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Ecological correlates of large carnivore depredation on sheep in Europe

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ABSTRACT

Sharing space with large carnivores on a human-dominated continent like Europe results in multiple conflictful interactions with human interests, of which depredation on livestock is the

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most widespread. We conducted an analysis of the impact by all four European large carnivores on sheep farming in 10 European countries, during the period 2010–2015. We ran a hierarchical Simultaneous Autoregressive model, to assess the influence of several ecological factors on the reported depredation levels. About 35,000 (SD = 4110) sheep kills were compensated in the ten countries as caused by large carnivores annually, representing 0.5% of the total sheep stock. Of them, 45% were recognized as killed by wolves, 24% by wolverines, 19% by lynx and 12% by bears. We found a positive relationship between wolf distribution and the number of compensated sheep, but not for the other three species. Depredation levels were lower in the areas where large carnivore presence has been continuous compared to areas where they disappeared and returned in the last 50 years. Our study shows that a few large carnivores can produce high damage, when the contribution of environmental, social, and economic systems predisposes for it, whereas large populations can produce a limited impact when the same components of the system reduce the probability that depredations occur. Time of coexistence plays in favour of a progressive reduction in the associated costs, provided that the responsible agencies focus their attention both on compensation and co-adaptation.

1. Introduction

The European continent is home to four species of large carnivores: brown bears (*Ursus arctos),* lynx (*Lynx lynx),* wolves (*Canis lupus)* and wolverines (*Gulo gulo*). After centuries of decline due to multiple causes (extermination policies, habitat destruction, reduction in the prey base, etc.) all these four species have progressively regained space, expanded their numbers, and recovered much of their former distribution during the last 50 years (Chapron et al., 2014). This happened mainly because of a set of international conventions, which modified their status from that of pest species to conservation priorities, creating the conditions for their legal protection at the national level. It was also due to a series of larger social, economic and historical processes, such as reforestation and the progressive abandonment of agricultural land (MacDonald et al., 2000), which reduced human impacts and released space for large carnivores and their wild ungulate prey. At present, 42 European large carnivore populations can be identified, 34 of which span over two or more (and up to nine) different countries (Chapron et al., 2014).

In the dichotomy between land sparing and land sharing conservation strategies (Phalan et al., 2011), the European situation reveals that humans and large carnivores can share the same landscape, with a series of potential benefits that range from restoring ecosystem function by re-establishing predators' ecological effects (Wolfe and Ripple, 2018), to supporting the economy of rural communities through eco-tourism (Palazón, 2017), to conveying the cultural, aesthetic or spiritual values associated to wilderness (Macdonald, 2001). The return of large carnivore, though, does not come without a reciprocal impact. On one hand, large carnivores often pay a high price to sharing space with humans, as witnessed by the persistently high levels of illegal killing in several European countries (Kaczensky et al., 2012). On the other hand, given the absence of large areas of wilderness in Europe (Venter et al., 2016), carnivores have almost entirely re-established their populations in rural, but highly human-modified landscapes, where humans raise livestock, keep bees for honey, hunt wild ungulates, and use forests and mountains for tourism and recreation (Chapron et al., 2014). Sharing space has therefore given rise to several forms of direct and indirect interaction between the ecological needs of large carnivores and the interests of rural humans (Bautista et al., 2019). These include depredation on livestock and destruction of beehives, dog killing, reduction of wild ungulate densities and other forms of impact that often generate conflicts which need to be managed (Melis et al., 2010; Linnell, 2013). Among such different forms of impact that large carnivore presence generates, depredation on livestock is by far the most widespread and relevant in economic terms (Linnell and Cretois, 2020).

In response to large carnivore recovery, most European governments have introduced compensation programs, under the assumption that such programs would progressively increase the social tolerance towards those species (Naughton-Treves et al., 2003). Compensation programs, in fact, rely on the social contract principle that the localized costs of human-large carnivore coexistence should be shared among all citizens (Schwerdtner and Gruber, 2007). This is an expensive strategy, considering that the European countries nowadays pay almost 30 million euros per year for damage compensation, a sum that has increased during the last decade (Bautista et al., 2019). Damage compensation programs are not expected to directly generate a reduction in depredation levels, because they do not operate on their primary causes, but only mitigate their negative economic effects. However, the expectation is that such programs will operate as a temporary buffer between large carnivores and farmers, increasing tolerance, while other management actions promote the establishment of the appropriate coexistence mechanisms (Nyhus et al., 2005). The main underlying assumption is that time will allow the refinement of such co-adaptation process, favouring a progressive reduction in the overall economic and social costs of human-large carnivore coexistence (Carter and Linnell, 2016).

This assumption, though, is not always supported by field experiences (Naughton-Treves et al., 2003; Bulte and Rondeau, 2005), and its validity varies with the socioeconomic and cultural contexts (Maclennan et al., 2009; Vynne, 2009). Several local studies have shown that compensation programs often fail to increase tolerance towards large carnivores and leave many stakeholders unsatisfied (Naughton-Treves et al., 2003; Vynne, 2009; Karanth et al., 2013). Moreover, many people feel that compensation schemes reward passivity and do not motivate producers to adopt effective mitigation strategies (Nyhus et al., 2005). Finally, compensation programs are often maintained for reasons which are poorly related to promoting human-large carnivore coexistence. In most of Europe and North America, economic incentives to farming (of which damage compensation is just a share) are used at the political level as a tool to subsidize the sector and to achieve a range of strategic goals which are not always related to conservation (Linnell et al., 2012). This

raises the question if the whole strategy will still be socially and economically sustainable in the future (Linnell, 2013), especially considering that large carnivores will likely further expand their range in future years (Chapron et al., 2014).

While the sustainability of compensation programs needs to be evaluated at many levels (ecological, economic, social, etc.), one relevant approach is to assess if the application of such programs has generally coincided with a parallel reduction in large carnivore depredation levels, and what factors might have contributed to such progressive reduction. In this sense, Europe appears as a mosaic of rather different situations. In some areas, humans and large carnivores have coexisted for many generations of uninterrupted sympatry, whereas other parts of the continent are now experiencing a challenging process of re-adaptation after several decades of absence (Kaczensky et al., 2012). Additionally, European countries differ in terms of large carnivore densities, livestock abundance and distribution, land use, landscape structure, and several other ecological and socio-economic factors, which are potentially relevant in affecting the levels of large carnivore damage on livestock (Kaczensky et al., 2012). Highlighting the differences between these local contexts in terms of large carnivore impact, and linking such differences to the variety of ecological and historical conditions in which humans and large carnivores interact, would be a relevant contribution to understanding the process. It would allow to identify virtuous experiences and challenging situations, while providing an insight into some of the underlying reasons behind the spatial and temporal variation in large carnivore impact on livestock farming.

