



How spatial scales shape the study of human-wildlife conflicts: Livestock farmers and Iberian wolves

Lucía Del Río^{a,*}, Jon Ander Zearra^a, Valentin Lauret^a, Rafael Mateo^b, Jorge Tobajas^a, Pablo Ferreras^a

^a Instituto de Investigación en Recursos Cinegéticos (IREC) CSIC- UCLM- JCCM, Ronda de Toledo, 12, 13005, Ciudad Real, Spain

^b Institute of Environmental Assessment and Water Research (IDAEA-CSIC), Jordi Girona 18, 08034, Barcelona, Spain

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ABSTRACT

Large carnivore populations are recovering across many regions, with populations of grey wolves (*Canis lupus*) being a prominent example. While their resurgence offers socioecological benefits, it also intensifies conflicts with livestock farmers, particularly in areas undergoing recent recolonization where traditional protection practices have diminished. Understanding local perceptions is therefore essential for designing management strategies that reconcile conservation objectives with rural livelihoods. We assessed human-wolf conflict across Spain at two spatial scales: a national scale through an online survey, and a regional scale through in-person questionnaires. Nationally, we compared perceptions between areas with ($n = 83$) and without ($n = 42$) wolves. Regionally, we focused on two wolf expansion areas: High Conflict Area (HCA) in La Rioja ($n = 30$) and Low Conflict Area (LCA) in Guadalajara ($n = 34$). We examined perceptions about wildlife damage, preventive measures, species responsible for losses, and perceptions toward coexistence. At the national scale, perceptions were largely homogeneous regardless of wolf presence. In contrast, regional results showed that conflict intensity strongly shaped perceptions. Farmers in HCA reported more wolf-related damage, lower trust in public administration, and stronger demands for better compensation and preventive measures than farmers in LCA. Wolves were consistently perceived as the weakest contributor to ecosystem balance, whereas livestock was ranked the highest. Perceptions of other wildlife species varied with conflict intensity, reflecting nuanced views of their ecological roles. These findings highlight the need for multi-scale management that integrates prevention, compensation, and stakeholder engagement to promote sustainable coexistence and support rural socio-economic resilience.

1. Introduction

Large carnivore populations are recovering in many parts of the world (Chapron et al., 2014), after decades of sustained decline (Ripple et al., 2014). Among them, the grey wolf (*Canis lupus*, hereafter wolf) is one of the most prominent examples of this resurgence (Di Bernardi et al., 2025). Several factors have contributed to this recovery, including decreasing human population densities in rural areas (Cimatti et al., 2021), widespread rural land abandonment (Bürge et al., 2017), implementation of stronger conservation policies (Hovardas and Marsden, 2018), and a gradual improvement in public attitudes toward large carnivores (Chapron et al., 2026).

Despite these advances, the recovery of large carnivores is unavoidably accompanied by important socio-ecological effects,

especially in the case of the wolf (Chapron et al., 2026). On the one hand, large predators provide important ecological benefits by removing sick or otherwise vulnerable prey through predation (Tanner et al., 2019), and help to restore and maintain trophic balance (Ripple and Beschta, 2003). On the other hand, their presence can result in livestock predation, fueling tensions with rural communities (Lino et al., 2024). The continued expansion of wolf populations in recent years has intensified human-wolf conflicts (Ausband and Mech, 2023; DeCesare et al., 2018). Negative attitudes toward wolves are especially prevalent in regions where the species has been absent for a long time and expands its range through recolonization (Gosling et al., 2019). In such areas, traditional livestock protection practices are no longer in use (Olson et al., 2015; Durá-Alemañ et al., 2024), leading to intense initial conflict that may decrease as communities gradually adapt to

* Corresponding author.

E-mail addresses: lucia.rio@csic.es, lucia.rio@uclm.es, lucialuciadrp@gmail.com (L. Del Río).

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coexistence with the species (Zimmermann et al., 2001). In regions with a long history of coexistence, communities often display more positive attitudes and greater acceptance of carnivore presence (Dorresteijn et al., 2014; Dressel et al., 2015).

In many rural regions, livestock farmers confront a suite of socio-economic pressures that jeopardize the sustainability of their livelihood. Farmers perceive vulnerabilities related to market uncertainty, rising feed and production costs, and unstable subsidy regimes, which threaten both food security and the multifunctional benefits of traditional livestock systems (Morales-Reyes et al., 2025). Furthermore, generational renewal is widely recognized as a critical challenge; ageing local populations and low rates of youth entry into farming pose structural threats to the continuity of family farms (Farkas et al., 2023). Livestock sectors also face broader structural challenges that affect competitiveness and adaptation to economic changes.

Human-wolf conflict emerges from a complex interplay of ecological, economic, and social factors that vary across scales. Studies of human perceptions regarding large carnivores help reveal the opinions, fears, and concerns of local communities coexisting with wildlife (Martínez-Jauregui et al., 2017), especially in areas undergoing recolonization by large carnivores (Herrero et al., 2021; Severino et al., 2025) and guide successful conservation and reintroduction programmes (Lopes-Fernandes et al., 2018). However, land users often perceive the recovery of wolves as a threat to their livelihoods (Acebes et al., 2024), highlighting the need to understand their perspectives to improve adaptive capacities during ongoing rural transitions (Pettersson et al., 2021). Studies from several European contexts highlight that attitudes toward wolves are not only heterogeneous but also strongly dependent on spatial scale and context (Sponarski et al., 2013; Treves et al., 2013). At broader (e.g., national or regional) scales, general patterns tend to emerge, such as more positive perceptions among urban dwellers and more negative attitudes among livestock farmers (Barmoen et al., 2024). However, these generalizations often obscure substantial variation at finer spatial scales, where local ecological conditions, livestock practices, and direct experience with wolves shape perceptions in more nuanced ways (Marino et al., 2022; Lino et al., 2024). Accounting for this local variation can help tailor management strategies to the specific challenges of a given area (Treves and Bruskotter, 2014). In Norway, negative perceptions increased immediately after wolf recolonization but decreased over time as local communities gained experience (Zimmermann et al., 2001), suggesting a spatio-temporal adaptation process. Conversely, in Poland, rural residents in areas with long-standing wolf presence and high predation rates exhibited less positive attitudes than those in recently recolonized areas (Gosling et al., 2019), highlighting how local intensity of conflict can override broader coexistence patterns. Similarly, in Germany, which was recolonized by wolves relatively recently, attitudes were more positive in areas with higher knowledge levels and trust in information sources (Arbieu et al., 2019), pointing to the role of social drivers that may vary across regions. These contrasting findings illustrate that human-wolf conflict cannot be fully understood without explicitly considering spatio-temporal scale, as patterns observed at national or continental levels may differ, or even reverse, when examined locally. Despite this, relatively few studies have simultaneously assessed attitudes across multiple spatial scales within the same socio-political context, limiting our ability to disentangle the relative influence of ecological, economic, and social drivers.

