Men and wolves: Anthropogenic causes are an important driver of wolf mortality in human-dominated landscapes in Italy

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Men and wolves: Anthropogenic causes are an important driver of wolf mortality in human-dominated landscapes in Italy

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A R T I C L E I N F O

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A B S T R A C T

Over the last 40 years the gray wolf (*Canis lupus*) re-colonized its historical range in Italy increasing human-predator interactions. However, temporal and spatial trends in wolf mortality, including direct and indirect persecution, were never summarized. This study aims to fill this gap by focusing on the situation of Tuscany and Emilia-Romagna regions, hosting a significant proportion of the Italian wolf population, by: (*i*) identifying the prevalent causes of wolf mortality, (*ii*) summarizing their temporal and spatial patterns and (*iii*) applying spatially-explicit Generalized Linear Models to predict wolf persecution. Between October 2005 and February 2021, 212 wolf carcasses were collected and subjected to necropsy, being involved in collisions with vehicles (n = 104), poisoned (n = 45), wounded with gunshot (n = 24) or blunt objects (n = 4) and being hanged (n = 2). The proportion of illegally killed wolves did not increase through time. Most persecution events occurred between October and February. None of our candidate models outperformed a null model and covariates such as the density of sheep farms, number of predations on livestock, or human density were never associated to the probability of having illegally killed wolves, at the municipal scale. Our findings show that conventional correlates of wolf persecution, combined with a supposedly high proportion of non-retrieved carcasses, fail to predict illegal wolf killings in areas where the species have become ubiquitous. The widespread spatial distribution of illegal killings indicates that persecution probably arises from multiple kinds of conflicts with humans, beyond those with husbandry. Wolf conservation in Italy should thus address cryptic wolf killings with multi-disciplinary approaches, such as shared national protocols, socio-

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ecological studies, the support of experts' experience and effective sampling schemes for the detection of carcasses.

1. Introduction

Over the last 40 decades, the gray wolf (*Canis lupus*) steadily expanded its distribution across Western Europe thanks to a synergy of multiple factors, including the abandonment of marginal rural areas and the increased availability of undisturbed areas, a boom in the populations of ungulates, as well as the widespread legal protection against unregulated culling (Chapron et al., 2014; Linnell et al., 2020; Cimatti et al., 2021). Such of a mix of different social and environmental dynamics, together with the huge degree of behavioral and ecological flexibility shown by the species (e.g. diet, Newsome et al., 2016; e.g. habitat selection, Muhly et al., 2019; Mancinelli et al., 2019), reverted the decrease and fragmentation which had characterized Western European wolf populations for centuries (Delibes, 1990; Mech, 1995; Dufresnes et al., 2018). Nowadays, it is estimated that more than 10,000 wolves live within the European Union and the Balkans (Boitani and Linnell, 2015).

Nonetheless, expanding large carnivore populations in Europe pose considerable challenges to contemporary wildlife management (Mech, 2017). As in other areas of the world, European carnivores can damage human activities like livestock farming (Van Eeden et al., 2018), and wolves make no exception (Janeiro-Otero et al., 2020). Furthermore, changing wildlife value orientations (Manfredo et al., 2020), can fragment attitudes towards the presence of wolves and complicate their management (Dressel et al., 2015).

Wolves living in regions with high human densities in Central and Northern Italy are particularly at risk of conflicts with anthropic activities, which can undermine the social support towards them and trigger illegal killing. In facts, the Italian wolf population, after the saturation of undisturbed areas (Bassi et al., 2015), is now widespread across almost all of its historical range (Galaverni et al., 2016), including rural and urbanized areas (e.g., the Po plain) (Meriggi et al., 2020).

This expansion raises many questions about conflicts with human activities. To date, most studies about human-wolf conflicts in Italy focused on those with livestock (Ciucci et al., 2005; Berzi, 2010; Boitani et al., 2011; Meriggi et al., 2020). However, in these new ecological conditions wolves are likely to raise conflicts with human activities other than herding. For example, the increase of wild boar distribution and abundance has led to nationwide practice of drives with dogs involving the culling of hundreds of thousands of boards each year, even around cities (e.g. Tuscany, 2018; Regione Toscana, 2018). It is thus plausible that new conflicts between wolves and hunters emerged, similarly to other European countries where ungulate hunting with dogs is widespread, as well as hunting dogs killed by wolves (Mykrä et al., 2017; Bassi et al., 2021). Also, wolves in these newly colonized areas are more likely to suffer from poisoned baits released against stray dogs, or from accidental poisoning with pesticides and anticoagulants (Bertero et al., 2020). Testing for the occurrence of these "hidden" conflicts is paramount for wolf management, because they can trigger cryptic persecution, an important limiting factor for wolf recovery (Liberg et al., 2012), or they can become politicized (Darimont et al., 2018) undermining any shared management policy for the species.

Wolf populations are mostly subjected to mortality rates driven by natural causes (e.g., diseases) (Mech et al., 1998; Cubaynes et al., 2014; Barber-Meyer et al., 2021); however, detailed information on the relative impact of anthropogenic mortality is still scarce across human-dominated European landscapes (Lovari et al., 2007a) and far from trivial (Treves et al., 2017). Current knowledge on the main causes of wolves' mortality is necessary to infer the limiting factors acting on this species and essential to implement effective conservation and management strategies.

