Men and wolves: are anthropogenic causes the main driver of wolf mortality in human-dominated landscapes in Italy?

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Abstract

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

Warning

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 [1][2][3]. 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 [4]; e.g. habitat selection [5][6]), reverted the decrease and fragmentation which had characterized Western European wolf populations for centuries [7][8][9]. Nowadays, it is estimated that more than 10,000 wolves live within the European Union and the Balkans [10].

Nonetheless, expanding large carnivore populations in Europe pose considerable challenges to contemporary wildlife management [11]. As in other areas of the world, European carnivores can damage human activities like livestock farming [12], and wolves make no exception [13]. Furthermore, changing wildlife value orientations [14], can fragment attitudes towards the presence of wolves and complicate their management [15].

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 [16], is now widespread across almost all of its historical range [17], including rural and urbanized areas (e.g., the Po plain) [18].

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 [18][19][20][21]. 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) [22]. 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 [23][24]. 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 [25]. 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 [26], or they can become politicized [27] undermining any shared management policy for the species.

Wolf populations are mostly subjected to mortality rates driven by natural causes (e.g., diseases) [28][29][30]; however, detailed information on the relative impact of anthropogenic mortality is still scarce across human-dominated European landscapes [31] and far from trivial[32]. 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 [17][33] 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 [34].

In this perspective, any recovery of wolf carcasses is an important source of information [35]. 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 [36][37]. 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 [38][39]. Finally, it is possible to study the health conditions, the presence of some etiological agents [40] and to conduct toxicological investigations [41]. Necropsy has the function of confirming suspicion, while subsequent laboratory tests on organic samples can determine possible positivity to a toxic substance [42]. 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 [43].

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 [26]. 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 [17], 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.

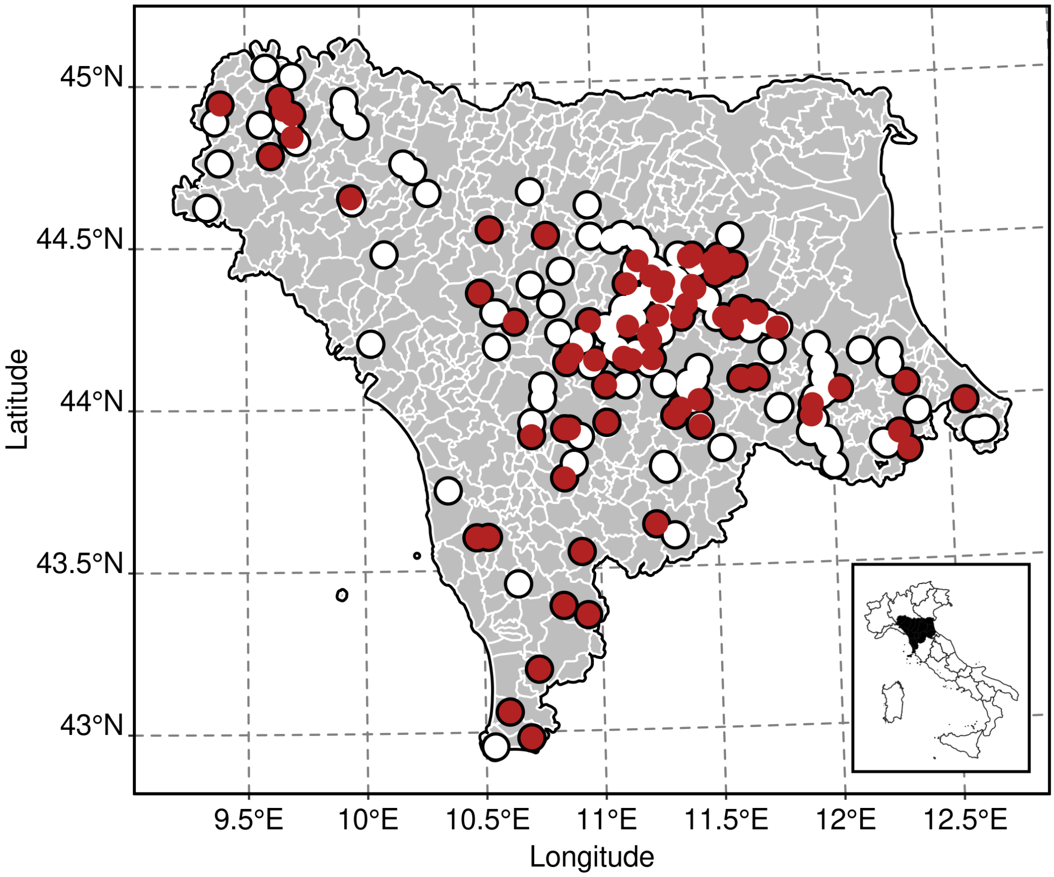

Figure 1: Study area with municipal boundaries, and the location of recovered wolf carcasses (in dark red those with signs of past persecution, in white all the others). The map on the bottom-right corner of the figure shows the Italian provinces covered by data collection.

Methods

Study area

The study area includes the entire Emilia-Romagna and about half of the Tuscany region, in Central Italy (Figure 1). In Tuscany, the provinces of Siena, Arezzo and Grosseto were not covered by our data collection scheme. 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/km^2 (mean ± sd).

Wolf populations expanded their distribution and numbers since the 1990s, with a population of at least 97 packs between 2014 and 2016 [44][45]. 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 [22][46][47].

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 [48]. While the Emilia-Romagna region co-financed and promoted prevention measures, which considerably decreased the number of predations on livestock [49], 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 problematic wolves was never authorized. The sterilization or captivation of hybrid individuals was sometimes undertaken with limited efforts within European and regional projects.

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 [50]. 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, 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 [44][45]. 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[51]. 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) [52] 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 [53]. Models were compared with the Widely Applicable Information Criterion (WAIC), the Deviance Information Criterion (DIC) and leave-one-out cross validation [54], 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) [55]. 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).

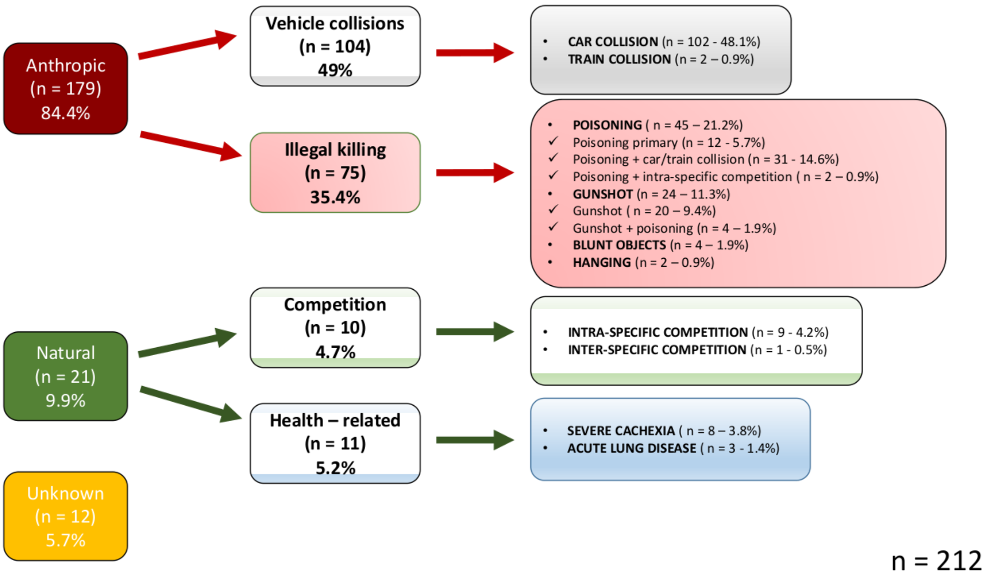

Figure 2: The causes of death were divided into three groups: "natural", "anthropic" and "unknown" in turn divided into subcategories, detailed with the specific causes of death. For "poisoning" and "gunshot" the primary causes and with contributing cause were distinguished.