Across the Iberian Peninsula, the Iberian wolf (*Canis lupus signatus*) is distributed in approximately 333 packs in the northwest of Spain (MITERD, 2025) and in approximately 58 packs in the north of Portugal (Pimenta et al., 2023). In recent years, conservation policies for the Iberian wolf have undergone significant changes in the region, particularly in Spain. Management differs geographically: wolves have been subject to regulated hunting quotas to the north of the Duero River, but are strictly protected to the south of the river (Ordiz et al., 2022). In Portugal, the species is legally protected since 1988 (Law No. 90/88). In Spain, wolves have largely stable populations to the northwest of the

Duero River, whereas to the south of it the species is currently expanding, and local livestock farmers generally report negative to neutral attitudes and often display a “not-in-my-backyard” response. This response refers to situations in which people accept conservation goals in principle but resist their implementation when they directly affect their own communities or livelihoods (Janeiro-Otero et al., 2023; Lino et al., 2024). In some regions, people have positive attitudes toward wolves, but knowledge remains limited and people continue to exhibit moderate levels of fear about wolves. More positive attitudes are linked to greater knowledge and less fear (Valente et al., 2024). Previous studies have shown that livestock farmers tend to express more negative perceptions than members of the general public and hunters (Lino et al., 2024). In Spain, the greatest challenges arise in newly recolonized areas, where traditional practices and memories of coexistence have been lost (Durá-Alemañ et al., 2024), and where population control remains prohibited due to the full legal protection of the wolf since 1992 (Ordiz et al., 2022).

Given these spatially structured dynamics, there is a clear need for approaches that integrate multiple dimensions of conflict. In this context, quantitative tools such as the Potential for Conflict Index (PCI₂) offer a valuable yet still underutilized framework to capture not only the direction but also the degree of agreement or disagreement among stakeholders. By assessing the distribution of survey responses, PCI₂ determines whether opinions are clustered (agreement) or widely dispersed (disagreement and polarization) (see in Methods) (Lauret et al., 2026). PCI₂ is widely used to assess human-wildlife interactions, offering insights into public perceptions and providing insights into management strategies aimed at reducing conflict (Manfredo et al., 2003; Vaske, 2018). This method has been applied in studies of conflicts with large carnivores such as cougars (*Puma concolor*), jaguars (*Panthera onca*), brown bears (*Ursus arctos*) and wolves (Frank et al., 2015; Engel et al., 2017). This is particularly relevant for complex socio-ecological systems such as Mediterranean agricultural landscapes, where conflict drivers operate simultaneously across ecological, political, economic, and social domains (Ravaglia et al., 2026). Accordingly, the main objective of the present study was to evaluate how perceptions of human-wolf conflict vary across spatial scales in Spain. Specifically, we assessed the conflict at two scales: (i) at a large scale (i.e., nationwide) by comparing perceptions of livestock farmers between areas with and without wolves, and (ii) at a local scale by comparing perceptions of livestock farmers between a region reporting high levels of conflict (HCA) and a region reporting low levels of conflict (LCA).

2. Methods

2.1. Surveys data

2.1.1. National scale

We conducted an online survey among livestock farmers of Spain via the Tickstat platform (<https://www.tickstat.com/>) between September and November 2024 to assess perceptions of wildlife-related risks. The survey was distributed opportunistically through various channels, mainly via website of the authors' institution (<https://www.irec.es/>) and social media, but also through a provincial farmers' association (APAG) to its members in Guadalajara and following a snowball distribution approach.

At the national scale, municipalities were classified as “wolf area” or “non-wolf area” based on the current distribution of the species in Spain (Fig. 1). However, this classification reflects present-day distribution rather than historical presence. The Iberian wolf historically occupied most of the Iberian Peninsula, and its current range is the result of a marked contraction during the 19th and 20th centuries (Clavero et al., 2023). Therefore, areas classified as “non-wolf areas” include regions where the species became locally extinct several decades ago, rather than areas outside its historical range. Conversely, “wolf areas” include both regions with long-term presence and areas that have been

