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

Alejandra Zarzo-Arias[1]*, María del Mar Delgado[1], Santiago Palazón[2], Iván Afonso Jordana[3], Giulia Bombieri[1,4], Enrique González-Bernardo[1], Andrés Ordiz[5], Chiara Bettega[1], Ricardo García-González[6] and Vincenzo Penteriani[1]*

[1]Research Unit of Biodiversity (UMIB, CSIC-UO-PA), Campus Mieres, 33600 Mieres, Spain.

[2]Fauna and Flora Service. Territory and Sustainability Department. Generalitat de Catalunya. Provença 204, 08036 Barcelona, Spain.

[3]General Council of Aran. Plaça d'Aran 1-2, 25530 Vielha

[4]Museo delle Scienze, Sezione Zoologia dei Vertebrati, Corso del Lavoro e della Scienza 3, I-38123, Trento, Italy

[5]Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Postbox 5003, NO-1432 Ås, Norway.

[6]Pyrenean Institute of Ecology (IPE), CSIC, Avda. Nuestra Señora de la Victoria 16, 22700 Jaca, Spain.

E-mail addresses: alejandra.zarzo@gmail.com (Zarzo-Arias, A.), delgado.mmar@gmail.com (Delgado, M.M.), santiago.palazon@gencat.cat (Palazón, S.), i.afonso@aran.org (Afonso Jordana, I.), giulipan91@gmail.com (Bombieri, G.), egonzalez@ebd.csic.es (González-Bernardo, E.), andres.ordiz@gmail.com (Ordiz, A.), chiara.bettega@gmail.com (Bettega, C.), rgarciag@ipe.csic.es (García González, R.) and v.penteriani@csic.es (Penteriani, V.).

*Corresponding authors

Phone number: +34628633938

Abstract

Coexistence of humans and large carnivores is a major challenge for conservation and management, especially in human-modified landscapes. 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. The increase in the number of damages varied in parallel with the increase in bear numbers, which is probably a primary cause determining the occurrence on damages. Damages also 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 conflicts, which is yet another call to apply preventive measures in carnivore damage to human property in seasons and years when natural 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.

Key words: brown bear, conflicts, human-modified landscapes, large carnivores, productivity, *Ursus arctos*.

1. INTRODUCTION

Coexistence with people is a major challenge for global large carnivore conservation (Treves and Karanth, 2003), which is key to preserving the ecological balance of ecosystems (Ordiz et al., 2013). 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), which, together with habitat loss as well as hunting, have led to a great 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 conservation efforts (e.g., protective legislation, reintroductions), allowing the partial recolonization of former ranges (Chapron et al., 2014). Nevertheless, in areas 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), as it happens in some populations (Bautista et al., 2017). But many factors can affect the occurrence and the frequency of these damages (Majić Skrbinšek and Krofel, 2014). Increasing damage could be due to sources of conflict (i.e., availability of livestock, hives or crops) (Molinari et al., 2016) 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 (e.g., Slovenia, Italy, Croatia, Kenya, Buhtan, and USA) 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 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 abundant large carnivores in Europe (approx 17,000 individuals), 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 recovering and recently interconnected after a long isolation (Gonzalez et al., 2016; Lamamy et al., 2019; Zarzo-Arias et al., 2019). Within their range, 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 several potential drivers that might influence 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 maximum 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, and Palencia for the Cantabrian population, and Lleida for Pyrenees), 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.

2. METHODS

2.1. Study area

Our study area comprises two mountainous systems in the north of Spain, the Cantabrian Mountains and the Pyrenees (Fig. 1). Description of the environmental characteristics of each bear nucleus and their range are summarized in Table 1.

In the Cantabrian Mountains elevation ranges from sea level 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 western Cantabrian subpopulation, estimated to hold around 280 bears (2017), inhabits an area of more than 7.000 km^2 with an average human population density of 10.9 inhabitants/km^2 and a road density of more than 0.5 km/km^2, while the eastern subpopulation, with around 50 bears (2017), occupies around 4.000 km^2 with c.a. 4.9 inhabitants/km^2 and about 0.3 km/km^2 of road density (Lamamy et al., 2019; htttp://www.fundacionosopardo.org/).Livestock farming is the most common human activity . Cattle is more common in the north slope of the Cantabrian Mountains (Asturias province), and together with horses they usually range free in the mountains. Sheep and goats are more common in the south (http://www.sadei.es/; http://www.atlas.itacyl.es/) and they are guarded with dogs and fences, sometimes electrical. Apiaries are also a widespread traditional activity in the area, usually surrounded by stonewalls (traditional constructions, especially found in the western bear nucleus) and/or electric fences (Naves et al., 2018). Other common activities in these areas are mining, tourism 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. The total bear population (43 individuals, 2017) occupies around 2000 km^2 of the Spanish Pyrenees, where the average human population density is ca. 5 inhabitants/km^2 and road density is around 0.2 km/km^2). The main human activities are forestry with associated road construction and maintenance and livestock herding. Sheep and goats are the most common species raised, generally protected by shepherds, guarding dogs, electric fences and night cabins. Cows and horses are free ranging, as in the Cantabrian Mountains. During summer and autumn, recreational tourism (e.g., hiking, hunting, and fishing) and mushroom picking stand out (Martin et al., 2012).

2.2. 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. All damages produced by bears in Spain are financially compensated by the administration after damage claims are reported by the owners of the property. Experienced rangers in each area check and confirm if the damaged was caused by a bear, and then the administration pays for the losses. 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 bear population; and in Lleida from 1998 to 2017, for the Pyrenean population.

