

Large carnivore damage in Europe: Analysis of compensation and prevention programs



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ABSTRACT

The mitigation of conflicts associated with large carnivore damage to livestock and agriculture is pivotal to their conservation. We evaluate current programs to compensate and prevent large carnivore damage in 27 European countries and the factors related to the economic costs of these programs. Overall, high compensation costs are associated with free-ranging livestock (68% of total costs) and with national economic wealth. Contrary to general belief, the return of large carnivores does not always translate into higher compensation costs. We identify a tendency towards prioritizing compensation over prevention; only a few wealthy countries pay the majority of the money allocated for prevention programs to adapt husbandry practices to the presence of large carnivores. We conclude that programs mainly focused on paying large compensation amounts will often fail to build tolerance towards predators. To mitigate conflicts and optimize the cost-effectiveness of publicly funded measures, responsible agencies should be proactive, focus on prevention-based policies and periodically evaluate

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the effectiveness of compensation and prevention programs in an adaptive manner. With this purpose and to identify further solutions for conflict mitigation, we call for a pan-European database of damage occurrence, management actions and associated costs.

1. Introduction

After centuries of decline, the density, abundance, and distribution of large carnivore populations have increased in most European countries during the last decades (Chapron et al., 2014). This recent recovery is due to legal protection, reforestation, the recovery of wild prey populations, and an increased social tolerance towards wildlife (Boitani and Linnell, 2015). Nevertheless, many of these populations are still threatened and their long-term viability relies on effective conservation efforts. A key conservation issue is the socio-political conflict that arises from the presence of large carnivores and the damage they do to human property, such as livestock (Can et al., 2014). This is a particularly sensitive problem when large carnivores return to areas where people have abandoned husbandry practices, which prevented damage (Linnell, 2013). Such situations can lead to high economic losses and intense social conflicts between conservationists and the farmers that feel threatened by the presence of large carnivores (Redpath et al., 2013). Accordingly, we define damage to human property (and the associated economic losses) as a wildlife impact on human livelihood that may fuel conflicts between different stakeholder groups over the desired conservation or management targets for damage-causing species.

Negative attitudes towards carnivores can hinder conservation efforts as they can result in illegal killings and public opposition to management policies (see Dressel et al., 2015). However, attitudes towards carnivores and their management are likely to change as circumstances change (e.g., Majić et al., 2011). In Europe, for instance, there is a trend for attitudes to become less positive with perceived increases in the abundance of large carnivores and risk of damage (Dressel et al., 2015; Eriksson et al., 2015; Heberlein and Ericsson, 2003; Majić et al., 2011). Thus, successful carnivore conservation largely depends on management policies that aim to maintain accepted population size of carnivores and enhance tolerance through ensuring low damage occurrence.

Wildlife agencies often implement compensation programs to mitigate conflicts emerging from damage-related losses and, therefore, to increase tolerance towards large carnivores of the local stakeholders sharing the landscape with these species (Boitani et al., 2010). Even though these programs have been operating since 1970 in many European countries (Bautista et al., 2017; Boitani et al., 2010), their conservation outcomes have been rarely evaluated and their effectiveness is still under debate (Ravenelle and Nyhus, 2017). Major flaws in compensation programs are insufficient and/or delayed payments, inefficient administrative procedures, failure to assess damage verification protocols, failure to condition compensation to prevention and ignoring the opinion of local stakeholders (Bulte and Rondeau, 2003; Marino et al., 2016; Nyhus et al., 2005; Ravenelle and Nyhus, 2017). Indeed, when responsible agencies tackle these limitations, compensation programs can successfully reduce the occurrence of damage and improve tolerance (Dalmasso et al., 2012; Stone, 2009).

In Europe, most large carnivore populations are transboundary, spanning up to eight countries (e.g., Carpathian lynx population; see Tables A1 and A2 in the Appendix A). Yet, the legal responsibility to conserve large carnivores falls on national and regional administrative levels. Despite the efforts to coordinate the management of large carnivores in Europe at the population level (Trouwborst, 2015), improving transboundary cooperation is still a key action for the conservation of large carnivores in the European Union (Boitani et al., 2015). In terms of damage management there is no common policy in Europe; policies differ among and within countries, even for shared

carnivore populations. Compensation programs are part of damage management policies and they differ between countries, leading to differences in the quantity of damage compensation across Europe (Bautista et al., 2017).