The main challenge in such effort, though, is given by the complexity and multi-dimensional nature of the depredation process. Part of this process is just another type of predation, and therefore operates according to the same mechanisms of predation ecology (Linnell et al., 2012). The relative densities of large carnivores and their domestic prey represent the numerical component of the predation process in a classical sense, (Holling, 1959), whereas landscape structure and land use can influence domestic prey encounter rates, accessibility, and hunting success, similarly to the way they can modulate predation risk and kill rates in the wild (Kauffman et al., 2015; Ghoddousi et al., 2016). Finally, the availability of alternative wild ungulate prey can also play a role in affecting the likelihood of depredation events on livestock (Gervasi et al., 2014; Khorozyan et al., 2015; Ciucci et al., 2020). Besides these ecological factors, however, cultural, historical, economic, and social aspects are expected to play a role in affecting the long causal chain that determines the costs of coexistence. Livestock husbandry practices, which are highly influenced by local historical and cultural traits, can strongly affect predation risk and the resulting magnitude of the depredation process (Eklund et al., 2017). Additionally, in most of the cases depredation events are neither directly nor accurately observed. Instead, they derive from a long chain of events that starts when the actual depredation occurs, implies a certain probability to detect the event, continues with a farmer's willingness to report it and claim compensation, and includes a different set of evaluation methods by local management authorities (Schwerdtner and Gruber, 2007). Such processes end with an administrative decision to classify the event as depredation, and therefore refund the farmer (see Fig. 1 for an illustration of the ecological and non-ecological factors linking predation ecology, livestock depredations and compensated losses).

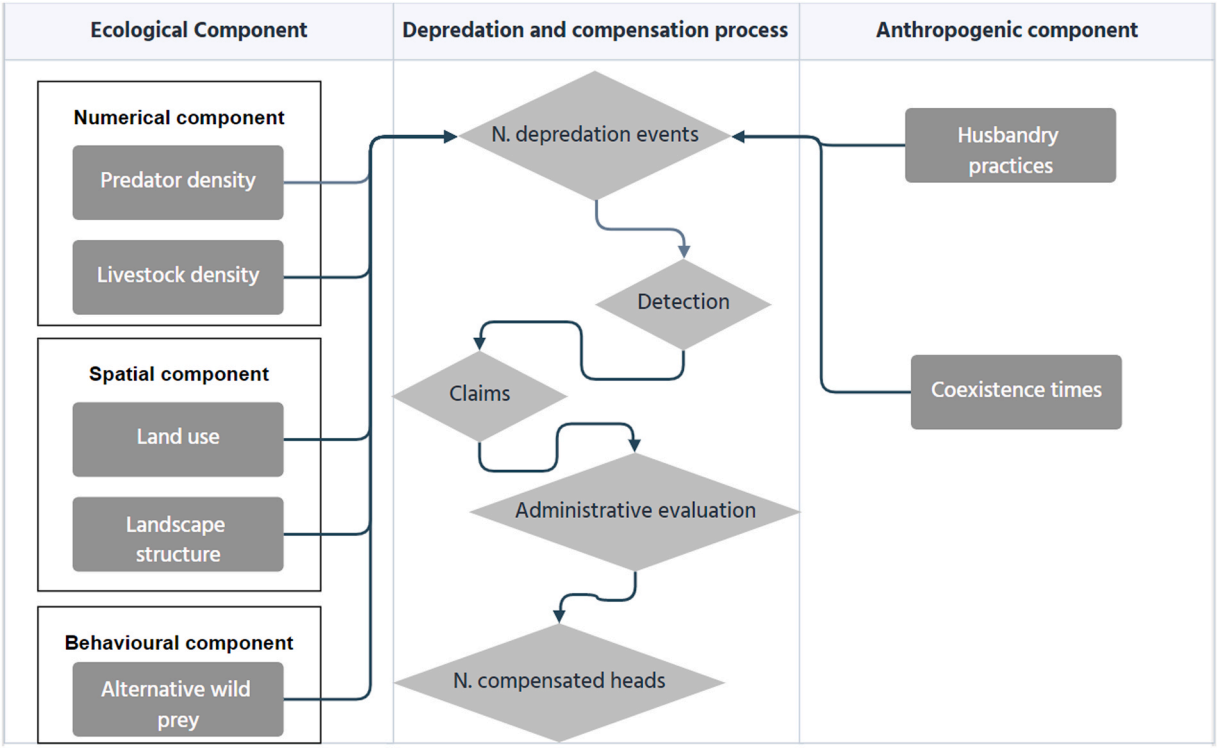

Fig. 1. Conceptual diagram of the ecological and anthropogenic mechanisms generating the number of annually compensated sheep losses to large carnivores. The diagram also illustrates the analytical framework used to analyse the spatial and temporal variation in the number of compensated sheep head in 10 European countries, years 2010–2015.

Therefore, looking at depredation through the filter of the different compensation systems requires accounting for the risk of getting a biased image of its relative magnitude in the different contexts.

Building on the above-described conceptual framework, we analysed the impact of all four European large carnivores on sheep farming in 10 European countries, during the period 2010–2015, with the aim to assess which ecological variables were correlated to the spatial and temporal variation in depredation levels. We collected data about the prevalent husbandry practices, the characteristics of the compensation schemes, and the number of confirmed depredation events in each of the administrative units in charge of large carnivore compensation in each country. Then, we ran a hierarchical Simultaneous Autoregressive model (SAR), to assess the influence of different ecological factors (prey and predator density, landscape structure, land use, etc.) on the emerging spatial and temporal patterns in the depredation levels across the continent. Although several domestic and semi-domestic species (sheep, goats, horse, cattle, reindeer) are affected by large carnivore predation in Europe (Linnell and Cretois, 2020), we narrowed our analyses to sheep depredation by the four European large carnivores, in order to keep model complexity to a manageable level and allow a more reliable interpretation of model results. Moreover, sheep alone represent more than 60% of all the compensation payments in Europe, with such percentage reaching 80% in some cases (Linnell and Cretois, 2020), thus making sheep depredation the most widespread, frequent, and expensive form of material impact of large carnivores on human interests.

In particular, we tested the following predictions, regarding the depredation process:

1. Large carnivore abundance in each administrative unit is a predictor of the number of verified sheep depredations.
2. There are differences among the four large carnivore species in terms of their relative impact on livestock husbandry, with bears, which are only occasional predators, exhibiting a lower impact than the other three species.
3. The geographic variation in land use, habitat types and landscape structure is related to the spatial variation in verified depredations.
4. The impact by large carnivores in recently re-colonized areas is higher than in the areas in which humans and large carnivores shared a longer history of co-occurrence.
5. A higher number of alternative wild ungulate species corresponds to a reduction in large carnivore impact on sheep in each administrative unit.

