apennine brown bears: Insights for conservation issues. Conserv. Sci. Pract. 1, e25. https://doi.org/10.1111/csp2.25

Gonsamo, A., Chen, J.M., Lombardozzi, D., 2016. Global vegetation productivity response to climatic oscillations during the satellite era. Glob. Chang. Biol. 22, 3414–3426. https://doi.org/10.1111/gcb.13258

Gonzalez, E.G., Blanco, J.C., Ballesteros, F., Alcaraz, L., Palomero, G., Doadrio, I., 2016. Genetic and demographic recovery of an isolated population of brown bear Ursus arctos L., 1758. PeerJ 4. https://doi.org/10.7717/peerj.1928

Graf, P.M., Bordjan, D., Fležar, U., Jerina, K., 2018. Feeding site use and food type preference of brown bears in Slovenia, prepared within the LIFE DINALP BEAR Project (LIFE13 NAT/SI/0005).

Gunther, K.A., Haroldson, M.A., Frey, K., Cain, S.L., Copeland, J., Schwartz, C.C., 2004. Grizzly bear–human conflicts in the Greater Yellowstone ecosystem, 1992–2000. Ursus 15, 10–22.

Hebblewhite, M., White, C.A., Nietvelt, C.G., McKenzie, J.A., Hurd, T.E., Fryxell, J.M., Bayley, S.E., Paquet, P.C., 2005. Human activity mediates a trophic cascade caused by wolves. Ecology 86, 2135–2144. https://doi.org/10.1890/04-1269

Herrero, S., Smith, T., Debruyn, T.D., Gunther, K., Matt, C.A., 2005. From the Field : Brown bear habituation to people — safety , risks , and benefits 33, 362–373.

Higashide, D., Miura, S., Miguchi, H., 2012. Are chest marks unique to Asiatic black bear individuals? J. Zool. 288, 199–206. https://doi.org/10.1111/j.1469-7998.2012.00942.x

Higham, J.E.S., Shelton, E.J., 2011. Tourism and wildlife habituation: Reduced population fitness or cessation of impact? Tour. Manag. 32, 1290–1298. https://doi.org/10.1016/j.tourman.2010.12.006

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965–1978. https://doi.org/10.1002/joc.1276

Hijmans, R.J., Phillips, S., Leathwick, J.R., Elith, J., 2017. Package "dismo." Circles 9.

Hrdy, S.B., 1979. Infanticide among animals: A review, classification, and examination of the implications for the reproductive strategies of females. Ethol. Sociobiol. 1, 13–40. https://doi.org/10.1016/0162-3095(79)90004-9

Huck, M., Jędrzejewski, W., Borowik, T., Miłosz-Cielma, M., Schmidt, K., Jędrzejewska, B., Nowak, S., Mysłajek, R.W., 2010. Habitat suitability, corridors and dispersal barriers for large carnivores in Poland. Acta Theriol. (Warsz). 55, 177–192.

Jedrzejewski, W., Jedrzejewska, B., Zawadzka, B., Borowik, T., Nowak, S., Mysłajek, R.W., 2008. Habitat suitability model for Polish wolves based on long-term national census. Anim. Conserv. 11, 377–390. https://doi.org/10.1111/j.1469-1795.2008.00193.x

Jerina, K., Debeljak, M., Džeroski, S., Kobler, A., Adamič, M., 2003. Modeling the brown bear population in Slovenia: A tool in the conservation management of a threatened species. Ecol. Modell. 170, 453–469. https://doi.org/10.1016/S0304-3800(03)00245-X

Jerina, K., Krofel, M., Maja, M., Matija, S., Marko, J., Seveque, A., 2015. Analysis of occurence of human-bear conflicts in Slovenia and neighbouring countries. Action A.1: Analysis of the damage cases and bear intervention group interventions, preparation of guidelines for

Intervention group protocols., University of Ljubljana, Biotechnical Faculty, Department of Forestry and Renewable Forest Resources.

Johnson, D., 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61, 65–71.

Kaartinen, S., Luoto, M., Kojola, I., 2009. Carnivore-livestock conflicts: Determinants of wolf (Canis lupus) depredation on sheep farms in Finland. Biodivers. Conserv. 18, 3503–3517. https://doi.org/10.1007/s10531-009-9657-8

Kaczensky P, Chapron G, von Arx M, Huber D, Andrén H, et al, 2013. Status, management and distribution of large carnivores - bear, lynx, wolf and wolverine - in Europe. Rep. to EU Comm. 272.

Kaiser, H.F., 1958. The varimax criterion for analytic rotation in factor analysis. Psychometrika 23, 187–200.

Kleiven, J., Bjerke, T., Kaltenborn, B.P., 2004. Factors influencing the social acceptability of large carnivore behaviours. Biodivers. Conserv. 13, 1647–1658. https://doi.org/10.1023/B:BIOC.0000029328.81255.38

Kobler, A., Adamic, M., 2000. Identifing brown bear habitat by a combined GIS and machine learning method. Ecol. Modell. 135, 291.

Koenig, W.D., Knops, J.M., 2000. Patterns of annual seed production by northern hemisphere trees: a global perspective. Am. Nat. 155, 59–69. https://doi.org/10.2307/3079016

Koike, S., Morimoto, H., Goto, Y., Kozakai, C., Yamazaki, K., 2008. Frugivory of carnivores and seed dispersal of fleshy fruits in cool-temperate deciduous forests. J. For. Res. 13, 215–222. https://doi.org/10.1007/s10310-008-0069-5

Kozakai, C., Yamazaki, K., Nemoto, Y., Nakajima, A., Koike, S., Abe, S., Masaki, T., Kaji, K., 2011. Effect of mast production on home range use of Japanese black bears. J. Wildl. Manage. 75, 867–875. https://doi.org/10.1002/jwmg.122

Kuemmerle, T., Radeloff, V.C., Perzanowski, K., Kozlo, P., Sipko, T., Khoyetskyy, P., Al, E., 2011. Predicting potential European bison habitat across its former range. 21, 830–843.

Kuijper, D.P.J., Sahlén, E., Elmhagen, B., Chamaillé-Jammes, S., H. Sand, K. Lone, J.P.G.M.C., 2016. Paws without claws ? Ecological effects of large carnivores in anthropogenic landscapes Paws without claws ? Ecological effects of large carnivores in anthropogenic landscapes. https://doi.org/10.1098/rspb.2016.1625

Lalleroni, A., Quenette, P.Y., Daufresne, T., Pellerin, M., Baltzinger, C., 2017. Exploring the potential of brown bear (Ursus arctos arctos) as a long-distance seed disperser : a pilot study in South-Western Europe. Mammalia 81, 1–9. https://doi.org/10.1515/mammalia-2015-0092

Lamamy, C., Bombieri, G., Zarzo-arias, A., González-Bernardo, E., Penteriani, V., 2019. Can landscape characteristics help explain the different trends of Cantabrian brown bear subpopulations ? Mammal Res. 1–9. https://doi.org/https://doi.org/10.1007/s13364-019-00440-7

Lande, R., 1988. Genetics and demography in biological conservation. Science. 241, 1455–1460.