Results

Only 21 of the 212 wolves examined (9.9%) died of natural causes (Figure 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) (Figure 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 (Figure 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 (Figure 3; Figure S2, Figure S3). Most wolves (n = 140) were found dead between October and March (Figure 3, Figure S2).

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 (Figure 4).

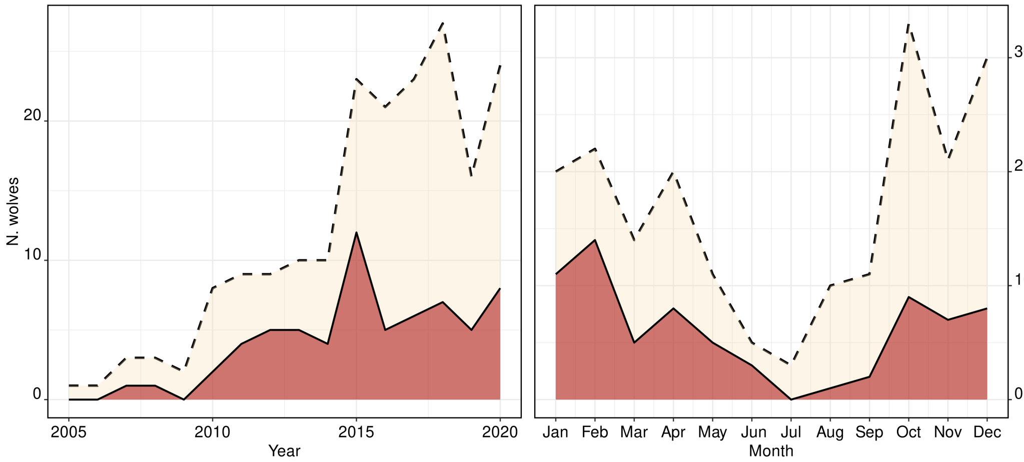

Figure 3: Temporal evolution (left) and seasonal distribution (right) of wolf recoveries (in dark red those with signs of poisoning or wounds, in light colour the total number of wolf recoveries).

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 [11]. 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 [31][56] and North America [57]. 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 [28]. In prey-rich Yellowstone National Park, intraspecific aggression regulated adult wolf survival in a density-dependent manner and independently from prey availability [29]. 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 Mörner et al. [58] in Scandinavia, it is far higher than values previously reported for Central Italy. Namely, Lovari *et al.* [31] 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 [59].

The very high proportion of wolves showing signs of human-driven mortality was certainly affected by our data collection methods 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 [26][31][56][58][60][61] and North America [32][57][62]. 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.* [58] and also with previous estimates from Central Italy (50.6%) [31]. 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 [63]. These two simultaneous processes should have produced a higher proportion of collisions involving young wolves, as observed by Lovari *et al.* [31]. 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.* [64] 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 [32][56][61][62], 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 [31].

Poisoning was particularly common (n = 45), in line with its widespread presence in Italy [41], 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 [65] 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 [44][45]. 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 [49]. 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

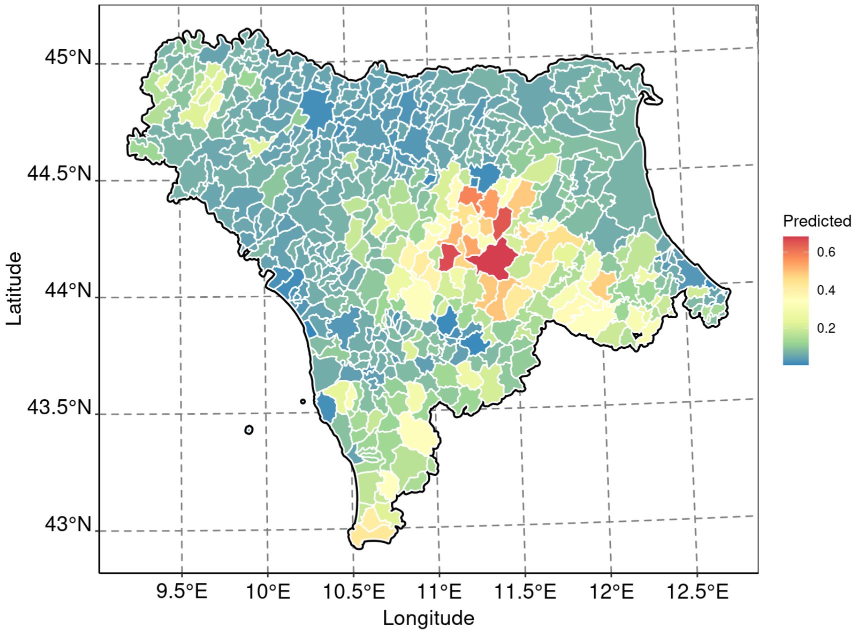

Figure 4: Predicted values of the Bayesian GLM, showing municipalities with the highest probability of having recorded illegally killed wolves between 2005 and 2021.

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 [66].

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 [23][67]; e.g. Scandinavia [26]). 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 [68]. 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 [32]. 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 [61].

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 [69], 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) [70] 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.

This study, besides pointing to the high portion of human-related causes of death among the retrieved wolf carcasses, wants to underline the importance of national and international coordination in the collection of carcasses of the gray wolf, and more broadly of large carnivores living in anthropized ecosystems. There are many doubts about the real magnitude, complexity and spatial scale of the persecution of the gray wolf in Italy: the same questions are arising elsewhere and for other species of large carnivores. It will be possible to answer them only through the analysis of carcasses collected and analyzed with the same protocol, and then put into 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.