Another important gap of knowledge, undermining targeted wolf conservation strategies in Italy, is represented by the limited information about population abundance (Caniglia et al., 2012; Galaverni et al., 2016) and its related parameters (e.g. birth, mortality and reproduction rates). Moreover, even less is known about individual body condition, in relation with environmental characteristics of the landscape. Wolves are elusive and strictly protected carnivores, requiring official permissions from national authorities to be live captured for scientific purposes. Furthermore, the effort required to reach a representative number of individuals is considerable and the researchers are constantly challenged to obtain robust and reliable datasets (Ciucci et al., 2007).

In this perspective, any recovery of wolf carcasses is an important source of information (Lovari et al., 2007b). Apart from the cause of mortality, many other relevant information can be obtained from a wolf carcass, including additional injuries and pathologies, sex, age and weight. An accurate observation of the phenotype can also contribute to evaluate anomalies in coat coloring or body characteristics likely attributable to hybridization (Anderson et al., 2009; Galaverni et al., 2017). The species or subspecies assignment, as well as past hybridization events with domestic dogs, can be confirmed applying molecular analyses on DNA obtained from blood or muscle samples (Randi et al., 2014; Caniglia et al., 2020). Finally, it is possible to study the health conditions, the presence of some etiological agents (Oleaga et al., 2015) and to conduct toxicological investigations (Rubini et al., 2019). Necropsy has the function of confirming suspicion, while subsequent laboratory tests on organic samples can determine possible positivity to a toxic substance (Mariacher and Fico, 2017). Any injury, disease or disorder that triggers the physiological imbalance that leads directly to the death of the individual is defined as the cause of death (Brooks Brownlie and Munro, 2016).

The limiting aspect of the collection of carcasses is associated with their detectability: this is often the case especially when illegal killings occur and hiding the carcasses is a common practice (Liberg et al., 2012). Moreover, environmental conditions, often characterized by limited visibility and/or accessibility can increase the difficulties of finding a wolf carcass.

Currently there is a common protocol for the collection of wolf carcasses in Italy, but the data obtained are not collected in a single database; this is preventing the possibility to combine high-quality and large-scale data across the country.

In this research, carried out in the Emilia-Romagna and Tuscany regions, which are estimated to host a considerable percentage of the whole wolf population in Italy (Galaverni et al., 2016), we aimed to: (*i*) identify the prevalent causes of wolf mortality, (*ii*) summarize their temporal and spatial patterns and (*iii*) test how well illegal wolf killing can be predicted from conventional environmental predictors of human-wolf conflicts and if spatial smoothing can identify hotspots of persecution.

2. Materials and methods

2.1. Study area

The study area includes the entire Emilia-Romagna and about half of the Tuscany region, in Central Italy (Fig. 1). In Tuscany, the provinces of Siena, Arezzo and Grosseto were not covered by our data collection scheme and we did not receive recovered wolves from there. Therefore we excluded them from out study area. The study area is characterized by a huge environmental heterogeneity, ranging from Mediterranean maquis to sub-alpine prairies and broad-leaved forests. High human density is restricted mostly to the Po plain, in the Emilia-Romagna region, and in the lower Arno basin, in Tuscany. Overall, the study area hosts 7,359,251 residents (http://demo.istat.it/) across ca. 33.900 km2, resulting in a human density of 252.01 ± 140.11 people/km2 (mean ± sd).

Wolf populations expanded their distribution and numbers since the 1990 s, with a population of at least 97 packs between 2014 and 2016 (Caniglia et al., 2014; Apollonio et al., 2016). This increase followed that of wild ungulate populations, which in these two regions attain densities among the highest in Europe and are subject to an intensive culling throughout the year, which now exceeds recreational hunting. Overall, more than 63,000 and 37,000 recreational hunters occur in Tuscany and in the Emilia-Romagna region, respectively (Cerri et al., 2018; Regione Toscana, 2018; Regione Emilia-Romagna, 2018).

Conflicts between wolves and shepherding occur, due to the economic impact of predation, the lack of long-term prevention and mitigation policies, as well as the decreasing economic viability of sheep farming (Pulina et al., 2018). While the Emilia-Romagna region co-financed and promoted prevention measures, which considerably decreased the number of predations on livestock (Berzi et al., 2021), the diffusion and co-financing of prevention measures is much scarcer in Tuscany, being restricted mostly to those provinces that were not included in our study area. Although Tuscany promoted prevention measures and paid compensations in the past, these did not entirely cover the real magnitude of damages suffered by farmers and were refunded after months. Lethal control of