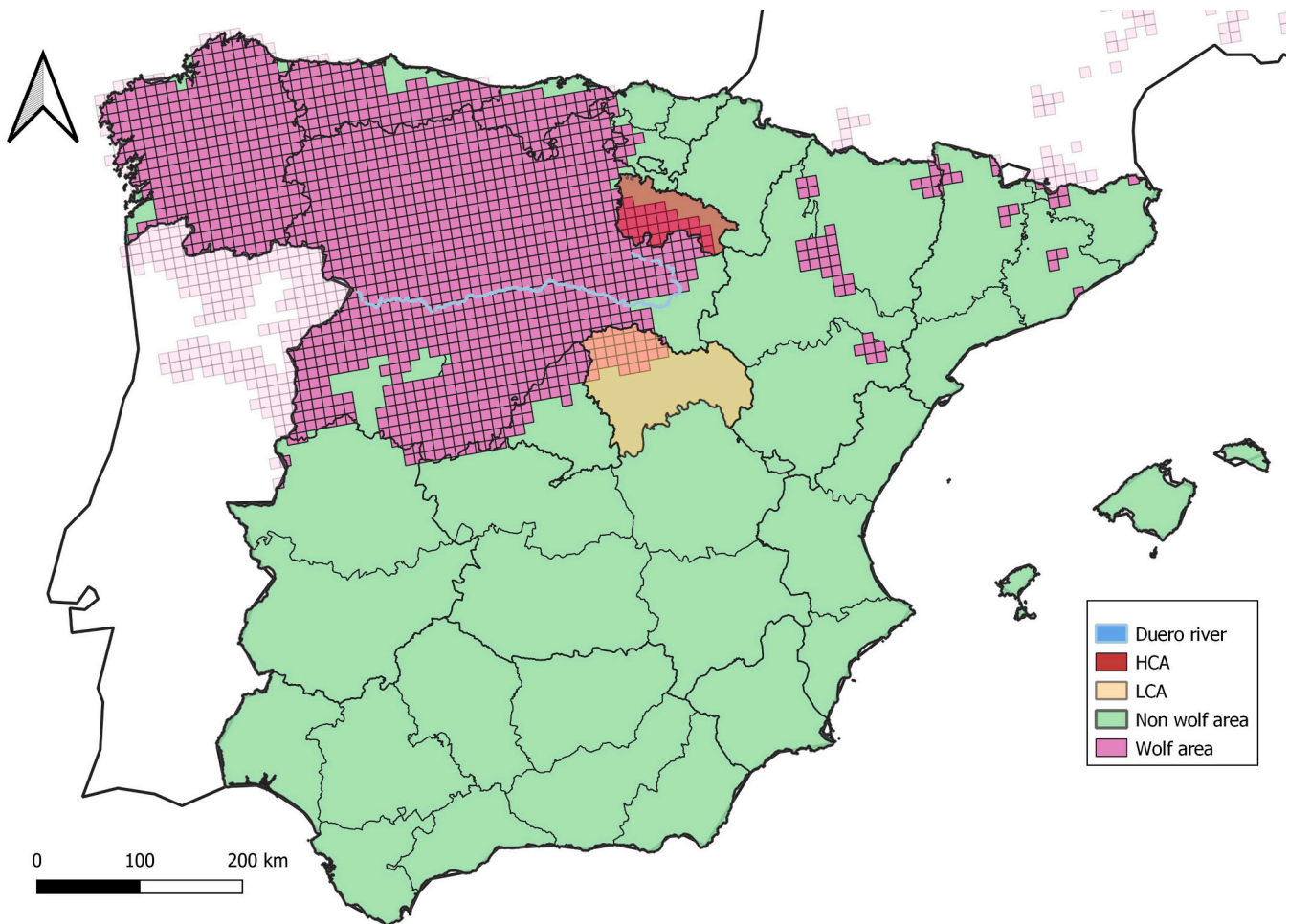


Fig. 1. Study areas at two spatial scales. Wolf area (pink) and non-wolf area (green) at the national scale, according to Kaczensky et al. (2024). HCA (La Rioja province) and LCA (Guadalajara province) at the regional scale. The Duero River marks the boundary between different wolf management schemes; to the south the hunting of wolves is prohibited, whereas to the north wolves are considered a game species subject to annual hunting quotas (except between 2021–2025). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

recolonized in recent decades. In addition, some “non-wolf areas” may be located near the current expansion front, where occasional dispersing individuals may occur. According to the most recent national census (2021–2024), a total of approximately 333 wolf packs have been identified in Spain, representing a very gradual increase compared to the 2012–2014 period (MITERD, 2025). Wolf populations are well established in the northwest of the Iberian Peninsula, while in the south and east the species is currently expanding into previously unoccupied areas. Management regimes differ spatially since 1992 according to the Habitats Directive (Directive 92/43/CEE): wolves north of the Duero River were subject to regulated hunting, whereas populations south of the river have been strictly protected. Between 2021 and 2025, however, wolves were granted full legal protection across the entire Spanish territory, temporarily homogenizing management conditions.

We conducted a structured questionnaire to assess farmers' perceptions of the prevalence and impacts of wildlife predation on livestock farming. We asked farmers whether their livestock had experienced attacks by wild animals specifying the species causing most attacks (Appendix A). The survey included questions addressing: (i) respondents' socio-demographic characteristics and rural context; (ii) experience with wildlife attacks on livestock, including predator species, attack frequency, and economic impact; (iii) perceived consequences of depredation for farming activity; (iv) use and perceived effectiveness of preventive measures, along with preferences for alternative management strategies; and (v) broader perceptions of wildlife-related risks,

coexistence, and impacts on both livestock and human activities.

2.1.2. Regional scale

Between January 2022 and March 2023, we conducted face-to-face interviews with livestock farmers in two areas that have experienced wolf recolonization in recent decades in Spain. These areas are located in regions with contrasting large-scale wolf population dynamics, with stable populations in the northwest of the Iberian Peninsula and expanding populations toward the east and south. Based on official records of wolf attacks over the previous four years (2020–2024), mean ($\pm$ SD) attack intensity was 4.91 ± 1.43 attacks per 100 km² per year in La Rioja and 0.49 ± 0.18 in Guadalajara, indicating an approximately ten-fold higher conflict intensity in La Rioja (Del Río et al., Under review) (Fig. 1). Thus, we considered Guadalajara as a low conflict area (LCA) and La Rioja as a high conflict area (HCA). These areas differ markedly in terms of wolf population status, livestock systems, and management regimes. In HCA (La Rioja province = 5045 km²), wolves recolonized the region in the 1990s and currently comprise up to five packs, some shared with neighboring provinces (MITERD, 2025). In LCA (Guadalajara province = 12,167 km²), recolonization occurred more recently (2000s), with up to four packs currently recorded. Thus, both areas represent expanding populations but differ in the duration of coexistence. Management frameworks also differ. HCA is located north of the Duero River, where wolves were historically subject to regulated lethal control under quotas, except during the 2021–2025 period when full

protection was implemented. In contrast, LCA lies south of the Duero River, where wolves have been strictly protected since 1992 and lethal control has not been permitted (Ordiz et al., 2022). Conflict intensity also differs substantially between areas. The two regions also represent contrasting livestock production systems. In HCA, livestock consists mainly of sheep managed under a seasonal (late spring-summer) transhumant grazing system in mountainous areas, where most wolf damage (94%) affects sheep. In LCA, livestock is dominated by cattle, followed by sheep managed under year-round extensive grazing systems, with lower overall predation pressure than in HCA.

In the LCA, wolf presence is restricted to the northwestern mountainous area (Sierra Norte de Guadalajara), where wolf-livestock interactions are concentrated and the study was conducted. According to the 2020 Agrarian Census of the National Statistics Institute (INE, 2020), approximately 51 livestock farms operate across the 35 municipalities with confirmed wolf presence in this area. We interviewed 34 livestock farmers from 20 municipalities, representing approximately 66.7% of the local farming population in the study area.

In the HCA, wolf presence is concentrated in the southwestern mountainous zones of La Rioja, including Alto Nájera, Sierra de Cameros, and Sierra de la Demanda, where interactions with livestock are most frequent. According to the 2020 Agrarian Census of National Statistics Institute (INE, 2020), approximately 46 livestock farms operate in these wolf-affected areas. We interviewed 30 livestock farmers across 11 municipalities, representing approximately 65.2% of the farming population in the study area. Overall, the surveyed municipalities were located within the main areas of confirmed wolf occurrence in both regions, ensuring that interviews were conducted in zones where human-wolf interactions are spatially relevant.

