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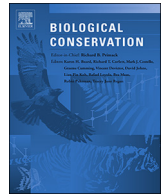
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Spatiotemporal depredation hotspots of brown bears, *Ursus arctos*, on livestock in the Pyrenees, France

Adrienne Gastineau^{a,b,*}, Alexandre Robert^b, François Sarrazin^b, Jean-Baptiste Mihoub^b, Pierre-Yves Quenette^a

^a Equipe Ours, Unité Prédateur-Animaux Déprédateurs, Office National de la Chasse et de la Faune Sauvage, impasse de la Chapelle, 31800 Saint-Gaudens, France

^b Centre d'Ecologie et des Sciences de la Conservation (CESCO), Muséum national d'Histoire naturelle, Centre National de la Recherche Scientifique, Sorbonne Université, CP 135, 43 rue Buffon, 75005 Paris, France

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ABSTRACT

One of the main factors limiting the acceptance of large carnivores is livestock depredation. Reducing damages on livestock requires understanding how depredation varies in space and time. The conservation of the brown bear (*Ursus arctos*) population in the Pyrenees offers a relevant study case to illustrate this issue, with a minimum population size of 41 individuals recorded in 2016 and an average of 103.3 ± 18.9 attacks per year on domestic animals between 2010 and 2016 during the summer pasture period. We analysed the spatial aggregation of depredation events by using the local Getis-Ord analysis of spatial dependence at the management scale (pastoral units) and at a finest scale (250×250 m grain). Our results uncover the absence of coldspots of brown bear depredation in the French Pyrenees and the presence of significant hotspots. Depredation hotspots are consistent in time, meaning that a hotspot in one year is likely to exist in the following year(s). The fine scale analysis allowed identifying both inter- and intra-pasture hotspots and we propose a simple method to rescale these fine scale results. We linked this spatial pattern of hotspots (at 250 m resolution) to environmental factors. Hotspot presence is characterized by being close to forest and buildings with a high proportion of grassland and on steep slopes. Moreover, a nonlinear relationship with brown bear activity describes the presence of hotspots. The assessment of depredation hotspots and their link with environmental factors offers some practical guidance about where to focus efforts in order to decrease this human-large carnivore conflict.

1. Introduction

Due to increasing human encroachment into natural habitats, interactions with wildlife are intensifying worldwide. Negative interactions, e.g. conflicts, arise especially when large animals return to areas they have left or from which they have been previously extirpated (Chapron et al., 2014; Redpath et al., 2013; Treves and Karanth, 2003; Woodroffe et al., 2005). The causes of conflicts are linked to direct and indirect effects of the presence of these animals on human activities. These effects include the destruction of agricultural produce (crops and livestock, Nyhus, 2016; Woodroffe et al., 2005) and the risk of attacks on humans (Støen et al., 2018), requiring to modify practices in many human activities (leisure, forestry activities, livestock breeding) to reduce risk exposure (Herrero et al., 2005; Swenson et al., 1999). Altogether, these impacts may diminish the local acceptance of the species and eventually increase persecution. In turn, these attitudes reduce the

efficiency of conflict management and can have deleterious effects on the viability of wildlife populations through direct removal of individuals (Treves et al., 2016, 2010), decrease of individual fitness following disturbances (Escobar et al., 2015; Ordiz et al., 2008), road kills (Chruszcz et al., 2003), increased competition between individuals (Gibeau et al., 2002) and fragmentation of distribution range (Fernández-Gil et al., 2016; Proctor et al., 2005).

For large carnivores, depredation on livestock is one of the major sources of conflict with humans (Carter and Linnell, 2016; Chapron et al., 2014) and remains one of the most critical factors affecting their acceptance and conservation worldwide (Treves and Bruskotter, 2014; Woodroffe et al., 2005). This is especially true in Europe, where human density is particularly high and wild natural areas are scarce and fragmented. The overlap between human activities and carnivore populations is thus compulsory (Chapron et al., 2014; Fernández-Gil et al., 2016; Linnell et al., 2001). Many management responses aiming at

* Corresponding author at: CESCO UMR 7204, CP 135, 43 rue Buffon, 75005 Paris, France.

E-mail addresses: adrienne.gastineau@mnhn.fr (A. Gastineau), alexandre.robert@mnhn.fr (A. Robert), francois.sarrazin@mnhn.fr (F. Sarrazin), jean-baptiste.mihoub@mnhn.fr (J.-B. Mihoub), pierre-yves.quenette@oncs.gouv.fr (P.-Y. Quenette).

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reducing or preventing the impact of depredation in conflict locations exist and include among others protective measures such as livestock guarding dogs (Marker et al., 2005; Treves and Karanth, 2003), aversive conditioning (Breck et al., 2006; Shivik and Martin, 2000; Smith et al., 2000), repellents and deterrents (Shivik et al., 2002; Smith et al., 2000), translocation (Linnell et al., 1997) or culling (Fernández-Gil et al., 2016; Treves et al., 2016). Since these mitigation responses can be costly, both financially and ecologically in terms of wildlife population dynamics, their implementation should be rationalized thanks to objective metrics and focused on very specific areas where their efficiency is supposed to be high (van Eeden et al., 2018).

For many reasons related to landscape features, to livestock management practices or to the spatial distribution and behavior of carnivores, the spatial pattern of depredation occurrences is not expected to be random. In this context, spotting areas where depredation occurs is one of the most common approaches to rationalize the management of human-carnivore conflicts.

Most of livestock-large carnivore depredation conflicts studies focus on the ecological aspect in a growing field known in the literature as *predation risk modeling* (Miller, 2015). *Predation risk modeling* aims at developing tools to inform decisions on livestock management and carnivore conservation. However, there is still some conceptual ambiguity hindering further developments of this field, for instance regarding the use of terms such as “depredation hotspot” and “depredation risk probability”. Distinguishing between these two terms is important, as they do not refer to similar conceptual or methodological approaches. The *depredation hotspot analysis* (hereafter, *DHA*) rigorously identifies high and low spatial clusters of depredation occurrences without making any a priori assumption on which underlying processes or factors generate the spatial pattern of the attacks (Baruch-Mordo et al., 2008; Meena et al., 2014; Wilson et al., 2005) but capturing all features at once. In contrast, *depredation risk probability analysis* (*DRPA*) provides a probability of depredation risk in space and allows a better understanding of the depredation process by linking environmental and/or management factors to risk probabilities (Miller et al., 2016).