The data included: (1) damage location (UTM); (2) date of damage occurrence; and (3) type of damage, i.e. beehives, crops (more than 95% trees as apple or hazel) or livestock (i.e. cow, sheep, goat 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 of the year for each Cantabrian subpopulation as a proxy of population size, since they are easier to locate and distinguish right after they exit the den after hibernation, as they stay in the same area for several weeks (Ordiz et al., 2007; Penteriani et al., 2018). For the Pyrenean population the total number of bears was available, because it is estimated by the different administrations based on direct observations, camera traps and genetic analyses of bear hair and scats. Approximately half of the population occurs within the French territory, while the other half primarily ranges in the Spanish Pyrenees (Gastineau et al., 2019). It is worth noting that, in all bear populations under study, a positive trend in bear number has been documented in the past years (Palazón, 2017; Pérez et al., 2014).

2.3. Productivity and climate indicators

To assess availability of natural food resources for bears, we used several annual indicators of productivity, which are summarized in Online Appendix Table A.1. First, we collected annual productivity data of cultivated tree crops (apple-tree (*Malus domestica*), cherry (*Prunus avium*) and hazel (*Corylus avellana*)) either rainfed (kg/ha) or scattered (kg/tree) for each province available from the Ministry of Agriculture, Fisheries and Food (http://www.mapama.org/) as a proxy of natural productivity. We used variables which included complete information for more than 3 years in each bear nuclei.

We also included productivity for the most common natural soft and hard mast items appearing in the diet of both Cantabrian and Pyrenean brown bears: acorn (*Quercus spp.*), chestnut (*Castanea sativa*), blueberry (*Vaccinium myrtillus*), cherry and beechnut (*Fagus sylvatica*), whose availability can vary from year to year depending on climate conditions. In the Cantabrian Mountains acorns, beech nuts and chestnuts are predominant, while in the Pyrenees acorns and hazel are easier to find. But, as bears can shift from one item to another depending on their availability, the diet of both populations it's very similar (Elosegi, 2010; Naves et al., 2006). For each of these natural food 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 annual mean of five variables: temperature, precipitation, North Atlantic Oscillation index (NAO), Normalized Difference Vegetation Index (NDVI), and sun radiation. We also included temperature, precipitation and NAO values for the previous year compared to the annual mean values of the variables in each year. So, for 2014 for example, we included annual mean temperature of that year, and for the previous one (2013), because plants might react with a certain delay to climate (Koenig and Knops, 2000); 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, 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.

2.4. Statistical analysis

First, we summarized and described the number and type of damages and performed a Man-Kendall trend test for the number of damages in each bear nucleus. To explore the spatio-temporal patterns of brown bear damages, we built two models: the first one included the registered damages 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 (to test if there was a seasonal pattern that was maintained over the years), bear nuclei, type of damage and its interaction with season and bear nuclei were included as potential explanatory variables. The number of brown bears was strongly correlated with the variable year in each bear nucleus (Pearson Correlation coefficient = 0.968 west Cantabrian, 0.924 east Cantabrian and 0.907 Pyrenean, and Variance Inflated Factor (VIF) = 15.67 west Cantabrian, 6.84 east Cantabrian and 5.63 Pyrenean), so we removed number of bears from the models, as the main objective is to test interannual variation in the number of damages. As a temporal series analysis, we explored the possibility of using generalized additive models (GAMs), but due to the almost linear pattern of the variable year in both 2008-2017 and 1997-2017 (edf = 2.59 and edf = 1, respectively), we chose generalized linear models (GLMs). Our response variable was discrete, thus we ran the GLMs with a negative binomial error distribution. We compared all possible candidate models and selected the most parsimonious one using the Akaike method (Burnham and Anderson, 2002).

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 nucleus. Each PCA creates several principal components (PC1-PC4) which are a set of values of linearly uncorrelated variables, with different importance in explaining the data. 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: the first one included 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*). The second set included only 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), MuMIn (Barton, 2018), and mgcv (Wood, 2015).

3. RESULTS

The type of damage varied in the different bear nuclei (Online Appendix Table A.2) 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 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 (Online Appendix Table A.2), and no damages to crops were reported.

The number of damage events (all types together) varied at the different spatio-temporal scales considered. Damages varied (A) across seasons (Table 2, Table 3), with the largest number of claims occurring during hyperphagia and the lowest during hibernation (Fig. 2), and (B) among years, with a significant positive trend in the western Cantabrian nuclei ($S = 154$, $\tau = 0.733$, $p<0.001$) and the Pyrenees ($S = 115$, $\tau = 0.507$, $p<0.005$), but not for the eastern Cantabrian subpopulation ($S = 25$, $\tau = 0.556$, $p<0.05$), which included a shorter study period (Fig. 3). We also found that the number of damages varied across study areas (Table 2, Table 3), with the lowest number of damages occurring in the Pyrenees, and then in the eastern Cantabrian subpopulation (Fig. 3). The number of damages of each type also depended on the bear population, damages to crops and livestock being lowest in the eastern Cantabrian subpopulation, while damages to livestock were significantly more numerous in the Pyrenees (Table 2, Table 3). The interaction between season and year appeared to be uninformative, suggesting that the seasonal patter showed by damages does not depend on the year (Table 2, Table 3).

The variation in the number of different types of damages across populations was related with some local factors (Online Appendix Table A.3). 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 conflicts with livestock were also positively related to hazel productivity.

4. 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 attraction to 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 bears is strongly correlated with year, which makes it a probable primary cause determining the occurrence on damages. 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 43 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 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 damage in each subpopulation seemed to be related to the availability of different resources (Online Appendix Table A.3). 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 (http://www.atlas.itacyl.es/). In contrast, conflicts with 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 damage (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 (Online Appendix Fig. A.1) of released bears coming from Slovenia (11 reintroduced so far), 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 damage livestock (Bereczky et al., 2011; Majić Skrbinšek and Krofel, 2014; Swan et al., 2017). Although before this bear population decreased damages to livestock were also common (Camarra, 1986).