A structured in-person questionnaire was used to assess livestock farmers' perceptions of predators in these two areas, with particular emphasis on wolves, their impacts, and management strategies (Appendix B). The survey included questions addressing perceived impacts of wolves and other predators, organized into three main topics. First, respondents were asked about the relative share of livestock attacks attributed to wolves and other predators (e.g. foxes, feral dogs, badgers, vultures, eagles). Second, they were asked about the economic, social, and psychological (stress-related) impacts associated with wolf damage. Third, they were asked about the ecological and socio-economic effects of wolves in the area, including population regulation of wild ungulates, carcass removal, impacts on game species, road-traffic accidents, and rural tourism. We also asked farmers to estimate annual economic losses caused by wolves, the costs and effectiveness of preventive measures (e.g. livestock monitoring, fencing, electric fences, guardian dogs, and deterrents), and to evaluate potential conflict mitigation actions such as compensation schemes, administrative support, scientific knowledge, and development of new preventive measures. The questionnaire also included items on personal experience with wolf attacks, number and trends of annual damages, undetected losses, perceptions of wolf population trends and abundance, trust in public administration, opinions on national wolf management, future conflict evolution, and the perceived ecological importance of predators and other wildlife species (Appendix B).

2.2. Statistical analysis

At the national scale, we compared responses from livestock farmers in wolf areas with those from farmers in non-wolf areas according to the distribution of wolves in Spain (Kaczensky et al., 2024). At the regional scale, we compared farmers from the LCA and the HCA to assess differences in perceptions and practices under different levels of conflict intensity within the wolf range. We selected statistical tests according to variable types and distribution. Categorical variables (nominal or dichotomous) were analyzed using chi-square tests of independence, or Fisher's exact test when expected counts were < 5 . Effect sizes were calculated using Cramér's V . For numerical variables expressed as

percentages, normality was assessed using the Shapiro-Wilk test. Depending on the results, we applied Student's t -tests (normal distribution) or Mann-Whitney U tests (non-normal distribution), reporting effect sizes as Cohen's d or Cliff's delta (δ), respectively (Naughton-Treves et al., 2003; Severino et al., 2025).

To assess patterns of agreement and disagreement in perceptions of wolf-related issues, we applied the second-generation PCI_2 (Vaske et al., 2010) at both spatial scales: wolf vs. non-wolf areas at the national level, and LCA vs. HCA within the wolf range at the regional level. At the national scale, we evaluated (using Likert scale) the respondents' perceptions of wolf management measures, whereas at the regional scale we evaluated the perceived effectiveness of wolf management measures, the effectiveness of preventive measures, and the ecological importance of different species in the ecosystem. This allowed the assessment of both inter-group differences and intra-group consensus across contrasting socio-ecological contexts. PCI_2 is a graphical and quantitative approach designed to identify the level of agreement within groups and the degree of divergence between them. It is particularly useful for detecting potential sources of conflict in human-wildlife relationships. The method uses Likert-scale responses (1 = "totally disagree" to 5 = "totally agree"), which are expanded according to their frequency and rescaled to a bipolar axis (-2 to $+2$). Mean values are plotted along the x-axis, indicating the overall direction of agreement, while responses are displayed as bubble plots in which bubble position reflects group mean agreement and the bubble size represents response dispersion (Manfredo et al., 2003).

PCI_2 values range from 0 to 1, where lower values indicate high consensus (smaller bubbles) and higher values indicate greater variability in responses and thus higher potential for conflict (larger bubbles). Inter-group differences (e.g. wolf vs. non-wolf areas) were assessed by comparing the position of group means along the x-axis, while intra-group consensus was evaluated based on bubble size. In addition, differences in mean responses between groups were statistically tested using the Mann-Whitney U test.

Furthermore, to assess differences in overall perceptions of wolf management and preventive measures, and species perceptions across areas, we fitted cumulative link mixed models (CLMMs) using ordinal Likert-scale responses as the dependent variable, and respondent identity as a random effect to account for repeated responses from the same individual. These models included different combinations of fixed effects (area, measures or species, depending on the question), depending on the scale of the analysis (national or regional) and the specific dependent variable considered. Model selection was evaluated using Akaike's Information Criterion (AIC). For each analysis, models were ranked according to AIC values, and ΔAIC was calculated relative to the best-supported model. We selected the model with the lowest AIC for each group of questions, unless the null model differed by less than 2 AIC units, in which case the null model was retained (Burnham and Anderson, 2002). We performed all analyses with R version 4.2.1 (R Core Team, 2021).

3. Results

3.1. National scale

A total of 125 responses were collected from livestock farmers at the national scale. Of these, 66.4% ($n = 83$) were obtained from farmers located in areas with established wolf presence, while 33.6% ($n = 42$) came from areas without wolves. Responses were obtained from multiple autonomous communities across Spain, including all regions with known wolf presence (i.e. Castilla y León, Asturias, Galicia, Cantabria, La Rioja, and parts of Aragón, Madrid, Catalonia and Castilla-La Mancha), as well as several regions without wolf populations (e.g. Comunidad Valenciana, Andalucía, and Extremadura).

Overall, most socio-demographic and management-related variables did not differ between farmers in wolf and non-wolf areas, indicating

broadly similar response patterns across groups. In terms of livestock depredation, the reported occurrence of attacks did not differ significantly between areas ($p = 0.142$). However, farmers differed strongly in the predator they believed was responsible for most attacks (Fisher's test, $p < 0.001$). In wolf areas, respondents most frequently attributed attacks to wolves (54.4%), whereas in non-wolf areas attacks were mainly attributed to foxes (15.2%), wolves (13.0%) and other wildlife species (8.6%). Notably, a substantial proportion of farmers reported no attacks at all, particularly in non-wolf areas (59.5% vs 33.7%) (Fig. 2a).

Perceived economic impacts showed limited differences between groups at national level. The proportion of annual income lost due to predation did not differ significantly between wolf and non-wolf areas ($p = 0.451$). However, farmers in wolf areas reported significantly higher costs associated with preventive measures relative to their annual expenses compared with those in non-wolf areas (38.3% vs. 23.7%; $W = 363.5$, $p = 0.039$) (Fig. 2b; Table S1).

Regarding the perceived impacts of livestock depredation, most variables did not differ significantly between wolf and non-wolf areas (Table 1). However, there was a non-significant tendency for farmers in wolf areas to report a higher willingness to abandon livestock farming due to predation compared to farmers in non-wolf areas (13.9% vs. 6.5%; $p = 0.060$). Economic losses and the proportion of annual costs attributed to depredation were similar between areas.

When evaluating management strategies with PCI_2 , respondents in both areas generally supported compensation increases and improved preventive measures, while lethal control and non-intervention received the least support (Fig. 3). Although preferences were broadly similar, farmers in wolf areas tended to show slightly stronger support for intervention-based management options (Table S1). Reducing predator population through quotas was also supported in both areas, although to a lesser extent (Fig. 3). Farmers from wolf areas tended to express stronger support for management measures. In contrast, the least preferred measures were removing problematic individuals, taking no action and removing the predator population in both areas (Table S1). The selected cumulative link mixed model (CLMM) was the null model, indicating that no wolf management measure was evaluated more positively than the others and that perceptions did not differ significantly among areas (Table S3).