Leblond, M., Dussault, C., Ouellet, J.P., 2013. Impacts of human disturbance on large prey species: do behavioral reactions translate to fitness consequences? PLoS One 8. https://doi.org/10.1371/journal.pone.0073695

Lenth, R. V., 2016. The R Package lsmeans. J. Stat. Softw. 69. https://doi.org/10.18637/jss.v069.i01

Lewis, D.L., Baruch-Mordo, S., Wilson, K.R., Breck, S.W., Mao, J.S., Broderick, J., 2015. Foraging ecology of black bears in urban environments: Guidance for human-bear conflict mitigation. Ecosphere 6, 1–18. https://doi.org/10.1890/ES15-00137.1

Libal, N.S., Belant, J.L., Leopold, B.D., Wang, G., Owen, P.A., 2011. Despotism and risk of infanticide influence grizzly bear den-site selection. PLoS One 6. https://doi.org/10.1371/journal.pone.0024133

Liberg, O., Chapron, G., Wabakken, P., Pedersen, H.C., Hobbs, N.T., Sand, H., 2012. Shoot , shovel and shut up: cryptic poaching slows restoration of a large carnivore in Europe. Proc. R. Soc. B 279, 910–915. https://doi.org/10.1098/rspb.2011.1275

Lima, S., Dill, L., 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68, 619–640.

Linnell, J.D.C., Odden, J., Kaczensky, P., Swenson, J.E., 1996. Strategies for the Reduction of Carnivore - Livestock Conflicts: A Review. Nor. Inst. Naturforskning Oppdragsmelding, Trondheim.

Linnell, J.D.C., Swenson, J.E., Andersen, R., 2001. Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. Anim. Conserv. 4, 345–349.

Linnell, J.D.C., Swenson, J.O.N.E., Andersen, R., 2000. Conservation of biodiversity in Scandinavian boreal forests : large carnivores as flagships , umbrellas , indicators , or keystones ? Biodivers. Conserv. 9, 857–868.

Löe, J., Röskaft, E., 2019. Large Carnivores and Human Safety: A Review. AMBIO A J. Hum. Environ. 33, 283–288.

Lowry, H., Lill, A., Wong, B.B.M., 2012. Behavioural responses of wildlife to urban environments. Biol. Rev. 88, 537–549. https://doi.org/10.1111/brv.12012

Mace, G.M., 2014. Whose conservation? Science. 345, 1558–1560. https://doi.org/10.1126/science.1254704

Majić Skrbinšek, A., Krofel, M., 2014. Defining, preventing, and reacting to problem bear behaviour in Europe, European Commission.

Marsden, K., Brandt, K., Hovardas, T., 2017. Report of the Fifth Regional Workshop of the EU Platform on coexistence between people and large carnivores.

Martin, J., Basille, M., Van Moorter, B., Kindberg, J., Allainé, D., Swenson, J.E., 2010. Coping with human disturbance: spatial and temporal tactics of the brown bear (Ursus arctos). Can. J. Zool. 88, 875–883.

Martin, J., Revilla, E., Quenette, P., Naves, J., Swenson, J.E., Ame, C., 2012. Brown bear habitat suitability in the Pyrenees : transferability across sites and linking scales to make the most of scarce data. J. Appl. Ecol. 49, 621–631. https://doi.org/https://doi.org/10.1111/j.1365-2664.2012.02139.x

Martin, J., van Moorter, B., Revilla, E., Blanchard, P., Dray, S., Quenette, P.Y., Allainé, D., Swenson, J.E., 2013. Reciprocal modulation of internal and external factors determines individual movements. J. Anim. Ecol. 82, 290–300. https://doi.org/10.1111/j.1365-2656.2012.02038.x

Martínez Cano, I., González Taboada, F., Naves, J., Fernández-Gil, A., Wiegand, T., 2016. Decline and recovery of a large carnivore: environmental change and long- term trends in an endangered brown bear population. Proc. R. Soc. B 283, 20161832. https://doi.org/10.1098/rspb.2016.1832

Mateo-Sánchez, M.C., Cushman, S.A., Saura, S., 2014. Connecting endangered brown bear subpopulations in the Cantabrian Range (north-western Spain). Anim. Conserv. 17, 430–440. https://doi.org/10.1111/acv.12109

Mateo-Sánchez, M.C., Gastón, A., Ciudad, C., García-Viñas, J.I., Cuevas, J., López-Leiva, C., Fernández-Landa, A., Algeet-Abarquero, N., Marchamalo, M., Fortin, M.J., Saura, S., 2016. Seasonal and temporal changes in species use of the landscape: how do they impact the inferences from multi-scale habitat modeling? Landsc. Ecol. 31, 1261–1276. https://doi.org/10.1007/s10980-015-0324-z

Mateo Sánchez, M.C., Cushman, S.A., Saura, S., 2013. Scale dependence in habitat selection: the case of the endangered brown bear (Ursus arctos) in the Cantabrian Range (NW Spain). Int. J. Geogr. Inf. Sci. 28, 1531–1546.

McGarigal, K., Cushman, S.A., Stafford, S., 2000. Multivariate statistics for wildlife and ecology research. Springer.

Mcloughlin, P.D., Case, R.L., Gau, R.J., 2002. Hierarchical habitat selection by barren-ground grizzly bears 132, 102–108. https://doi.org/10.1007/s00442-002-0941-5

Merow, C., Smith, M.J., Silander, J.A., 2013. A practical guide to MaxEnt for modeling species' distributions: What it does, and why inputs and settings matter. Ecography (Cop.). 36, 1058–1069. https://doi.org/10.1111/j.1600-0587.2013.07872.x

Miller, B., Dugelby, B., Foreman, D., Martinez, C., Noss, R., Phillips, M., Reading, R., Willcox, L., 2001. The Importance of Large Carnivores to Healthy Ecosystems. Endanger. Species Updat. 18, 202–210.

Miller, S., White, G., Sellers, R., Reynolds, H., Schoen, J., Titus, K., Barnes, V.J., Smith, R.B., Nelson, R.R., Ballard, W.B., Schwartz, C.C., 1997. Brown and black bear density estimation in Alaska using radio telemetry and replicated mark–resight techniques. Wildl. Monogr. 133, 3–55.

Milleret, C., Ordiz, A., Chapron, G., Andreassen, H.P., Kindberg, J., Månsson, J., Tallian, A., Wabakken, P., Wikenros, C., Zimmermann, B., Swenson, J.E., Sand, H., 2018. Habitat segregation between brown bears and gray wolves in a human-dominated landscape. Ecol. Evol. 1–17. https://doi.org/10.1002/ece3.4572

Moe, T.F., Kindberg, J., Jansson, I., Swenson, J.E., 2007. Importance of diel behaviour when studying habitat selection: examples from female Scandinavian brown bears (Ursus arctos). Can. J. Zool. 85, 518–525.

Moen, G., Ordiz, A., Sundell, J., Kindberg, J., Swenson, J.E., Støen, O.-G., 2019. Behavioral reactions of brown bears to approaching humans in Fennoscandia. Ecoscience 26, 23–33.

Moen, G.K., Støen, O.G., Sahlén, V., Swenson, J.E., 2012. Behaviour of solitary adult Scandinavian brown bears (Ursus arctos) when approached by humans on foot. PLoS One 7. https://doi.org/10.1371/journal.pone.0031699

Molinari, P., Krofel, M., Bragalanti, N., Majić, A., Černe, R., Angeli, F., Huber, D., Groff, C., Hipolito, D., Jerina, K., Jonozovič, M., Mohorović, M., Reljić, S., Seveque, A., Stergar, M., Molinari-Jobin, A., 2014. Comparison of the Occurrence of Human-Bear Conflicts Between the Northern. Carniv. Damage Prev. News.

Moran, A., 1950. A Test for the Serial Independence of Residuals. Biometrika 37, 178–181.