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 bear conflict. 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 (Online Appendix Fig. A.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, higher beehive activity 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.

5. CONCLUSIONS

The increase in recent years in the number of damages produced by brown bears in all bear nuclei located in Spain (western Cantabrian, eastern Cantabrian and Pyrenean) varied differently among bear populations and also among seasons and years. These variations mainly depended on the local availability of natural food items, weather conditions and probably on the different availability and husbandry and protective methods of apiaries and livestock. However, the increase in the number of bears is strongly correlated with year, which makes it a probable primary cause determining the occurrence on damages. Fluctuating availability of food items may explain the frequency of conflicts, which is yet another call to apply and improve preventive measures of carnivore damage to human property. Understanding and preventing damage is indeed essential to mitigate conflicts where humans and large carnivores share the same landscape, especially now that several large carnivore populations are recovering (e.g., Chapron et al., 2014).

ACKNOWLEDGEMENTS

We thank the Administrations of the Gobierno del Principado de Asturias, the Junta de Castilla y León and the Conselh Generau d'Aran, Generalitat de Catalunya for providing the brown bear databases. In particular, we would like to thank Teresa Sánchez Corominas, Víctor Vázquez, Pedro García-Rovés and Paloma Peón Torre of the Principado de Asturias, David Cubero, Mercedes García Dominguez and María Ángeles Osorio Polo of the Junta de Castilla y León, and Antoni Batet, Jordi Guillén, Xavier Garreta and Nicolàs Espinós of Generalitat de Catalunya for their continuous assistance and work during this study. During this research, V.P., A.O., R.G.G. and A.Z.A. were financially supported by the Excellence Project CGL2017-82782-P financed by the Spanish Ministry of Science, Innovation and Universities, the Agencia Estatal de Investigación (AEI) and the Fondo Europeo de Desarrollo Regional (FEDER, EU). V.P. was also funded by a GRUPIN research grant from the Regional Government of Asturias (Ref.: IDI/2018/000151). G.B. was financially supported by a collaboration contract with the MUSE – Museo delle Scienze of Trento (Italy). M.M.D. was financially supported by the Spanish Ramon y Cajal grant RYC-2014-16263.

REFERENCES

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

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.

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.

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

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

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

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

Camarra, J.J., 1986. Changes in Brown Bear Predation on Livestock in the Western French Pyrenees from 1968 to 1979. Bears Their Biol. Manag. 183–186.

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

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

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

Enserink, M., Vogel, G., 2006. The carnivore comeback. Science (80-.). 314, 746–749. https://doi.org/10.1126/science.314.5800.746

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

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, e0151541. https://doi.org/10.1371/journal.pone.0151541

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, 403–408.

Gastineau, A., Robert, A., Sarrazin, F., Mihoub, J.B., Quenette, P.Y., 2019. Spatiotemporal depredation hotspots of brown bears, Ursus arctos, on livestock in the Pyrenees, France. Biol. Conserv. 238, 108210. https://doi.org/10.1016/j.biocon.2019.108210

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.

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.

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

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

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

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

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

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., 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

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

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

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., 2016. Comparison of the Occurrence of Human-Bear Conflicts Between the Northern Dinaric Mountains and the South-Eastern Alps. Carniv. Damage Prev. News 9–17.

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

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

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.

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., 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.

Ordiz, A., Bischof, R., Swenson, J.E., 2013. 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

Palazón, S., 2017. The Importance of Reintroducing Large Carnivores: The Brown Bear in the Pyrenees., in: Catalan J., Ninot J.M., A.M. (Ed.), High Mountain Conservation in a Changing World. Springer International Publishing, pp. 231–249.

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., 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., 2018. 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., 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

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.

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

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., 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 (80-.). 343, 1241484.

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

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

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

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

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., 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

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

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

Wood, S., 2015. Package "mgcv." R Packag. version 1, 29.

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

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

FIGURE AND TABLE LEGENDS

Table 1. Summary of the three study areas' environmental characteristics.

Bear nucleus	Bear population	Area (km2)	Elevation range (m)	Human population density (hab/km2)	Road density	Main anthropogenic resources	Protection measures
Western Cantabrian	280	7000	0 - 2648	10.9	0.5	Apiaries	Stonewalls and electric fences
						Cattle (north)	None
						Sheep (south)	Fences and dogs
Eastern Cantabrian	50	4000	0 - 2648	4.9	0.3	Apiaries	Electric fences
						Sheep	Fences and dogs
Pyrenees	43	2000	500 - 3404	5	0.2	Sheep	Fences, dogs, shepherds, night cabins
						Apiaries	Electric fences

Table 2. Comparison of the firs 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. 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 and its evaluation graphs are summarized below (B).

Bear nucleus	Bear population	Area (km2)	Elevation range (m)	Human population density (hab/km2)	Road density	Main anthropogenic resources	Protection measures
Western Cantabrian	280	7000	0 - 2648	10.9	0.5	Apiaries	Stonewalls and electric fences
						Cattle (north)	None
						Sheep (south)	Fences and dogs
Eastern Cantabrian	50	4000	0 - 2648	4.9	0.3	Apiaries	Electric fences
						Sheep	Fences and dogs
Pyrenees	43	2000	500 - 3404	5	0.2	Sheep	Fences, dogs, shepherds, night cabins
						Apiaries	Electric fences

Table 2. Comparison of the firs 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. 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 and its evaluation graphs are summarized below (B).