The main goal of this policy analysis is to identify weaknesses and strengths of current policies to manage large carnivore damage in Europe and to give recommendations for effective conflict mitigation. To this end, we provide an overview of the damage compensation programs in 27 European countries involving four species of large carnivores: the brown bear (*Ursus arctos*), the Eurasian lynx (*Lynx lynx*), the grey wolf (*Canis lupus*), and the wolverine (*Gulo gulo*). We compiled data on the type and costs of compensation programs and analyzed these costs in relation to different socioeconomic metrics. We quantified the costs of compensation programs in each country, based on Kaczensky et al. (2012). We standardized the costs of compensation across countries using purchasing power parities and divided the compensation expenditures by the estimated number of each species in each country or region separately (see Online Appendix for detailed explanation of the methods). We investigated the link between compensation expenditures and husbandry practices, the countries' economic status, the rate of large carnivore recolonization and tolerance towards large carnivores. In a second step, taking the brown bear as a case study, we compiled information about the type and costs of the measures subsidized in damage prevention programs. As for compensation expenditures, we standardized prevention costs using purchasing power parities and evaluated their relationship with compensation expenditures, the countries' economic status, and the rate of large carnivore recolonization. Finally, we proposed strategies to optimize the effectiveness of compensation and prevention programs to reduce damage-related economic losses and encourage coexistence between large carnivores and people.

2. Large carnivores and damage compensation programs in Europe

Europe harbours approximately 17,000 brown bears, 12,000 wolves, 9000 Eurasian lynx and 1200 wolverines (excluding Belarus, Russia and Ukraine, Chapron et al., 2014). Lynx occur in eleven populations, bears and wolves in ten populations each, and wolverines in two populations (Fig. 1). Of these 33 large carnivore populations, eight are small and highly isolated (of which six are reintroduced or augmented), whereas 14 have > 1000 individuals each. Altogether, large carnivores occur in 27 countries in Europe and 25 of the 33 populations are transboundary (Tables A1 and A2). All but seven countries have compensation programs for one or more large carnivore species (Table A2). In most countries, compensation is paid a posteriori, based on damage verification. Only Swedish authorities implement a different approach for reindeer, paying Sámi reindeer herders a priori based on the estimated large carnivore abundance or reproduction, regardless of the amount of the damage-related economic losses (Zabel and Holm-Müller, 2008).

3. The costs of compensation for large carnivore damage: a continental overview

The annual compensation for large carnivore damage in Europe comprises approximately 28.5 million Euros. The average cost per year and individual carnivore during 2005–2012 was over 6300 Euros for wolverines, 2400 Euros for wolves, 1800 Euros for bears, and 700 Euros for lynx (valued at 2011 purchasing power parity, hereafter PPS; see