Muhly, T.B., Musiani, M., 2009. Livestock depredation by wolves and the ranching economy in the Northwestern U. S. Ecol. Econ. 68, 2439–2450. https://doi.org/10.1016/j.ecolecon.2009.04.008

Müller-Haubold, H., Hertel, D., Seidel, D., Knutzen, F., Leuschner, C., 2013. Climate Responses of Aboveground Productivity and Allocation in Fagus sylvatica: A Transect Study in Mature Forests. Ecosystems 16, 1498–1516. https://doi.org/10.1007/s10021-013-9698-4

Muntifering, J.R., Dickman, A.J., Perlow, L.M., Hruska, T., Ryan, P.G., Marker, L.L., Jeo, R.M., 2006. Managing the matrix for large carnivores: A novel approach and perspective from cheetah (Acinonyx jubatus) habitat suitability modelling. Anim. Conserv. 9, 103–112. https://doi.org/10.1111/j.1469-1795.2005.00008.x

Muscarella, R., Galante, P.J., Soley-Guardia, M., Boria, R.A., Kass, J.M., Uriarte, M., Anderson, R.P., 2014. ENMeval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. Methods Ecol. Evol. 5, 1198–1205.

Naves, J., Fernández-Gil, A., Rodríguez, C., Delibes, M., 2006. Brown Bear Food Habits At the Border of Its Range: a Long-Term Study. J. Mammal. 87, 899–908. https://doi.org/10.1644/05-mamm-a-318r2.1

Naves, J., Ordiz, A., Fernández-Gil, A., Penteriani, V., Delgado, M.M., López-Bao, J.V., Revilla, E., Delibes, M., 2018. Patterns of brown bear damages on apiaries and management recommendations in the Cantabrian Mountains , Spain. PLoS One 13, e0206733. https://doi.org/https://doi.org/10.1371/journal.pone.0206733

Naves, J., Wiegand, T., Revilla, E., Delibes, M., 2003. Endangered Species Constrained by Natural and Human Factors : the Case of Brown Bears in Northern Spain 17, 1276–1289.

Naves, L., 2016. Comportamiento del oso pardo y actividades humanas: factores explicativos y propuestas de manejo. Trab. Fin Grado. Universida.

Nellemann, C., Støen, O.G., Kindberg, J., Swenson, J.E., Vistnes, I., Ericsson, G., Katajisto, J., Kaltenborn, B.P., Martin, J., Ordiz, A., 2007. Terrain use by an expanding brown bear population in relation to age, recreational resorts and human settlements. Biol. Conserv. 138, 157–165. https://doi.org/10.1016/j.biocon.2007.04.011

Nestby, R., Percival, D., Martinussen, I., Opstad, N., Rohloff, J., 2010. The European Blueberry (Vaccinium myrtillus L.) and the Potential for Cultivation. A Review. Eur. J. Plant Sci. Biotechnol. 5, 5–16.

Newsome, T.M., Boitani, L., Chapron, G., Ciucci, P., Dickman, C.R., Dellinger, J.A., López-Bao, J. V., Peterson, R.O., Shores, C.R., Wirsing, A.J., Ripple, W.J., 2016. Food habits of the world's grey wolves. Mamm. Rev. 46, 255–269. https://doi.org/10.1111/mam.12067

Nores, C., Ballesteros, F., Blanco, J.C., García-Serrano, A., Herrero, J., Palomero, G., 2010. Evidence of non-hibernation in Cantabrian brown bears. Acta Theriol. (Warsz). 55, 203–209. https://doi.org/10.4098/j.at.0001-7051.085.2008

Nyhus, P., Fischer, H., Madden, F., Osofsky, S., 2003. Taking the Bite out of Wildlife Damage The Challenges of Wildlife Compensation Schemes. Conserv. Pract. 4, 37–43.

Nyhus, P., Osofsky, S.A., Ferraro, P., Fischer, H., Madden, F., 2005. People and Wildlife: Conflict or Coexistence?, in: Bearing the Costs of Human-Wildlife Conflict: The Challenges of

Compensation Schemes. pp. 107–121.

Oberosler, V., Groff, C., Iemma, A., Pedrini, P., Rovero, F., 2017. The influence of human disturbance on occupancy and activity patterns of mammals in the Italian Alps from systematic camera trapping. Mamm. Biol. 87, 50–61. https://doi.org/10.1016/j.mambio.2017.05.005

Ordiz, A., Bischof, R., Swenson, J.E., 2013a. Saving large carnivores, but losing the apex predator? Biol. Conserv. 168, 128–133. https://doi.org/10.1016/j.biocon.2013.09.024

Ordiz, A., Rodríguez, C., Naves, J., Fernández, A., Huber, D., Kaczensky, P., Mertens, A., Mertzanis, Y., Mustoni, A., Palazón, S., Quenette, P.Y., Rauer, G., Swenson, J.E., 2007. Distance-based Criteria to Identify Minimum Number of Brown Bear Females with Cubs in Europe. Ursus 18, 158–167. https://doi.org/10.2192/1537-6176(2007)18[158:dctimn]2.0.co;2

Ordiz, A., Sæbø, S., Kindberg, J., Swenson, J.E., Støen, O.G., 2017. Seasonality and human disturbance alter brown bear activity patterns: implications for circumpolar carnivore conservation? Anim. Conserv. 20, 51–60. https://doi.org/10.1111/acv.12284

Ordiz, A., Støen, O.-G., Delibes, M., Swenson, J.E., 2011. Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. Oecologia 166, 59–67. https://doi.org/10.1007/s00442-011-1920-5

Ordiz, A., Støen, O.G., Sæbø, S., Kindberg, J., Delibes, M., Swenson, J.E., 2012. Do bears know they are being hunted? Biol. Conserv. 152, 21–28. https://doi.org/10.1016/j.biocon.2012.04.006

Ordiz, A., Støen, O.G., Sæbø, S., Sahlén, V., Pedersen, B.E., Kindberg, J., Swenson, J.E., 2013b. Lasting behavioural responses of brown bears to experimental encounters with humans. J. Appl. Ecol. 50, 306–314. https://doi.org/10.1111/1365-2664.12047

Oriol-Cotterill, A., Valeix, M., Frank, L.G., Riginos, C., Macdonald, D.W., 2015. Landscapes of Coexistence for terrestrial carnivores: the ecological consequences of being downgraded from ultimate to penultimate predator by humans. Oikos 124, 1263–1273. https://doi.org/10.1111/oik.02224

Packer, C., Holt, R.D., Hudson, P.J., Lafferty, K.D., Dobson, A.P., 2003. Keeping the herds healthy and alert : implications of predator control for infectious disease. Ecol. Lett. 6, 797–802. https://doi.org/10.1046/j.1461-0248.2003.00500.x

Palomares, F., Ferreras, P., Fedriani, J., Delibes, M., 1996. Spatial relationships between Iberian lynx and other carnivores in an area of south-western Spain. J. Appl. Ecol. 33, 5–13.

Palombit, R.A., 2015. Infanticide as sexual conflict: Coevolution of male strategies and female counterstrategies. Cold Spring Harb. Perspect. Biol. 7, 1–31. https://doi.org/10.1101/cshperspect.a017640

Palomero, G., Ballesteros, F., Blanco, J., García-Serrano, A., Herrero, J., C, N., 2011. Osas. El comportamiento de las osas y sus crías en la Cordillera Cantábrica. Fundación Oso Pardo, Fundación Biodiversidad, Madrid.

Palomero, G., Ballesteros, F., Nores, C., Blanco, J.C., Herrero, J., García-Serrano, A., 2007. Trends in Number and Distribution of Brown Bear Females with Cubs-of-the-year in the Cantabrian Mountains, Spain. Ursus 18, 145–157.

Parco Naturale Adamello e Brenta, B.B.R. and C.G., 2007. Influence of human disturbance towards brown bear - expert opinion based survey.