(A)

Intercept	Type of damage	Season	Bear nucleus	Year	Type of damage *Season	Type of damage *Bear nucleus	Season*Year	df	AICc	ΔAICc	R^2 (adj.)	weight
-172.7	**+**	**+**	**+**	**0.08713**	**+**	**+**		**16**	**1106**	**0**	**0.8536**	**0.818**
-68.1	+	+	+	0.03515	+	+	+	18	1109	3.01	0.8554	0.182
2.584	+	+	+		+	+		15	1129.5	23.5	0.8275	0
-166.1	+	+	+	0.08378		+		12	1147.2	41.16	0.7983	0
-80.85	+	+	+	0.04144		+	+	14	1150.8	44.75	0.7998	0
2.5	+	+	+			+		11	1162.7	56.69	0.7743	0
-199.8	+	+	+	0.1006	+			13	1180.6	74.62	0.7547	0
-65.55	+	+	+	0.03394	+		+	15	1182.9	76.86	0.7587	0
2.696	+	+	+		+			12	1200.6	94.52	0.7178	0
-193.5	+	+	+	0.09746				9	1202.1	96.08	0.7023	0

(B)

EXPLANATORY VARIABLE	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	-172.72916	33.67506	-5.129	2.91E-07***
Mating	1.78389	0.18839	9.469	< 2e-16***
Hyperphagia	2.26934	0.18731	12.115	< 2e-16***
Crops	-1.97955	0.43899	-4.509	6.50E-06***
Livestock	-1.44176	0.2815	-5.122	3.03E-07***

Eastern Cantabrian subpopulation	-1.32099	0.14785	-8.934	< 2e-16***
Pyrenean population	-3.11411	0.21473	-14.503	< 2e-16***
Year	0.08713	0.01673	5.208	1.91E-07***
Crops*Mating	-0.41193	0.49724	-0.828	0.407429
Crops*Hyperphagia	1.83544	0.47946	3.828	0.000129***
Livestock*Mating	-0.01777	0.33716	-0.053	0.957957
Livestock*Hyperphagia	0.14193	0.33424	0.425	0.671112
Crops* Eastern Cantabrian subpopulation	-3.36458	0.56223	-5.984	2.17E-09***
Livestock* Eastern Cantabrian subpopulation	-1.71904	0.39104	-4.396	1.10E-05***
Livestock* Pyrenean population	1.51568	0.28761	5.27	1.37E-07***

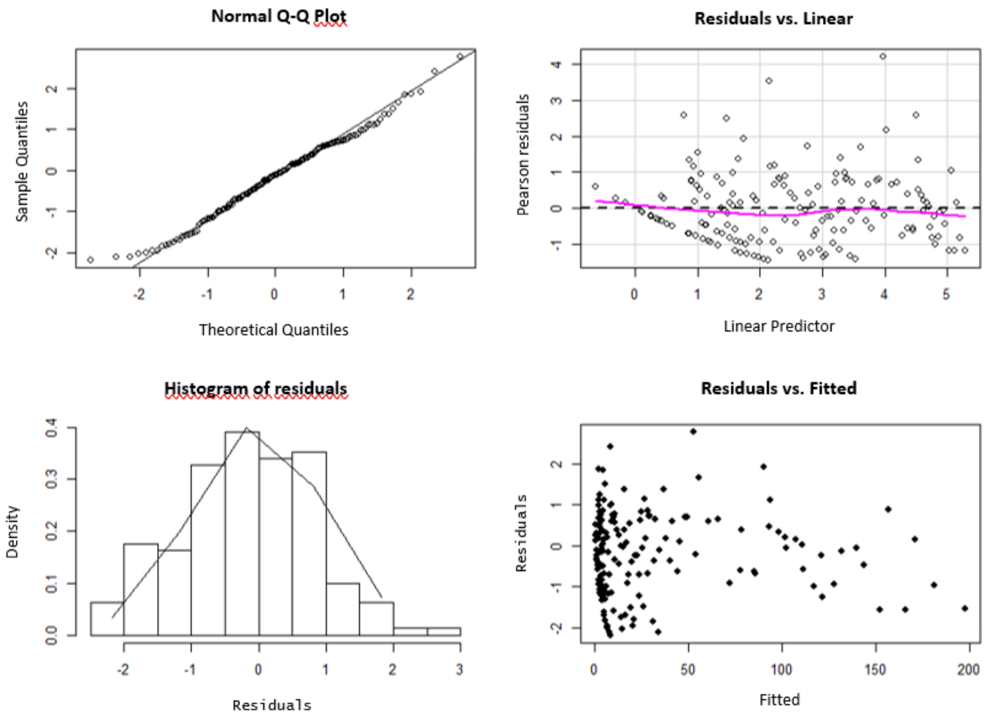


Table 3. Comparison of the first ten generalised linear models explaining the number of damages produced by bears in the western Cantabrian subpopulation and the Pyrenees (1997-2017) (A). Models are ranked from the lowest (best model) to the highest AIC value. Positive cells show when a categorical variable 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 and its evaluation graphs are summarized below (B).