The *DHA* is based on a spatial statistical test that associates each area with a score given a certain significance threshold indicating clusters where carnivores tend to depredate the most (hotspots) or in contrast where depredation is very unlikely (i.e. coldspots, Baruch-Mordo et al., 2008; Fortin and Dale, 2005; Getis and Ord, 1992). Doing so, the *DHA* provides a statistical description of the spatial dependence between depredation occurrences. The *DHA* and *DRPA* approaches are complementary in the *predation risk modeling* framework, although the applicability of these two methods is highly context-dependent. In particular, the *DRPA* requires knowledge that is more detailed than the *DHA* to select a priori factors supposed to trigger attacks and necessitates adequate data on the processes underlying the spatial pattern of depredations. Moreover, despite generating depredation risk probabilities, it does not allow identifying depredation hotspots and coldspots per se. Identifying depredation hotspots through a statistical description of spatial patterns of attacks however represents the primary information needed to prevent and mitigate conflicts through focusing efforts on areas identified as depredation hotspots and may help identify areas where more information is needed to predict actual risks (Baruch-Mordo et al., 2014, 2008; Miller, 2015). The *DHA* approach also represents the most widely applicable method in practice, since the spatial location of attacks is the primer most accessible information. In many depredation contexts, official declaration reports of depredation gathering some basic pieces of information on the attack such as its location are mandatory for obtaining compensation payments or related measures aiming at mitigating injuries and losses of livestock (Bautista et al., 2017; Dhungana et al., 2016).

In the Pyrenees, depredations on livestock by brown bears (*Ursus arctos*) constitute probably the main issue for the social acceptance of the species (Piédallu et al., 2016). Each summer, shepherds lead hundreds of thousands of domestic animals (mainly sheep but also goats,

cattle, horses and sometimes donkeys) into mountainous pastoral areas, which offer grazing areas where livestock would remain all summer. This period coincides temporally with the mating season for brown bears as well as the rearing of cubs and the establishment of subadults in their new home ranges (Støen et al., 2006; Swenson et al., 2000), implying key behaviors of learning for young and of large movements for adults. Overall, regular damages on livestock by brown bears each year create intense conflicts with humans. The impact of brown bear across the French Pyrenees represents 50% of the damage claims, of which 95% occur on livestock.

In this study, we combined a *DHA* with a *DRPA*-like approach to characterize the spatial pattern of depredation on livestock by brown bears in the French Pyrenees, and to identify the potential drivers of this pattern. As a first step, we used a seven-year depredation dataset to identify potential hotspots and coldspots of depredation occurrences and to characterize their temporal dynamics. We also investigated the sensitivity of our results to the spatial unit considered in the analysis (a *fine scale* with small and homogenous spatial units versus a *management-scale* with larger and heterogeneous spatial units corresponding to pastoral areas). As a second step, we modeled the intensity of hotspots as a function of a spatial index of bear activity density and several environmental descriptors. The environmental descriptors were chosen based on the bear ecology. We predict that the more intense the hotspot i) the farthest the human activities (disturbance hypothesis). We expect individuals (mainly dominant individuals as adult males and lone adult females) to avoid humans in order to benefit from the best foraging areas and intake (Nellemann et al., 2007), ii) the closest the forest edge (brown bears: Martin et al., 2013; Ordiz et al., 2011; tigers: Miller et al., 2015), iii) the more important the proportion of grassland, since the proportion of grassland could be a proxy of the density of domestic preys within grazing areas iv) the more difficult the terrain (steep slope and high ruggedness, lynx: Stahl et al., 2001).

2. Material and methods

2.1. Study area

The Pyrenees Mountains are enlarged on an east-west axis ranging between France, Spain and Andorra (Fig. 1). The study area consists of large valleys and steep mountains with elevation between 500 and 3400 m. Forests of deciduous (beeches *Fagus sylvatica*, oaks *Quercus*, Birches *Betula pubescens*) and coniferous (firs *Abies alba*, spruces *Picea alba*, pines *Pinus sylvestris*) trees cover a large part of the landscape. Between the forest patches, large grasslands represent the majority of open areas encroached by few shrubs such as rhododendron *Rhododendron ferrugineum* and wild blueberry *Vaccinium myrtillus* above 1800 m. These open areas are taken over by a traditional pastoral activity called transhumance, which involves the seasonal migration of hundreds of thousands of livestock brought by shepherds into the mountains roughly from June to October (approximately around 500,000 domestic animals as 82% sheep, 15% cattle, 2% equine, 1% caprine and some donkeys). Besides pastoral activity, human activities in the study area consist mainly in forestry and recreational activities like hunting and hiking. Human density in the area is relatively low (5 inhabitants per km², Martin et al., 2012) and restricted to the bottom of the valleys.

2.2. Brown bear population and monitoring

The Pyrenean brown bear population is divided into two nuclei, one with only two males in the west (Occidental nucleus) and the other in the center-east of the Pyrenees (Central nucleus; Fig. 1). Each year, brown bear presence signs are collected both systematically (systematic monitoring of bear presence along transects) and non-systematically (opportunistic observations by hikers, hunters, foresters, shepherds, and validated by wildlife technicians; Piédallu et al., 2017). Over the