Model	ELPD	WAIC	Classification accuracy	AUC
Emilia-Romagna region				
illegal killing ~predations + farm density + human density + wolf presence	-113.9 ± 11.8	226.8	0.78	0.79
illegal killing ~predations + farm density + human density + wolf presence + marginal area + offset(log(n. wolves))	-91.1 ± 9.4	181.4	0.79	0.89
illegal killing ~log(predations) + farm density + human density + wolf presence + marginal area + offset(log(n.wolves))	-88.0 ± 9.2	175.8	0.81	0.91
illegal killing ~log(predations) + farm density + human density + wolf presence + marginal area + offset(log(n.wolves)) + BYM structure	-87.4 ± 9.3	173.4	0.84	0.96
illegal killing ~log(predations) + human density + wolf presence + offset(log(n.wolves)) + BYM structure	-85.7 ± 9.1	170.4	0.85	0.96
illegal killing ~log(predations) + wolf presence + offset(log(n.wolves)) + BYM structure	-85.3 ± 8.9	169.8	0.84	0.95
illegal killing ~log(predations) + offset(log(n.wolves)) + BYM structure	-84.8 ± 8.7	168.7	0.85	0.96
illegal killing ~offset(log(n. wolves)) + BYM structure	-86.9 ± 8.8	172.3	0.88	0.98
illegal killing ~1 + BYM structure	-90.0 ± 10.1	162.7	0.93	0.98
Study area (Emilia-Romagna + Tuscany)				
illegal killing ~farm density + human density + wolf presence + marginal area	-170.5 ± 14.5	341.0	0.63	0.68
illegal killing ~farm density + human density + wolf presence + marginal area + offset(log(n.wolves))	-133.3 ± 11.1	266.5	0.82	0.92
illegal killing ~human density + wolf presence + marginal area + offset(log(n.wolves)) + BYM structure	-127.8 ± 11.3	254.4	0.84	0.97
illegal killing ~human density + wolf presence + offset(log(n.wolves)) + BYM structure	-126.9 ± 11.0	252.7	0.84	0.97
illegal killing ~human density + offset(log(n.wolves)) + BYM structure	-126.2 ± 10.8	251.5	0.81	0.97
illegal killing ~1 + offset(log(n.wolves)) + BYM structure	-128.0 ± 10.5	254.9	0.85	0.98
illegal killing ~1 + BYM structure	-136.0 ± 12.2	246.9	0.91	0.99

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 selection was based on leave-one-out cross validation, while WAIC, ROC and classification accuracry were supplementary criterions.

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Author's contribution

C.M., J.C., M.G., R.C., E.F., F.C., D.B., G.M2 and M.D. conceived the ideas and designed methodology; C.M., G.M.1, M.C.F., L.G., A.P., A.R., C.G., L.F., F.C., D.B. and G.M.2 collected the data; J.C. performed the statistical analyses; C.M., J.C., M.G., R.C., E.F., M.A., N.M., P.B., D.B., G.M.2, and M.D. led the writing of the manuscript. All authors significantly interpreted results and contributed to writing and editing.

Dataset and reproducible software code

The dataset, altogether with the reproducible software code, are available on the Open Science Framework repository, at the following link: https://osf.io/3guh4/

Appendix S1

Protocol for necropsy and genetic analysis

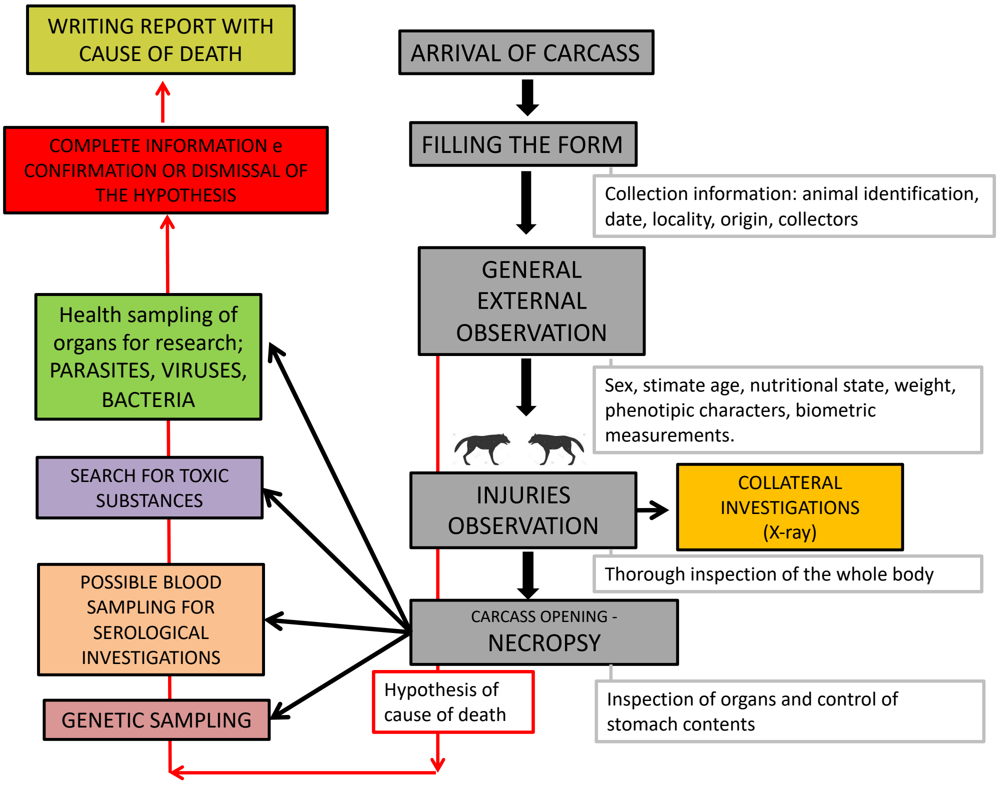


Figure S1: Overview of the data collection process.

Necropsy examinations on wolf carcasses were conducted by the IZSLER, the Italian acronym of Experimental Zooprophylactic Institute of Lombardy and Emilia Romagna, situated in Parma, Piacenza, Reggio Emilia, Modena, Bologna, Forlì-Cesena, and by the Wildlife and Exotic Service of the University of Bologna.

At the arrival of each carcass, a first form containing the following information was filled (Figure S1): subject's identification data with the attribution of a unique ID code, the discovery location (reported as GPS coordinates), the sex, the weight (in kg) and the nutritional status (obtained through the direct observation and palpation of the locations where the fat accumulates, thus: flank fossa, ribs, lumbar vertebrae and pelvic bones; see below). The age of the animal was estimated on the basis of dental development, body size and weight [58]. Here, all individuals were aged using 3 categories as follows: class 1: 12 months; class 2: 1–2 years; class 3: $>$ 2 years. The aging (based on months of life) was executed in relation to the reproductive cycle of the Italian wolf, which defines May as pups' birth month [71].

The biometric information and phenotypic characteristics were also recorded: in particular, were noted: total length (from the nose to the junction of the tail), length of the tarsus, length of the tail, height of the ear, chest circumference, neck circumference and finally the presence of spurs, stripes, white nails and the coloring of the coat (Figure S1). Then, an external examination of the carcass was made by disposing the carcass in lateral decubitus: such position allows for straight evaluation of the nutritional and health status of the subject (Figure S1). During this first inspection, we established whether radiographic investigations were needed to identify foreign bodies (such as bullets, blunt objects) or fractures in the skeletal system (i.e. due to traumatic-contusive lesions) (Figure S1). At this stage, it was also possible to assess the nutrition, skin and mucosal status as well as the explorable lymph nodes and proceed with tongue sampling to be preserved in 95% ethyl alcohol for the genetic determination of the species (Figure S1). After finalizing the first physical inspection, the carcass was placed in dorsal decubitus to proceed with its flaying. The complete necropsy examination started with the opening of the abdominal cavity and was followed by the opening of the thoracic one. At each of these two steps, all organs were inspected and evaluated individually before being sampled for additional laboratory analysis (Figure S1).