Table 1

Perceived impacts of livestock depredation in the wolf and non-wolf areas at national scale. Values are percentages or mean $\pm$ SD.

Variable	Wolf areas	Non-wolf areas
Willingness to abandon livestock (yes)	13.9%	6.5%
Would abandon if damage increases	35.4%	21.7%
Unwilling to abandon livestock	15.2%	17.4%
Uncertainty ("don't know")	35.4%	54.3%
Percentage of annual income lost (mean $\pm$ SD)	23.2 $\pm$ 21.7	27.3 $\pm$ 27.2
Percentage of annual costs (mean $\pm$ SD)	23.7 $\pm$ 29.0	38.3 $\pm$ 32.6

3.2. Regional scale

At the regional scale, clear differences emerged between the high-conflict area (HCA) and the low-conflict area (LCA), particularly in the perceived frequency and trends of wolf-related damage. Farmers in the HCA reported a higher number of wolf-related damages in the previous year compared to those in the LCA ($W = 232.5$, $p = 0.002$). In addition, a significantly larger proportion of farmers in the HCA indicated that damages had increased over the last five years ($\chi^2 = 12.14$, $p < 0.001$). Farmers in the HCA also more frequently estimated losses associated with missing animals that were not recovered ($W = 221$, $p = 0.040$). With respect to long-term perceptions, farmers in the HCA perceived higher wolf abundance ($p < 0.001$) and were more likely to expect future increases in wolf populations ($p = 0.030$). They also reported lower trust in public administration ($p = 0.003$) and weaker expectations of long-term coexistence ($p = 0.027$).

Despite these differences in perceived damage patterns, no significant differences were found in actual annual economic losses attributed to wolves between regions (Table 2), nor in annual expenditures on preventive measures. Similarly, support for increased administrative assistance for preventive actions did not differ between regions (Table 2).

Regarding perceived responsibility for livestock damage, farmers in both regions generally attributed higher impact to wolves. However, significant regional differences were found in the attribution of damage to feral dogs ($p < 0.001$) and vultures ($p = 0.025$), which were reported more frequently in the LCA, whereas wolf-related damage ($p < 0.001$)

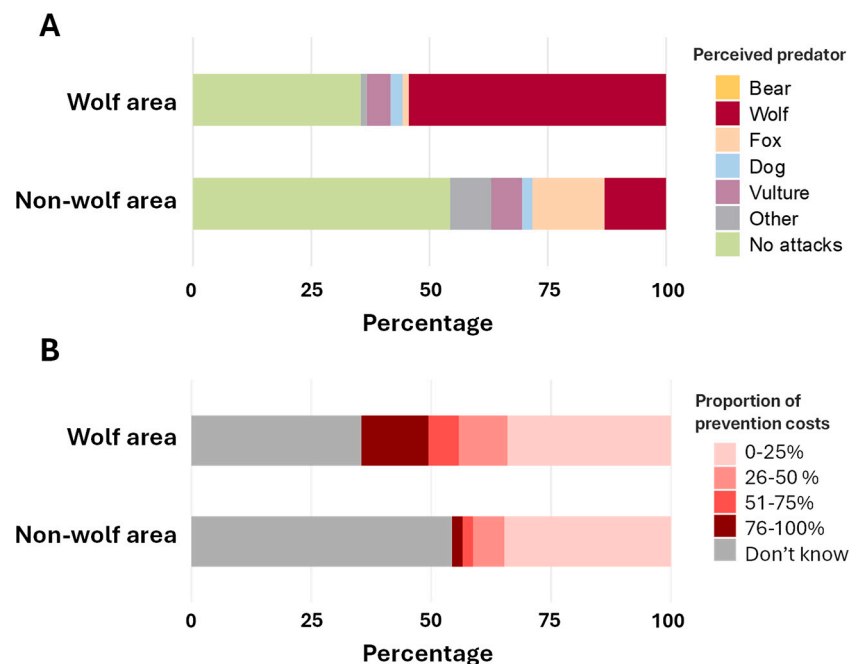


Fig. 2. Results at the national scale of study: A) Percentage of main species responsible for attacks on livestock according to livestock farmers' perception in wolf and non-wolf areas. B) Percentage of annual farming costs represented by measures implemented to prevent predation damage in wolf and non-wolf areas.

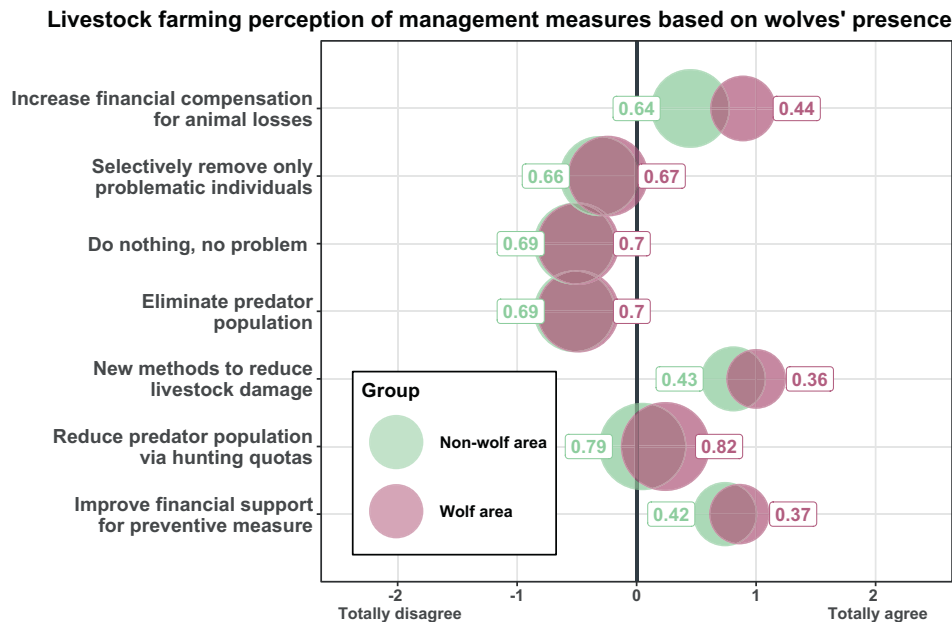


Fig. 3. Potential for Conflict Index (PCI_2) of livestock farmers' perception on management measures according to wolf presence at the national scale of study. Bubble position on the horizontal axis indicates the mean value associated with a 5-points scale ranging from -2 (Totally disagree) to 2 (Totally agree). The size of the bubbles reflects the PCI_2 values in each wolf area (in purple) and non-wolf area (in green), with larger bubble size representing higher disagreement within the group. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2

Statistical results of responses from livestock farmers in the LCA ($n = 34$) and the HCA ($n = 30$). The question, mean $\pm$ SD or percentage in each area, the statistical test used and the p value are included. Each question row corresponds to a specific species or problem. The p values indicate the significance of the difference between the LCA and the HCA.