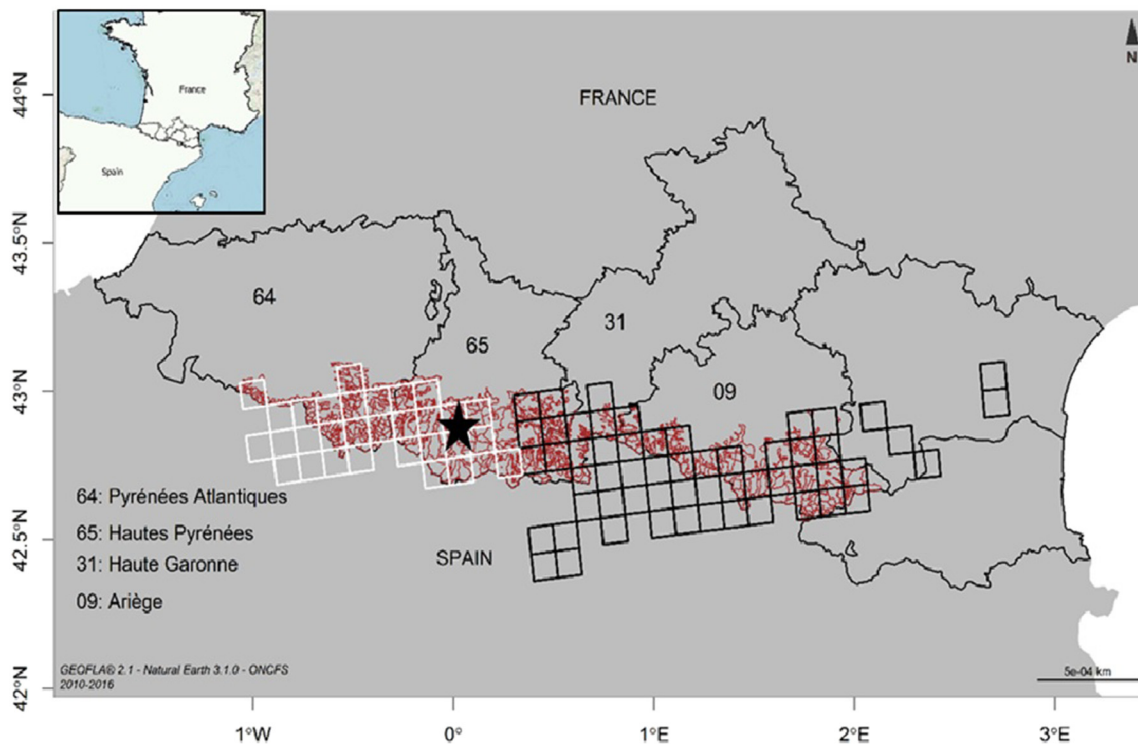


Fig. 1. Map of the presence area of the brown bear population from 2010 to 2016 in the Pyrenees (Occidental nucleus, white grid cells; Central nucleus, black grid cells). Our study focuses on the Central nucleus of the population. Brown lines inside the presence area represent pastures. The star indicates the location of the Pyrenean National Park (PNP). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

study period (2010–2016), the brown bear presence area is described as a grid of 10×10 km cells in which at least one bear sign (e.g. hairs, scats, claw marks) has been detected. It represents 8700 km² for the 7-year grid cell presence (Fig. 1). In 1995, the size of the remnant population was only five individuals. A reinforcement program was initiated in 1996 and bears currently occurring in the Pyrenees mostly descend from individuals translocated from Slovenia (nine individuals translocated from 1996 to 2016; Chapron et al., 2003; Quenette et al., 2000). In 2016, the minimum population size was 41 individuals (Fig. A1) of which 39 were in the Central nucleus.

The French National Game and Wildlife Agency (Office National de la Chasse et de la Faune Sauvage, ONCFS) drives brown bear management and monitoring in France. ONCFS' agents are in charge of reporting official damage claims. In line with the national compensation program, shepherds or breeders request the ONCFS services to send an expert officer on the field each time a domestic animal is suspected to be killed or wounded by bears in pastures in order to certify the claim of depredation and to register the damage in a standardized report form. It collects the location of the damage as well as the estimated date of the attack, the number of domestic animals damaged and any evidences useful to assess if this was a depredation event. Then, the damage claim is classified either as depredation by brown bear, death not related to brown bear or undetermined causes of death. Here, we only considered damage claims classified as depredation by brown bears.

2.3. Spatial analysis

This study focuses on the Central nucleus of the Pyrenean brown bear population (Fig. 1 central eastern part of the map, outside the Pyrenean National Park) as this area contains the main bear population (Section 2.2). The database used for this study consists of records of brown bear depredations in pastures on the French side of the Central nucleus between 2010 and 2016 from June 1st to September 30th. We indeed focused on the summer period to maximize the probability of

presence of all domestic herds in the mountain pastures at the same time for grazing (*prey availability hypothesis*, Hebblewhite et al., 2005; Hopcraft et al., 2005; Miller, 2015).

2.3.1. Management-scale analysis

Both declaration reports and management responses of livestock depredations occur at the scale of pastoral units (ranging from 0.009 to 46.1 km² in our study area). Consequently, we ran spatial analyses at this scale (hereafter referred as the management-scale). Data about the actual presence of livestock in each pasture was not available at the time, but we assumed that all pastoral units in our study area potentially contain livestock based on our field knowledge and because sheep husbandry is the main agricultural activity in the Pyrenees. We identified pastoral units from shape files collected thanks to the administrative services of the departments of Ariège (DDT 09) and Haute-Garonne (DDT 31, Chambre d'Agriculture 31). Two temporal resolutions were chosen to examine depredation clustering: (1) as a pooled analysis, we determined the clustering from pastoral units contained within the Central brown bear presence area over the whole study period and, (2) as a year-by-year analysis, we only selected pastoral units included within the Central presence area of brown bears for each given year (for the pooled analysis, $n = 216$ pastoral units, for the year-by-year analysis, $n = 105.6 \pm 30.6$ pastoral units per year).

Since, administrative borders do not reflect the functionality of pastures, pastoral units' polygons were attributed the depredations that were located inside the pastoral unit or within a buffer of 500 m around each unit ($n = 543$ brown bear depredations during the pasture period from June to September for the French Central nucleus).

2.3.2. Fine scale analysis

Whereas the management-scale may be relevant and useful to report and to manage conflicts, it is not necessarily appropriate to understand the process of depredation by brown bears. This process relies on complex interactions between the ecology and the behavior of bears

within their environment, which occur independently of administrative borders. We thus also considered a finer and more ecologically relevant scale than the management-scale, to which we refer hereafter as the fine scale. To perform analyses at the fine scale, we superimposed a grid of 250×250 m cell on the shape file of pastoral units. We selected cells that were simultaneously 1) inside pastoral units or within a 500 m buffer around each pastoral unit, and 2) inside the brown bear presence area (for pooled analysis, whole study period area and for year-by-year analysis, annual areas). As for the management scale, each cell was attributed a depredation number (for pooled analysis $n = 30,009$ cells with 369 cells with depredations, for year-by-year analysis $n = 12,762.57 \pm 4280.291$ cells per year with 68.3 ± 14.2 cells with depredations).

2.3.3. Depredation hotspots analysis

To identify the existence and the locations of hotspots or coldspots from depredations data, we used the Getis-Ord analysis (Getis and Ord, 1992) at both spatial scales (management- and fine-scales) and at both temporal scales (pooled and year-by-year). For both analyses, the spatial statistics were solely based on a spatial clustering score of depredations numbers associated with spatial units. We used the centroid i to define each spatial units (pasture or cell). The number of depredations recorded in the spatial unit defines the weight x of each centroid. The local Getis-Ord $G_i^*(d)$ statistic then measures for each point i the spatial association that results from the concentration of weighted points j_x (or area represented by a weighted point) and all other j_x included within a radius of distance d from the focal weighted point i_x . The neighboring distance d , represents the maximum distance beyond which spatial dependence between two points can be considered as negligible (Fortin and Dale, 2005). The local Getis-Ord $G_i^*(d)$ statistic is defined as followed:

$$G_i^*(d) = \frac{\sum_j w_{ij}(d) x_j}{\sum_j x_j}, j \text{ may equal } i,$$

where G_i^* measures the degree of dependence in the variable x (count of attacks) for j points located within a distance d of the focal point i , as compared to total value of all j points across study extent (Getis and Ord, 1992). The symmetric binary weighted matrix $w_{ij} = 1$ if j is within d of focal point i and $w_{ij} = 0$ if not (Getis and Ord, 1992). To compute the expected G_i^* under the null hypothesis of spatial independence, $n!$ random permutations of x values at the j points are equally likely (where n is the number of regions in our area, Getis and Ord, 1992).