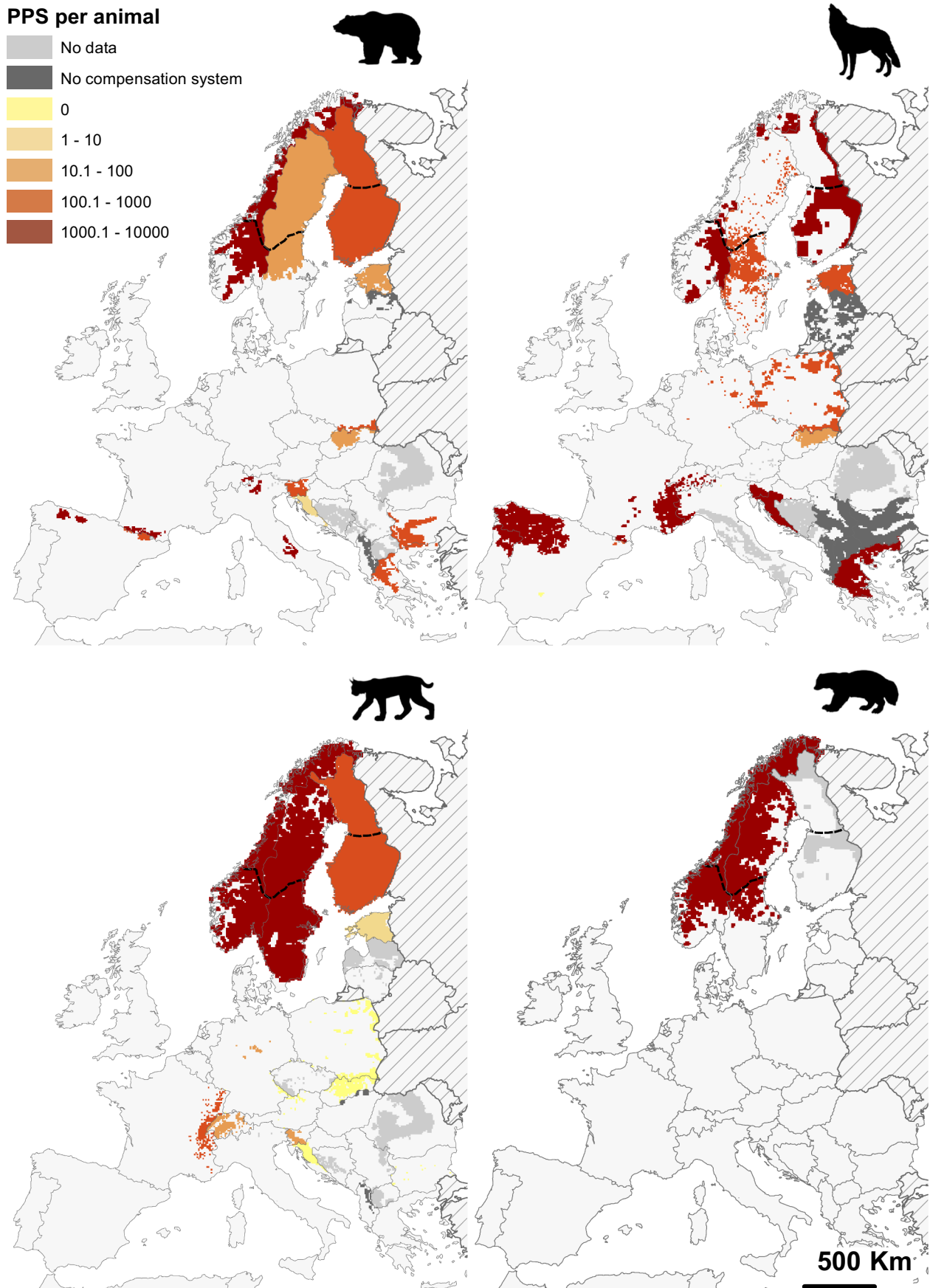


Fig. 1. Compensation costs for damage caused by the brown bear, wolf, Eurasian lynx and wolverine in Europe. Costs are expressed in PPS per animal (Supplementary methods in Appendix A). Black dashed lines show the southern edge of the semi-domestic reindeer husbandry area. Countries with grey dashed lines were not included in this study. Species distributions were extracted from [Chapron et al. \(2014\)](#).

Supplementary methods and Table A2). However, there is a lot of variation among and within countries depending on the species. For instance, in Italy and Poland the costs of compensation per animal are higher for bears than for wolves (see Table A2). In the case of Poland, the occurrence of wolf damage is rare in most of the species' range because livestock density is low and wild ungulates are highly abundant (Nowak et al., 2011), whereas bear damage occurs across most of its range (Bautista et al., 2017). In Italy, the occurrence of wolf damage may be underestimated because many regional administrations do not keep formal records on the compensation schemes and some just do not compensate at all (Boitani et al., 2010). Currently, the brown bear in Italy is fully protected and occurs in two separated small populations, which are the focus of large conservation efforts, also in the form of damage compensation (Bautista et al., 2017; Kaczensky et al., 2012).

3.1. The toll of free-ranging livestock

Differences in compensation costs among species and countries are largely related to husbandry practices. The amount paid per individual carnivore differed by up to three orders of magnitude between countries (e.g., ca 9400 PPS per bear in Norway vs. 9 PPS per bear in Croatia, Table A2). Whereas compensation for lynx depredation on livestock was zero in six countries, Sámi communities raising semi-domestic reindeer in Fennoscandia received up to 75% of the total compensation paid for lynx damages in Europe (Fig. 1, Table A2). Reindeer herding is deeply anchored in the culture of Sámi people and represents a key component of their livelihood. Depredation on reindeer by all large carnivore species together accounted for 41% of the total compensation costs in Europe (approximately 9.2 million PPS annually, half of which is paid a priori in Sweden). Nordic authorities implement damage management policies to build tolerance towards large carnivores, either as a priori (Zabel and Holm-Müller, 2008) or a posteriori compensation (Sippola et al., 2005). However, they rarely implement techniques to prevent reindeer predation (e.g., artificial feeding in sensitive periods to protect reindeer, Table 1). National laws specify different management policies for large carnivores inside and outside reindeer herding areas. For example, the law permits wolf extermination in reindeer herding

areas in Finland, Norway and Sweden (Kojola et al., 2005; Wabakken et al., 2010). As a consequence, resident packs do not occur in reindeer areas (see Fig. 1).