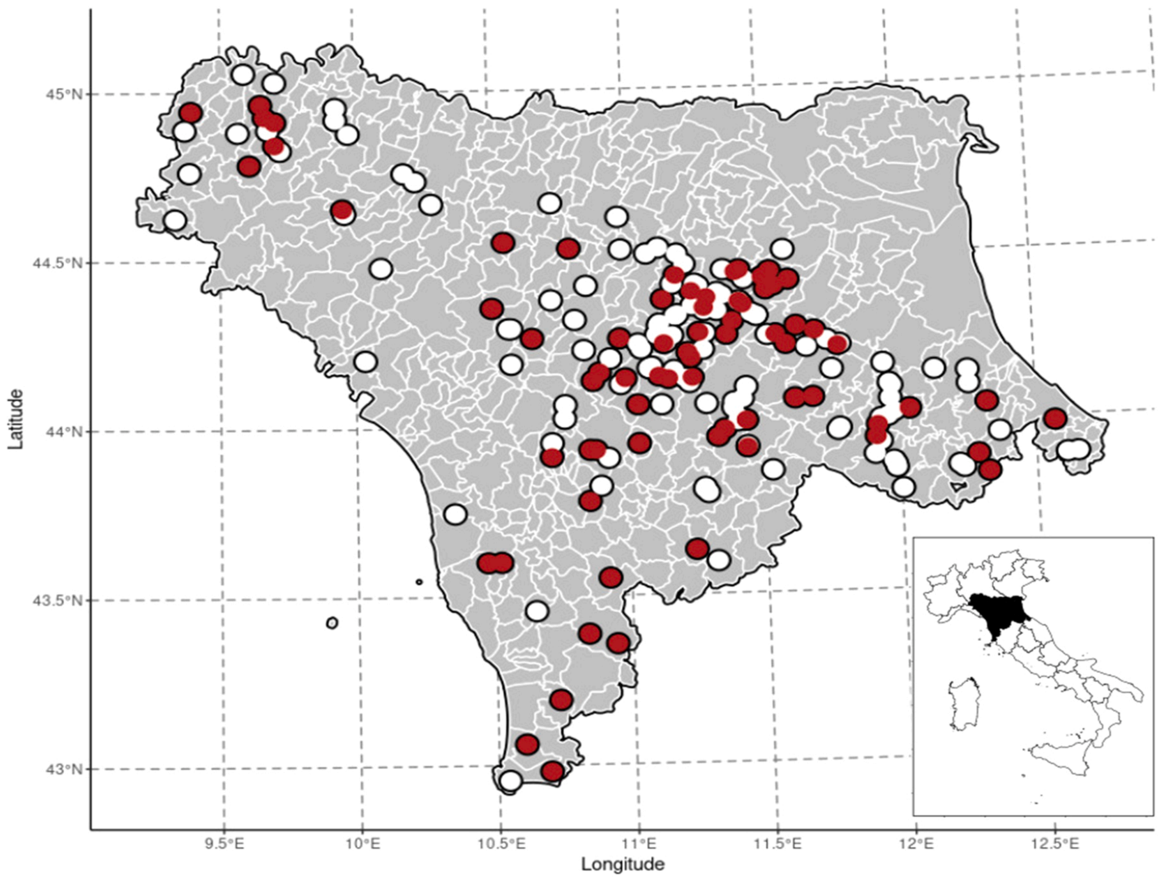

Fig. 1. Study area with municipal boundaries, and the location of recovered wolf carcasses (in dark red those with signs of past persecution, in white all the others). The map on the bottom-right corner of the figure shows the Italian provinces covered by data collection.

problematic wolves was never authorized. The sterilization or captivation of hybrid individuals was sometimes undertaken with limited efforts within European and regional projects.

2.2. Data collection and statistical analysis

Between October 2005 and February 2021, a total of 212 wolf carcasses were collected after being notified to public authorities. All carcasses were collected according to the National Action Plan for the wolf conservation. Specifically, the plan requires that each wolf carcass is checked and collected by the public authority in charge (depending on the regional/provincial regulations, as a duty of the Forestry Police, Provincial Police, Local Health Authority and/or Park Authorities). Carcasses were subsequently delivered to authorized centers in order to proceed with the necropsy (i.e., Institutes for the Prevention of Animal Diseases, Universities and Park Authorities) and genetic analyses (Genovesi, 2002). A complete overview of necropsy and genetic analysis is given in Appendix 1. After having excluded 12 individuals (5.7%), for which no reliable information could be obtained from necropsy due to their advanced state of decomposition, thus classified as "unknown" cause category, we retained 200 wolves for data analysis. We summarized data in terms of temporal and spatial distribution, sex ratio, age classes and mortality causes, namely "natural", "anthropic" and "unknown", in turn divided into subcategories including poisoning or gunshots that can indicate persecution from humans.

To identify drivers of illegal wolf killing we fit a spatially explicit Bayesian Generalized Linear Model (GLM), with a twofold scope. On the one hand, our model aimed to see if conventional predictors of human-wolf conflicts, mostly associated to livestock, predicted the presence of illegally killed wolves. On the other hand, model predictions enabled spatial smoothing and the visualization of hotspots of illegal wolf killing. Although our data were geostatistical points with coordinates, we assigned them to municipalities ($n = 494$), as predictors were available at this spatial scale as areal data. Moreover, we coded the presence of illegally killed wolves as a dichotomous variable, indicating the presence/absence of at least one killed wolf in a certain municipality between 2005 and 2021, and modeling its probability with a Bernoulli distribution and a log-link. We opted for this choice because only 12 municipalities had 2 or more wolves, and a Poisson or an ordered-logit structure did not adequately fit the data.

Covariates captured: (*i*) proxies of conflicts with livestock, the major expected source of human- wolf conflicts in the study area, (*ii*) drivers of wolf presence producing differences between municipalities and (*iii*) factors affecting wolf carcass detection and therefore the total number of illegally killed wolves. Proxies of conflicts with livestock included the number of farms per squared kilometer, extracted from the national livestock dataset (Ministry for Agriculture and Forestry) (https://www.vetinfo.it/j6_statistiche//). For the Emilia-Romagna region ($n = 328$) we fit a separate model where we also included the logarithm of predation events on livestock, that had occurred in each municipality between 2011 and 2016. Unfortunately, we had to fit a separate model because predation events were not available for the Tuscany region. Also, we adopted a dichotomous variable that classified each municipality as a marginal rural area or not, based on the national classification (https://www.reterurale.it/areerurali). Marginal rural areas are expected to be more prone to see the escalation of human-wolf conflicts, because of their decreased level of financial viability of farming activities, which make farmers less able to cope with economic losses from predations. We also accounted for the permanent presence of wolves,