When clustering is higher or lower than expected under the null model of random spatial distribution of attacks, the resulting G_i^* has large positive or negative values. Thus, each region (pasture or cell) is given a $Zscore$ defined as follow:

$$Z_i = \frac{G_i^*(d) - E[G_i^*(d)]}{\sqrt{\text{Var}[G_i^*(d)]}}$$

A large $Zscore$ implies a strong spatial dependence of point i with its neighboring points j within d . Thus, a large positive $Zscore$ describes a hotspot, whereas a large negative $Zscore$ a coldspot. Results are described as empirical $Zscore$ comparison.

Lastly, in order to get a more direct correspondence for comparing with the management-scale analysis, we rescaled the fine-scale results at the pastoral units. Specifically, we calculated the mean $Zscore$ of each pasture (which adjusts the intensity of the intra-pasture aggregation to the size of the pasture), its maximum $Zscore$ (only reflecting the intensity of the intra-pasture aggregation) and the sum of its $Zscores$ (mechanistically reflecting both the size of the pasture and the intensity of aggregation) from all grid cells within each pastoral unit to define the aggregated score of the pastoral unit. In order to illustrate the relevance of the scale considered to describe the spatial depredation patterns as well as the practical implications of this methodological choice, we ranked pastures according to their local Getis-Ord $Zscore$ at the

management-scale and at the fine scale once rescaled to the management scale using the aggregation functions described above (MEAN, SUM, MAX).

2.3.4. Sensitivity analysis

A critical step in Getis-Ord analysis is to define appropriate neighboring distance. The neighboring distance allows analyzing conveniently noncontiguous polygons such as pastoral units, although it does not take into account for shape and area of polygons.

For the management-scale, we determine the most appropriate neighboring distance by investigating the sensitivity of $Zscores$ to two global statistics: the Moran's $I(d)$ test for spatial autocorrelation and the global Getis-Ord $G(d)$, which measures the overall concentration (or lack of concentration) of all pairs of (x_i, x_j) such that i and j are within neighboring distance d of each other.

We then compared global Moran's $I(d)$ and global Getis-Ord $G(d)$ through their $Zscores$, respectively $Z(M)$ and $Z(G)$, for the entire study area at incremental distances from 2000 m to 10,000 m per steps of 1000 m. We additionally computed $Z(M)$ and $Z(G)$ at $d = 3836$ m and $d = 7800$ m. The former distance corresponds to the theoretical radius for the largest pastoral unit size of 46.13 km^2 . The latter distance corresponds to the distance at which each unit within a radius of this length or longer is connected to at least one other unit. The distance at the first peak of intensity of Moran's $I(d)$ and global Getis-Ord $G(d)$ was taken as the neighboring distance d for the local Getis-Ord $G_i^*(d)$ analysis for hotspots of depredation ($d = 3836$ m, see Fig. A2).

For the analysis at the fine-scale, we computed Getis-Ord $G_i^*(d)$ at $d = 1367$ m that is the theoretical radius for the mean area of pastoral unit of 5.86 km^2 . With this, each cell possesses on average 72 neighbors. We assessed the effect of neighboring distance through increasing distances at both management and fine-scale (for details about distances we used, please refer to Figs. A3a and A3b).

At the fine-scale, another critical step is the choice of the grain size that may have strong consequences on the outcomes of the analysis and largely depends on the goal of the study (Baruch-Mordo et al., 2008). To assess the sensitivity of results to different grain size, we computed a sensitivity analysis of our results to grain size by using grids with cells of half (125×125 m) and twice (500×500 m) the initial resolution (250×250 m) at the same neighboring distance ($d = 1367$ m, see Fig. A3c).

2.3.5. DHA spatiotemporal dynamics

We performed a complementary analysis to assess whether and how hotspots locations change through time (at the fine scale). To do so, we computed local Getis-Ord $G_i^*(d)$ for each year over the brown bear presence area from 2010 to 2016 (see details and justifications in Figs. A4a and A4b).

To evaluate the temporal trend of Getis-Ord $Zscore$ for each cell, we then computed a Mann Kendall non parametric test (Mann, 1945). Each pair of time steps was compared over the 7-year series, generating a Mann-Kendall statistics for each cell describing its temporal trend. In absence of any temporal trend, the expected value of the Mann-Kendall statistics is zero. Based on the Getis-Ord $Zscores$ variance for each cell, we assessed whether a temporal trend exists for each cell thanks to the Mann-Kendall $Zscore$ statistics. The clusters and trends resulting from the combination of Getis-Ord $G_i^*(d)$ and Mann-Kendall statistics were then used to categorize each cell (Harris et al., 2017) to characterize the overall spatiotemporal pattern of depredation by brown bears.

We only ran and displayed spatiotemporal analysis for cells that had at least one significant Getis-Ord $Zscore$ over the study period. To select these cells, we applied a false discovery rate correction (the proportion of false positives among all significant results) for cut-off value of significance given the great number of neighbors (average number of links = 72) implying multiple testing. It allowed lowering our type I error rate while controlling for the type II error rate.

2.4. Relationship between hotspot presence and environmental factors

Following the analysis of hotspots of depredations, and as a post-hoc analysis, we further examined whether hotspot presence may be related to environmental factors. As explanatory variables reflecting environmental factors, we considered the nearest distance to forest, the nearest distance to buildings, the elevation, the slope, the ruggedness (details for the terrain variables calculations are in Appendix A6) and three different grassland proportion buffers at $r = 500$, $r = 1000$ and $r = 1367$ m (Table A6a). We also computed an index of brown bear activity density (per year), corresponding to the mean number of bear signs within seven buffers (Table A6a and Appendix A6 for justification). We standardized these variables and evaluated the collinearity among them (Fig. A6b). Because hotspots and brown bears are mainly in the core area of the Central nucleus, we restricted our analysis to this area (see Fig. A6a). The fine scale hotspots *Zscores* did not follow any probability distribution, thus they were further transformed into a binary response variable such as cells with *Zscore* < 1.96 were assigned 0 (i.e. no hotspot) and those with *Zscore* \geq 1.96 were assigned 1 (i.e. hotspot). To account for the potential temporal autocorrelation, we used a binomial generalized linear mixed effects model with the year as a random factor. Spatial autocorrelation being the core of this process, we took the spatial position of each of our points as the second random factor.