(A)

Intercept	Type of damage	Season	Bear nucleus	Year	Type of damage *Season	Type of damage *Bear nucleus	Season*Year	df	AICc	ΔAICc	R^2 (adj.)	weight
-115.2	**+**	**+**	**+**	**0.05844**	**+**	**+**		**13**	**1553.5**	**0**	**0.7874**	**0.874**
-95.33	+	+	+	0.04856	+	+	+	15	1557.4	3.88	0.7881	0.126
-115.4	+	+	+	0.05855		+		9	1598.6	45.05	0.73	0
2.251	+	+	+		+	+		12	1598.9	45.36	0.7375	0
-102	+	+	+	0.05187	+			12	1601.8	48.31	0.734	0
-84.08	+	+	+	0.04294		+	+	11	1602.4	48.82	0.7308	0
-88.62	+	+	+	0.04522	+		+	14	1604.9	51.34	0.7358	0
2.251	+	+	+		+			11	1631.7	78.17	0.6934	0
2.177	+	+	+			+		8	1635.8	82.22	0.6787	0
-104.1	+	+	+	0.05285				8	1643	89.43	0.6682	0

(B)

EXPLANATORY VARIABLE	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	-1.15E+02	1.53E+01	-7.514	5.72E-14***
Mating	1.82E+00	1.99E-01	9.17	< 2e-16***
Hyperphagia	2.09E+00	1.98E-01	10.534	< 2e-16***
Crops	-1.72E+00	3.98E-01	-4.327	1.51E-05***
Livestock	-1.22E+00	2.53E-01	-4.811	1.50E-06***

Pyrenean population	-2.78E+00	1.92E-01	-14.486	< 2e-16***
Year	5.84E-02	7.63E-03	7.658	1.88E-14***
Crops*Mating	-6.50E-01	4.58E-01	-1.42	0.155725
Crops*Hyperphagia	1.52E+00	4.35E-01	3.492	0.000479***
Livestock*Mating	-4.23E-01	3.05E-01	-1.388	0.165016
Livestock*Hyperphagia	2.89E-01	3.02E-01	0.959	0.337436
Livestock* Pyrenean population	1.83E+00	2.39E-01	7.647	2.05E-14***

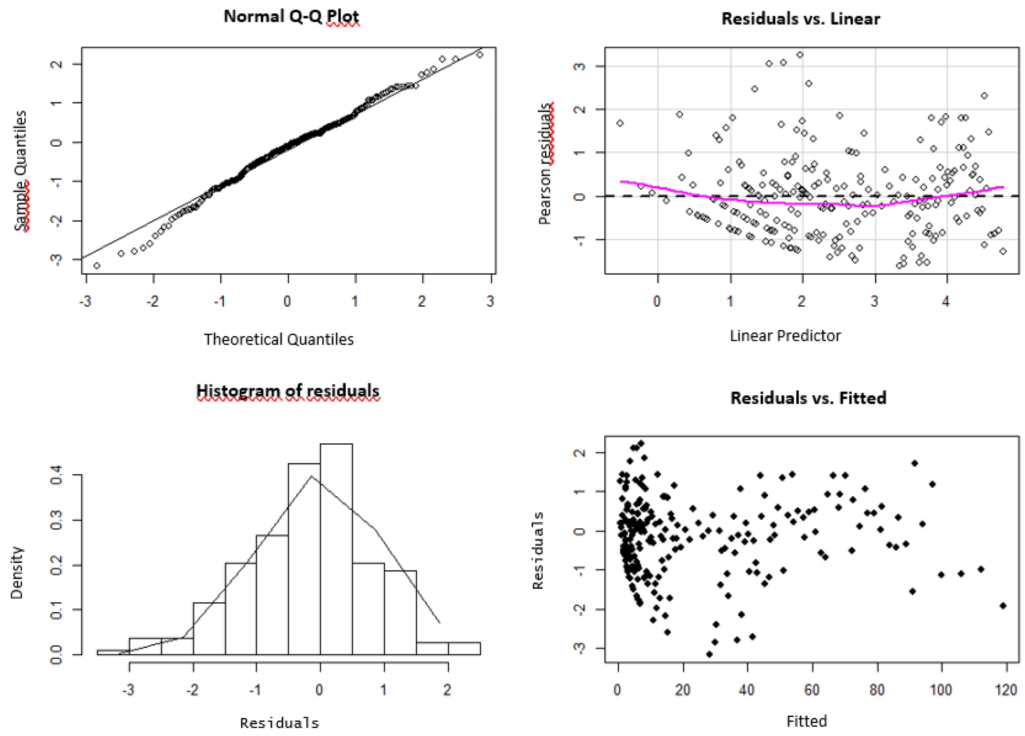
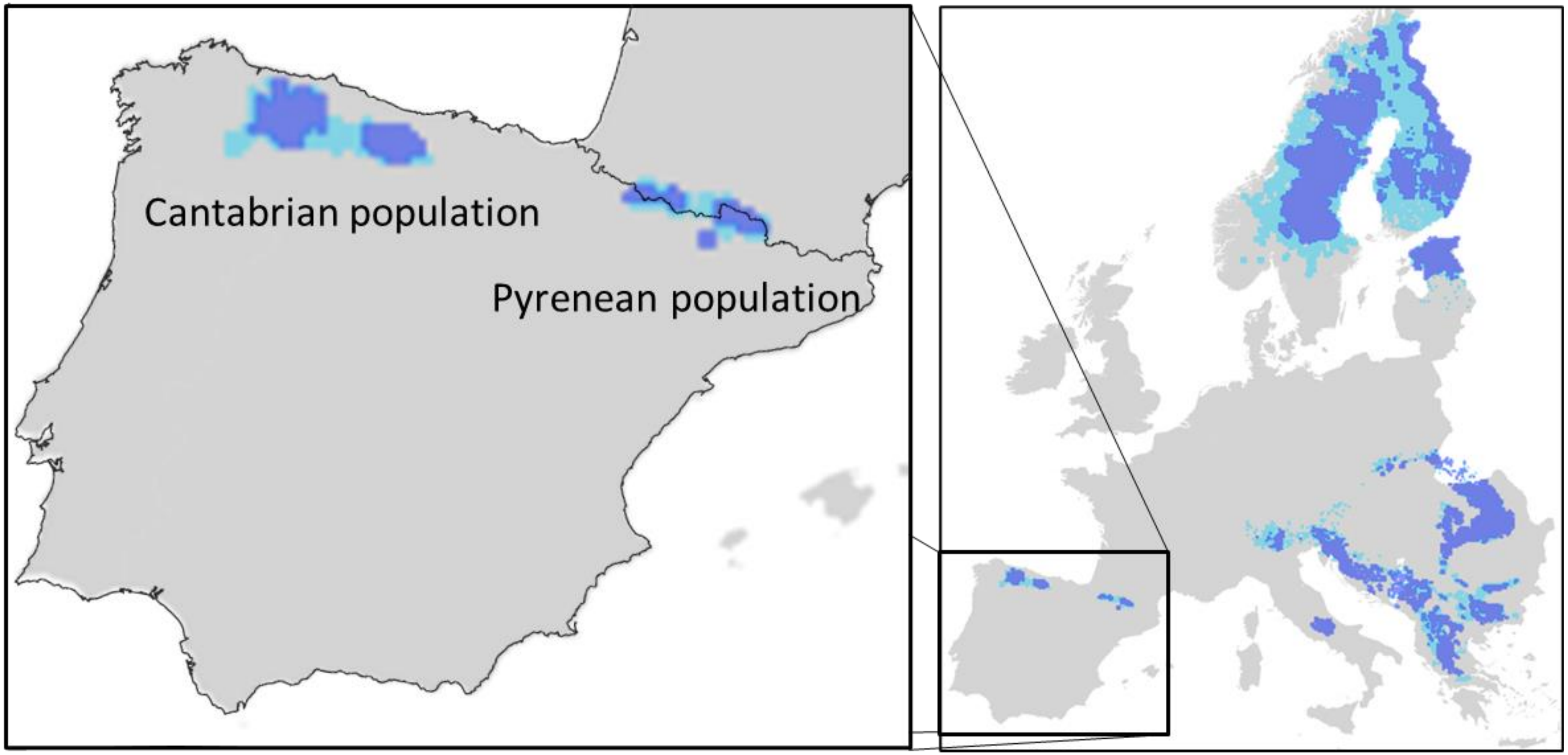