Next in magnitude is the predation on free-ranging sheep in Norway, which represented almost 25% of total compensation payments in Europe. Despite the disproportionate amount paid, the conflict around free-ranging sheep predation remains chronic, resulting in very low population goals for large carnivores set by the Norwegian Parliament. For instance, in 2016 authorities approved plans to kill over two-thirds of the Norwegian wolf population (Immonen and Husby, 2016), disregarding that wolf experts had previously identified the very small population size as the main threat to wolves in Norway (Kaczensky et al., 2012).

3.2. Wealthier countries pay more

The annual compensation cost per individual carnivore is positively related to national economic wealth measured as gross domestic product per capita in PPS (model 1 in Table A3). This association is not due to differences in the price of livestock or agricultural products across countries, because we expressed both variables at a uniform price level (Supplementary methods). The link between wealth and conservation expenditures has been reported globally (Balmford et al., 2003; Barnes et al., 2016). Our findings suggest that, in wealthier countries, damage management policies receive more institutional support to cover the costs of damage compensation. However, spending more money for damage management does not necessarily imply an effective reduction of damage occurrence and its costs (see below).

3.3. The return of large carnivores does not always translate into higher compensation costs

The rate of carnivores' range change (calculated for each country/region as the ratio of the species' range sizes in the year 2012 in relation to the species' range sizes in the 1950–70s based on maps published by Chapron et al. (2014); Appendix A) was larger in wealthier countries, which tend to pay more for compensation (model 5 in Table A3; see also

Table 1

List of measures subsidized in prevention programs to mitigate brown bear damage across 14 European countries in 2003–2015.

| Measures subsidized in prevention programs ^a | Countries and regions in which the measure is subsidized on a yearly basis | Countries and regions in which the measure is occasionally subsidized |
|---|--|---|
| Electric fences | CM, CAT, EST ^a , FR, NO, SLO, SW, TR | CI, CR, PO |
| Livestock guarding dogs | CAT, FR, GR, NO, SLO, TR | CI, PO |
| Physical barriers (i.e., fences and gates) | CAT | CI, CM, PO |
| Alarm pistols and firecrackers | – | PO |
| Public awareness with documents (e.g., leaflets) | – | CM |
| Shepherds ^b | CAT, FR | – |
| Helicopter transportation of cabins and other equipment to the summer pastures ^b | FR, TR | – |
| Food for livestock guarding dogs ^b | CAT | – |
| Late release and early removal of sheep from the summer pastures ^b | NO | – |
| Translocation of livestock to areas free of large carnivores ^b | NO | – |
| Facilitation of grazing areas near villages protected with predator-proof fences ^b | NO | – |
| Supplementary feeding in sensitive periods to protect reindeer ^b | NO | – |
| Patrolling of grazing areas to look for signs of dead or injured livestock ^c | NO | – |
| Electronic surveillance (i.e., GPS-radio collar for livestock) in grazing areas ^c | NO | – |
| Dogs to find livestock carcasses ^c | NO | – |

Countries and regions as follows: CM: Cantabrian Mountain (NW Spain); CAT: Catalonia (NE Spain); CI: Central Italy; CR: Croatia; EST: Estonia; FR: France; GR: Greece; NO: Norway; PO: Poland; SLO: Slovenia; SW: Sweden; TR: Trentino (N Italy).

^a Citations for the subsidized measures available in Tables A4 and A5 in the online Appendix.

^b Starting from 2013.

^c Measures related to restructuring husbandry practices.

^d Measures related to damage verification and compensation.