2. Methods

2.1. Data collection

We obtained data from 10 European countries, namely Croatia, Estonia, Finland, France, Greece, Italy, Norway, Slovenia, Sweden and Switzerland. Data from Italy were limited to the Alpine wolf and bear populations (Chapron et al., 2014). We chose the above-mentioned countries and regions because they allowed us to cover a north-south geographical gradient of the European continent, which involved a range of environmental, social, and economic differences, such as climate, habitat productivity, availability of wild prey, national economic wealth, traditions and practices in animal husbandry, etc. The choice was also based on the availability of organised and accessible national or regional datasets, which contained the type of information needed to compile the review and run the subsequent analyses. We collected data according to the NUTS3 (Nomenclature of Territorial Units for Statistics) classification, which is the highest resolution of the hierarchical system which divides the territories of the European Union for statistical purposes. Such classification corresponds in most countries to the administrative level of departments, cantons, provinces, etc.

For each year and each NUTS3 unit, we collected data about the estimated abundance of each large carnivore species whenever available, or the minimum number of individuals known to be present. We also collected the number of registered sheep and the number of sheep compensated as killed by large carnivores. Additionally, for each country, we compiled a summary description of the prevalent sheep husbandry practices, of the most common damage prevention systems employed by sheep farmers, and of the main characteristics of the national compensation system, whose results are summarized in Table A4 and in the Appendix 1 in the Additional Supporting Information. As data on husbandry practices was mostly available at the national scale, and never at the NUTS3 spatial resolution of our study, we did not explicitly include it in the following statistical analyses, but rather used it as a qualitative set of information to discuss the results of the SAR models. We received data from national and regional wildlife agencies, from published literature and reports, as well as from researchers and practitioners. The complete description of the data sources for each data type included in the review is available in tables A1, A2 and A3.

2.2. Modelling

To explore the main patterns in the number of sheep heads compensated each year as killed by large carnivores in the 10 countries included in the study, we used Bayesian hierarchical SAR Poisson models (Zhu et al., 2008) in Jags (Plummer, 2003). Our approach was similar to the one usually applied for risk modelling or species-environment predictive spatial models, but with compensated sheep as the response variable. Similar approaches have been used by Bautista et al. (2017) for brown bear damage in Europe, and by Treves et al. (2011) for wolves in the U.S.

One of the objectives of our study was to test and estimate the effect of large carnivore abundance at a large scale on the expected number of annually compensated sheep (objective 1). As not all countries included in the study were able to provide large carnivore abundance data at the NUTS3 spatial resolution, the surface of the species distribution area in each sampling unit was the only common metric we could resort to. The relationship between the area occupied by a species and the number of individuals living in that area,

though, is not expected to be a constant (Carbone and Gittleman, 2002). Habitat productivity, body size and several other factors influence home range size and the area needed to sustain a given animal population (Harestad and Bunnell, 1979; Nilsen et al., 2005). Therefore, the use of distribution as a proxy for abundance, at the scale of the whole European continent, could potentially introduce a bias in all subsequent analyses. To account for and prevent such bias, we built the first level of the hierarchical SAR Poisson model (Eq. (1)) to analyse the species-specific area/abundance relationship for each of the four large carnivore species. To this aim, we defined the number of individuals of each large carnivore species s detected in each NUTS3 region i on year t (period 2010–2015) as a Poisson random variable with parameter ($\gamma_{s,i,t}$). This parameter was modelled (on the log scale) as a function of the area occupied by the species in the same region. To account for the large-scale spatial variation in climate and habitat productivity, we included the latitude of each NUTS3 region in the model as a predictor. As large carnivore home range size is also influenced by prey availability, we used presence/absence distribution maps for the main wild ungulate species in Europe (roe deer *Capreolus capreolus*, red deer *Cervus elaphus*, wild boar *Sus scrofa*, moose *Alces alces*, chamois *Rupicapra rupicapra*, wild reindeer *Rangifer tarandus*; Linnell and Cretois, 2020) and calculated the number of wild ungulate prey species available in each NUTS3 unit. We used this factor variable as an additional predictor for large carnivore abundance. Additionally, we used sheep abundance in each NUTS3 unit as a predictor of large carnivore abundance, to test if any predator numerical response occurred. To account for the spatial correlation of neighbouring NUTS3 units, we also added a normally distributed individual random term $\varepsilon_{i,s}$ for each region i and species s in the model. The random effect had mean equal to zero and variance defined as $\sigma^2(D - \phi W)$, in which σ was the standard deviation, W was a binary adjacency matrix (1 = bordering, 0 = not bordering), D was the diagonal matrix of W, and ϕ was an estimated parameter controlling the intensity of the spatial correlation. Finally, we also added a time-dependent random effect $\tau_{t,s}$ accounting for the nested structure of the data, in which six abundance data points (one for each year) were available for each large carnivore species in each region. A log link function was used to run the Poisson regression model.

$$\begin{aligned} log\left(\gamma_{s,i,t}\right) = \alpha_{0,s} + \quad \alpha_{1,s} * LCspecies_s + \quad \alpha_{2,s} * LCarea_{s,i} + \\ \alpha_{3,s} * latitude_i + \quad \alpha_{4,s} * alternative_{prey_i} \quad + \quad \alpha_{5,s} * sheep_i \\ + \quad \varepsilon_{i,s} + \quad \tau_{t,s} \end{aligned} \tag{1}$$

The second level of the Bayesian hierarchical model (Eq. (2)) was meant to interpret part of the variation in the number of compensated sheep heads in each NUTS3 unit and in each country. Model structure was similar to the one used for the first level of the model. We initially ran the model using a common intercept and slope for all the four large carnivore species, in order to reveal any common pattern in compensation levels. Then, we ran another version of the model, which included separate intercepts and slopes for each large carnivore species, with the aim to highlight species-specific patterns and the relative impact of each large carnivore species (objective 2). We used sheep abundance and the index of large carnivore abundance (derived from Eq. (1)) as linear predictors, in order to include the numerical component of the predation process and to test to what extent the area occupied by large carnivores in each NUTS3 unit affected the resulting number of compensated losses. We also included three large-scale spatial variables, to test for the effect of land use and landscape structure on the sheep compensation process, under the expectation that more forested areas, rugged areas, and ecotone areas would exhibit a higher impact by large carnivores (objective 3). Using a Digital Elevation Model for Europe (DEM, resolution 25 m) and the Corine Land Cover map (EEA-ETC/TE, 2002), we extracted the proportion of land occupied by forest (conifer, broadleaved or mixed), the edge density index as an estimate of the availability of ecotone areas, and the landscape ruggedness index for each NUTS3 spatial unit. Following Riley et al. (1999), the ruggedness index was calculated as the average of the squared differences in elevation between a centre cell and the eight cells immediately surrounding it. The topographic ruggedness index is then derived by taking the square root of this average. We added these variables as three additional linear predictors in the Poisson regression model (Eq. (2)), under the hypothesis that areas of interspersed forest patches, especially in rugged terrains, would reduce visibility, prevent the effective use of protection measures such as fences, and increase livestock accessibility to large carnivores.