All individuals were also examined for the presence of zoonotic parasitic infections such as Trichinella spp. and Leishmania infantum. Specifically, diaphragm and the tibialis muscles were analyzed to detect *Trichinella* spp. [72], whereas spleen and popliteal lymph nodes were examined to detect *Leishmania infantum* [73]. In all individuals, stomach and liver were also analyzed to detect the presence of toxic substances (such as zinc phosphide, strychnine, organophosphate pesticides, metaldehyde and anticoagulants) [74], Figure S1. Moreover, further investigations on the possible presence of *Sarcoptes scabiei* were only performed in case of suspicious skin lesions, which could have been caused by sarcoptic mange. In the case of mangy subjects, staging was established according to the methodology described in Pence and Ueckermann [75]. Each step of the necropsy process was photographed.

We collected and stored in 95% ethanol a fragment of lingual tissue in 141 carcasses to carry out genetic analyses to confirm the belonging of samples to the Italian subspecies and detect possible traces of dog ancestry.

DNA extraction was performed using the genomic DNeasy Blood Tissue Kit (Qiagen Inc., Hilden, Germany), following the manufacturer's instructions, in a QIAcube (Qiagen Inc., Hilden, Germany) extractor. Subsequently, each DNA sample was amplified by Polymerase Chain Reaction (PCR), sequenced at 500 bp of the mtDNA control-region (diagnostic for the Italian wolf population) [76], and genotyped through a multiple-tube approach at 39 unlinked autosomal microsatellites (STR, which differentiate between wolves, dogs and their first two generation hybrids) as listed in Randi *et al.* [38]. A marker on the Amelogenin gene was used to identify the sex of the samples. Additionally, four Y-chromosome microsatellites were used to identify paternal haplotypes [38], whereas a dominant 3-bp deletion (named KB or CBD103DG23) at the b-defensin CBD103 gene, correlated to black coat and likely of dog origin (the K-locus) [36][37] was also genotyped. Any sign of past hybridization with domestic dog (*Canis lupus familiaris*) was investigated using a Bayesian genetic clustering procedures implemented in STRUCTURE 2.3.4 [77] and described in Caniglia *et al.* [39]. In particular, we categorized an individual as wolf, hybrid or introgressed based on their membership proportions to the wolf cluster (qwolf). We further considered as introgressed individuals presenting a mtDNA or Y-haplotype of canine origin, or the deletion at the K-locus [38] regardless of their qwolf values [39]. Extraction, amplification and post-amplification procedures were carried out in three separate rooms at the Unit for Conservation Genetics (BIO-CGE Ozzano dell'Emilia, Bologna, Italy), which is part of the Italian Institute for Environmental Protection and Research (ISPRA).

Not all wolves covered by this study were genetically tested, in fact 33.5% were not sent for species attribution. This information gap is given by the lack of national coordination and a solid network that guarantees the genetic determination of species for each canid examined. So, a total of 137 out of the 141 analysed samples was successfully genotyped at 39 STR, Amelogenin and K loci, four STR Y-Linked and mtDNA control-region. Among them, 105 (74.5%) resulted pure wolves, showing a qwolf >= 0.995 and no other genetic signals of dog origin; 13 (9.2%) resulted wolf x dog hybrids, showing a qwolf <= 0.954, and 23 (16.3%) were classified as introgressed individuals, showing a lower genetic dog derivate component represented by qwolf < 0.995 but > 0.954 or by the presence of a dog Y-haplotype (N=4) and/or the Kb allele (N=3). No dog mtDNA haplotype was identified, since all the analysed animals shared the private Italian wolf mtDNA haplotype (named W14 by Randi *et al.* [78] and by Montana *et al.* [76]).

The molecular gender, genetically identified by analysing the Amelogenine marker, always confirmed the autopsy visual examination.

The causes of mortality were grouped into three main categories: anthropic, natural and unknown. A schematic representation of each category (numbers included and contributing causes) is shown in Figure 2, details on each group are shortly defined as: *i*) Natural: it included health-related (i.e., presence of disease and/or starvation to death) and natural competition (interspecific and intraspecific) as causes of mortality; *ii*) Anthropic: it included vehicle collisions caused by cars and trains, hereafter called ACC, and illegal killing (linked to poisoning, fire weapons and other minor) – hereafter called IK. In case no precise information relative to the cause of death was identified during the necropsies, the subjects examined were assigned to the category "unknown" [43]. Moreover, additional processes that were not directly causes of death, but could still trigger the physiological imbalance, were noted as "contributing causes of death".

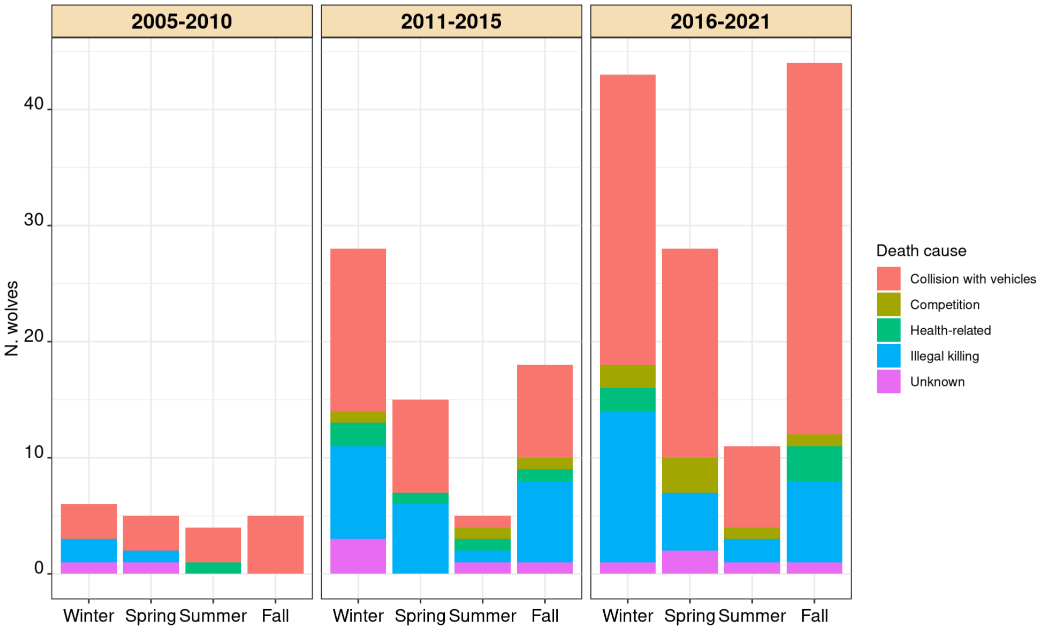


Figure S2: Causes of death of recovered wolves, in three periods between 2005 and 2021. Data collection in 2005 started in October and 2021 data refer to January and February only.