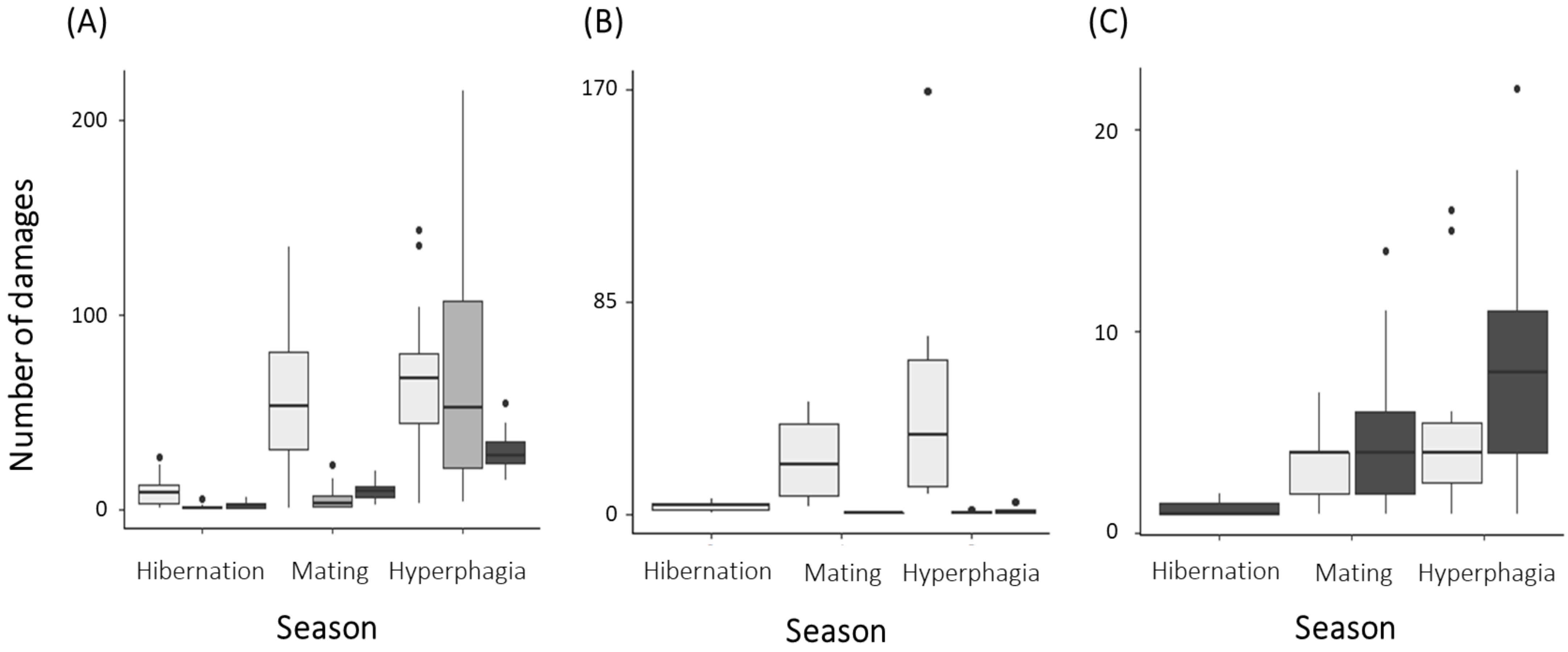
Figure 1. Distribution of the brown bear in Europe and focus populations of this study: the Cantabrian (western and eastern) and the Pyrenean (extracted from https://www.lcie.org/Large-carnivores/Brown-bear).