To test for the effect of time since large carnivore re-colonization (objective 4), we overlaid the study area with the estimated large carnivore distribution referring to the period 1950–1970 (Chapron et al., 2014), and produced a binary variable for each NUTS3 region, indicating if a given large carnivore species was already present at that time or returned in more recent years. Similarly to what was done for the first level of the hierarchical model, we used the number of wild ungulate prey available in each sampling unit as an additional predictor of compensation levels, under the hypothesis that a wider spectrum of alternative wild prey would reduce the number of compensated sheep heads (objective 5). Three additional random effects were added to the depredation model: an individual random effect $\mu_{i,s}$ for each region i and species s, accounting for the spatial auto-correlation in the data in the same way as described for the first level of the hierarchical model; a time-specific random effect $\theta_{t,s}$ for each year t and species s; a country and species-specific random effect $\rho_{k,s}$, which estimated the residual variation in compensated sheep heads, which could not be explained by the other terms of the model. With respect to the conceptual differentiation between ecological and anthropogenic predictors of large carnivore damage, the explicit variables represented the ecological component of the process (numerical, spatial, behavioural), whereas the effect of the unexplained factors was summarized through the random effects.

$$log(\delta_{s,k,i,t}) = \beta_{0,s} + \beta_{1,s} * \gamma_{s,i,t} + \beta_2 * sheep_i + \beta_3 * ruggedness_i + \beta_4 * forest_i + \beta_5 * edge_i + \beta_6 * historical_{dist\,s,i} + \beta_7 * alternative\_prey_i + \rho_{k,s} + \mu_{i,s} + \theta_{t,s} \quad (2)$$

Finally, we also predicted the number of compensated sheep heads using a model which excluded the individual and country-specific random effects. This allowed us to produce an estimate of what compensation levels would be expected in a country if only the numerical, spatial and behavioural component of the depredation process were operating. The comparison of these predictions with the observed compensation levels allowed us to infer the positive/negative effect of the additional country-specific components that were not explicitly tested in the depredation model. We also estimated the proportion of variance explained by the two models (R^2), in order to highlight the relative importance of the explicit and implicit terms in the compensation process. To this aim, we calculated the difference between the model residuals and the residuals of an intercept-only model (Nakagawa and Schielzeth, 2013). We used a log link to run also this part of the Poisson model. Models converged in Jags, using 10,000 iterations and a burning phase of 5000 iterations.

3. Results

3.1. Descriptive statistics

Overall, the 10 countries considered in the analysis hosted about 26 million sheep, of which about 7.6 million (29%) overlapped with the distribution of at least one large carnivore species (Table 1). In the same geographic area, a minimum of about 2000 wolves, 7600 bears, 1300 wolverines and 5600 lynx were estimated to live (Table 1), for a total of 16,500 individuals.

On average, about 35,000 sheep (SD = 4110) were annually compensated in the ten countries as killed by large carnivores (Table 1 and Fig. 2). Out of them, about 45% were recognized as killed by wolves, 12% by bears, 24% by wolverines and 19% by lynx. On average, 2.12 sheep were annually compensated for each large carnivore individual, but large species-specific differences emerged: 7.6 sheep were compensated for each wolf, 0.55 sheep for each bear, 6.55 for each wolverine and 1.24 for each lynx.

In absolute terms, Norway was the country with the highest number of compensated sheep heads (N = 19,543, 54% of the total, see Table 1) followed by France (N = 5574) and Greece (N = 4201). Finland, Sweden and Switzerland exhibited the lowest absolute numbers of compensated heads, with an average of less than 1000 compensated heads per year (Table 1). In relative terms, Norway was still the country exhibiting the highest costs of sheep-large carnivore co-occurrence, as about 5.6% of all sheep living in the country were compensated as killed by one of the four large carnivore species each year. All the other countries lost less than 1% of their national sheep flock to large carnivores.

3.2. Drivers of damage compensation across Europe

For all four large carnivore species, the first level of the Bayesian hierarchical model highlighted a positive relationship between the area occupied by the species in each NUTS3 unit and the number of individuals detected by the monitoring system. Species-specific slopes for this relationship varied between 0.048 for lynx (SD = 0.015, 95% CIs = 0.019 – 0.079) and 0.327 for wolves (SD = 0.074, 95% CIs = 0.181 – 0.470). The effect of latitude on the area/abundance relationship was only significant for wolves (β = −0.069, SD = 0.030, 95% CIs = −0.139 to −0.019), but not for the other three species. At the average latitude, 549 km^2 of permanent distribution area were needed to host one wolf territory (Fig. 3a). This value increased to 1369 km^2 at the northernmost latitude and decreased to

Table 1
Summary statistics of sheep husbandry, large carnivore estimated abundance and total compensated sheep heads in the 10 European countries included in the large carnivore impact analysis, years 2010–2015.

Country	Sheep abundance in large carnivore distribution areas (thousands)	Large carnivore abundance (Minimum number detected)				N. compensated heads per year (mean)				
		Wolf	Bear	Wolverine	Lynx	Wolf	Bear	Wolverine	Lynx	Total
Croatia	418	193	1000	0	50	1674	1	0	0	1675
Estonia	91	230	650	0	460	806	5	0	23	834
Finland	134	157	1700	240	2485	85	164	0	32	281
France	998	250	25	0	108	5285	289	0	0	5574
Greece	4729	700	450	0	0	3972	229	0	0	4201
Italy (Alps)	217	157	35	0	0	251	117	0	0	368
Norway	330	33	105	360	396	2037	2942	8469	6095	19,543
Slovenia	81	46	608	0	20	1083	478	0	6	1567
Sweden	489	295	3300	692	1650	308	23	0	463	794
Switzerland	224	13	0	0	166	220	0	0	16	236
Total	7711	2074	7873	1292	5335	15,721	4248	8469	6635	35,073