Question	HCA	LCA	Test	p value
Which of the following species do you believe are causing attacks on livestock?				
Foxes	9.7 $\pm$ 12.6	12.0 $\pm$ 16.6	Fisher	0.06
Feral dogs	4.8 $\pm$ 6.1	1.7 $\pm$ 5.5	Fisher	0.01
Wolves	81. $\pm$ 21.4	62.0 $\pm$ 27.1	Fisher	0.01
Badgers	0.1 $\pm$ 0.9	0.1 $\pm$ 0.8	Fisher	1
Vultures	16.8 $\pm$ 24.1	14.0 $\pm$ 17.9	Fisher	0.02
Eagles	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	–	–
What problems does the presence of wolves cause for livestock farming?				
Economic	76.4%	50.0%	Fisher	< 0.001
Social	0.0%	14.7%	Fisher	0.49
Psychological	11.7%	44.1%	Fisher	0.01
Do you believe in the possibility of coexistence with wolves?	16.6%	29.4%	Fisher	0.02
Do you trust the administration?	0.0%	1.7%	Fisher	0.003
Has the wolf population increased in your region?	96.6%	76.4%	Fisher	0.03
Do you think wolf abundance is high in your area?	50%	35.2%	Fisher	< 0.001
Has the number of damages increased since the first attack?	76.6%	38.2%	Chi ₂	<0.001
Number of damages received last year?	8.4 $\pm$ 1.7	2.4 $\pm$ 0.4	Wilcoxon	0.002
What proportion of damages is not found?	51.5 $\pm$ 4.7	36.1 $\pm$ 5.5	Wilcoxon	0.04

was reported more frequently in the HCA. For foxes, a similar tendency was observed but did not reach statistical significance ($p = 0.07$). Perceptions of damage caused by badgers and eagles were uniformly low across regions, and no significant regional differences were detected (Table 2).

In terms of the perceived problems associated with wolf presence, economic impacts were reported significantly more frequently in the HCA than in the LCA (76.4% vs. 50.0%; $p < 0.001$). Conversely, psychological impacts were significantly more common in LCA respondents (44.1% vs. 11.7%; $p = 0.012$). Social problems were infrequently reported in both regions and did not differ significantly between groups (0.0% vs. 14.7%; $p = 0.494$). Despite these differences in the type of perceived impacts, the overall evaluation of wolf effects on livestock

activities did not differ between the regions (Table 2).

No significant regional differences were found in reported annual livestock losses or in expenditure on preventive measures (Table 2). However, farmers in the HCA were significantly more likely to report the experience of wolf attacks ($p < 0.001$).

Regarding management strategies, all proposed measures were generally positively evaluated in both regions (Fig. 4a). Nevertheless, farmers in the LCA showed significantly stronger support than those in the HCA for maintaining wolves as a game species ($W = 741$, $p < 0.001$), increasing financial compensation ($W = 317$, $p = 0.005$), and accelerating compensation payments ($W = 664$, $p = 0.008$). In contrast, both groups expressed similarly high levels of support for developing new preventive tools and increasing scientific knowledge about wolves

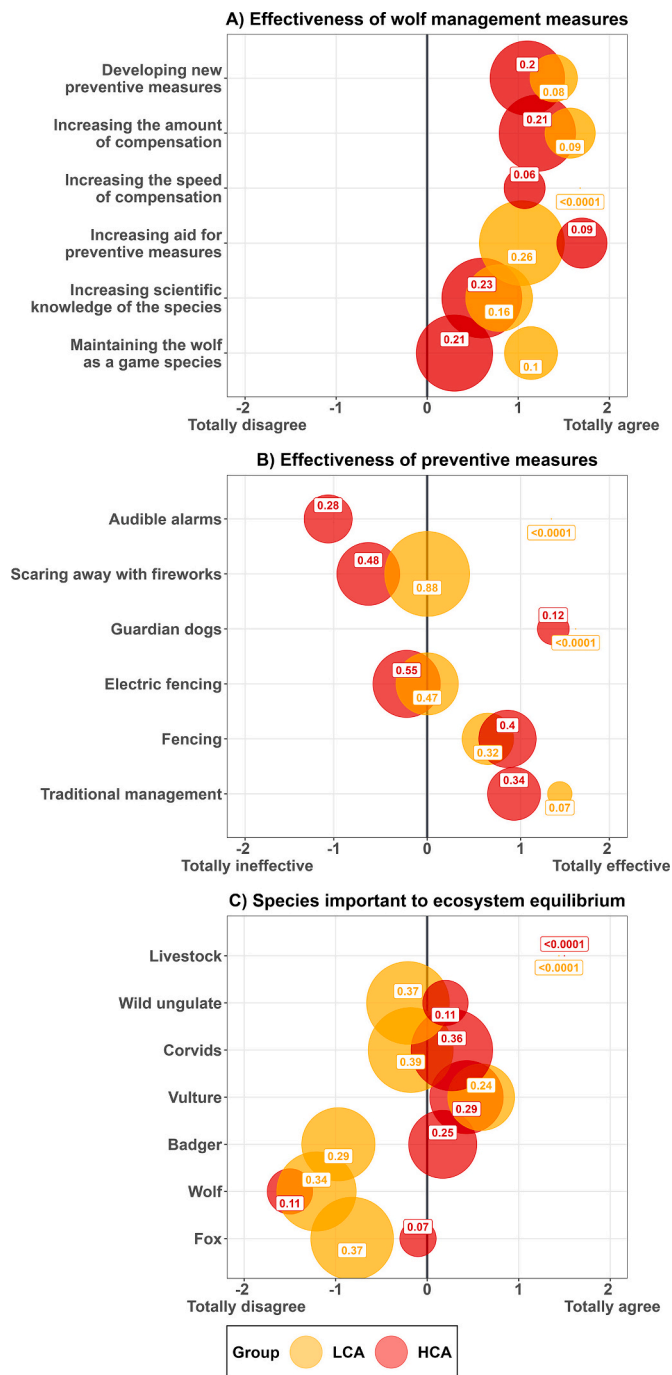


Fig. 4. Potential for Conflict Index (PCI_2) values are related to areas with different conflict intensity for: A) perceived effectiveness of wolf management measures, B) perceived effectiveness of preventive measures and C) importance for the ecosystem equilibrium attributed to each species in the two study areas. Position of each bubble on the horizontal axis indicates the mean value associated with a 5-points scale ranging from -2 (Totally disagree) to 2 (Totally agree). Bubble size indicates the PCI_2 value associated to values in Low Conflict (in yellow) or High Conflict (in red) areas. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Fig. 4a; Table S2). Respondents considered reducing wolf populations through hunting quotas to be the most effective management measure, assigning significantly higher importance to this option than to increasing financial compensation for livestock losses and implementing new methods to reduce damage in CLMM models. In contrast, scientific

knowledge and financial support for preventive measures were rated similarly to predator removal. Respondents from the HCA assigned lower overall importance scores to management measures than those from the LCA (Table S4).