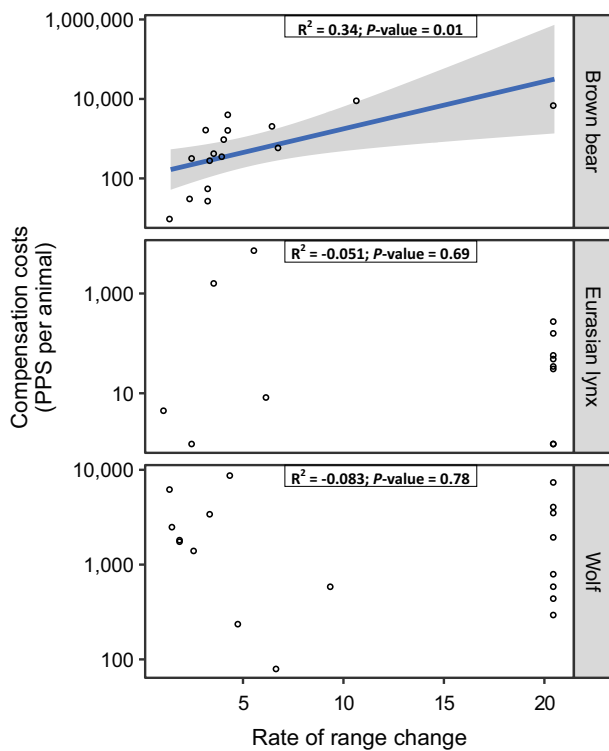


Fig. 2. Annual costs of compensation for large carnivore damage in relation to the rate of large carnivore range change over the last five decades in Europe (see Supplementary methods in Appendix A). Costs are log-scaled and expressed in PPS per animal (Supplementary methods in Appendix A). Complete return and reintroduction to places with no population a few decades ago were given the maximum value of range change rate, which corresponds to a 20-fold lynx range increase in Finland. No wolf population has been reintroduced in Europe (Table A2).

Kojola et al., 2018). This may suggest that compensation costs tend to be higher in countries with higher recolonization rates. However, our analysis shows that, at the European scale, this positive relationship only occurs in the case of the brown bear (Fig. 2 and model 7, 12 and 15 in Table A3). It seems that the costs of bear damage compensation are higher in countries where bears have returned or expanded after decades of absence than in countries with a long history of coexistence and where the use of preventive measures was never abandoned (Linnell, 2013).

The lack of relationship between recolonization rates and compensation costs for wolf and lynx damages may be related to land-use dynamics in the areas of expansion. Land abandonment in Europe and the decline of the rural population (17% since 1961) have resulted in an increase in forest and scrubland cover (Pereira and Navarro, 2015). These changes have favoured an increase in the abundance of wild prey, which has likely further promoted the expansion of large carnivores into abandoned lands (Boitani and Linnell, 2015), and may have helped to keep livestock predation at very low rates. This is the case in Western and Central Poland and Eastern Germany, where wolves have expanded into areas with low farming activity, high forest cover and high abundance of wild prey (Nowak et al., 2011; Wagner et al., 2012). Furthermore, costs can be kept low in recolonized rural areas if responsible authorities help farmers to adapt husbandry practices to the presence of large carnivores, by ensuring financial support for preventive measures (e.g., wolf expansion in Piedmont, NW Italy; Dalmasso et al., 2012). On the contrary, when these expansions occur into areas where husbandry practices are not adapted to the presence of large carnivores and where proper prevention is not a precondition for compensation, the costs of damage compensation tend to be high. These are the cases of bear recolonization in Norway (Swenson and Andrén, 2005), wolf expansion in

most of Italy (Boitani et al., 2010), and lynx reintroduction in the Jura Mountains in France (Stahl et al., 2001). Finally, in the case of reintroduced and/or reinforced populations, compensation expenditures tend to be higher due partly to authorities' huge efforts to increase tolerance as a critical component for the success of reintroduction programs (Clark et al., 2002; Tosi et al., 2015).

3.4. Compensation alone is not enough to improve tolerance towards large carnivores

The tolerance for large carnivores is a highly complex and context-dependent issue (Linnell and Boitani, 2012). The attitudes towards different species involved in conflict situations are taxonomically biased (Kansky et al., 2014). Farmers in Europe tend to have more negative attitudes towards wolves than towards other predators (Dressel et al., 2015), even though in a few countries compensation costs are lower for the wolf than for other species (see France, Italy, Norway and Poland in Table A2). Attitudes are usually more strongly associated with intangible costs (e.g., risk perception) than with economic costs (e.g., livestock predation) (Kansky and Knight, 2014). This can partly explain why the return of extirpated populations is often unwelcome by local communities (independent of economic losses), whereas decades of human-carnivore coexistence result in a greater tolerance (Kaczensky et al., 2004; Majić and Bath, 2010; see the previous section). In addition, tolerance towards large carnivores is strongly linked to cultural values (Dickman, 2010). There are great cultural differences across Europe that play a role in how various societies deal with and tolerate carnivores. For instance, levels of tolerance seem to be lower in Norway than in Sweden, and especially low in rural areas with free-ranging sheep and strong hunting traditions (Gangaas et al., 2013).