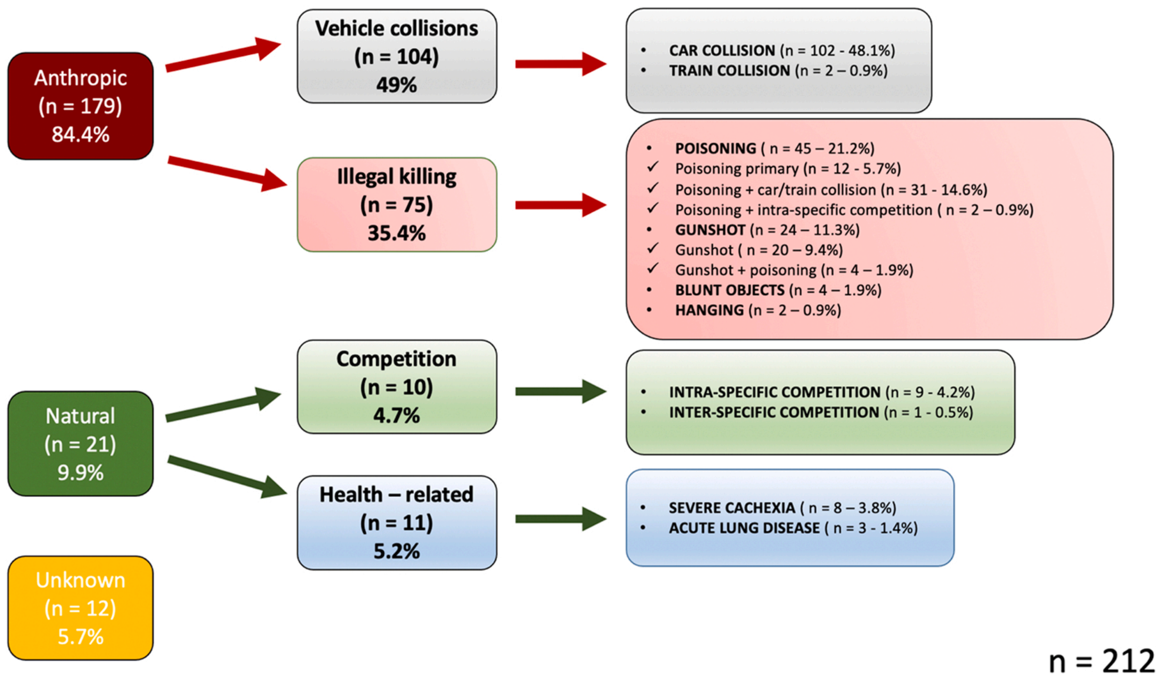

Fig. 2. The causes of death were divided into three groups: "natural", "anthropic" and "unknown" in turn divided into subcategories, detailed with the specific causes of death. For "poisoning" and "gunshot" the primary causes and with contributing cause were distinguished.

because it could confound both the detection of carcasses and the occurrence of predation and conflicts (absent wolves, there are neither recovered carcasses, nor predations). Therefore, we used a dichotomous variable, obtained by manually classifying municipalities according to existing maps of wolf presence (Caniglia et al., 2014; Apollonio et al., 2016). This variable identified those municipalities where wolves had been regularly present between 2005 and 2021, distinguishing them from municipalities where occasional records were available and from municipalities where wolves were never recorded (e.g. highly urbanized areas). Finally, we also included two variables that aimed to represent drivers of the underlying detection process that generated wolf records. The first one was human density, as areas with many people are most likely to be those where wolf carcasses are found and reported, as a consequence of the higher number of persons wandering around the municipal area (e.g. hikers, drivers, dog-owners). Also, areas with many people are probably those where illegal wolf killing is somehow harder, due to the higher probability of being discovered while shooting wolves or displacing their corpses (Suutarinen and Kojola, 2018). The second one was an offset variable, with a log-link modeling the influence of the total number of wolves that were found at a certain municipality over the probability of having at least one wolf killed there.

Predictors were standardized and centered, and we used weakly informative prior distribution of slope parameters (a Normal distribution with mean equal to 0 and variance equal to 1, see Lemoine, 2019) to improve model regularization. Collinearity between predictors was checked before model fitting, with the Variance Inflation Factor, whose values were below the conventional threshold of 1.8. Models were fit with 4 MCMC with 5000 iterations each. We also included a Besag-York-Mollié structure, to account for spatial autocorrelation between adjacent municipalities (Moraga, 2019). Models were compared with the Widely Applicable Information Criterion (WAIC), the Deviance Information Criterion (DIC) and leave-one-out cross validation (Vehtari et al., 2017), through a backwise approach, where non-significant predictors were progressively discarded from the full model. A predictor was deemed significant according to the overlap between its posterior distribution and a Region of Practical Equivalence between − 0.18 and + 0.18 (ROPE, Kruschke and Liddell, 2018). Finally, we also carried out the exploration of model residuals, to detect non-linear effects of covariates, and also posterior predictive checks, to see how well our data fit to the chosen distribution of the error term. The overall quality of model performance was calculated with the classification accuracy and the Area Under the Curve (AUC).

3. Results

Only 21 of the 212 wolves examined (9.9%) died of natural causes (Fig. 2), mostly diseases or starvation (n = 11) and injuries from other wolves or dogs (n = 9). One wolf was most probably killed by a red or fallow deer. Sarcoptic mange was present in 41 carcasses (n = 41).