Perceived effectiveness of preventive measures was also broadly similar across regions. No differences were found for traditional herding practices, fencing (including electric fencing), livestock guardian dogs, scaring devices, or fladry (Fig. 4b). The only exception was audible alarm systems, which were rated more positively in the HCA than in the LCA ($W = 47.5$, $p = 0.017$).

Finally, perceptions of ecological value attributed to wildlife and livestock species varied across regions. The wolf was the least valued species in both areas, with no differences between them (Fig. 4c). In the LCA, all carnivore species were rated negatively, whereas in the HCA foxes and badgers were rated more neutrally or slightly positively. Accordingly, farmers in the HCA assigned significantly higher ecological value to foxes ($p = 0.010$) and badgers ($p < 0.001$) than those in the LCA. No significant differences were found for corvids or wild ungulates, although similar trends were observed. Vultures were consistently rated positively and were the most highly valued wild species in both regions. Livestock was rated most positively and showed the highest level of agreement among respondents, surpassing all wild species, with no differences between areas (Fig. 4c). Regarding the ecological importance derived from the CLMM models, respondents from the HCA assigned higher scores overall than those from the LCA. Livestock was rated as significantly more important than the reference species (badger), whereas no significant differences were detected among the remaining species, including wolves, foxes, vultures, corvids, and wild ungulates (Table S4).

4. Discussion

Our results indicate that differences in the interpretation of livestock farmers' perceptions of wolves depend on the spatial scale of the analysis. At the national scale, survey responses did not differ markedly between areas with and without wolf presence, except regarding the species perceived to cause most attacks and the reported costs of implementing preventive measures. This suggests that, at broader spatial scales, perceptions toward wolves tend to be relatively homogeneous and may not necessarily reflect farmers' direct experiences with coexistence (Capitain et al., 2025). In contrast, livestock farmers' responses at a finer regional scale varied significantly in two areas that were recently occupied by wolves and differed in conflict intensities. More negative perceptions were observed in the area experiencing higher levels of conflict, highlighting how the intensity and frequency of damage can exacerbate negative perceptions (Naughton-Treves et al., 2003). These findings underscore the importance of considering local context when interpreting human-wildlife interactions.

4.1. National scale

As shown in this study, the perceptions of livestock farmers were generally similar across all areas surveyed in Spain, regardless of the presence or absence of wolves. This contrasts with previous findings from Norway, where more negative perceptions were reported in areas where the wolves were present (Zahl-Thanem et al., 2020). This suggests that livestock farmers in Spain do not represent a classic "not-in-my-backyard" case, but instead share a generalized perception toward wolves, as described for other species (Morales-Reyes et al., 2018; Ashish et al., 2022). In this context, perceptions toward wolves may be influenced not only by direct experience with predation, but also by media narratives associated with recolonization phases and periods of heightened social and political attention (Ravaglia et al., 2026). Most attacks in wolf-occupied areas were attributed to wolves, whereas farmers in non-wolf areas frequently attributed them to foxes or wolves. These reports could be related to occasionally dispersing wolves near the

current distribution range (Miller et al., 2016). In addition, predation by other carnivores, particularly foxes and feral dogs, can be an important cause of mortality in young lambs, which may further contribute to uncertainty in attributing mortality cases. A marginal trend suggested that losses due to predation increase livestock farmers' intentions to abandon livestock farming, although this decision appears to be influenced by a broader set of other pressures, including ecological constraints (e.g. biodiversity requirements), economic challenges (e.g. low market prices for livestock products, rising production costs and competition with forestry productivity), and landscape-related factors, as observed before in earlier studies (Benjamin et al., 2007; Morales-Reyes et al., 2025). Our findings indicate that farmers in wolf areas reported significantly higher expenditure on preventive measures compared to those in non-wolf areas, a pattern consistent with previous research (Rigg et al., 2011; Bautista et al., 2019). Nevertheless, the relative economic losses attributed to depredation did not differ between wolf and non-wolf areas. Perceptions of the effectiveness of preventive measures were generally similar between groups, suggesting that coexistence strategies are viewed as comparable regardless of wolf presence. Reducing predator populations through culling was the measure that generated the highest level of disagreement among respondents. This lack of consensus is consistent with a growing body of literature questioning the effectiveness of lethal control. Several studies have shown that culling often has limited or only localized effects (Grente et al., 2025), and, in some cases, studies have shown no clear relationship between the number of wolves removed and reductions in livestock losses (Kutal et al., 2024). Moreover, lethal control can disrupt pack social structure, potentially increasing the number of solitary individuals, which in some cases can lead to higher depredation rates on livestock (Wielgus and Peebles, 2014). These ecological mechanisms may contribute to the uncertainty and disagreement observed among farmers regarding the effectiveness of culling as a management strategy. Nevertheless, this finding should be treated cautiously due to the limited sample size at the national scale, when comparing respondents from areas with and without wolves. The reduced sample size may have constrained our ability to detect significant differences and could bias the results toward more homogeneous responses. Therefore, the absence of detected differences should not be interpreted as evidence of true equivalence between groups.

4.2. Regional scale

The results at the regional scale indicate that the level of conflict between livestock farmers and wolves is influenced more by social factors and individual perceptions than by the actual extent of damages, consistent with findings from other studies (Karlsson and Sjöström, 2007; Mahajan et al., 2022). Respondents from the HCA primarily characterized the problem as economic, whereas respondents from the LCA perceived it as both economic and psychological. Higher levels of reported damage were associated with more negative perceptions of the economic impact of wolves and a greater likelihood of having experienced a wolf attack (Eriksson et al., 2015). Previous research has shown that individuals directly affected by livestock losses due to wolf depredation tend to express more negative perceptions than those without such experiences (Barmoen et al., 2024). A similar pattern emerged for other potentially involved species, such as feral dogs and vultures, suggesting a negative perception of wildlife in high-conflict areas (Dickman et al., 2013). Perceptions of higher wolf abundance and population growth in the region were associated with higher levels of conflict. The perceived overabundance of large carnivores appears to be driven more by the frequency of negative experiences and the social context surrounding conflict than by actual ecological data (Suárez-Tangil and Luna, 2023; Colomer et al., 2026).