Pato, J., Obeso, J.R., 2012. Fruit mass variability in Vaccinium myrtillus as a response to altitude, simulated herbivory and nutrient availability. Basic Appl. Ecol. 13, 338–346. https://doi.org/10.1016/j.baae.2012.05.003

Patterson, B.D., Kasiki, S.M., Selempo, E., Kays, R.W., 2004. Livestock predation by lions (Panthera leo) and other carnivores on ranches neighboring Tsavo National Parks, Kenya. Biol. Conserv. 119, 507–516. https://doi.org/10.1016/j.biocon.2004.01.013

Penteriani, V., Del Mar Delgado, M., López-Bao, J.V., García, P.V., Monrós, J.S., Vigón Álvarez, E., Corominas, T.S., Vázquez, V.M., 2017a. Patterns of movement of three rescued and released female brown bears in the Cantabrian Mountains, northwest Spain. Ursus 28, 165–170. https://doi.org/10.2192/URSU-D-16-00012.1

Penteriani, V., Delgado, M.D.M., Krofel, M., Jerina, K., Ordiz, A., Dalerum, F., Zarzo-Arias, A., Bombieri, G., 2018a. Evolutionary and ecological traps for brown bears Ursus arctos in human-modified landscapes. Mamm. Rev. 48. https://doi.org/10.1111/mam.12123

Penteriani, V., Delgado, M.D.M., Pinchera, F., Naves, J., Fernández-Gil, A., Kojola, I., Härkönen, S., Norberg, H., Frank, J., Fedriani, J.M., Sahlén, V., Støen, O.-G., Swenson, J.E., Wabakken, P., Pellegrini, M., Herrero, S., López-Bao, J.V., 2016. Human behaviour can trigger large carnivore attacks in developed countries. Sci. Rep. 6, 20552.

Penteriani, V., Delgado, M.M., López-Bao, J. V., Vázquez García, P., Monrós, J.S., Vigón Álvarez, E., Sánchez Corominas, T., Vázquez, V., 2017b. Patterns of movement of three rescued and released female brown bears in the Cantabrian Mountains, northwest Spain. Ursus 28, 165–170. https://doi.org/10.2192/URSUS-D-16-00012.1

Penteriani, Vincenzo, López-Bao, J.V., Bettega, C., Dalerum, F., Delgado, M. del M., Jerina, K., Kojola, I., Krofel, M., Ordiz, A., 2017. Consequences of brown bear viewing tourism: A review. Biol. Conserv. 206, 169–180. https://doi.org/10.1016/j.biocon.2016.12.035

Penteriani, V., Zarzo-Arias, A., Bombieri, G., Cañedo, D., Díaz García, J., Delgado, M.M., Peón Torre, P., Fernández Otero, M., Vázquez García, P., Vázquez, V.M., Sánchez Corominas, T., 2018b. Density and reproductive characteristics of female brown bears in the Cantabrian Mountains, NW Spain. Eur. Zool. J. 85. https://doi.org/10.1080/24750263.2018.1499826

Penteriani, V., Zarzo-Arias, A., Delgado, M.M., Dalerum, F., Gurarie, E., Peón Torre, P., Sánchez Corominas, T., Vázquez, V.M., Vázquez García, P., Ordiz, A., n.d. Females brown bear use areas with infanticide risk in a spatially confined population. Ursus.

Penteriani, V., Zarzo-Arias, A., Novo-Fernández, A., Bombieri, G., López-Sánchez, C.A., 2019. Responses of an endangered brown bear population to climate change based on predictable food resource and shelter alterations. Glob. Chang. Biol. 25, 1133–1151. https://doi.org/10.1111/gcb.14564

Perdue, B., 2016. The Effect of Computerized Testing on Sun Bear Behavior and Enrichment Preferences. Behav. Sci. (Basel). 6, 19. https://doi.org/10.3390/bs6040019

Pérez, T., Naves, J., Vázquez, J.F., Fernández-Gil, A., Seijas, J., Albornoz, J., Revilla, E., Delibes, M., Domínguez, A., 2014. Estimating the population size of the endangered Cantabrian brown bear through genetic sampling. Wildlife Biol. 20, 300–309.

Pérez, T., Naves, J., Vázquez, J.F., Seijas, J., Corao, A., Albornoz, J., Domínguez, A., 2010. Evidence for improved connectivity between Cantabrian brown bear subpopulations. Ursus 21, 104–108. https://doi.org/10.2192/09SC018.1

Phillips, S.J., Anderson, R.P., Dudík, M., Schapire, R.E., Blair, M.E., 2017. Opening the black box: an open-source release of Maxent. Ecography (Cop.). 40, 887–893.

Phillips, S.J., Anderson, R.T., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecol. Modell. 190, 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026

Phillips, S.J., Dudík, M., 2008. Modeling of species distribution with Maxent: new extensions and a comprehensive evalutation. Ecograpy 31, 161–175. https://doi.org/10.1111/j.2007.0906-7590.05203.x

Pinheiro, J.C., Bates, D.M., 2000. Mixed-Effects Models in S and S-PLUS. Springer. Sci. Bus. Media.

Pohja-mykrä, M., Kurki, S., 2014. Strong community support for illegal killing challenges wolf management. Eur. J. Wildl. Res. 60, 759–770. https://doi.org/10.1007/s10344-014-0845-9

Posillico, M., Meriggi, A., Pagnin, E., Lovari, S., Russo, L., 2004. A habitat model for brown bear conservation and land use planning in the central Apennines. Biol. Conserv. 118, 141–150. https://doi.org/10.1016/j.biocon.2003.07.017

Pyare, S., Cain, S., Moody, D., Schwartz, C., Berger, J., 2004. Carnivore re-colonisation: reality, possibility and a non-equilibrium century for grizzly bears in the southern Yellowstone ecosystem. Anim. Conserv. 7, 71–77.

Quenette, P.Y., Alonso, M., Chayron, L., Cluzel, P., Dubarry, E., Dubreuil, D., Palazon, S., Pomarol, M., 2001. Preliminary results of the first transplantation of brown bears in the French Pyrenees. Ursus 12, 115–120.

R: A Language and Environment for Statistical Computing. R Foundationfor Statistical Computing, Vienna, Austria <http://www.R-project.org/>, 2018. R. Core Team. https://doi.org/10.1093/hmg/ddu272

R Development Core Team, 2013. A language and environment for statistical computing.

Richardson, L., Loomis, J., 2009. The total economic value of threatened, endangered and rare species: An updated meta-analysis. Ecol. Econ. 68, 1535–1548. https://doi.org/10.1016/j.ecolecon.2008.10.016

Rigg, R., Finďo, S., Wechselberger, M., Gorman, M.L., Sillero-Zubiri, C., MacDonald, D.W., 2011. Mitigating carnivore-livestock conflict in Europe: Lessons from Slovakia. Oryx 45, 272–280. https://doi.org/10.1017/S0030605310000074

Ripley, B., Venables, B., Bates, D.M., Hornik, K., Gebhardt, A., Firth, D., Ripley, M.B., 2013. Package "MASS." Cran R.

Ripley, B., Venables, W., Ripley, M.B., 2016. Package "nnet." R Packag. version 7, 3–12.

Ripple, W.J., Beschta, R.L., 2012. Trophic cascades in Yellowstone: The first 15years after wolf reintroduction. Biol. Conserv. 145, 205–213. https://doi.org/10.1016/j.biocon.2011.11.005

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D., Wirsing, A.J., 2014. Status and Ecological Effects of the World's Largest Carnivores. Science. 343, 1241484.