Moreover, compensation programs can sometimes further motivate negative attitudes and can be a source of conflict over large carnivore management. For instance, programs that aim to improve tolerance by only paying compensation can perpetuate a negative perception of carnivores (Berger, 2006). When prevention payments are not used efficiently, damage incidence does not decrease and conflicts over large carnivore conservation escalate (Boitani et al., 2010). Furthermore, poorly functioning compensation programs, in which damage verification processes are unreliable and slow, may discourage people from claiming damage and fail to promote positive attitudes (Dickman et al., 2011; Nyhus et al., 2005). Finally, compensation programs can benefit from an adaptive approach and should adjust to changes in the conflict situations over time (e.g., increase of damage occurrence) and being integrated in participatory processes (i.e., engaging stakeholders to manage conflicts) (Anthony and Swemmer, 2015). Failing to do so can hamper efforts to improve tolerance (Marino et al., 2016) and to achieve effective conflict mitigation (Redpath et al., 2013, 2017). In such participatory processes, providing information about benefits stemming from the presence of predators to the parties involved can also help to build tolerance (Slagle et al., 2013).

There are some examples of low costs of compensation and high tolerance that partly relate to the prerequisite of using effective prevention practices in order to receive compensation. In Sweden, compensation payments outside the reindeer herding area are among the lowest in Europe because compensation is conditional on the proper protection of livestock and wildlife agencies strongly focus on subsidizing preventive measures (Widman and Eloffsson, 2018). The management of brown bear damage in Croatia is another example. Hunter organizations are responsible for damage compensation and stipulate the use of protection measures as a condition for compensation (Bautista et al., 2017). The members of hunting organizations are local people (mainly farmers) who profit from hunting bears, are involved in bear management, and protect well their livestock to avoid a conflictive coexistence (Hipólito et al., 2018). As a result, costs for compensation of bear damage are among the lowest in Europe (Fig. 1) and local

communities accept and value the presence of bears (Majić et al., 2011).

4. The costs of prevention programs: the case of brown bears

4.1. Heterogeneity in prevention programs

National administrations routinely compensate for brown bear damage in most of Europe, whereas only half of the countries systematically subsidize preventive measures (Tables 1, A4 and A5). The majority of the funds for preventive measures come from public

agencies at the national or regional level, and in some cases from the European Union (mostly through LIFE NATURE projects) and non-governmental organizations (Tables A4 and S5).

In almost every country and region damage prevention programs cover the costs of electric fences and livestock guarding dogs, which represented ca 20% of the overall annual cost to prevent bear damage in Europe (Fig. 3, Table A4). These measures are effective in preventing damage only if properly implemented and maintained (Van Eeden et al., 2017). Improper use of these measures, such as inadequate fence design, uncharged batteries, or chained dogs, can result in up to 40% of the funded measures being ineffective (di Vittorio et al., 2016; Rigg