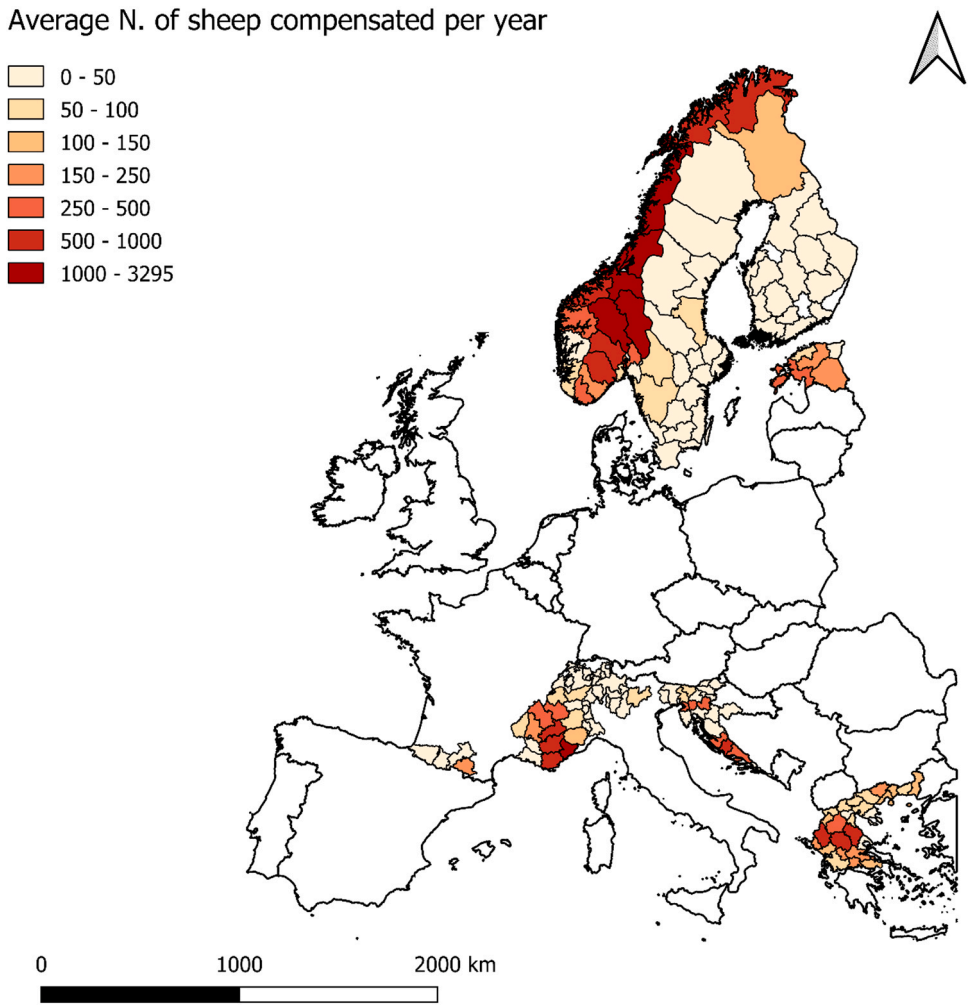

Fig. 2. Average number of sheep heads totally compensated as killed by large carnivores in 171 administrative units and 10 countries in Europe (NUTS3 level).

216 km^2 at the southernmost latitude. The estimated values were consistent with field-based estimates derived from radio-collared wolves in Europe (Kusak et al., 2005; Mattisson et al., 2013; but see Mancinelli et al., 2018). The model also revealed an effect of the number of wild ungulate species on the area/abundance relationship for wolves ($\beta = 0.498$, SD = 0.149, 95% CIs = 0.219 – 0.788) and lynx ($\beta = 0.933$, SD = 0.287, 95% CIs = 0.406 – 1.485). As shown in Fig. 3b for wolves, a higher number of wild prey species corresponded to a smaller area required for one wolf territory. The model revealed no significant numerical response of large carnivore abundance to variations in sheep abundance.

The second level of the Bayesian hierarchical model revealed a positive relationship between the area occupied by large carnivores in each NUTS3 administrative unit and the number of compensated sheep (objective 1; $\beta = 0.012$, SD = 0.001, 95% CIs = 0.011–0.013). A positive relationship also existed between sheep abundance and the number of sheep compensated ($\beta = 0.084$, SD = 0.029, 95% CIs = 0.024–0.141). Both these slopes refer to a model comprising a pooled effect for all the four large carnivore species considered in the analysis. When parameterizing the model with species-specific intercepts and slopes, the model revealed significant differences between the four large carnivore species (objective 2). After accounting for all the other factors, verified wolf damage was significantly higher than that attributed to the other three species, as indicated by the higher intercept value in the model. In addition, wolves were the only species exhibiting a positive relationship between their distribution area and the expected number of compensated sheep per year ($\beta = 0.131$, SD = 0.004, 95% CIs = 0.123–0.139). The model reported no significant effects of any of the landscape variables (objective 3), but it did reveal an effect of the historical continuity of large carnivore presence in reducing the expected number of compensated sheep per year (objective 4; $\beta = -0.973$, SD = 0.471, 95% CIs = −1.914 to −0.069). The number of alternative wild ungulate prey species available in a given geographic area did not correspond to a reduction in the expected large carnivore impact on sheep farming (objective 5; $\beta = -0.042$, SD = 0.247, 95% CIs = −0.516 to 0.449).

The estimation of random effects in the second level of the hierarchical model revealed large differences in the expected compensation levels among countries and among large carnivore species, a pattern that was also confirmed by the comparison between

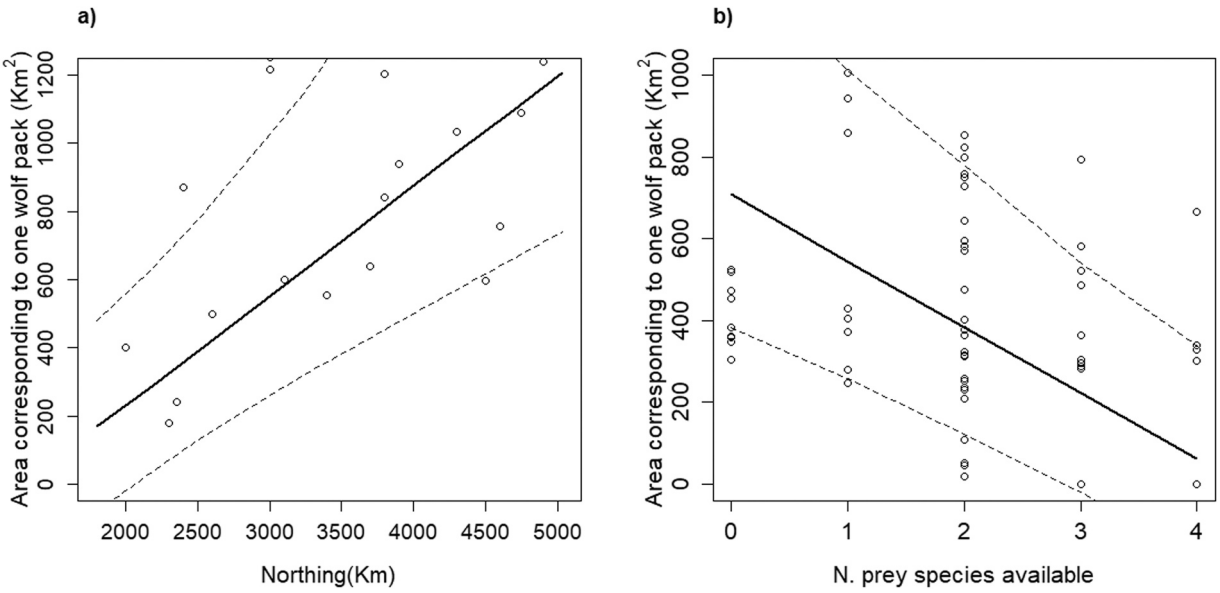

Fig. 3. Relationship between latitude (a), the number of wild ungulate prey species available (b) and the area corresponding to one wolf territory in Europe.

the observed number of sheep annually compensated and the one predicted by a model which accounted only for the ecological component of the process (Fig. 4). Norway, for example, was predicted to generate 4348 compensated sheep per year, as opposed to the 19,543 observed. Similarly, France reported more than 5000 compensated heads per year, while the explicit part of the model predicted no more than 400. On the other hand, Sweden and Finland generated only 10–15% of the damage levels predicted by the number of large carnivores present in those countries and by the size of their national flocks (Fig. 4).