We ran all combinations nested within the full model (including all environmental factors) described above (Zuur et al., 2009), with correlated ($r > 0.7$) variables excluded from similar models (Fig. A6b) and ranked models according to their AIC (Table A6b, Burnham and Anderson, 1998). We checked the residuals of the best model (Figs. A6c, A6d) and predicted the relation between the binary response hotspot variable and each of the selected explanatory variable (with other variables maintained at their mean).

We performed all statistical analyses with the R Core Team (2017) free software version 3.5.1 with the main packages *spdep* (Bivand and Piras, 2015) for local Getis-Ord $G_i^*(d)$, *trend* (Pohler, 2018) for Mann Kendall statistics, *glmmTMB* (Brooks et al., 2017) for mixed modeling and *MuMIn* (Barton, 2017) for model selection. We computed some representations and exploratory mapping on ArcGIS version 10.3.1.

3. Results

In the Central nucleus, the 2010–2016 brown bear presence area included 216 pastures (Fig. 2A), of which 43 were associated with depredation events (26% of the total surface of pastoral units). Over that period and in this area, there were on average 103.3 ± 18.8 depredations per year with 181.6 ± 42.2 domestic animals killed per year (of which 99% on sheep).

3.1. Depredation hotspots pattern

At the management scale, the Getis-Ord statistics confirmed the existence of depredation hotspots in the core of the Central nucleus (Fig. 2B). At the neighboring distance of 3836 m, each of the 216 pastoral units was on average linked to four neighbors, except 12 pastures without any neighbor. Among the 216 pastures located within the brown bear presence area, only 16 pastures could be considered as significant depredation hotspots (i.e. *Zscore* over 1.96).

The analysis at the fine-scale revealed further heterogeneity in depredation hotspots both within and between pastures (Fig. 2C). Local hotspots indicated spatial clustering of depredations inside pastures as well as overlapping between pastures. Interestingly, the 1970 cells considered as significant hotspots only represented 6.6% of the surface of the study area but contained 88% of depredation events data.

Whatever the spatial scale at which the Getis-Ord *Zscores* were calculated (management or fine scale), the depredation ranking of pastoral units were not necessarily associated with the maximum

number of attacks (Table 1). In addition, although ranks associated to the exposure of a given pasture unit to depredation were generally consistent among the different metrics calculated from *Zscores* (mean, sum or maximum *Zscores*), the ranking could change depending on the spatial scale considered. As an example, the pasture Aouzout was ranked second with the management scale analysis and no more listed in the top eight management units with the grid cell-scale analysis.

3.2. Depredation hotspots dynamics

The year-by-year analysis of depredation hotspots indicated the occurrence of “annual” hotspots (Fig. A4a), which was not necessarily expected. The existence of annual depredation hotspots implied that hotspots did not solely result from aggregation over a large period (several years pooled) but also occurred for each single year. Visual assessment of annual maps of hotspots (Fig. A4a) and the Mann-Kendall analysis (Fig. 3) suggested that hotspots locations remained consistent over time, whereas a westward shift started from 2016: hotspots in center east became less intense in term of *Zscore* and those in the west became more intense (Fig. A4a). Moreover, the spatiotemporal analysis performed through the combination of spatial Getis-Ord clusters and temporal Mann-Kendall trends allowed us to confirm a discrimination between hotspots that tended to be less intensively depredated over time and those that showed intensifying depredation through time (Fig. 3).

3.3. Factors associated with hotspots presence

After checking the collinearity between explanatory variables, we excluded the following pairs of variables from a given model: slope and ruggedness, grassland proportions, and elevation and nearest distance to forest. The best model (conditional R^2 (based on random and fixed effects) = 0.70; marginal R^2 (based only on fixed effects) = 0.15) indicated the bear activity density, the proportion of grassland ($r = 1367$ m), the nearest distance to building, the nearest distance to forest and the slope as the most important factors associated with depredation hotspots presence (Table 2, Fig. 4), with the probability of hotspot presence strongly increasing where the brown bear activity density and the proportion of grassland were high, and to a lower extent where the distances to forest and buildings were low.

4. Discussion

Depredation on livestock by the brown bear is one of the major issues for the social acceptance of the species in the Pyrenees. Raw depredation counts may highlight pastures with the largest numbers of attacks but they are insufficient to provide information on the clustering of these attacks in space. The DHA is a powerful approach to understanding the spatial dependence of spatial units along the depredation process. Our study indicates that most depredation events are spatially clustered in hotspots of depredations. Besides, whereas hotspots concentrate depredation into very few locations, the vast majority of space within the range of brown bear presence is not undergoing any depredation, as suggested by the absence of coldspots in the study area whatever the scale of the analysis. Similar patterns of depredation hotspots have been found in other bear populations (e.g. black bear, Baruch-Mordo et al., 2008; brown bear, Bautista et al., 2017; grizzly bear, Wilson et al., 2005) and more generally in large carnivores (e.g. tiger, Miller et al., 2016; lynx, Stahl et al., 2001). Here, we further showed that depredation hotspots occur for several consecutive years and that they can be characterized for each single year at both fine (i.e., 250×250 m cells) and larger scales (i.e., pastoral units of 0.009 to 46.1 km²).