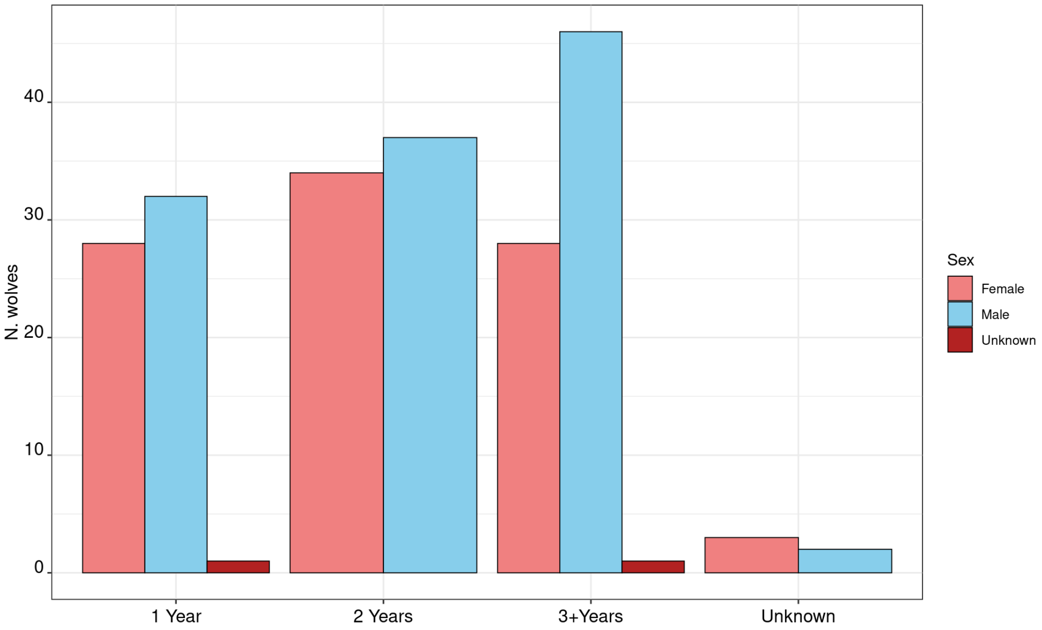


Figure S3: Distribution of recovered wolves between the two sexed and three age classes (1 year, 2 years, 3 or more years).

Appendix 2 - Model selection and diagnostics

Introduction

The following documents aim to provide a quick overview about model selection and diagnostics. A more comprehensive overview about statistical analyses can be found in the reproducible script.

Emilia-Romagna region

To start with, let's start with the Emilia-Romagna data, whose datasets contains the following variables of interest:

- "illegal.ever" - a dichotomous variable indicating if any illegally killed wolf was found at a certain municipality, between 2005 and 2021. Municipalities with more illegally killed wolves are nevertheless coded in this binary way, because those with 2 or 3 wolves were few.
- "predations" - the total number of domestic animals (cattle, sheep, goats) that had been killed by wolves in each municipality.
- "log.pred.events" - a natural logarithm of the total number of predations by wolves on domestic animals (number of events). The variable was log-converted to smooth out its extremes.
- "farm.density" - the total number of farms in each municipality, divided per its total surface in hectares.
- "human density" - the total number of residents in each municipality, divided per its total surface in hectares.
- "wolf.presence" - a dummy variable indicating whether wolves had been recorded on a certain municipality on some consecutive monitoring initiatives, between 2006 and 2016 (see Apollonio et al., 2016, reference n. 45).
- "marginal.area" - a dummy variable indicating if a certain municipality was considered to be marginal for agriculture. Based on the National Agricultural Network (https://www.reterurale.it/flex/cm/pages/ServeBLOB.php/L/IT/IDPagina/1)
- "wolf.found offset" - a variable indicating the number of wolves that were found, between 2005 and 2021 on a certain municipality. Used as an offset.

All continuous variables were standardized an centered, before their inclusion as predictors.

We compared the following models, with a backwise selection approach based on leave-one-out cross validation, and supplemented by some other measures of fitness. Such as the WAIC, area under the curve and classification accuracy:

Let's calculate the VIF on an analogous frequentist logistic regression, before fitting the full model (without BYM structure)

```
vif(glm(illegal.ever ~ log.pred.events + farm.density.std + human.density.std + wolf.presence +
        marginal.area + wolf.found.std,
        family=binomial(link="logit"), data=d.er))
```

```
##   log.pred.events  farm.density.std human.density.std     wolf.presence
##          1.449720          1.123598          1.424633          1.714927
##     marginal.area    wolf.found.std
##          1.916923          1.508884
```

VIF looks good and there is no sign of strong collinearity between predictors:

```
#mod.a.er <- brm(illegal.ever ~ predations.std + farm.density.std + human.density.std +
#                wolf.presence + marginal.area,
#                family=bernoulli(link = "logit"), data=d.er,
#                chains=4, cores=4, iter=5000, warmup=1000, thin = 10,
#                control = list(adapt_delta = 0.99, max_treedepth = 10),
#                prior=c(prior(normal(0, 1), class=b, coef = predations.std),
#                        prior(normal(0, 1), class=b, coef = farm.density.std),
#                        prior(normal(0, 1), class=b, coef = human.density.std),
#                        prior(normal(0, 1), class=b, coef = wolf.presence1),
#                        prior(normal(0, 1), class=b, coef = marginal.area1)))
#
#mod.b.er <- brm(illegal.ever ~ predations.std + farm.density.std + human.density.std +
#                wolf.presence + marginal.area +
#                offset(log(wolf.found.offset)), family=bernoulli(link = "logit"),
#                data=d.er,
#                chains=4, cores=4, iter=5000, warmup=1000, thin = 10,
#                control = list(adapt_delta = 0.99, max_treedepth = 10),
#                prior=c(prior(normal(0, 1), class=b, coef = predations.std),
#                        prior(normal(0, 1), class=b, coef = farm.density.std),
#                        prior(normal(0, 1), class=b, coef = human.density.std),
#                        prior(normal(0, 1), class=b, coef = wolf.presence1),
#                        prior(normal(0, 1), class=b, coef = marginal.area1)))
#
#mod.c.er <- brm(illegal.ever ~ log.pred.events.std + farm.density.std +
#                human.density.std + wolf.presence + marginal.area +
#                offset(log(wolf.found.offset)), family=bernoulli(link = "logit"),
#                data=d.er,
#                chains=4, cores=4, iter=5000, warmup=1000, thin = 10,
#                control = list(adapt_delta = 0.99, max_treedepth = 10),
#                prior=c(prior(normal(0, 1), class=b, coef = log.pred.events.std),
#                        prior(normal(0, 1), class=b, coef = farm.density.std),
#                        prior(normal(0, 1), class=b, coef = human.density.std),
#                        prior(normal(0, 1), class=b, coef = wolf.presence1),
#                        prior(normal(0, 1), class=b, coef = marginal.area1)))
#
#mod.d.er <- brm(illegal.ever ~ log.pred.events.std + farm.density.std +
#               human.density.std + wolf.presence + marginal.area +
#               offset(log(wolf.found.offset)) + car(W, type = "bym2"),
#               family=bernoulli(link = "logit"),
#               data=d.er, data2 = list(W = m.er),
#               chains=4, cores=4, iter=5000, warmup=1000, thin = 10,
#               control = list(adapt_delta = 0.99, max_treedepth = 10),
#             prior=c(prior(normal(0, 1), class=b, coef = log.pred.events.std),
#                     prior(normal(0, 1), class=b, coef = farm.density.std),
#                     prior(normal(0, 1), class=b, coef = human.density.std),
#                     prior(normal(0, 1), class=b, coef = wolf.presence1),
#                     prior(normal(0, 1), class=b, coef = marginal.area1)))
#
#mod.e.er <- brm(illegal.ever ~ log.pred.events.std + human.density.std + wolf.presence +
#                offset(log(wolf.found.offset)) + car(W, type = "bym2"),
#                family=bernoulli(link = "logit"),
#                data=d.er, data2 = list(W = m.er),
#                chains=4, cores=4, iter=5000, warmup=1000, thin = 10,
```

```
#                control = list(adapt_delta = 0.99, max_treedepth = 12),
#                prior=c(prior(normal(0, 1), class=b, coef = log.pred.events.std),
#                        prior(normal(0, 1), class=b, coef = human.density.std),
#                        prior(normal(0, 1), class=b, coef = wolf.presence1)))
#
#mod.f.er <- brm(illegal.ever ~ log.pred.events.std + wolf.presence +
#                offset(log(wolf.found.offset)) + car(W, type = "bym2"),
#                family=bernoulli(link = "logit"),
#                data=d.er, data2 = list(W = m.er),
#                chains=4, cores=4, iter=5000, warmup=1000, thin = 10,
#                control = list(adapt_delta = 0.99, max_treedepth = 12),
#                prior=c(prior(normal(0, 1), class=b, coef = log.pred.events.std),
#                        prior(normal(0, 1), class=b, coef = wolf.presence1)))

#mod.g.er <- brm(illegal.ever ~ log.pred.events.std +
#                offset(log(wolf.found.offset)) + car(W, type = "bym2"),
#                family=bernoulli(link = "logit"),
#                data=d.er, data2 = list(W = m.er),
#                chains=4, cores=4, iter=5000, warmup=1000, thin = 10,
#                control = list(adapt_delta = 0.99, max_treedepth = 12),
#                prior=c(prior(normal(0, 1), class=b, coef = log.pred.events.std)))

#mod.h.er <- brm(illegal.ever ~ offset(log(wolf.found.offset)) + car(W, type = "bym2"),
#                family=bernoulli(link = "logit"),
#                data=d.er, data2 = list(W = m.er),
#                chains=4, cores=4, iter=5000, warmup=1000, thin = 10,
#                control = list(adapt_delta = 0.99, max_treedepth = 12))

#mod.i.er <- brm(illegal.ever ~ 1 + car(W, type = "bym2"),
#                   family=bernoulli(link = "logit"),
#                   data=d.er, data2 = list(W = m.er),
#                   chains=4, cores=4, iter=5000, warmup=1000, thin = 10,
#                   control = list(adapt_delta = 0.99, max_treedepth = 12))
```