Based on the R^2, the full model explained 62% of the variation in the number of compensated sheep per year in each NUTS3 region. A model including only the fixed terms (predator and prey abundance, landscape structure and the historical large carnivore presence) explained 13% of the variation, leaving the remaining 49% to the random part.

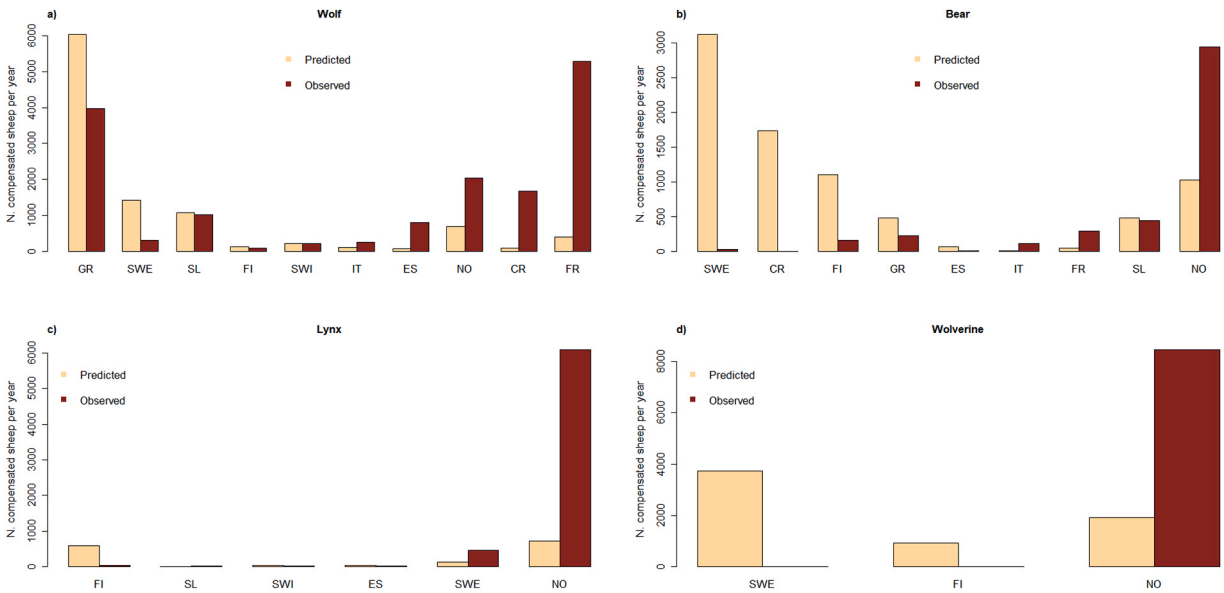

Fig. 4. Comparison between the observed sheep compensation frequencies referring to four large carnivore species in 10 European countries and the ones predicted by the Bayesian hierarchical Simultaneous Autoregressive model (CR = Croatia; ES = Estonia; FI = Finland; FR = France; GR = Greece; IT = Italy (Alps); NO = Norway; SL = Slovenia; SWE = Sweden; SWI = Switzerland).

4. Discussion

4.1. Spatial variation in the observed patterns

Our analysis revealed a wide variation with respect to all the components of the sheep depredation and compensation process in the ten countries examined. Large carnivore densities, husbandry practices, protection measures, compensation systems, length of time exposed to large carnivores, etc., all varied among and within the European countries considered in the study. Compensation systems mainly exhibited a country-to-country variation, except for the Italian case in which the issue is managed at the regional level, with each administration following a different legislation and a different set of procedures. All the other variables considered, though, varied widely among the different NUTS3 units within the same country. In particular, husbandry practices and the use of livestock protection measures, which can have a strong effect on the reduction of large carnivore impact (Eklund et al., 2017), did not exhibit a consistent pattern in most of the countries (see Table A4 and Appendix 1). Instead, they varied from region to region, likely as the result of a combination of environmental, social, and historical processes, and due to the complexity of their implementation. Such multi-scale spatial variation is at the core of the challenges that human-large carnivore coexistence faces (Linnell, 2015): large carnivore populations are inherently trans-boundary and need a trans-boundary approach to their management (Linnell and Boitani, 2012), but several of the factors that determine the magnitude of their impact on human activities are influenced by local factors and require a local approach to be fully understood (van Eeden et al., 2018).

Among such local factors, the structure and effectiveness of the different damage compensation systems is expected to be a relevant component, which calls for caution in the interpretation of model results. It should be noted that our analysis mainly addressed the management dimension of large carnivore damage on livestock (i.e. basing the data on compensation payments), not the true depredation levels. Impact estimated through compensation inevitably filters true depredation levels by accounting for at least two fundamental components: the willingness of the afflicted farmers to make a claim, and the rules and procedures of the compensation scheme in place. Both these components varied widely between and sometimes within (e.g., Italy) the countries included in our study. In countries in which compensation for damage is inefficient or just slow, farmers often avoid reporting a suspected depredation and do not claim compensation. "Marino et al. (2016) found that only 5% of the farmers in central Italy subscribed an insurance for having damages compensated, while at least 34% of the farmers suffered damages without declaring it to the authorities" Consequently, large carnivore depredation levels can be underestimated when these conditions occur. On the other hand, countries with subsidised economies can use loose criteria for damage compensation as a way to increase tolerance towards carnivores, reduce social conflict, or simply as a political tool to generate consensus. In Norway, for example, only a small proportion of the sheep that go missing during summer are found and inspected (typically from 5% to 10%), but compensation payments are paid also for many of the sheep for which there is no verification of their cause of death (Mabille et al., 2015). This can cause an overestimation of the damage caused by large carnivores, when depredation is analysed through the filter of such liberal compensation criteria. Therefore, caution should be used when comparing the estimated impact levels among countries, because different attitudes and compensation schemes can play a role in the country-to-country differences. On the other hand, some of the differences revealed in our study are so large that their interpretation should be robust to the potentially confounding effect of the different national compensation schemes. To this regard, our analytical framework provided us with an answer to all the six research questions.