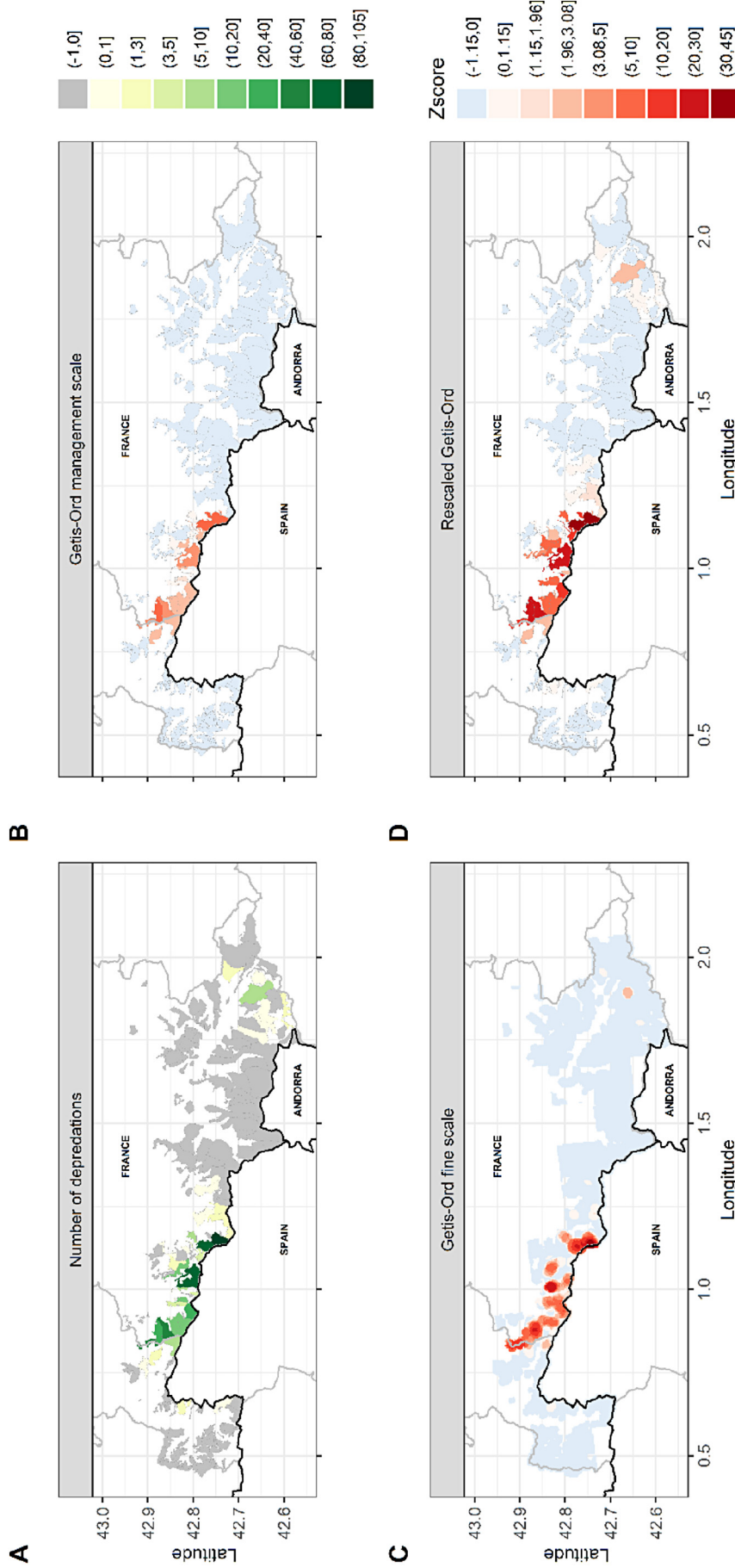


Fig. 2. Four types of spatial representation of brown bear depredation events between 2010 and 2016. **A)** Number of depredations per pastures (raw data, legend is at the top right). **B)** Getis-Ord Zscore at the management scale. **C)** Getis-Ord Zscore at the fine scale. **D)** Getis-Ord Zscore from the fine scale rescaled to the management scale. For the intensity of the Getis-Ord Zscore the legend is at the bottom right. Neighboring distances used for the Getis-Ord at the management scale and at the fine scale are $d = 3836$ m and $d = 1367$ m respectively.

Table 1

Ranking of pasture units (vertically) reflecting depredation exposure according to depredation numbers (within brackets in the left column), *Zscore* of Getis-Ord analysis at the management scale, rescaled mean *Zscore*, rescaled max *Zscore* and rescaled sum *Zscore* (only the 8 first units are shown). *Zscores* are within brackets in the right four columns. In Appendix 5, we mapped the pastoral unit names used in this table.

Depredation count ranking	Depredation clustering ranking			
	Management scale	Grid cell scale Mean (rescaled)	Grid cell scale Max (rescaled)	Grid cell scale Sum (rescaled)
POUILH (102)	AULA (7.33)	POUILH (17.03)	POUILH (44.27)	POUILH (3915.99)
TRAPECH (67)	AOUZOUT (7.15)	AULA (12.45)	AULA (34.04)	AULA (2738.06)
AULA (63)	POUILH (7.15)	UGET (11.55)	TRAPECH (25.75)	BARESTET (2557.87)
BARESTET (58)	ESTREMAILLE (6.51)	BARESTET (8.44)	UGET (25.28)	TRAPECH (2233.13)
IZARD (44)	LA PLAGNE (4.38)	ESTREMAILLE (6.88)	ESTREMAILLE (21.95)	ESTREMAILLE (1520.19)
ESTREMAILLE (28)	BARESTET (4.27)	IZARD (6.70)	IZARD (21.48)	IZARD (1400.57)
URETS (28)	TRAPECH (4.06)	LASPE (5.23)	DUL (21.34)	URETS (1031.95)
LARECH (16)	IZARD (3.45)	URETS (4.89)	BARESTET (19.06)	UGET (658.28)

4.1. Comparing spatial scales of hotspot determination

In spite of the importance of the management scale for decision-making, this scale does not reflect accurately the spatial heterogeneity of domestic herds nor the actual habitat use by the brown bear (Martin et al., 2013, 2012). In this context, the use of a finer scale allowed us to take into account the heterogeneity of the pastures' sizes and for getting rid of the administrative boundaries delimitating pastoral unit thus better reflecting the spatial continuity of livestock availability, landscape heterogeneity and connectivity of bears' habitat. Such finer scale analysis then revealed some spatial connection between hotspots. For example, hotspots occurring on the western part of the study area are connected between pastures, whereas, the hotspot on the eastern part is isolated.

By assessing hotspots at a much smaller scale than the pastoral unit, we were able (i) to identify hotspots within pastoral units, thus determining areas of particular interest to focus depredation management actions within each pastoral unit, (ii) to assess hotspots within and between pastoral units, thus providing precise information to help disrupting this hotspot connection, (iii) to uncover hotspots of particularly high intensity (e.g. compare Fig. 2B and C) which might not be apparent if hotspots are primarily determined at the scale of pastoral units.

4.2. Temporal scale and lifetime of hotspots

In line with *DHA*, hotspots are locations where depredations are significantly clustered, which implies that local mitigation responses could have disproportionately high beneficial impact. Here, we formally showed that depredation hotspots by the brown bear in the Pyrenees (i) occur for each single year (Fig. A4b) and (ii) that their locations are overall consistent in time (Fig. 3). Although our results show that the intensity of depredation hotspots may gradually change over a few consecutive years (Fig. 3 and Appendix 4) possibly reflecting slight changes in individual bear behavior and/or local mitigation measures, this finding implies that depredation data from one single year can be sufficient to diagnose hotspots that would very likely persist over several years if no environmental or management changes occur.