Overall, anthropic mortality was identified on 179 wolf carcasses (84.4%). Among them, 104 individuals had been involved in collisions with vehicles, and 75 wolves had signs compatible with illegal human persecutions, namely poisoning with toxic substances (n = 45), wounds from gunshot (n = 24), from blunt objects (n = 4) and hanging (n = 2) (Fig. 2). These latter were classified as potentially subjected to illegal killing, although we will further comment this decision, with respect to poisoning, in the Discussion section. Wolves with and without signs of illegal killing did not markedly differ in their distribution of age classes (Illegally killed: 1 year = 27.8%, 2 years = 37.5%, 3 + years = 34.7%; Others: 1 year = 32.3%, 2 years = 34.7%, 3 + years = 33.1%) and sex (Illegally killed: Males = 58.3%; Others: Males = 52.4%), nor in their spatial location (Fig. 1). The number of carcasses showing signs of illegal killing increased throughout the years, and varied across seasons, similarly to the total number of death wolves (Fig. 3; Figs. S2 and S3). Most wolves (n = 140) were found dead between October and March (Fig. 3, Fig. S2).

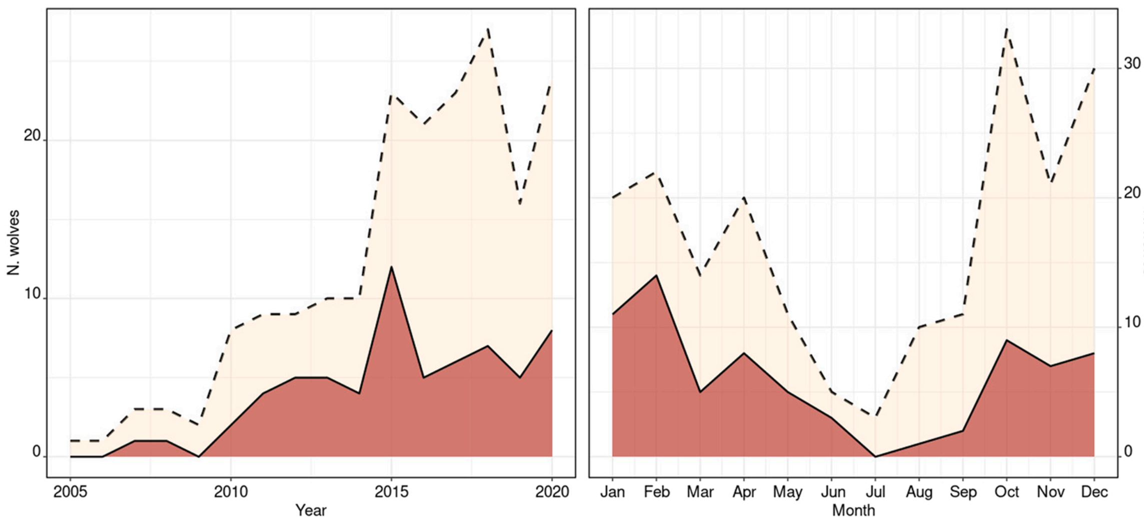

Fig. 3. Temporal evolution (left) and seasonal distribution (right) of wolf recoveries (in dark red those with signs of poisoning or wounds, in light colour the total number of wolf recoveries).

Bayesian GLM converged, and the analysis of model residuals and posterior predictive checks did not highlight any particular issue in model fitting. A complete overview of model selection and diagnostics is available in the Supplementary Information (Appendix 2). Model selection revealed that none of our candidate models outperformed a null model: covariates were not effective at predicting the probability that municipalities had at least one wolf killed, between 2005 and 2021. In the full model, using the logarithm of the total number of wolves as an offset seemed to improve model performances, but this variable lost any effect once that spatial correlation between neighboring municipalities was accounted for (Table 1).

Spatial smoothing, carried out by plotting predicted values from the best candidate model for the whole study area, revealed that municipalities in the Apennines, between Florence and Bologna, had the highest probability of having recorded killed wolves on their area (Fig. 4).

4. Discussion

During the last 40 years, gray wolves have become increasingly abundant and widespread in the Tuscany and Emilia-Romagna regions in Italy, raising considerable questions about their co-existence with human activities, similarly to other areas of Europe and North America (Mech, 2017). Our work summarizes the effects of this strong demographic increase and the spatial trends on the mortality causes of the species, while at the same time raising the alarm for the potential occurrence of hidden conflicts with human activities and diffused wolf persecution in these two regions.

In our study area, natural mortality was relatively low among the analyzed animals (9.9%), in line with previous studies from Europe (Huber et al., 2002; Lovari et al., 2007a) and North America (Fuller, 1989). Despite their low number, a considerable proportion of these wolves had died due to attacks from conspecifics. This point is in accordance with previous findings stating that wolves tend to regulate their numbers when other causes of mortality are low (Mech et al., 1998). In prey-rich Yellowstone National Park, intraspecific aggression regulated adult wolf survival in a density-dependent manner and independently from prey availability (Cubaynes et al., 2014). While the opportunistic sampling used in this study did not allow to make inference about the role of intraspecific aggression on the population parameters of wolves, our findings indicate that this dynamic can systematically occur even in environments characterized by a much stronger pressure by humans.

A number of individuals ($n = 41$) also were affected by sarcoptic mange, although this disease was never identified as the primary cause of death, but rather a concurrent cause. Interestingly, while this proportion of individuals with mange (19.5%) is similar to that found by Morner et al. (2005) in Scandinavia, it is far higher than values previously reported for Central Italy. Namely, Lovari et al. (2007a) found mange on 2 wolf carcasses out 154 in 2007. Our findings could indicate that the circulation of sarcoptic mange could have increased through time, and it can have a significant impact on fitness of wolves living in Central-Northern Italy. To date, no epidemiological study was carried out on mange in Italian wolves, and future initiatives adopting camera trapping designs can be useful to address its prevalence and spatio-temporal dynamics (Carricondo-Sanchez et al., 2017).