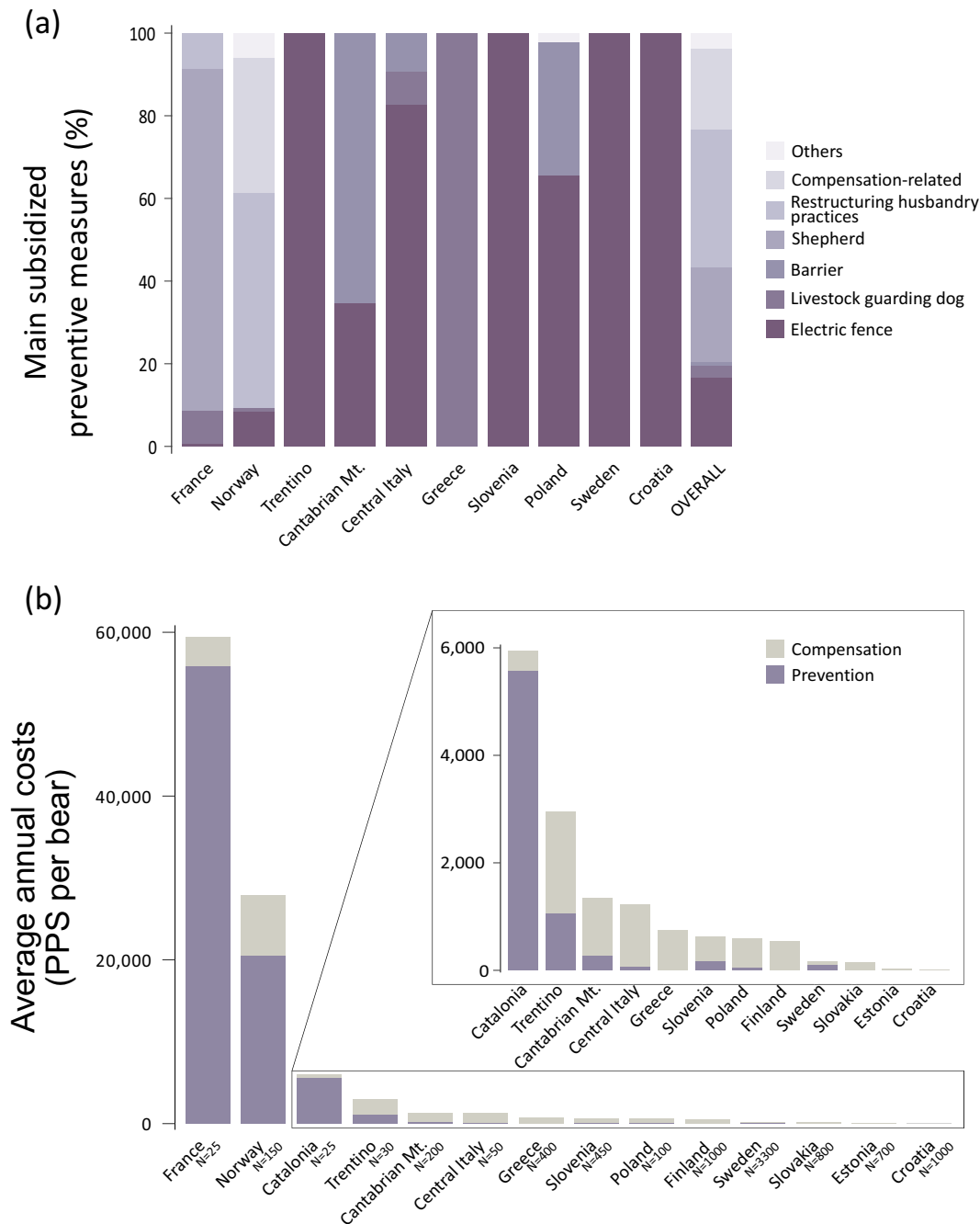


Fig. 3. Relative distribution of the average annual costs of the main measures officially subsidized to prevent brown bear damage (a); and average annual compensation and prevention expenditures for brown bear damage in Europe in 2005–2012 (b). In (b), *N* indicates the bear population estimation (see details in Table A5). No data were available for Catalonia about the cost of each subsidized measure, neither about prevention costs for Finland and Slovakia (Table A4). Costs are expressed in PPS per bear (Supplementary methods in Appendix A). Detailed information about the different measures included in each category in (a) is presented in Tables 1 and A4.

et al., 2011). We identified a substantial portion of the prevention subsidies allocated to assist in restructuring husbandry practices in places where extensive farming has emerged after the temporary absence of large carnivores (Linnell, 2013). Payments for shepherd dog food or relocation of herds to areas where large carnivores are absent were among these husbandry-supportive measures (Table 1). Together with the cost of the salaries for shepherds in the French Pyrenees (23% of the total), husbandry-supportive measures represented ca 56% of the total annual expenditures allocated for damage prevention in Europe (Fig. 3). These measures were subsidized in prevention programs implemented in countries or regions with reintroduced bear populations (France, Catalonia in Spain, and Trentino in Italy) and in Norway, where the bear range has increased tenfold in the last decades (Kaczensky et al., 2012; Tables 1, A2 and A4).