4.3. Factors affecting hotspots presence

Although hotspot characterization provides useful information about the spatial dynamics of attack patterns and their possible persistence on the short-term, better understanding the mechanisms underlying depredation is critical to increase the power and the robustness of predictions of hotspot locations in space and time. Our post-hoc *DRPA*-like analysis relating hotspots to environmental factors indicates a positive relationship between hotspot presence and brown bear activity density, confirming that depredation are more likely to occur in

areas frequently used by brown bears. Similarly, the proportion of grassland is also positively related with hotspot presence, corroborating that this metric can be interpreted as a proxy of prey density. These positive relationships are in line with the knowledge about prey-predator relationship as they are shaped by the predator's foraging strategies and the prey's anti-predatory behavior, thus areas where both the activity of bears is high and where preys can roam (*prey availability hypothesis*, Miller, 2015; Woodroffe et al., 2005) are associated not only with higher density of attacks, but also with high spatial clustering of these attacks. Surprisingly however, hotspots tend to occur at the proximity of buildings. This counter-intuitive result might reflect the positive effect of the aggregation of preys near human presence through night grouping rather than any direct negative effect of humans (*prey accessibility hypothesis*, Hebblewhite et al., 2005; Hopcraft et al., 2005). In line with the last hypothesis, the steep terrain and the proximity of forest edges ease the bear hunting process to access domestic preys, as in several other predators (Mech et al., 2000; Miller et al., 2015; Stahl et al., 2001), the former creating an advantage for the bear as isolating preys and easing its movement, the latter providing cover to approach the herd.

However, with a marginal R^2 lower than the conditional R^2 and spatial autocorrelation still found in the residuals of the best model (Fig. A6c), our results suggest that some factors associated with the pattern of depredations are missing in order to improve this model and the explanation of the spatial pattern of depredation hotspots.

4.4. Management implications and recommendations

The analysis of depredation hotspots is usually treated as a purely retrospective analysis, which limits its management implications. Our results indicate that the combination of this hotspot approach with some post-hoc *DRPA*-like analysis makes it possible to establish the link between spatial clusters of attacks and some spatial environmental features, therefore providing both reactive and proactive answers to crucial management questions. Beyond the intrinsic efficiency of local management responses to brown bear depredation, the implementation of these mitigation measures in hotspot areas is expected to be more efficient than in non-hotspot areas. In terms of herd and pasture management, the location of intra-pasture hotspots that may last several years and of factors associated with their occurrences could allow (i) the creation of exclusion zones, i.e. no go zones for the domestic herd, based on both the presence of identified hotspots and relevant environmental factors associated with their presence, and (ii) the implementation or enhancement of specific mitigation measures on these areas. Furthermore, the implementation of such measures all over the mountain chain (in a proactive or reactive way) would decrease depredations (Woodroffe et al., 2005) and bear's depredation-prone behavior through learning the negative association by individual experience or by cultural transmission through cubs (Hopkins, 2013; Noyce

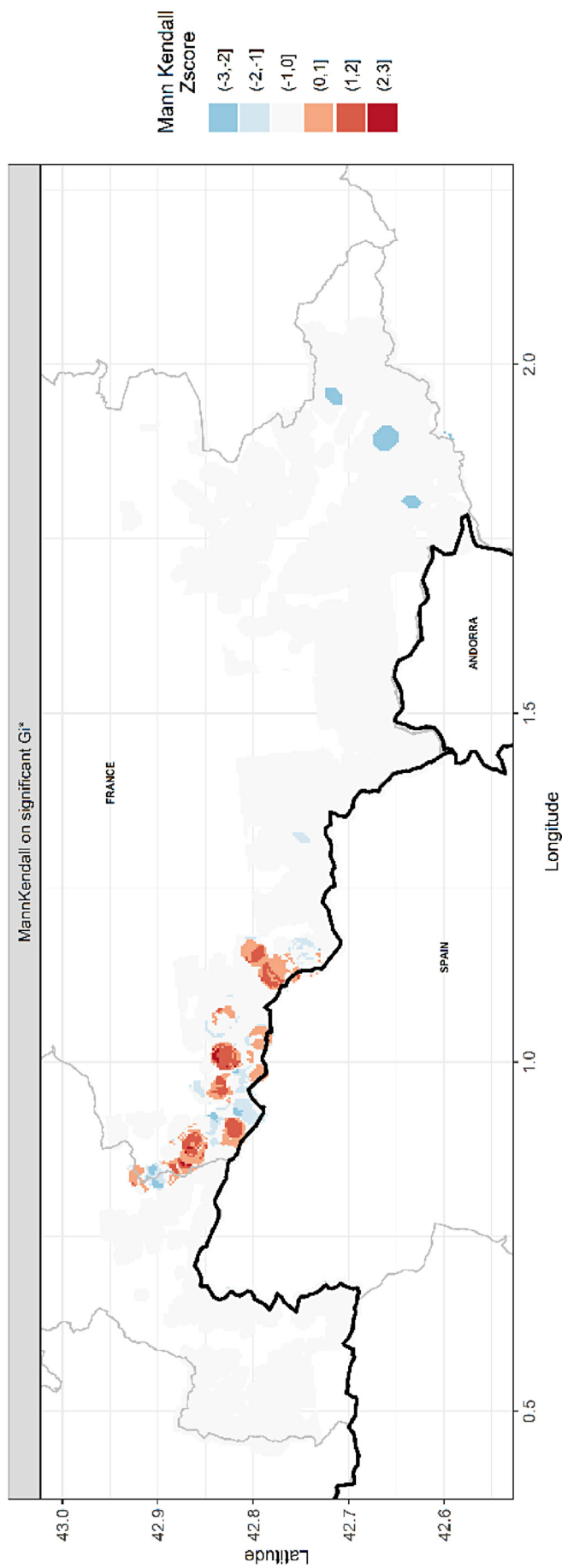


Fig. 3. Spatiotemporal hotspot analysis (combination of local Getis-Ord analysis and Mann-Kendall test) of brown bear depredation in the French Central nucleus of the Pyrenees from 2010 to 2016. The Mann-Kendall map allows highlighting temporal correlation of depredation hotspot locations with negative score indicating a decrease of the intensity of the hotspot in time rather a positive score highlight an intensifying one.

Table 2
Effects of environmental variables on the probability of being a hotspot. Summary of best model after model selection based on AIC. Random factors are the years and the spatial position of points, $n = 57,036$ ($n_{year} = 8\ 148$).

Explanatory variables	β	SE	Z	p
Intercept	-3.17975	0.17344	-18.33	< 2e-16
Grassland proportion ($r = 1367\text{ m}$)	2.79702	0.08439	33.14	< 2e-16
Nearest building	-0.67424	0.08350	-8.07	6.77e-16
Slope	0.31422	0.08469	3.71	0.000207
Nearest forest	-0.28515	0.6634	-4.3	1.72e-05
Bear activity	0.38519	0.04046	9.52	< 2e-16

and Garshelis, 2014).