Rode, K.D., Farley, S.D., Robbins, C.T., 2006. Sexual dimorphism, reproductive strategy, and human activities determine resource use by brown bears. Ecology 87, 2636–2646. https://doi.org/10.1890/0012-9658(2006)87[2636:SDRSAH]2.0.CO;2

Rodríguez, C., Naves, J., Fernández-Gil, A., Obeso, J.R., Delibes, M., 2007. Long-term trends in food habits of a relict brown bear population in northern Spain: The influence of climate and local factors. Environ. Conserv. 34, 36–44. https://doi.org/10.1017/S0376892906003535

Roff, D., 1992. The evolution of life histories; theories and analysis. Chapman and Hall, New York.

Rondinini, C., Stuart, S., Boitani, L., 2005. Habitat suitability models and the shortfall in conservation planning for African vertebrates. Conserv. Biol. 19, 1488–1497. https://doi.org/10.1111/j.1523-1739.2005.00204.x

Ruiz-Villar, H., Morales-González, A., Bombieri, G., Zarzo-Arias, A., Penteriani, V., 2019. Characterization of a brown bear aggregation during the hyperphagia period in the Cantabrian Mountains, NW Spain. Ursus 29, 93–100.

Sangay, T., Vernes, K., 2008. Human-wildlife conflict in the Kingdom of Bhutan: Patterns of livestock predation by large mammalian carnivores. Biol. Conserv. 141, 1272–1282. https://doi.org/10.1016/j.biocon.2008.02.027

Sanzol, J., Herrero, M., 2001. The "effective pollination period" in fruit trees. Sci. Hortic. (Amsterdam). 90, 1–17. https://doi.org/10.1016/S0304-4238(00)00252-1

Schadt, S., Revilla, E., Wiegand, T., Knauer, F., Kaczensky, P., Breitenmoser, U., Bufka, L., Cerveny, J., Koubek, P., Huber, T., Stanisa, C., Trepl, L., 2002. Assessing the suitability of central European landscape for the reintroduction of Eurasian lynx. J. Appl. Ecol. 39, 189–203. https://doi.org/10.1046/j.1365-2664.2002.00700.x

Schlaepfer, M.A., Runge, M.C., Sherman, P.W., 2002. Ecological and evolutionary traps. Trends Ecol. Evol. 17, 474–480.

Schmitz, O.J., Hawlena, D., Trussell, G.C., 2010. Predator control of ecosystem nutrient dynamics. Ecol. Lett. 13, 1199–1209. https://doi.org/10.1111/j.1461-0248.2010.01511.x

Sergio, F., Marchesi, L., Pedrini, P., Penteriani, V., 2007. Coexistence of a generalist owl with its intraguild predator: distance-sensitive or habitat-mediated avoidance? Anim. Behav. 74, 1607–1616. https://doi.org/10.1016/j.anbehav.2006.10.022

Shannon, G., Larson, C.L., Reed, S.E., Crooks, K.R., Angeloni, L.M., 2017. Ecological Consequences of Ecotourism for Wildlife Populations and Communities. In: Blumstein D., Geffroy B., Samia D., Bessa E. (eds), in: Ecotourism's Promise and Peril. Springer, Cham.

Shivik, J.A., 2006. Tools for the Edge: What ' s New for Conserving Carnivores. BioSience 56, 253–259.

Skuban, M., Find'o, S., Kajba, M., 2018. Bears napping nearby: daybed selection by brown bears (Ursus arctos) in a human-dominated landscape. Can. J. Zool. 96, 1–11. https://doi.org/10.1139/cjz-2016-0217

Skuban, M., Finďo, S., Kajba, M., Koreň, M., Chamers, J., Antal, V., 2017. Effects of roads on brown bear movements and mortality in Slovakia. Eur. J. Wildl. Res. 63, 1–9. https://doi.org/10.1007/s10344-017-1138-x

Smith, J.A., Suraci, J.P., Clinchy, M., Crawford, A., Roberts, D., Zanette, L.Y., Wilmers, C.C., 2017. Fear of the human ' super predator ' reduces feeding time in large carnivores. Proc. R. Soc. B 284, 20170433.

Smith, T.S., Herrero, S., DeBruyn, T.D., 2005. Alaskan brown bears, humans, and habituation. Ursus 16, 1–10. https://doi.org/10.2192/1537-6176(2005)016[0001:ABBHAH]2.0.CO;2

St John, F.A.V., Keane, A.M., Edwards-Jones, G., Jones, L., Yarnell, R.W., Jones, J.P.G., 2012.

Identifying indicators of illegal behaviour: Carnivore killing in human-managed landscapes. Proc. R. Soc. B Biol. Sci. 279, 804–812. https://doi.org/10.1098/rspb.2011.1228

Stahl, P., Vandel, J.M., Herrenschmidt, V., Migot, P., 2001. Predation on livestock by an expanding reintroduced lynx population: Long-term trend and spatial variability. J. Appl. Ecol. 38, 674–687. https://doi.org/10.1046/j.1365-2664.2001.00625.x

Steyaert, S.M.J.G., Endrestøl, A., Hackländer, K., Swenson, J.E., Zedrosser, A., 2012. The mating system of the brown bear Ursus arctos. Mamm. Rev. 42, 12–34. https://doi.org/10.1111/j.1365-2907.2011.00184.x

Steyaert, S.M.J.G., Kindberg, J., Swenson, J.E., Zedrosser, A., 2013. Male reproductive strategy explains spatiotemporal segregation in brown bears. J. Anim. Ecol. 82, 836–845. https://doi.org/10.1111/1365-2656.12055

Steyaert, S.M.J.G., Leclerc, M., Pelletier, F., Kindberg, J., Brunberg, S., Swenson, J.E., Zedrosser, A., 2016. Human shields mediate sexual conflict in a top predator. Proc. R. Soc. B Biol. Sci. 283. https://doi.org/10.1098/rspb.2016.0906

Steyaert, S.M.J.G., Swenson, J.E., Zedrosser, A., 2014. Litter loss triggers estrus in a nonsocial seasonal breeder. Ecol. Evol. 4, 300–310. https://doi.org/10.1002/ece3.935

Støen, O.G., Ordiz, A., Evans, A.L., Laske, T.G., Kindberg, J., Fröbert, O., Swenson, J.E., Arnemo, J.M., 2015. Physiological evidence for a human-induced landscape of fear in brown bears (Ursus arctos). Physiol. Behav. 152, 244–248. https://doi.org/10.1016/j.physbeh.2015.09.030

Suraci, J.P., Clinchy, M., Dill, L.M., Roberts, D., Zanette, L.Y., 2016. Fear of large carnivores causes a trophic cascade. Nat. Commun. 10698. https://doi.org/10.1038/ncomms10698

Swan, G.J.F., Redpath, S.M., Bearhop, S., McDonald, R.A., 2017. Ecology of Problem Individuals and the Efficacy of Selective Wildlife Management. Trends Ecol. Evol. 32, 518–530. https://doi.org/10.1016/j.tree.2017.03.011

Swanepoel, L.H., Lindsey, P., Somers, M.J., van Hoven, W., Dalerum, F., 2013. Extent and fragmentation of suitable leopard habitat in South Africa. Anim. Conserv. 16, 41–50. https://doi.org/10.1111/j.1469-1795.2012.00566.x

Swenson, J., Andrén, H., 2005. A tale of two countries: large carnivore depredation and compensation schemes in Sweden and Norway, in: People and Wildlife, Conflict or Co-Existence? p. 323.

Swenson, J.E., Dahle, B., Sandegren, F., 2001. Intraspecific predation in Scandinavian brown bears older than cubs-of-the-year. Ursus 12, 81–92.

Swenson, J.E., Gerstl, N., Dahle, B., Zedrosser, A., 2000. Action plan for the conservation of the brown bear (Ursus arctos) in Europe. Nat. Environ. Counc. Eur. 69.