The very high proportion of wolves showing signs of human-driven mortality was certainly affected by our data collection methods

Table 1

Model comparison, between nested models. Measures of fitness include the expected log-pointwise predictive density (ELPD) of the leave-one-out cross validation, with its standard error, the Widely Applicable Information Criterion (WAIC), the classification accuracy and the Area Under the Curve, calculated over the training sample.

Model	ELPD ± S.E.	WAIC	Classification accuracy	AUC
Emilia-Romagna region				
illegal.ever ~ predations.std + farm.density.std + human.density.std + wolf.presence + marginal.area	-113.9 ± 11.8	226.8	0.78	0.79
illegal.ever ~ predations.std + farm.density.std + human.density.std + wolf.presence + marginal.area + offset(log(wolf.found.offset))	-91.1 ± 9.4	181.4	0.79	0.89
illegal.ever ~ log.pred.events.std + farm.density.std + human.density.std + wolf.presence + marginal.area + offset(log(wolf.found.offset))	-88.0 ± 9.2	175.8	0.81	0.91
illegal.ever ~ log.pred.events.std + farm.density.std + human.density.std + wolf.presence + marginal.area + offset(log(wolf.found.offset)) (BYM structure)	-87.4 ± 9.3	173.4	0.84	0.96
illegal.ever ~ log.pred.events.std + human.density.std + wolf.presence + offset(log(wolf.found.offset)) (BYM)	-85.7 ± 9.1	170.4	0.85	0.96
illegal.ever ~ log.pred.events.std + wolf.presence + offset(log(wolf.found.offset)) (BYM)	-85.3 ± 8.9	169.8	0.84	0.95
illegal.ever ~ log.pred.events.std + offset(log(wolf.found.offset)) (BYM)	-84.8 ± 8.7	168.7	0.85	0.96
illegal.ever ~ offset(log(wolf.found.offset)) (BYM)	-86.9 ± 8.8	172.3	0.88	0.98
illegal.ever ~ 1 (BYM)	-90.0 ± 10.1	162.7	0.93	0.98
Study area (Emilia Romagna + Tuscany)				
illegal.ever ~ farm.density.std + human.density.std + wolf.presence + marginal.area	-170.5 ± 14.5	341.0	0.63	0.68
illegal.ever ~ farm.density.std + human.density.std + wolf.presence + marginal.area + offset(log(wolf.found.offset))	-133.3 ± 11.1	266.5	0.82	0.92
illegal.ever ~ farm.density.std + human.density.std + wolf.presence + marginal.area + offset(log(wolf.found.offset))	-127.8 ± 11.3	254.4	0.84	0.97
illegal.ever ~ human.density.std + wolf.presence + offset(log(wolf.found.offset))	-126.9 ± 11.0	252.7	0.84	0.97
illegal.ever ~ human.density.std + offset(log(wolf.found.offset))	-126.2 ± 10.8	251.5	0.81	0.97
illegal.ever ~ 1 + offset(log(wolf.found.offset))	-128.0 ± 10.5	254.9	0.85	0.98