Locating, quantifying and ranking areas where mitigation measures are the most necessary is then of first importance if resources to implement these measures are limited. A right implementation is especially crucial in a complex social context towards brown bears. According to Piédallu et al. (2016), the residents of the two counties of Central Pyrenees display opposite attitudes towards brown bears: the residents of the Ariège county (Fig. 1) displays more negative attitudes than residents of Haute-Garonne. One possible reason for this heterogeneity is that, in Ariège, 44.5% of the area used by brown bears (over the 2010-2016 period) overlaps with pastoral areas, which is more than twice the percentage of overlap occurring in Haute-Garonne (17.4%). In order to match with the county scale used in the study of Piédallu et al.

(2016) and based on the same methods as the rescaling at the management scale used in the present study (Section 2.3.3), the maximum rescaled Zscore for the Ariège county is 44.3 while it is 19.1 for Haute-Garonne. Thus, the spatial heterogeneity of the negative attitude could be linked to the area used by brown bears and, more importantly, to the intensity of the major conflict opposing human activities to the presence of this species, which might relate to different types, sizes and protective measures of herds. Our framework of fine scale depredation analysis and rescaling the outcomes at appropriate management scale (i.e. pastoral units as well as any territorial units such as municipality or at NUTS for EU level) may allow stakeholders (i.e. wildlife managers, stockbreeders, scientists, pastoral organizations) to identify hotspots, assess their spatial and temporal scales, and to enhance mitigation planning, efforts and funds accordingly.

In France, each year we map administrative areas (municipalities) that can claim for public subsidies for preventive measures (<http://www.ariège.gouv.fr/Actualites/Pastoralisme-en-zone-de-presence-de-lours-l-Etat-soutient-et-accompagne-les-eleveurs>). For now, these maps do not result from any scientific and systematic assessments. Our study should help improving such spatial planning through better adapting the funding to areas that are particularly vulnerable to predation (hotspots). Moreover, it would also improve the classification of adjacent areas with a score: being adjacent to hotspots would be different than being adjacent to areas with low Z scores. For example, if some adjacent municipalities are actually surrounded by municipalities with

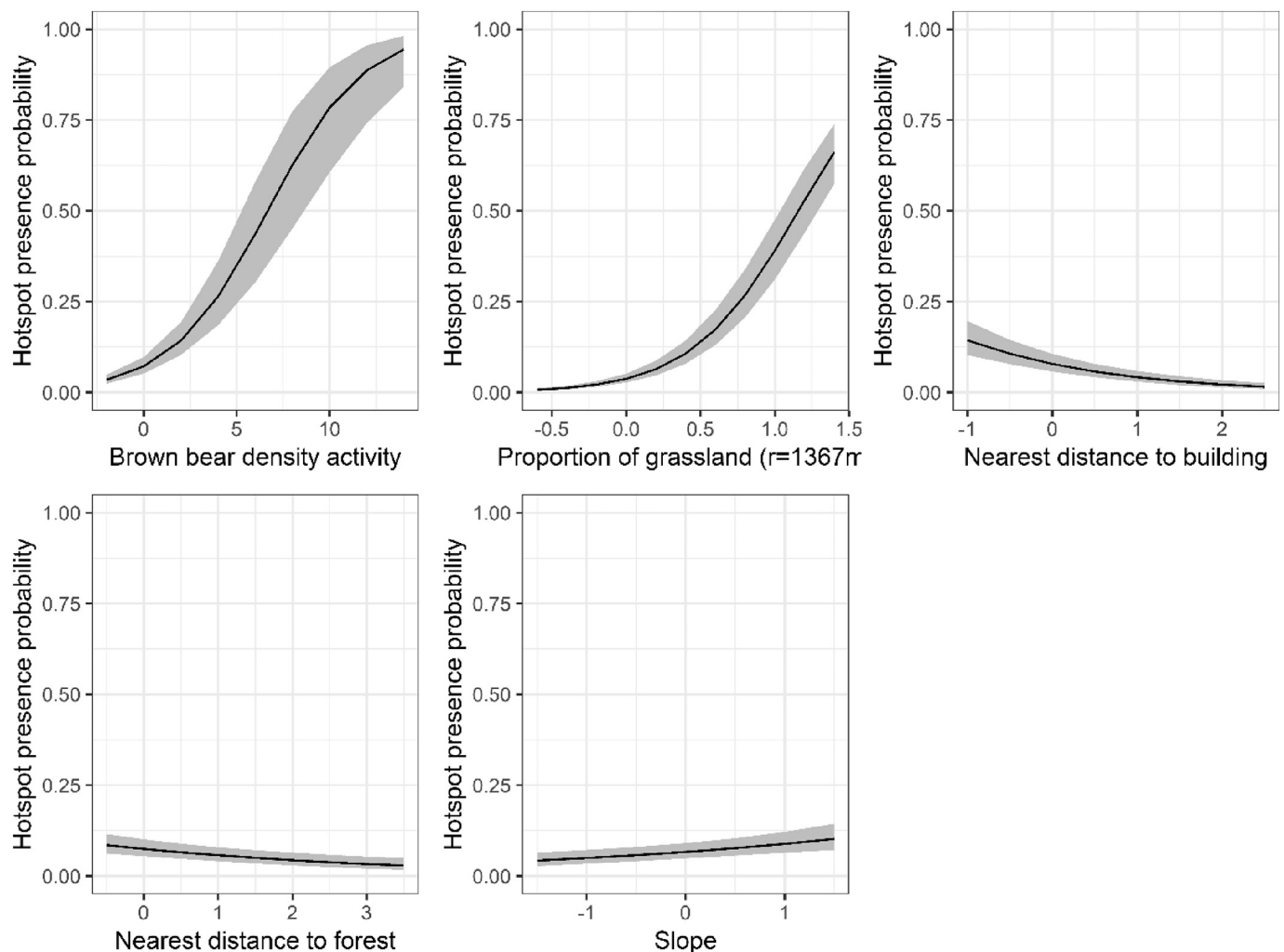


Fig. 4. Hotspot presence probability predicted from the best model for each explanatory variable. Predictions for each variable are shown in the original range of the variable while other explanatory variables are maintained at their mean (Zuur et al., 2009).

depredations, their score might be much higher than external municipalities. In addition, recently, brown bear scaring measures have been carried out in some predation areas. The initiation of these operations should be based, for example, on whether or not they are in a hotspot area in order to quantify the depredation risk incurred in this area and to quantify the effectiveness of these frightening measures. Thus, together with decreasing the number of attacks by appropriate mitigation measures, locally improving the attitude towards species tolerance by focusing on evidence-based communication is a major issue to help solving human–carnivore conflicts (Dickman, 2010; Linnell and Boitani, 2011; Woodroffe et al., 2005).

Declaration of competing interest

No conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2019.108210>.

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