Swenson, J.E., Taberlet, P., Bellemain, E., 2011. Genetics and conservation of European brown bears Ursus arctos. Mamm. Rev. 41, 87–98. https://doi.org/10.1111/j.1365-2907.2010.00179.x

Tanner, E., White, A., Acevedo, P., Balseiro, A., Marcos, J., Gortázar, C., 2019. Wolves contribute to disease control in a multi-host system. Sci. Rep. 9, 7940. https://doi.org/10.1038/s41598-019-44148-9

Tattoni, C., Bragalanti, N., Groff, C., Rovero, F., 2015. Patterns in the use of rub trees by the Eurasian brown bear. Hystrix 26, 118–124. https://doi.org/10.4404/hystrix-26.2-11414

Team, Q.G.D., 2015. QGIS Geographic Information System. Open Source Geospatial Foundation Project <http://qgis.osgeo.org>.

Treves, A., 2009. Hunting for large carnivore conservation. J. Appl. Ecol. 46, 1350–1356. https://doi.org/10.1111/j.1365-2664.2009.01729.x

Treves, A., Karanth, K.U., 2003. Human-Carnivore Conflict and Perspectives on Carnivore Management Worldwide. Conserv. Biol. 17, 1491–1499. https://doi.org/10.1111/j.1523-1739.2003.00059.x

Treves, A., Naughton-treves, L., Harper, E.K., Mladenoff, D.J., Rose, R.A., Sickley, T.A., Wydeven, A.P., 2004. Predicting Human-Carnivore Conflict : A Spatial Model Derived from 25 Years of Data on Wolf Predation on Livestock 18, 114–125. https://doi.org/10.1111/j.1523-1739.2004.00189.x

Tukey, J.W., 1949. Comparing Individual Means in the Analysis of Variance. Int. Biometric Soc. 5, 99–114.

Tuomainen, U., Candolin, U., 2011. Behavioural responses to human-induced environmental change. Biol. Rev. 86, 640–657. https://doi.org/10.1111/j.1469-185X.2010.00164.x

Ulrich, W., Almeida-Neto, M., Gotelli, N.J., 2009. A consumer's guide to nestedness analysis. Oikos. https://doi.org/10.1111/j.1600-0706.2008.17053.x

Valeix, M., Hemson, G., Loveridge, A.J., Mills, G., Macdonald, D.W., 2012. Behavioural adjustments of a large carnivore to access secondary prey in a human-dominated landscape. J. Appl. Ecol. 49, 73–81. https://doi.org/10.1111/j.1365-2664.2011.02099.x

van Schaik, C., Janson, C., 2000. Infanticide by males and its implications. Cambridge University Press, Cambridge.

Venter, O., Sanderson, E.W., Magrach, A., Allan, J.R., Beher, J., Jones, K.R., Possingham, H.P., Laurance, W.F., Wood, P., Fekete, B.M., Levy, M.A., Watson, J.E.M., 2016. Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. Nat. Commun. 7, 1–11. https://doi.org/10.1038/ncomms12558

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J., Hoegh-guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. Nature 416, 389–395.

Warren, D.L., Seifert, S.N., 2011. Ecological niche modeling in Maxent: The importance of model complexity and the performance of model selection criteria. Ecol. Appl. 21, 335–342. https://doi.org/10.1890/10-1171.1

Watson, F.G.S., Becker, M., Milanzi, J., Nyirenda, M., 2015. Human encroachment into protected area networks in Zambia: implications for large carnivore conservation. Reg. Environ. Chang. 15, 415–429. https://doi.org/10.1007/s10113-014-0629-5

Wei, T., Simko, V., 2016. corrplot: Visualization of a Correlation Matrix. R package version 0.77.

Whiteman, A., Passoni, G., Rowcliffe, J.M., Ugarković, D., Kusak, J., Reljić, S., Huber, D., 2017. Identifying key denning habitat to conserve brown bear (Ursus arctos) in Croatia. Wildl. Res. 44, 309–315. https://doi.org/10.1071/WR16164

Wiegand, T., Naves, J., Stephan, T., Fernandez, A., 1998. Assessing the Risk of Extinction for the Brown Bear (Ursus arctos) in the Cordillera Cantabrica, Spain. Ecol. Appl. 68, 539–570.

Wielgus, R.B., Bunnell, F.L., 1995. Tests of Hypotheses for Sexual Segregation in Grizzly Bears. J.

Wildl. Manage. 59, 552–560.

Wilmers, C.C., Schmitz, O.J., 2016. Effects of gray wolf--induced trophic cascades on ecosystem carbon cycling. Ecosphere 7, e01501.

Wilson, S.M., Madel, M.J., Mattson, D.J., Graham, J.M., Burchfield, J.A., Belsky, J.M., 2005. Natural landscape features, human-related attractants, and conflict hotspots: a spatial analysis of human–grizzly bear conflicts. Ursus 16, 117–129. https://doi.org/10.2192/1537-6176(2005)016[0117:nlfhaa]2.0.co;2

Wolf, C., Ripple, W.J., 2016. Prey depletion as a threat to the world ’ s large carnivores. R. Soc. Open Sci. 3, 160252.

Woodroffe, R., 2000. Predators and people: using human densities to interpret declines of large carnivores. Anim. Conserv. 3, 165–173.

Young, N., Carter, L., Evangelista, P., 2011. A MaxEnt model v3. 3.3 e tutorial (ArcGIS v10). Fort Collins, Color. Nat. Resour. Ecol. Lab. Color. State Univ. Natl. Inst. Invasive Species Sci. 1–30.

Zarzo-Arias, A., Delgado, M. del M., Ordiz, A., García Díaz, J., Cañedo, D., González, M.A., Romo, C., Vázquez García, P., Bombieri, G., Bettega, C., Russo, L.F., Cabral, P., García González, R., Martínez-Padilla, J., Penteriani, V., 2018. Brown bear behaviour in human-modified landscapes: The case of the endangered Cantabrian population, NW Spain. Glob. Ecol. Conserv. 16. https://doi.org/10.1016/j.gecco.2018.e00499

Zarzo-Arias, A., Penteriani, V., Del Mar Delgado, M., Torre, P.P., García-González, R., Mateo-Sánchez, M.C., García, P.V., Dalerum, F., 2019. Identifying potential areas of expansion for the endangered brown bear (Ursus arctos) population in the cantabrian mountains (NW Spain). PLoS One 14, 1–15. https://doi.org/10.1371/journal.pone.0209972

Zedrosser, A., Steyaert, S.M.J.G., Gossow, H., Swenson, J.E., 2011. Brown bear conservation and the ghost of persecution past. Biol. Conserv. 144, 2163–2170.

Zimmermann, A., Baker, N., Inskip, C., Linnell, J.D.C., Marchini, S., Odden, J., Rasmussen, G., Treves, A., 2010. Contemporary views of human–carnivore conflicts on wild rangelands, in: Wild Rangelands: Conserving Wildlife While Maintaining Livestock in Semi-Arid Ecosystems. pp. 129–151.