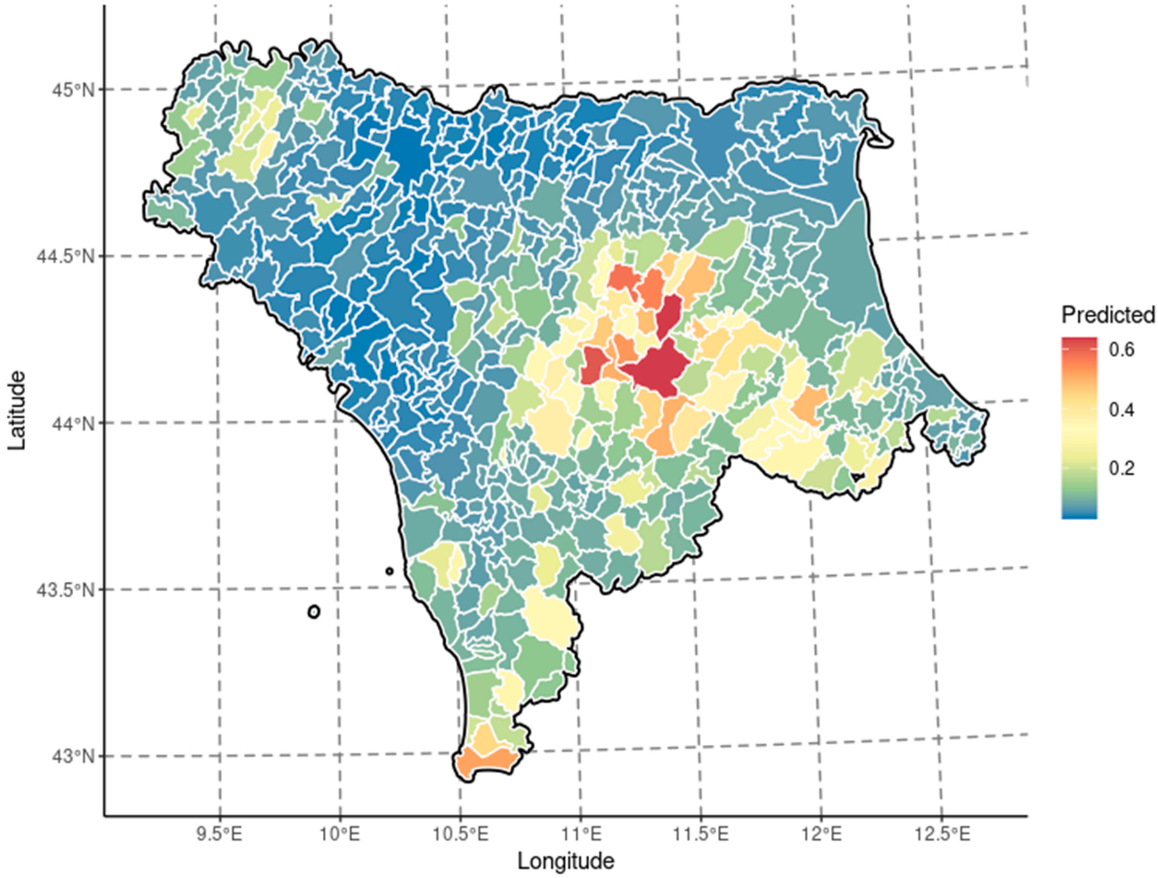

Fig. 4. Predicted values of the Bayesian GLM, showing municipalities with the highest probability of having recorded illegally killed wolves between 2005 and 2021.

and the consequent detection probabilities (e.g., road-killed wolves are easier to find than those who die in the wild). Nevertheless, our findings are highly suggestive that human-driven wolf mortality in our study area can be considerable, similarly to other studies conducted in Europe (Huber et al., 2002; Morner et al., 2005; Lovari et al., 2007a; Liberg et al., 2012, 2020; Sunde et al., 2021) and North America (Fuller, 1989; Murray et al., 2010; Treves et al., 2017). For all causes of anthropogenic mortality, there were no statistically significant differences between sex and age classes, suggesting a rather even impact on all of them.

Most anthropogenic mortality was accidental, through collisions with vehicles (49%). This finding is consistent with data from a similar study on European wolf mortality by Morner et al. (2005) and also with previous estimates from Central Italy (50.6%) (Lovari et al., 2007a). Most collisions occurred between September to December. This period in Italy coincides with the phase of increased independence of young wolves that are more mobile than during summer. Therefore, adults leave the surroundings of rendez-vous sites for hunting as the pups do not more necessitate continuous care. Moreover, pups start moving and hunting with adults (Mech and Boitani, 2007). These two simultaneous processes should have produced a higher proportion of collisions involving young wolves, as observed by Lovari et al. (2007a). The fact that we did not observe age-specific differences could have been caused by the fact that the expansion of wolves in more road-rich areas affects mortality not only in young, but also in adults. A study by Zimmermann et al. (2014) analyzed a group of 19 GPS-collared resident wolves, observing that some individuals have adapted in using the roads to facilitate their movements. This behavioral plasticity may have been important in enabling successful recovery of wolf populations in industrialized countries, while being also an important cause of susceptibility to anthropogenic mortality. While other studies found even higher prevalence of illegal killing (Huber et al., 2002; Murray et al., 2010; Treves et al., 2017; Sunde et al., 2021), our findings confirm the prominent role of persecution by humans over wolf mortality, being this the second leading cause of death for the animals examined in this study (n = 75), in line with similar studies from Central Italy (Lovari et al., 2007a).

Poisoning was particularly common (n = 45), in line with its widespread presence in Italy (Rubini et al., 2019), and often masked by other forms of mortality. For example, out of 45 poisoned wolves, 31 of them traveled on fast-moving roads or on tracks, and collided with vehicles or trains. Toxic substances can undermine the capacity of wolves to react to dangerous situations (Fournier-Chambrillon et al., 2004) and almost certainly these changed the behavior of poisoned individuals, possibly reducing their natural fear towards man. This data demonstrates the importance of the toxicological investigation of all dead animals, even when the cause seems evident. If we had stopped our investigations to the apparent fatal injuries, we would have underestimated poisoning by 75.5%, concealing the so-called "cryptic poisoning".

Injuries from firearms were also common. However, this cause of mortality could have been underestimated, because shot wolves could be hidden, thus harder to detect.

Most anthropogenic mortality was concentrated between September and March. As mentioned above, during this period both young and adult wolves increase their spatial activity. However, this period in the study area also coincides with the wild boar hunting and truffle season, when opportunities to shot wolves during drives with dogs increase and truffle collectors sometimes use poison to deter competitors to use their searching dogs.

The average density of sheep farms per squared kilometer, or the total number of predation events were not good predictors of wolf mortality, despite these are proxies of human-wolf conflicts that can trigger wolf persecution globally. The only case that at first increased model performances was the inclusion of an offset variables, linking the total number of wolves to the probability of illegally killed wolves. Still, even this solution was better replaced by a conventional Besag-York-Mollié structure for spatial correlation, which averaged observations across neighboring municipalities. This indicates that even wolf detection was probably not important per-se, but it reflected the spatially-varying distribution of wolves, which in turn placed most of recovered carcasses in the mountains between Florence and Bologna, a historical stronghold for the species (Caniglia et al., 2014; Apollonio et al., 2016). The simultaneous occurrence of widespread signs of wolf persecution, the lack of any clear spatial cluster, and the absence of relationships with conventional predictors of human-wolf conflicts is puzzling. We can offer three different, non-mutually exclusive, explanations for this pattern.

First, records of illegally killed wolves included many cases of poisoning, also from substances adopted for rodent control in croplands and peri-urban areas, like Brodifacoum. Some wolves could have suffered from intoxication due to their predation on rodents or their consumption of poisonous baits. Moreover, although the use of poisonous baits for pest control is regulated in Italy, they are adopted to illegally kill mesocarnivores and other wild animals, and sometimes to kill competitors' truffle dogs. If the use of rodenticides and the use of poisonous baits were segregated in space, with rodenticides being clustered around cities and baits being scattered far away from human settlements, such of a mixture of two processes could have produced the lack of any clear spatial pattern. Unfortunately, our dataset was relatively small, and we could not analyze poisoning data separately, as this would have meant a further reduction in the number of observations, with severe impacts on statistical power.