4.2. Drivers of large carnivore impact

The first prediction we were able to test regarded the link between large carnivore distribution, their abundance, and the resulting damage on livestock. The debate about large carnivore impact often focuses on the questions of how many carnivores occur in a certain area, if they should be numerically reduced, and, if so, how many should be culled. On this and similar issues, the debate is usually highly polarized, under the implicit assumption that numbers are crucial when it comes to large carnivore damage (Treves et al., 2016). Overall, the fact that a linear relationship existed between the area occupied by a species in each NUTS3 unit and the number of individuals detected revealed that the use of large carnivore distribution area, corrected by the above-mentioned factors, was a reliable proxy for large carnivore abundance in each NUTS3 unit. Moreover, distribution and abundance in this context need to be viewed at different scales. Distribution may more directly account for a geographic effect of large carnivore presence, which generates a cumulative impact at the scale of a country. This is exactly the type of impact we explored in our work. Abundance can be relevant at the local scale (i.e., management unit), where more predators have higher chances of causing a higher number of livestock depredations. Moreover, it should be stressed that also competition between sympatric large carnivore species can potentially affect the species-specific depredation levels. Although we were not able to directly test such effect of competition in our dataset, previous local studies have highlighted responses and diet shifts by one predator after re-colonization by a competing species. Leopards (*Panthera pardus*) in India, for instance, shifted their diet towards a significantly higher intake of domestic prey, after tiger (*Panthera tigris*) recovery and increased competition for wild prey (Harihar et al., 2011).

Regarding the link between large carnivore abundance and depredation levels, our results provide a nuanced answer. In the case of wolves, and looking at the large-scale continental gradient, a larger distribution (and likely higher abundance) implied higher levels of reported depredation; on the other hand, the link between large carnivore distribution and damage was weak and not significant for the other three large carnivore species, although the model suggested a positive relationship for them, too. Bautista et al. (2019) also found contrasting evidence of the link between large carnivore numbers and compensated damage. They revealed a positive relationship between the rate of range change in the last five decades and the costs for damage compensation in brown bears, but not in wolves and lynx (Bautista et al., 2019). These results suggest that large carnivore numbers cannot be disregarded as irrelevant factors

in livestock damage, and that management actions aimed at influencing them should be evaluated as an option, because they can affect damage. On the other hand, numbers alone are likely to be poor and weak predictors of large carnivore impact. Our analytical framework shows that a few carnivores can produce high levels of damage, when the sum of the environmental, historical, social and economic system favours it, whereas large populations can produce a very limited material impact, when the same components of the system reduce the probability that depredations occur.

Norway and Sweden, for example, share similar habitat and climatic conditions (although rather different landscape and terrain structures) and they have both experienced an expansion of large carnivore ranges and numbers during recent decades, after a long period of absence or drastic reduction (Chapron et al., 2014). They display large differences, though, when it comes to the prevalent sheep husbandry practices and to the characteristics of their damage compensation systems. Sheep in Norway are traditionally free-ranging and unguarded on summer pastures and do not gather in flocks, whereas in Sweden the vast majority of them are raised in fenced fields all year round (Linnell and Cretois, 2020, see also Table A4). Also, in Sweden the vast majority of compensation claims are based on a field inspection by state inspectors and only verified depredations are compensated, whereas in Norway only about 5–10% of damage compensations stem from a field inspection of a carcass, whereas the remaining 90–95% refers to payments made for missing animals which are assumed to be killed by large carnivores (Swenson and Andrén, 2005). Likely as a result of these social and administrative differences, Norway exhibited four times more compensated sheep heads than it would be expected based on large carnivore abundance in the country, whereas in Sweden compensation levels were about six times lower than expected by large carnivore abundance (Fig. 4).

A similar example of how relevant the anthropogenic component of the depredation process can be is provided by the Croatian results. Croatia hosts about 1000 bears and 200 wolves, which overlap with about 400,000 sheep (Table 1). While there are by far more bears than wolves in the country, bear impact on livestock is close to zero (Majić et al., 2011), whereas about 1700 sheep are compensated each year as killed by wolves (Majić and Bath, 2010). A partial explanation for such differences lies in the fact that bears are omnivorous and feed on many other sources besides livestock, while wolves rely almost entirely on meat for their diet. Moreover, bears only partially overlap with the distribution of sheep farming areas in the country. Also, the bear population in Croatia is extensively supported through supplemental feeding. Still, other components need to be considered. Bears are traditionally managed as a de facto game species in Croatia and the maintenance of a large population secures income for hunters in rural areas (Knott et al., 2014). Moreover, bear damage to sheep (and to beehives) is paid by local hunting associations, which are willing to pay the costs of compensation as a way to gain social acceptance for bear presence in the country (Majić et al., 2011). The whole system, which benefits from a traditional human-large carnivore relationship based on hunting and management at the local level, seems to be both socially and economically sustainable. On the other hand, wolves in Croatia are not a game species and therefore not perceived as a recreational or economic resource for hunters. Rather, they are seen mainly as human competitors both for livestock and for game, with social conflict being especially high in recently re-colonized areas (Majić and Bath, 2010). In this sense, the wolf damage compensation system in Croatia is similar to the ones commonly found in most European countries: compensation is managed at the national level and livestock losses are refunded after a field inspection, but farmers are often unsatisfied with the amount of the compensation and the long transaction times (Kaczensky et al., 2012). Overall, the number of wolf-related compensation payments in Croatia is several times higher than it would be expected based on wolf population size in the country, whereas bear damage is much lower than predicted by bear abundance (Fig. 4). Such differences in depredation patterns between two large carnivore species within the same country also highlight that solutions to human-large carnivore coexistence issues are bound to be species-specific, and that no recipes are valid for all contexts and all species. While comparative studies are useful to reveal patterns, actions, and policies, they should be grounded in each local context and finely tuned for each large carnivore species.