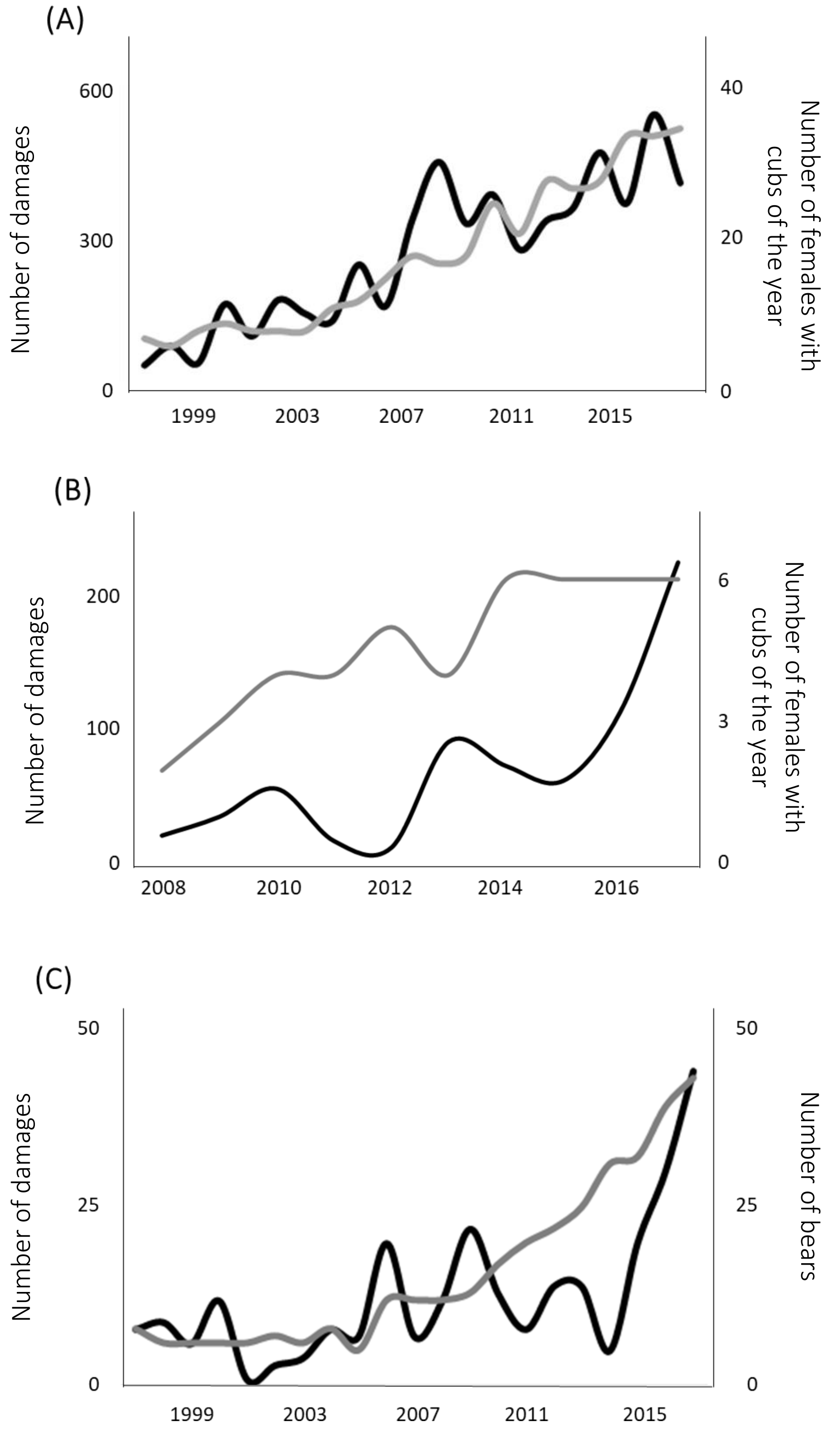
Figure 2. Amount of damage by type produced in each season (hibernation, mating and hyperphagia) during the periods: (A) 1997-2017 in the western Cantabrian brown bear subpopulation; (B) 2008-2017 in the eastern Cantabrian subpopulation; and (C) 1997-2017 in the Pyrenees. Beehives = light grey, crop = grey and livestock = dark grey. Outliers are represented with black dots, the median as a black line and the errors as upper and lower lines for each box. Note that the scale of the Y axis is different for each study area.

Figure 3. Trend 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 of the year for A and B and the total number of bears in C.