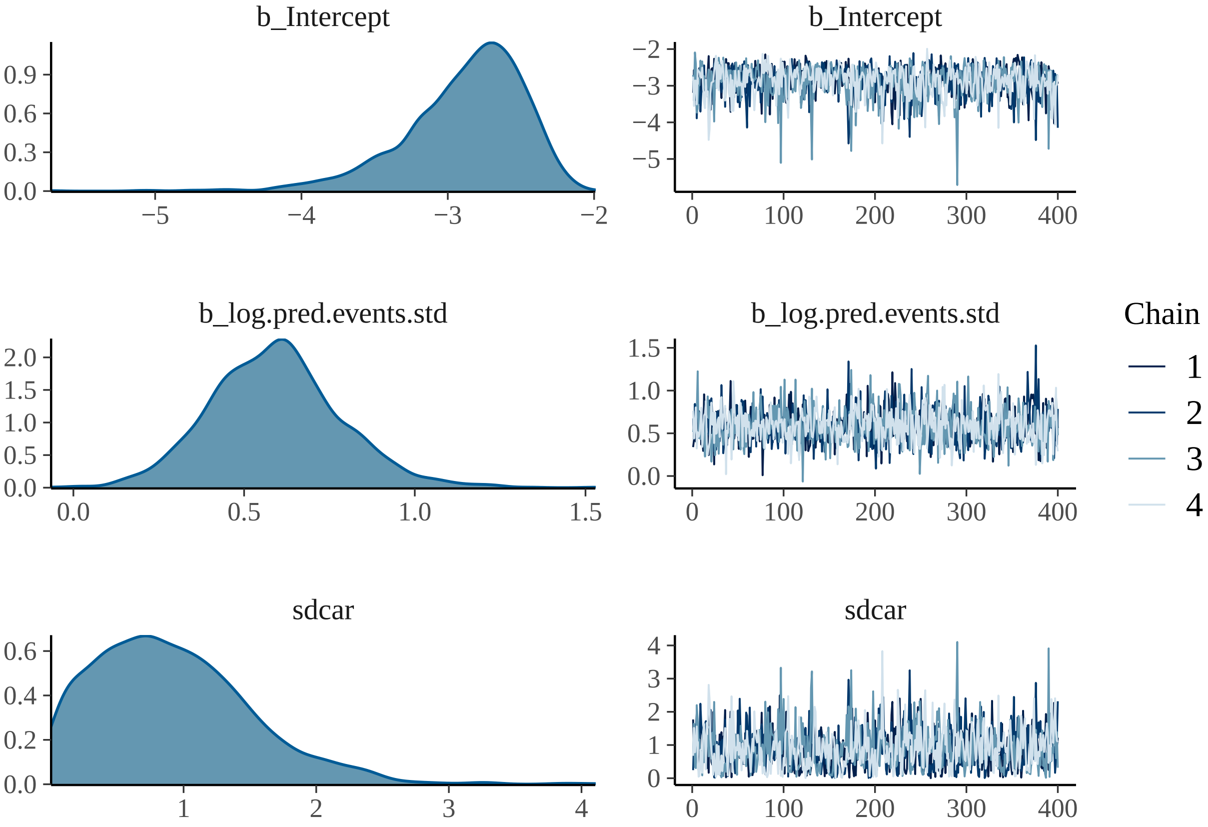
From Table 1 you can see that a model with the logarithm of predations as a predictor, the total number of wolves found as an offset and a Besag-York-Mollié structure seems to be the best choice. In the BYM structure, we used “Queen neighbours”: two municipalities were deemed to be neigbours if they shared at least one point in common, on their perimeter. Although differences are not so pronounces between models. Let’s see if this model converged:

```
mod <- mod.g.er
summary(mod)
```

```
##  Family: bernoulli
##   Links: mu = logit
## Formula: illegal.ever ~ log.pred.events.std + offset(log(wolf.found.offset)) + car(W, type = "bym2")
##    Data: d.er (Number of observations: 328)
## Samples: 4 chains, each with iter = 5000; warmup = 1000; thin = 10;
##          total post-warmup samples = 1600
##
## Correlation Structures:
##       Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sdcar     0.92      0.59     0.05     2.28 1.00      699     1143
##
```

```
## Population-Level Effects:
##                      Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## Intercept               -2.88      0.41    -3.86    -2.28 1.00      991     1273
## log.pred.events.std      0.59      0.19     0.24     0.99 1.00     1411     1414
##
## Samples were drawn using sampling(NUTS). For each parameter, Bulk_ESS
## and Tail_ESS are effective sample size measures, and Rhat is the potential
## scale reduction factor on split chains (at convergence, Rhat = 1).
```

```
plot(mod)
```