This also highlights a partial limitation of our continental approach to the study of large carnivore impact, as some information on the relevant factors in the depredation process were simply not available at the appropriate local scale and for the appropriate geographic extent required. One component we could not explicitly test in our model is the potential confounding effect of dog depredation on livestock. Free-ranging and stray dogs are common in some European countries, especially in the southern portion of the continent (e.g., Ciucci and Boitani, 1998), whereas they are usually rare further north. We know that dogs can and do kill livestock, and that field methods are not always effective in telling apart wolf and dog predation signs. In Greece, for instance, about 6–10% of the compensations paid for sheep depredation are due to dog attacks (Iliopoulos, personal communication), whereas in Estonia up to 15% of sheep depredation can be due to dogs, with about 7% of the field inspections mistakenly attributing dog depredation to wolves (Plumer et al., 2018). The issue is less relevant for the other large carnivore species, whose killing patterns are easier to distinguish. Ideally, such a potentially confounding factor should be explicitly accounted for in a statistical analysis of large carnivore depredation at the continental scale, but reliable data on the incidence of dog depredation on sheep were not available at the geographic extent of our study. Further adding to the complexity of wolf-dog-sheep interactions is the fact that wolves kill both sheep and dogs. Therefore, wolf presence can have a direct negative effect on livestock through depredation, but also an indirect positive effect through a reduction of free-ranging dogs' density in the area. While the complexity of such interactions goes beyond the general scope of our study, it should be noted that unaccounted dog depredation on sheep could have caused an overestimation of wolf impact on sheep, especially in southern European countries. On the bright side, molecular methods based on saliva samples are becoming increasingly common during field inspections for suspected large carnivore depredations (Sundqvist et al., 2007). The increasing availability of reliable species identification tools will allow the production of more accurate estimates of the relative impact of wild and domestic predators on livestock.

An additional, potentially relevant factor is represented by the possibility that part of the predator-related mortality might be compensatory with respect to other sources of sheep mortality. No straightforward conclusion, though, can be drawn about it. There are contexts, such as Norway, in which it is reasonable to think that some part of large carnivore predation on sheep might be

compensatory. Sheep are left unguarded in a rough terrain in boreal forests or tundra and do not have a strong flocking behaviour. Moreover, weather can be inclement also in summer, and human surveillance is absent or minimal, so that ill or wounded animals can roam alone for days, and eventually be killed by predators. All these elements point in the direction of some compensation in predator-related mortality. Accordingly, Mabille et al. (2016) have shown that sheep mortality in Norway is related to large carnivore density, but also to food availability and spring weather conditions. Tveraa et al. (2014) presented similar results for semi-domestic reindeer in Norway. Such situation of wide ranging, unguarded domestic animals living in harsh environments is also similar to the one described by Allen and Sparkes (2001) for dingo predation on sheep in Australia. A rather different situation, though, exists in most of the other European countries we examined. Sheep are almost entirely fenced and guarded in Sweden, Estonia, and Finland. In the Alpine countries, such as France, Italy, and Switzerland, large but compact flocks are usually kept in high mountain pastures in summer, where human surveillance is almost uninterrupted and supported by life-guarding dogs, with night fencing being a common practice. Similar practices are also used in Greece (see Appendix 1). In these conditions, the mechanisms leading to compensatory predator-related mortality, such as long chasing, or the solitary roaming of injured, ill animals, are supposed to be harder to realize, suggesting that most of large carnivore predation in these contexts should be additive. Moreover, the existence of surplus (or even massive) killing events, would go in the direction of a super-additive mortality. Van Liere et al. (2013), for instance, estimated an average of 4 sheep killed per attack by wolves in Slovenia; in the Arezzo province in Italy, Gazzola et al. (2008) reported that in 30% of wolf attacks more than 10 sheep or goats were killed. Surplus killing, though, is not a universal, and in some cases not even a common, trait of large carnivore predation on domestic animals: Jeremić et al. (2014) reported 1.7–2.1 sheep killed per attack by wolves in Croatia, with a decreasing trend during their study period; Ciucci and Boitani (1998) estimated that only 2.3% of wolf attacks on sheep in Tuscany produced massive killings, but accounted for 19% of all sheep losses.

4.3. Management implications

The good news resulting from our analysis of large carnivore depredation in Europe is that time seems to play in favour of a progressive reduction in the costs associated with human-large carnivore coexistence. Despite the potentially confounding effect of the unaccounted factors, our model provides a clear indication that longer periods of exposure are associated with a reduced impact of large carnivores on livestock. It is likely that the factor variable we used as a proxy for sympatry times was strongly correlated with a set of other variables, such as the level of human guarding of flocks, the use of livestock guarding dogs and electric fences, the choice of appropriate flock size, etc., which have been shown to reduce depredation levels in local studies (Eklund et al., 2017). Therefore, we could expect that time will allow the re-establishment of the appropriate co-adaptation tools (*sensu* Carter and Linnell, 2016), which in turn will favour a reduction of the costs associated with sharing space with large carnivores in multiuse landscapes. However, there may well be more challenges with restoring traditional grazing practices with their associated protection measures in areas where they have been lost, as compared to maintaining them in areas where their use has been continuous. Moreover, the entire livestock industry is slowly changing due to social and economic drivers, which are causing the gradual abandonment of pastoral lifestyles (Linnell and Cretois, 2020). Without the appropriate management of the issues related to large carnivore impact on livestock husbandry, time may correspond to a progressive disappearance of small livestock breeding. This trend is further facilitated by the rules provided for by the Common Agricultural Policy (CAP, Scown et al., 2020) that has been applied in EU countries, and which tend to favour holdings with large numbers of heads, often difficult to manage in a compatible way with the presence of predators (Iliopoulos et al., 2009). Finally, large carnivore populations are still expanding in most of the European countries (Chapron et al., 2014), making the economic sustainability of the whole compensation model unsure. Other models, such as risk-based or insurance-based compensation, are being tested, with contradictory results about their effectiveness and social acceptance (Marino et al., 2016). To be effective, compensation programs should be coupled with a set of reliable procedures to verify alleged claims, and with a parallel system of enforcement of protection measures, which stimulates livestock owners to adhere to minimal standards of responsible husbandry practices. Lacking such standards, compensation costs may become (and in some cases have already become) an unsustainable expense, within socio-ecological systems in which damage is a chronic trait (Gervasi et al., 2021).

The other relevant issue is that social conflict is often poorly related to material impact (Linnell, 2013). So, while technical tools and the appropriate mitigation policies might decrease the material impact of large carnivore presence on human livelihoods, the socio-cultural context may still generate conflict within and between stakeholders, unless careful attention is paid to governance structures (Linnell, 2013). Therefore, responsible agencies should try and focus their attention both on compensation and co-adaptation. In this perspective, the acceptance of all the regulations connected with damage reduction and compensation by the local farmers can be the result of a participatory process among all interest groups, with rules collectively designed and frequently revised. While the reduction of large carnivore impact is a fundamental pre-requisite for the establishment of a sustainable long-term coexistence, there is also an urgent need for those participatory actions that consider the socio-cultural component of the process (Redpath et al., 2013; Salvatori et al., 2020) and that are more likely to increase the speed of the human-large carnivore re-adaptation process, thus progressively moving from an armed co-occurrence to a sustainable coexistence.

CRediT authorship contribution statement

V. Gervasi, O. Gimenez, J. Linnell and L. Boitani conceived the ideas and designed the methodology; All authors contributed to data collection; V. Gervasi and O. Gimenez analysed the data; V. Gervasi, O. Gimenez, J. Linnell and P. Ciucci led the writing and revising of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2021.e01798.

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