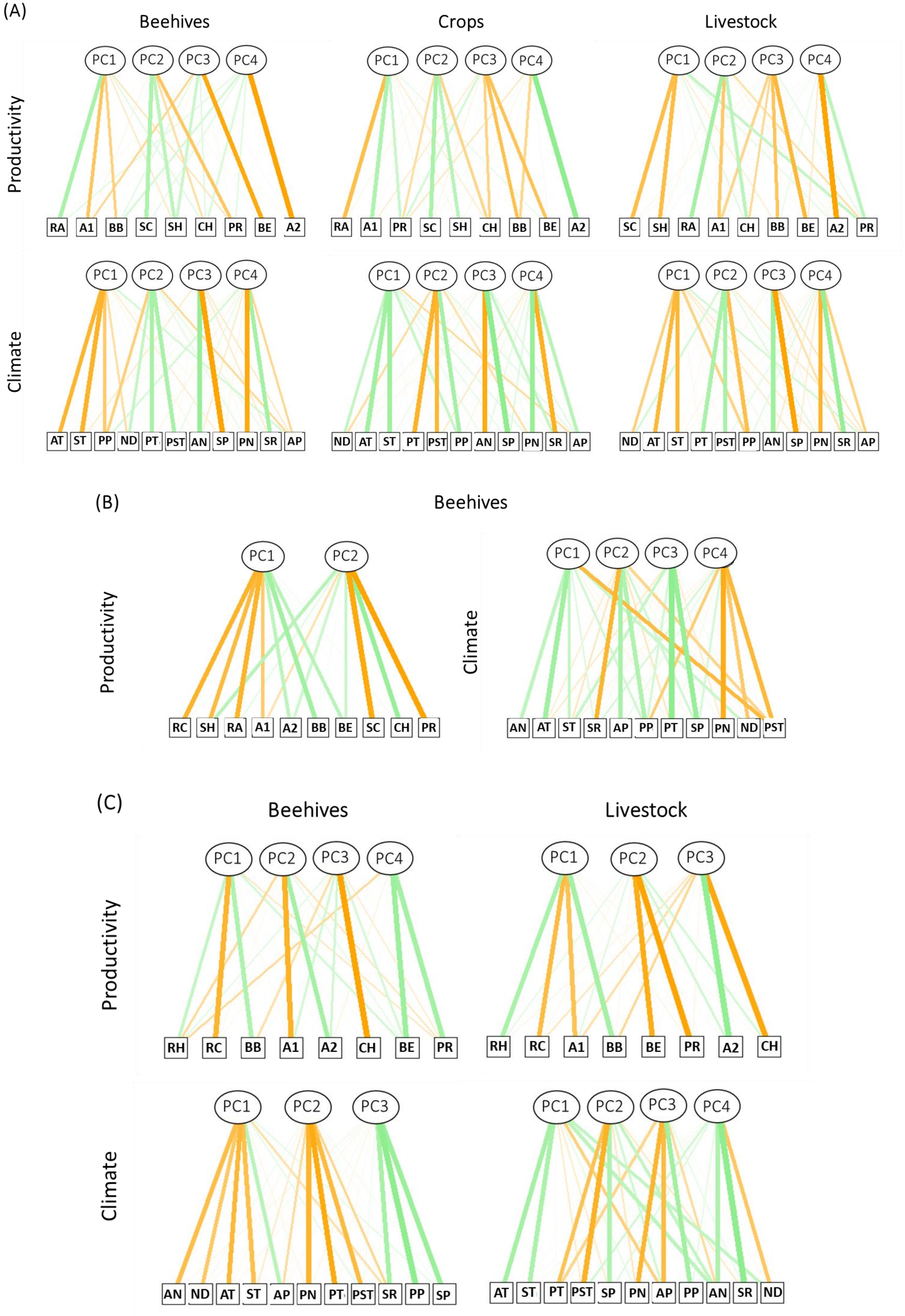
Figure 4. Correlations between varimax rotated variables and the principal components selected (with an eigenvalue > 1) in: the (A) western and (B) eastern Cantabrian subpopulations, and (C) the Pyrenean population, explained by productivity (upper panels) and climatic (lower panels) indicators. Green lines correspond to positive correlations, while orange lines denote negative correlations. The thickest lines represent high loading values. Productivity indicators: (SC) scattered cherry, (RC) rainfed cherry, (SH) scattered hazel, (RH) rainfed hazel, (RA) rainfed apple-tree, (A1) September precipitation (acorn), (A2) spring precipitation (acorn), (CH) mean temperature August (chestnut), (BB) mean winter temperature (blueberry), (BE) mean temperature previous June-July (beech), (PR) minimum temperature Nov-Feb (prunus); climatic indicators: (AN) annual NAO, (PN) previous year NAO, (SR) sun radiation, (ND) NDVI, (AT) mean annual temperature, (ST) mean temperature April-August, (TP) mean temperature previous year, (PST) mean temperature April-August previous year, (AP) annual precipitation, (PP) precipitation previous year and (SP) summer precipitation.


Cantabrian population
Pyrenean population


(A)
(B)
(C)
Number of damages
200
100
0
170
85
0
20
10
0
Hibernation
Mating
Hyperphagia
Season



(A)
Number of damages
Number of females with cubs of the year
600
300
0
40
20
0
1999
2003
2007
2011
2015
(B)
Number of damages
Number of females with cubs of the year
200
100
0
6
3
0
2008
2010
2012
2014
2016
(C)
Number of damages
Number of bears
50
25
0
50
25
0
1999
2003
2007
2011
2015


(A)
Beehives
Crops
Livestock
Productivity
Climate
PC1 PC2 PC3 PC4
RA A1 BB SC SH CH PR BE A2
RA A1 PR SC SH CH BB BE A2
SC SH RA A1 CH BB BE A2 PR
AT ST PP ND PT PST AN SP PN SR AP
ND AT ST PT PST PP AN SP PN SR AP
ND AT ST PT PST PP AN SP PN SR AP
(B)
Beehives
Productivity
PC1 PC2
RC SH RA A1 A2 BB BE SC CH PR
Climate
PC1 PC2 PC3 PC4
AN AT ST SR AP PP PT SP PN ND PST
(C)
Beehives
Livestock
Productivity
PC1 PC2 PC3 PC4
RH RC BB A1 A2 CH BE PR
PC1 PC2 PC3
RH RC A1 BB BE PR A2 CH
Climate
PC1 PC2 PC3
AN ND AT ST AP PN PT PST SR PP SP
PC1 PC2 PC3 PC4
AT ST PT PST SP PN AP PP AN SR ND