Low trust in public institutions reinforces a cycle of institutional mistrust, negatively affecting the implementation of preventive measures, the acceptance of compensation, and perceptions of fairness in

conflict management (Janeiro-Otero et al., 2023). High levels of conflict were also linked to lower trust in public administrations and decreased confidence in the feasibility of long-term coexistence. For instance, our study found that livestock farmers often consider compensation schemes and administrative tools insufficient to improve tolerance toward wolves, regardless of wolf presence and damage intensity, as described by Marino et al. (2016). Perceptions toward management measures varied according to conflict level: farmers experiencing lower conflict were more supportive of maintaining the wolf as a game species, despite the species being fully protected in that region since 1992 (Ordiz et al., 2022). Conversely, economic support for preventive measures was more positively evaluated in the HCA, whereas faster compensation was more frequently mentioned in the LCA, indicating that the perceived effectiveness of management actions does not always align with conflict intensity. Compensation programmes have been described as an essential tool for increasing tolerance and alleviating the financial burden posed by large carnivores (Agarwala et al., 2010; Morehouse et al., 2018). These patterns underscore that management preferences are shaped by conflict intensity, highlighting the need for regional policies that are better adapted to local realities (Braczkowski et al., 2023). Regarding preventive measures, opinions were generally similar across conflict levels, except for audible alarms perceived as more effective in areas with high conflict. Global reviews across large carnivore species also concluded that the most effective measures for reducing damage include livestock-guarding dogs, deterrents, and enclosures (Eklund et al., 2017; Van Eeden et al., 2018; Oliveira et al., 2021).

Overall, livestock farmers in both areas perceived domestic livestock as the most important component for maintaining ecosystem balance, while carnivores were generally considered less important. This pattern reflects a production-oriented view of ecosystems, in which livestock farming is regarded as a key structuring element, despite the well-documented ecological role of large carnivores as top predators (Ripple et al., 2014; Ripple and Beschta, 2012). Similar perceptions have been reported in other pastoral systems, where farmers prioritize the ecological and socio-economic role of livestock over that of predators (Redpath et al., 2017). In contrast, differences between areas were mainly observed in the valuation of wild carnivores, particularly mesopredators. The relatively more positive perception of mesopredators in high-conflict areas suggests that negative perceptions were primarily directed toward wolves, the main source of conflict, while other carnivores were viewed less negatively. This pattern is consistent with the context-dependent nature of wildlife perceptions reported by Morales-Reyes et al. (2018). It may also indicate that negative perceptions associated with large carnivores, particularly wolves, can extend to or overshadow perceptions of other carnivores, thereby influencing the overall valuation of mesopredator guilds (Martínez-Jauregui et al., 2017; Colomer et al., 2026). In addition, perceptions of mesopredators may vary across contexts depending on perceived risks, such as disease transmission or impacts on game species (Bouchez-Zacria et al., 2023; Colomer et al., 2026).

4.3. Management implications for spatially adapted coexistence

Our results indicate that coexistence strategies should be designed at multiple spatial scales. At the national scale, livestock farmers showed broadly similar perceptions regardless of wolf presence, suggesting that general policies can provide a common framework for compensation schemes, legal procedures, and technical support (Oliveira et al., 2021). However, the marked differences observed at the regional scale demonstrate that the acceptance and perceived effectiveness of management measures are strongly influenced by local conflict intensity, previous experiences with depredation, and trust in institutions (Karlsson and Sjöström, 2007; Capitain et al., 2025).

Preventive measures were generally perceived similarly across study areas, indicating that most tools are broadly accepted by livestock farmers. This suggests that management efforts should focus less on

promoting individual measures and more on improving their accessibility, technical implementation, and long-term maintenance. Global reviews have shown that preventive tools such as livestock-guarding dogs, fencing, and deterrents can substantially reduce depredation when properly implemented and adapted to local husbandry systems (Eklund et al., 2017; Van Eeden et al., 2018). In our study, farmers in high-conflict areas reported greater expenditure on prevention and assigned higher importance to financial support for preventive measures, highlighting the need to prioritize subsidies and technical assistance where conflict is most intense (Bautista et al., 2019).

Compensation schemes also emerged as an important management tool, although their perceived importance varied with conflict context. Farmers in low-conflict areas placed greater value on faster compensation, whereas those in high-conflict areas emphasized support for prevention. Compensation programmes have been described as a key mechanism for mitigating the economic burden of large carnivores and increasing tolerance, particularly when payments are timely, transparent, and perceived as fair (Agarwala et al., 2010; Morehouse et al., 2018; Marino et al., 2016). Our results suggest that compensation should be integrated with preventive support rather than implemented as a stand-alone measure.

Finally, the strong association between conflict intensity and lower trust in public administration indicates that effective wolf management depends not only on reducing damages but also on strengthening institutional legitimacy. Low trust can undermine the uptake of preventive measures, reduce satisfaction with compensation schemes, and exacerbate perceptions of injustice (Janeiro-Otero et al., 2023). Participatory processes that actively involve livestock farmers and other stakeholders in the design and evaluation of management actions have been shown to improve transparency, legitimacy, and social acceptance (Salvatori et al., 2020; Salvatori et al., 2021). Therefore, coexistence strategies should combine evidence-based preventive measures, efficient compensation systems, and inclusive governance tailored to local socioecological conditions (Redpath et al., 2017). Such approaches are more likely to reduce conflict, maintain the economic viability of extensive livestock farming, and support long-term coexistence between rural communities and wolves.

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All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript.

CRediT authorship contribution statement

Lucía Del Río: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Jon Ander Zearra:** Writing – review & editing, Methodology, Data curation. **Valentin Lauret:** Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **Rafael Mateo:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Jorge Tobajas:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Methodology, Investigation, Conceptualization. **Pablo Ferreras:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Ethics statement

Our study adhered to the basic ethical principles for conducting research that involves human subjects. In particular, the participants in

the questionnaire were informed about the safeguard of the privacy, confidentiality, and anonymity of all the information they provided, according to Spanish law of data protection and its adaptations to European Union regulations on data privacy (i.e. Royal Decree-Law 5/2018, of 27 July, concerning urgent measures for adaptation of Spanish law to European Union regulations on data privacy). The final questionnaire and its protocol were approved by CSIC Ethics Board, certificate 211/2021.

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Declaration of competing interest

The authors declare no conflicts 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.2026.112018>.

Data availability

The data are available in Zenodo. doi:<https://doi.org/10.5281/zenodo.18923613>

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