Zimmermann, J., Hauck, M., Dulamsuren, C., Leuschner, C., 2015. Climate Warming-Related Growth Decline Affects Fagus sylvatica, But Not Other Broad-Leaved Tree Species in Central European Mixed Forests. Ecosystems 18, 560–572. https://doi.org/10.1007/s10021-015-9849-x

SUMMARY AND CONCLUSIONS

General introduction

Large carnivores are in general species with large territories and great capacity for movement, high energy requirements and low reproduction rates and population density. They are iconic species, but at the same time in precarious conservation status. Furthermore, they are key to maintaining the ecological balance of the habitats they inhabit. Being at the top of the food chain, they control interactions between all trophic levels. Furthermore, because they are such charismatic and striking ("flagship" species) and have such wide range and sometimes specific habitat requirements, they serve as "umbrellas" for the conservation of other species that are included in their same habitat and may not attract as much attention. They also bring large economic benefits associated with nature tourism. But this does not deny that large carnivores also produce conflicts arising from their presence in human-dominated areas, often associated with threats to property or the safety of people. As a result, the potential benefits linked to these species have generally been underestimated by society, which has persecuted them for centuries due to these conflicts. Currently, thanks to more protective and tolerant legislation that advocates the recovery and maintenance of their populations, and the implementation of important conservation and management actions, their precarious situation is being reversed.

But they face multiple, and generally concurrent, threats that put their survival at risk. Now that they are recovering and re-colonising former territories after their long persecution, which are sometimes characterized by a high human density, the emergence of conflicts arise. For this reason, illegal hunting or poisoning is still used to avoid conflicts and even for commercial purposes, making their conservation very difficult. Also, the loss, degradation and fragmentation of habitat increasingly promoted by growing human populations compromises the viability of large carnivores. And the reduction and deterioration of their prey populations, which suffer similar threats and on which they depend for their livelihoods, further aggravates their situation. Climate change also affects their habitats and food resources. Furthermore, human presence and activity can also influence the behavior of large carnivores.

Facilitating coexistence with large carnivores is one of the main objectives, and also challenges, of management and conservation plans, especially after the recovery of these species in many parts of the world and the increasing occupation of the territory by humans. But the viability of their populations depends very much on their capacity to adapt to highly humanized environments, which can be promoted by applying the appropriate strategies that allow their coexistence with human populations and also do not harm their development. Public support and cooperation are crucial to the success of these actions. Achieving effective conservation depends largely on the ability to translate the global value of carnivores into tangible benefits large enough to drive conservation at the local level, promoting collaborative action and public acceptance of wildlife management. Conservation programs therefore include conflict mitigation measures (e.g. electric fencing, livestock protection) and economic compensation for damage and losses, aimed at improving the viewpoint of those most affected. These actions should be based on a better understanding of the ecology and behaviour of carnivores, as well as on accumulated knowledge and local experiences of conflict.

Although the population of brown bears located in the Cantabrian Mountains has increased considerably over the last two decades, the current status of the population does not yet guarantee its viability and the effect that human activities have on it has not been studied in depth. The main motivations of this thesis have been to produce new scientific information focused essentially on promoting and facilitating the coexistence with the brown bear in a highly humanized landscape such as the Cantabrian Mountains, and to contribute in the correct management of the species for conservation purposes.

Increasing the knowledge about large carnivore’s ecology, as well as about the conflicts posed by their interactions with humans, is of vital importance in promoting their conservation and achieving sustainable coexistence between them, especially in highly human dominated landscapes. Given the recovery of many populations of large carnivores and the colonization of new territories in recent decades, we could witness an increase in the interactions of these species with human activities, which puts the sustainability of these populations at risk.

Objectives

The main objective of this thesis is to produce new scientific information, while updating the information already available, on the ecology and behaviour of the brown bear population in the Cantabrian Mountains. Focusing on the effect that a highly humanized environment can have on this population, as well as on the study and mitigation of conflicts between bears and humans, the aim of this thesis is to achieve an improvement in the management and conservation of this population, as well as to develop and provide the scientific community with new methodologies applicable to other populations of large carnivores. It explores four key elements: (1) the characteristics of the population's habitat and its potential expansion areas, as well as (2) the habitat selection of the different groups of bears in the breeding season (females with first-year and second-year cubs and breeding areas), (3) the possible changes in behaviour as a function of proximity to different human infrastructures and (4) the spatial-temporal patterns that can affect the appearance of damage to livestock, beehives and crops. The results presented serve in turn as a basis for making management and conservation recommendations for the species, highlighting threats and situations that may affect the viability of this brown bear population in this geographical environment.

Chapter 1. Identifying potential areas of expansion for the endangered brown bear (Ursus arctos) population in the Cantabrian Mountains (NW Spain).

Chapter 1 discusses the characterization of the preferred areas for bears in this population, as well as its expansion and possible consequences. In the Cantabrian Mountains, bears prefer rugged forests with low human population density at high altitude, which are quite inaccessible to humans. But in the western part of Asturias most of the areas that meet these conditions are already occupied by bears, so their increase and dispersion to nearby territories would put them in more contact with people in lower altitude areas and greater presence of human activities and infrastructures. Population growth also favours the connection between the two subpopulations of the Cantabrian Mountains, although the infrastructures that separate them are a great barrier to dispersion. The improvement of the connectivity between both subpopulations could facilitate the expansion to areas in the east of Asturias, where the species still has favourable unoccupied habitats. The identification of the potential areas of brown bear range expansion is crucial to facilitate proactive conservation and management strategies towards promoting a further recovery of this small and isolated population. At the same time, the application and maintenance of preventive measures against damage, as well as their incorporation in the identified expansion areas, would allow the level of conflicts to remain low.

Chapter 2. Female brown bears use areas with infanticide risk in a spatially confined population.

The main aim of chapter 2 was to identify landscape features that may differentiate the habitat use of females with cubs of the year from areas frequented by females with yearlings and bear mating areas, since infanticide is an important cause of mortality of the cubs in the Cantabrian Mountains. Although in this population females also resort to polygamy to protect their offspring and reduce the chance of infanticide, selecting areas that do not overlap with those chosen by breeding individuals can also be an advantage. But given the restricted area of distribution and limited habitat availability for bears in the Cantabrian Mountains, the need for both shelter and food in early spring may trap females with cubs in the Cantabrian Mountains in the same areas used by breeding individuals, which increases the likelihood of risky encounters. Proactive conservation of areas where these females are located is an important management recommendation, especially when such places are close to human settlements and outdoor human activities (e.g. hiking and climbing areas), which are a potential source of disturbance and may cause displacement of these females from these sensitive areas.

Chapter 3. Brown bear behaviour in human-modified landscapes: the case of the endangered Cantabrian population, NW Spain.

In Chapter 3, changes in behaviour as a function of distance from human infrastructures are studied. Although the preferred areas for bears are usually linked to little human influence, bears in these mountains have had to get used to their presence due to the high humanization of the environment. Our findings suggest that the bear's general pattern of avoiding humans is adapted to the human-modified landscape in which they live. The main changes in warning behaviours reflect the dominance relationships and avoidance patterns among different types of bears in each season. This suggests that bears may have previously chosen areas where the effect of human activities is lower, and therefore their disturbances are tolerable. It may also suggest an adaptation of bear behaviour to human presence in such humanized areas, as the waste of time in alert behaviours reduces the time spent on other necessary behaviours such as feeding or nursing the cubs. Coexistence between large carnivores and humans in human-modified landscapes is possible, even when human encroachment is high, provided that carnivores are not heavily persecuted and direct interactions are avoided. Further research should also document the potential existence of other responses to human presence and activity, e.g., hunting, traffic noise, and measuring stress levels with physiological indicators.

Chapter 4. Seasonality, local resources and environmental factors drive patterns of brown bear damages: implications for management.

Chapter 4 discusses spatial and temporal patterns of conflict occurrence, specifically bear damages to livestock, crops and beehives in the two bear populations located in Spain. The presence of these animals in human-dominated landscapes produces difficulties for people, as they sometimes take advantage of more easily accessible resources and create conflict. Compensation and damage payments are necessary to reduce the bad reputation of these animals, but prevention measures are even more important, as reducing the amount of conflict makes living together much easier. However, understanding the drivers triggering conflicts is a conservation priority which helps prevent and reduce damages. Damages varied among years, seasons and bear populations, and seemed to mainly depend on the local availability of natural food items, weather conditions and the availability of the different human activities. Fluctuating availability of food items may explain the frequency of damages, which is yet another call to apply preventive measures in carnivore attacks to human property in seasons and years when food availability is lower than usual. Thus, this chapter highlights the need for particular studies, since conflicts depend greatly on each population and its behaviour, as well as on land uses, climate conditions and even the legislation and management of each territorial unit.