In the case of Norway, additional measures included in damage prevention programs do not involve guarding or active herding, but other actions rather related to damage verification and compensation; e.g., patrolling of the grazing area to look for signs of dead or injured sheep (Mabille et al., 2015; Tables 1 and A4). These measures represented as much as 20% of the total annual expenditures incurred on prevention programs in Europe (Fig. 3).

4.2. Payments for bear damage prevention almost double compensation costs

On average, the annual costs for prevention of brown bear damage were almost twice the costs for compensation of bear damage in Europe (ca 5 million vs. ca 3 million PPS; Table A5). Prevention costs per bear differed by four orders of magnitude among countries: ca 56,000 vs. 1 PPS paid per bear and year in France and Croatia, respectively (Fig. 3). Approximately 90% of the total prevention costs in Europe were paid in Norway and France, where free-ranging sheep herding is an important socio-economic activity (Kaczensky et al., 2012).

Our analyses indicate that the annual costs of compensation per individual bear are positively related to costs of prevention per individual bear, which, in turn, tend to be higher in wealthy countries (Models 16 and 24 in Table A3). However, only the costs of compensation, but not prevention, are positively related to the rate of the bear's range change (Models 16 and 25 in Table A3). The lack of relationship between prevention costs and bear recolonization rate is probably due to a lack of systematic prevention before the “problem appears”, especially in countries where the bear populations have increased considerably during the last decades (e.g., Cantabrian Mountains in Spain, see Tables A2 and A5). This indicates a tendency to prioritize compensation over prevention programs in Europe and a lack of proactive approaches to mitigate conflict (i.e. act before the problem appears).

We did not find any relationship between compensation costs and previous investments in prevention (Model 29 in Table A3), probably due to the heterogeneity of measures classified and subsidized as prevention (Tables 1, A4 and A5). Additional local-scale analyses would help to test whether prevention has actually reduced compensation costs in resident bear populations and whether administrations have sufficiently subsidized preventive measures to mitigate damage in recently recolonized areas. For example, in an area of the Cantabrian bear population in Spain, where the species' range has quadrupled in the last 30 years, an investment of around 1000 PPS in prevention of damage to apiaries reduced compensation costs more than threefold. Therefore, a small investment in prevention reduced compensation costs in that area by 30,000 PPS, which is equivalent to a 30–50% reduction compared to previous years (Seijas et al., 2016).

5. Implications for management and conservation

Effective conflict mitigation implies facilitating coexistence and reducing damage to human property and associated economic losses

(Van Eeden et al., 2017). To achieve that, responsible agencies should focus on damage-prevention programs that help to adapt husbandry practices to the presence of large carnivores. Because large carnivore populations are expected to expand further across Europe (Milanesi et al., 2017; Scharf and Fernández, 2018), damage management strategies need to be proactive and anticipate emerging conflicts to ensure the success of large carnivore recolonization. For this purpose, responsible agencies should integrate compensation and prevention programs into participatory processes that consider socio-cultural aspects at the national, regional and local levels (Anthony and Swemmer, 2015; Marino et al., 2016; Redpath et al., 2017; Tosi et al., 2015).

In Europe, research studies and LIFE NATURE projects sometimes evaluate the outcome of compensation and prevention programs (e.g., di Vittorio et al., 2016), but these evaluations are rarely led by the responsible authorities. Examples of the latter include the assessment of programs to compensate and prevent bear damage in Asturias in northern Spain and the evaluation of measures to prevent wolf damage in the French Alps funded by the regional and national Ministries of Environment, respectively (Naves et al., 2010; de Roince, 2016). Such assessments are not compulsory in LIFE projects and they only occasionally evaluate whether compensation programs succeed to improve attitudes towards large carnivores or whether subsidized preventive measures are effectively reducing damage to human property. To ensure that damage management policies alleviate conflicts, responsible agencies should be obliged to evaluate the effectiveness of compensation and prevention programs periodically and adapt these programs according to the results of such evaluations.

Finally, to enable a proper assessment of the effectiveness of compensation and prevention programs, we encourage the administrations and organizations working on damage mitigation to establish a common pan-European database of damage occurrence, management actions and associated costs. A common criterion to properly classify measures as compensative, preventive or supportive would be desirable. Such efforts would allow for optimizing the cost-effectiveness of public funds invested in damage management and the identification of the most adequate solutions for conflict mitigation in Europe in a more adaptive manner.

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Data accessibility

Data from this study are available online from Figshare <https://figshare.com/s/64131ade28b9d20154fa>.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2019.04.019>.

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