Second, the lack of any predictive power of wolf-livestock conflict might indicate that predations are poorly recorded. Even if the Emilia-Romagna region collected data about predations, it was through self-reported methods, like interviews with farmers (Berzi et al., 2021). These methods can suffer from misreporting, especially from those farmers who mistrust regional agencies and public authorities. If some farmers concealed predations from wolves, then probably this measure is unable to properly describe the amount of conflicts. Furthermore, it can also be hypothesized that in areas where predations are under-reported, farmers are also more careful at concealing illegal killing. Other approaches should be used to capture under-reporting of human-wolf conflicts, including stricter controls on livestock numbers, the use of whistleblowing from members of local communities, or specialized questioning techniques (Cerri et al., 2021).

Third, our results could indicate that illegal wolf killing is widespread in the study area, due to conflicts other than those with livestock. This should not be a surprise, because hunters in some European countries already conflict with wolves and poach them, deeming them to be a pest which can reduce the abundance of game and wild ungulates (despite the growing numbers of ungulates occurring throughout central Italy) and interfere with their traditional hunting habits killing their hunting dogs (e.g. Finland, Mykrä et al., 2017; Suutarinen and Kojola, 2017; e.g. Scandinavia, Liberg et al., 2012). Considering that wild boar and deer hunting is now carried out throughout most of the regions, it is plausible that illegal killing of wolves by hunters is not restricted in space but occurs at multiple locations. The hunting community however, never really expressed its concerns about the presence of wolves, at least to an extent comparable to what hunters did in some other European areas (Ericsson and Heberlein, 2003). However, this lack of any communication could have depended upon the protected status of the species in Italy, the strong level of polarization surrounding its management and maybe from mistrusts towards regional wildlife agencies.

We believe that all these three hypotheses need to be adequately investigated, because each one of them poses various threats to wolves and possibly other wildlife species in the study area. If wolves are getting accidentally poisoned by baits for pest management, these are probably also affecting other species of conservation concern. On the other hand, if persecution arises from cryptic conflicts with shepherd, hunters or other categories, not measuring them can have extremely negative consequences for wolf populations, in case lethal control will be considered in the future without accounting for extra human-related mortality (Treves et al., 2017). Also, ignoring these conflicts can prevent agencies from designing adequate mitigation and communication initiatives, at the local scale, which could further exacerbate mistrust and the polarization of public attitudes toward their presence and management (Sunde et al., 2021).

To address these three questions multiple approaches should be combined, including human dimensions studies, based on qualitative methods and structured surveys, elicitation studies with experts and members of local communities (Burgman, 2016), as well as ecological sampling schemes aimed at discovering wolf carcasses. Although, to the best of our knowledge, no-one ever conducted ecological sampling schemes for detecting wolf carcasses, similar initiatives existed for other mammal species, like wild boar (*Sus scrofa*, e.g. for the African Swine Fever, Jo and Gortázar, 2021) and similar methods can be adopted for wolves as well. The use of structured ecological sampling can regularize data collection and it reveal areas of anomalous wolf mortality. Indeed, it is unclear on whether local authorities could implement a similar form of data collection, due to practical restrictions in trained staff and economic resources.

Therefore, we also recommend that members of local communities and outdoor recreationists (e.g. hunters, anglers, mushroom pickers) should be encouraged to report wolf carcasses in the wild, by means of tailored communication campaigns.

We particularly encourage the design and implementation of human dimension studies, exploring how the various segments of society perceive wolves and their environmental and socio-economic impacts, also according to their values or emotions (Jacobs and Vaske, 2019; Manfredo, 2008). While many human dimensions studies so far focused on small social groups (e.g. farmers, Franchini et al., 2021; e.g. hunters, Vaske et al., 2021), broadening the coverage of the resident population can be extremely useful to better understand if, and in case the extent to which, wolf presence is accepted (Behr et al., 2017). These types of studies can be extremely precious to identify unexpected human-wolf conflicts and they can be extremely precious to explain widespread wolf mortality (Gangaas et al., 2013). Of course, we also encourage the use of qualitative methods, especially those based on deliberation (Mukherjee et al., 2018). These techniques can be a valuable complement to survey, as they can provide conservationists with nuanced, high-quality, insights on how wolves are perceived by local stakeholders. These methods have been adopted in participatory initiatives with shepherds in Southern Tuscany (https://ec.europa.eu/environment/nature/conservation/species/carnivores/regional_platforms.htm), but indeed we believe that much would be gained by decision makers, if they were extended to the provinces from our study area, as well as to other stakeholders.

5. Conclusions

This study, besides pointing to the high portion of human-related causes of death among wolves found dead in Central Italy, raises many doubts about the real magnitude, complexity and spatial scale of the persecution of gray wolf in Italy. As these questions are arising in other anthropized environments in Europe, our findings emphasize the need for national and international coordination in the collection of carcasses of large carnivores in anthropized ecosystems. A deeper understanding of large carnivore persecution will be gained only through the analysis of carcasses collected and analyzed with standardized protocols, and then put in a harmonized database. Moreover, carcasses will hardly be sufficient to identify persecution hotspots: this study also wants to encourage researchers to integrate multiple sources of information about the presence and mortality of wolves, and more generally large carnivores, in Italy and across Europe, to answer relevant questions about illegal killing and cryptic conflicts with human activities, which can seriously affect the conservation status of their populations despite their increasing abundance.

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.e01892.

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