General discussion

The present thesis focuses on producing new scientific information focused essentially on promoting and facilitating the coexistence between humans and brown bears in a highly humanized space such as the Cantabrian Mountains, and helping the correct management of the species for conservation purposes. In general, the results of this thesis, which are discussed below, aim to improve our knowledge and better understanding of the coexistence between humans and large carnivores in an illustrative context, inspiring possible future research and providing practical tools for the conservation of this small and isolated bear population in southern Europe.

Chapters one and two confirm the avoidance of human-driven disturbance by brown bears. In turn, they define the most suitable areas for the species, which are characterized by high altitude and slope, as well as forest cover, which represents key feeding and shelter areas. However, this fact results in a trap for females with first year cubs, which use very specific areas where they find both refuge and food availability. In the western area and given that adult individuals also try to avoid human disturbance, the areas where these females are located are similar to the breeding areas, which, together with the higher density of bears, increases the probability of infanticide. Therefore, proactive conservation of steep terrain, especially during the spring, is an important management recommendation, especially when these places are frequented by leisure activities such as hiking or climbing, can reduce disturbance and prevent the movement of these females.

In contrast, in the eastern area there are still large extensions of favourable areas in Asturias in which there are hardly any bears located, and where there is great availability of refuges. These areas have not yet been colonized due to the combination of the small size of the eastern subpopulation, its lower growth rate and litter size compared to the western subpopulation, and its lower genetic diversity. The increased growth of the larger subpopulation and its dispersion could enhance the recovery of the eastern subpopulation and the occupation of these favourable territories. But the reduced connectivity between both subpopulations, which limits the flow of individuals, delays the colonization of these areas. Another added problem could be the lower quality of natural foods in this sector, which would encourage the use of anthropogenic resources and the appearance of conflicts. These results serve as a tool for the prevention and mitigation of potential conflicts, as well as for developing information campaigns, by identifying priority areas where bear density may increase, or where the bear is currently absent but is expected to expand to. In addition, future direct monitoring of the use of space, movements and activity patterns of females with cubs, dispersing individuals and other groups of bears will be crucial to understanding the development and dynamics of this population.

Nevertheless, having coexisted for so many years with humans, bears have been able to adapt and get used to the disturbances, for example, by selecting areas where their impact is less severe. Consequently, as shown in chapter three, the appearance of warning behaviours in this population mainly reflects the relationships of dominance and avoidance patterns between the different types of bear at each time of year, but they do not increase according to the proximity to the main human infrastructures. In addition, recorded females with cubs were often located closer to some human infrastructures such as villages during the times of greatest risk of infanticide, which can be interpreted as an adaptive advantage when using as areas of greater protection those closer to human disturbances, since they are generally avoided by solitary adult individuals. Effectively preventing human-caused mortality, while reducing interactions that could potentially negatively influence stress and behavior in these animals, is crucial to the persistence and recovery of bears and other carnivores in humanized environments. Future research should focus on responses to different human-derived activities, such as hunting, trafficking, or mountain tourism, taking into account temporal patterns of avoidance of these disturbances and considering physiological stress levels.

As mentioned above, the location of potentially conflictive areas is crucial for coexistence. But it is not only necessary to locate the areas where the bear could appear, but also to define the variables that determine the occurrence of conflicts. As shown in chapter four, the number of damages varies according to the time of year and the size of the population in the Cantabrian Mountains. Differences in the management of the territory by the different administrations, together with the availability of human resources and the different methods of raising and protecting livestock and other activities, also have an important influence on the number of damages that occur in each place. At the same time, the fact that these animals have always shared the same territory means that the human populations of the Cantabrian Mountains have maintained the use of preventive measures. On the other hand, in areas where bears disappeared, but where they have recently been reintroduced, this type of practice has been abandoned. Furthermore, a reduced availability of natural food resources at specific times can promote the consumption of anthropogenic food and the appearance of damage to livestock, beehives or crops. The climatic conditions in each territory affect each type of damage differently, which may be due to the specific characteristics of the area, differences in management, or even the bear's ability to change its food source depending on its availability. In addition, climate change has the potential to encourage these conflicts. Therefore, local studies on the occurrence of damage and its relationship to the availability of food resources, as well as the development and implementation of protection measures, are crucial to prevent and reduce conflict and thus promote coexistence with this and other large carnivores.

In conclusion, the results obtained by the work carried out in this thesis can be an important predictive tool with implications for conservation, suggesting proactive and multi-level management strategies that address both the human factor and landscape conservation, thus minimizing the negative effects of bear coexistence with humans. These strategies are of crucial importance especially when dealing with a small, isolated and endangered brown bear population such as that in the Cantabrian Mountains. These results also provide new information about potential threats to this population, as well as new perspectives about their coexistence with people in such a humanized environment. Human populations that share territory with them should in turn try to minimize the disturbances they produce as much as possible, to avoid events that compromise the viability of the species. The results of this thesis provide a vision of the capacity to coexist between humans and large carnivores, raising the possibility of adequate and successful coexistence in the future. It also highlights the need to combine research with management, and to spread the knowledge acquired by these means to the general public, improving the perception of these species and involving all parties in their conservation.

Conclusions

1. The study of large carnivores' ecology in humanized environments allows us to acknowledge the relationship between their populations and human activities and to better understand the path towards coexistence in order to develop optimal management and conservation measures.
2. Brown bears in the Cantabrian Mountains prefer high altitude and rugged forested areas with low human impact. This population still has favourable habitat for its expansion, especially in the eastern zone where the smallest subpopulation is found.
3. Increased connectivity between the two subpopulations is crucial to encourage their expansion and ensure the viability of the eastern subpopulation, as well as to increase the

protection of these areas and create information and damage prevention campaigns in the potential expansion areas.

4. Infanticide is a threat to the Cantabrian brown bear, as habitat fragmentation and human encroachment on the territories traps females with first year cubs in the same areas used by adult individuals for reproduction.
5. Protecting and reducing human activity in areas where females with first year cubs are found in spring can help reduce the likelihood of infanticide, but a better monitoring of these bears and their activity patterns is needed.
6. Bears in the Cantabrian Mountains have adapted their behavior to living with humans, showing the same patterns of alert behavior regardless of proximity to human infrastructures. Future studies should focus on their responses to different human activities (hunting, traffic, tourism), taking into account physiological stress levels and time patterns of avoidance of these disturbances.
7. Bear damage occurrence patterns are very complex. The number of damages caused by bears in the Cantabrian Mountains and the Pyrenees varies according to the type of damage, the season, the year, the province and changes in productivity and climatic conditions. But locally, other economic and social factors, such as the availability of livestock or beehives, breeding methods and preventive measures, can influence their dynamics.
8. Reducing the occurrence of conflicts is necessary to maintain peaceful coexistence with human populations that share territory with large carnivores. To this end, local studies on their occurrence must be strengthened, including better monitoring of food availability, in order to be able to anticipate where and when damage may occur and to apply preventive measures in an optimal way.
9. Coexistence between large carnivores and humans in human-modified landscapes is possible, provided that carnivores are not highly persecuted and direct interactions are avoided. In addition, collaboration between researchers, management agencies and the general public is necessary for a proper management and conservation of these species.

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