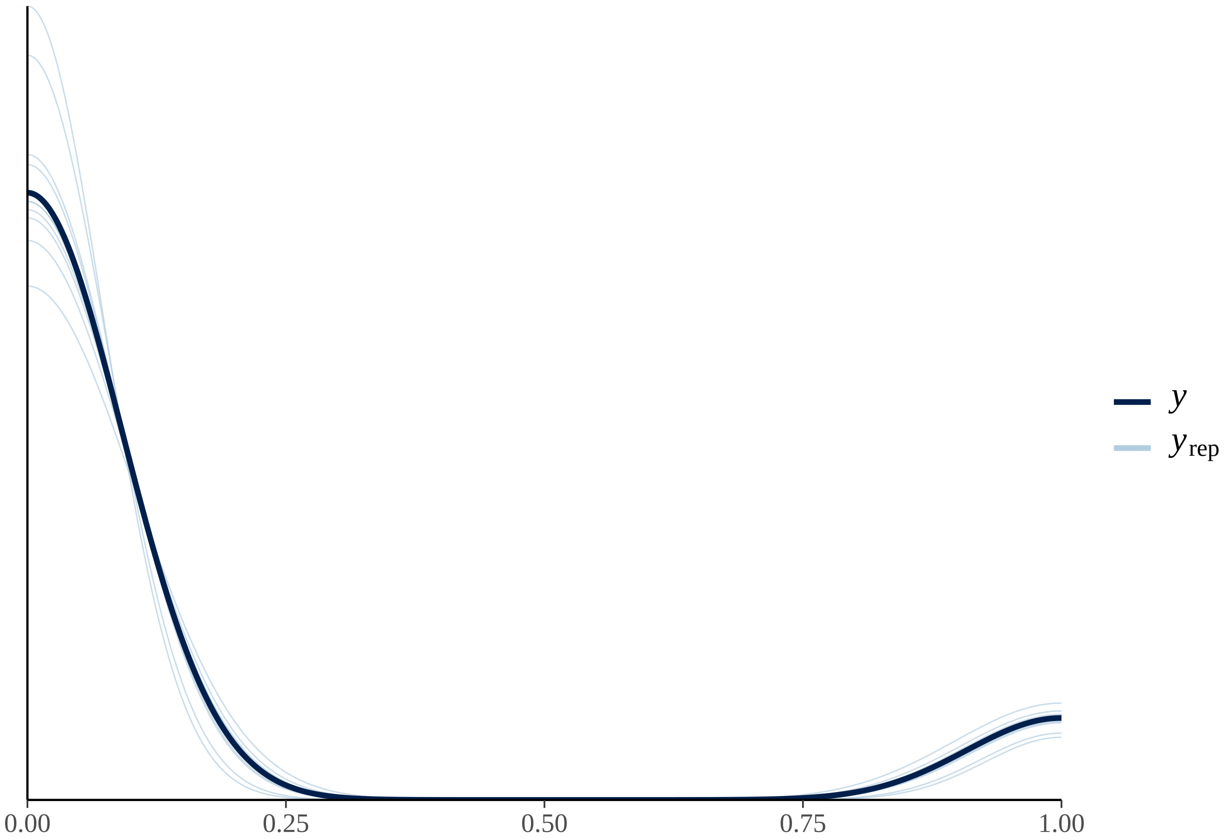


Yest, MCMC have mixed well and model parameters seem to have a nice posterior distribution. But will the model fit the data? Let's compare the observed response variable with simulated datasets from the posterior predictive distribution:

```
brms::pp_check(mod)
```

```
## Using 10 posterior samples for ppc type 'dens_overlay' by default.
```

```
## Warning: Using CAR terms without a grouping factor is deprecated. Please use
## argument 'gr' even if each observation represents its own location.
```



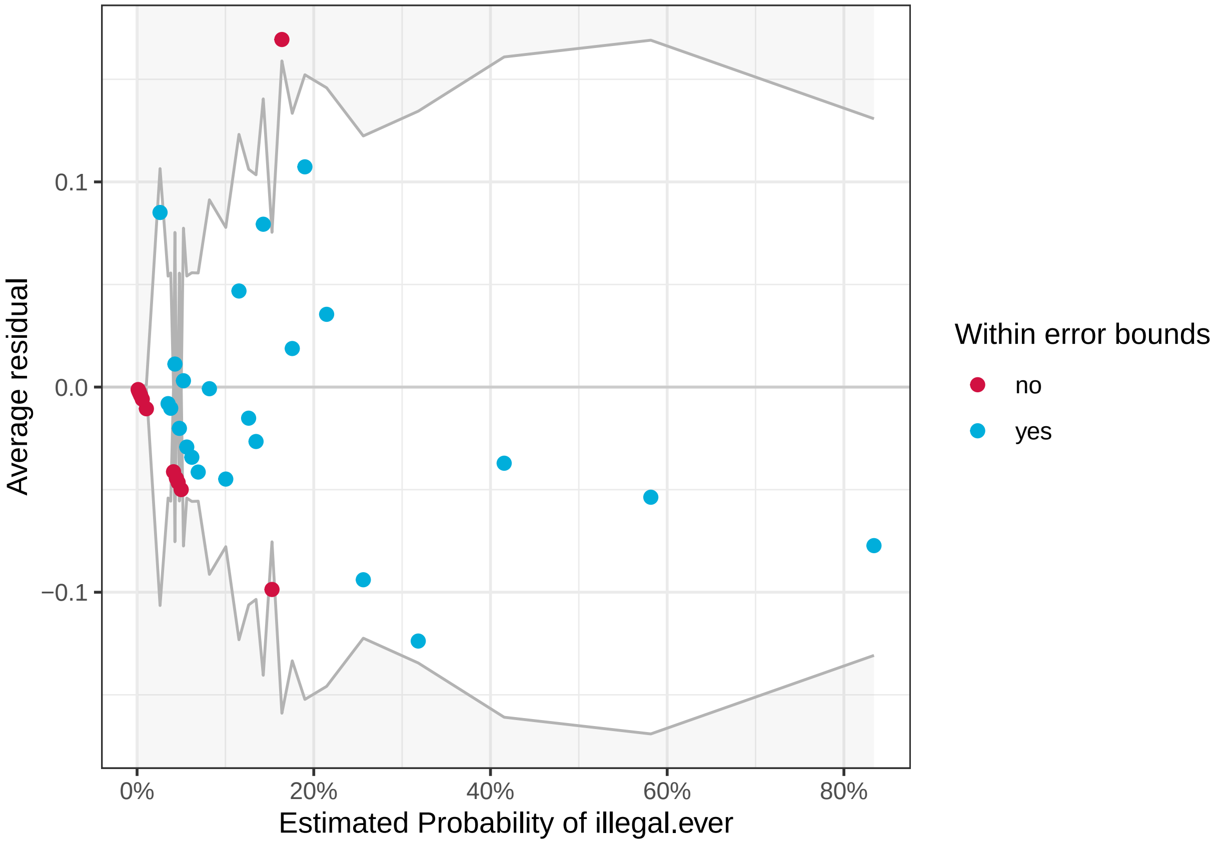
Now, let try to make model binned residuals plot. In this plot, data are partitioned into categories based on their fitted values and then average residuals are plotted against the average fitted value. In case of a good fit, one would expect 95% of residuals to fall within the error bounds:

```
binned_residuals(mod)
```

```
## Warning: Using CAR terms without a grouping factor is deprecated. Please use
## argument 'gr' even if each observation represents its own location.
```

```
## Warning: Following potential variables could not be found in the data: W
```

```
## Warning: Probably bad model fit. Only about 64% of the residuals are inside the error bounds.
```



About 45% of model residuals are outside of error bounds: the model does not fit really well the data, as confirmed by our progressive elimination of the various covariates. Let' check also the role of the logarithm of predations:

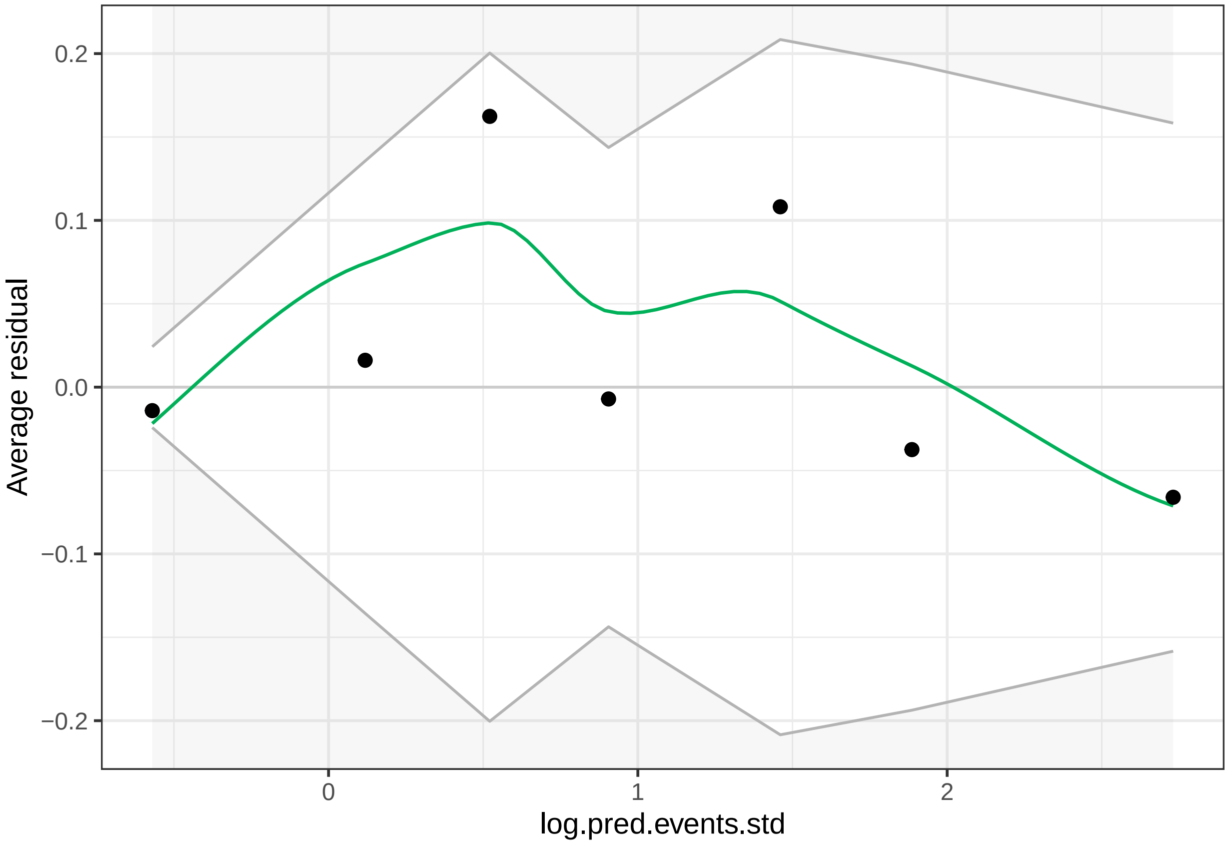
```r
binned_residuals(mod, term=c("log.pred.events.std"))
```

```
## Warning: Using CAR terms without a grouping factor is deprecated. Please use
## argument 'gr' even if each observation represents its own location.
```

```
## Warning: Following potential variables could not be found in the data: W
```

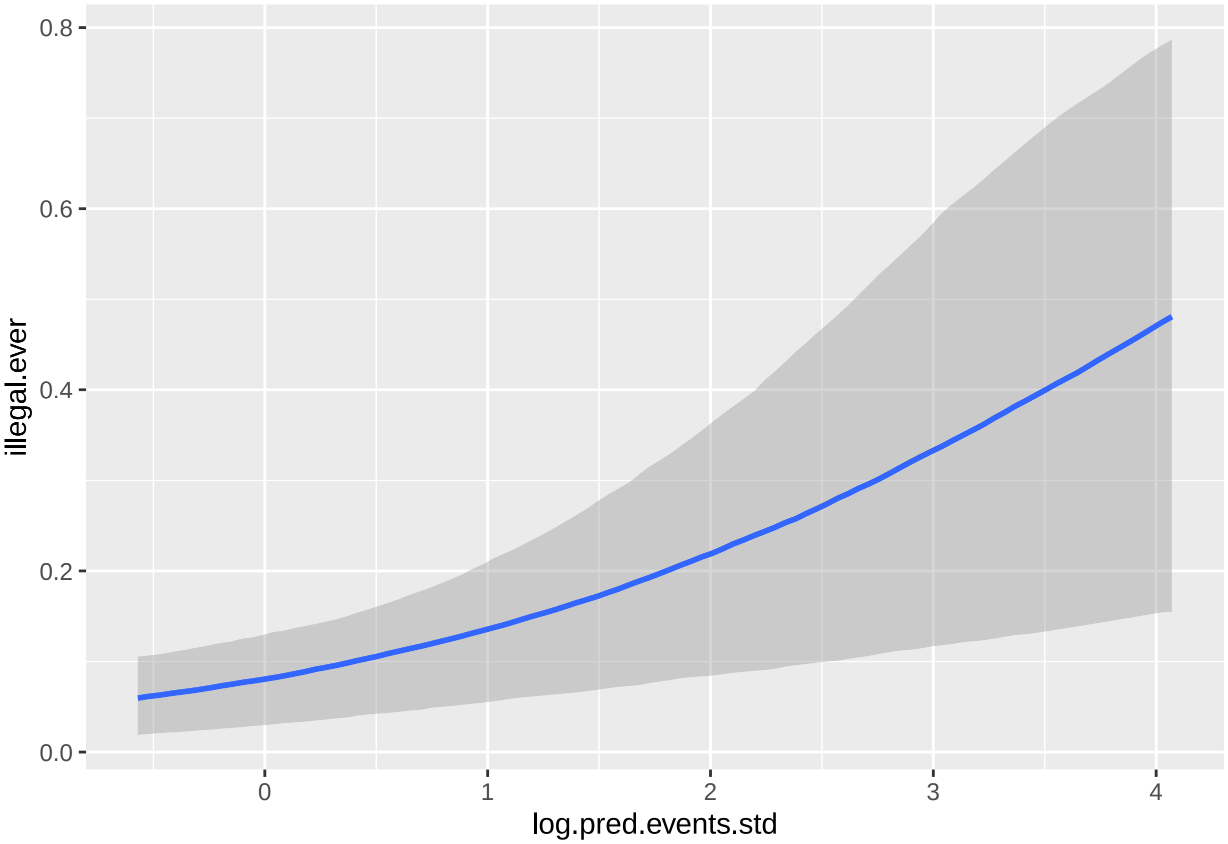
```
## Ok: About 100% of the residuals are inside the error bounds.
```

```
## `geom_smooth()` using formula 'y ~ x'
```



Indeed, all residuals fall into error bounds. This indicate that the association with the covariate was modelled relatively well. Now let's plot the marginal effect of the covariate:

```
conditional_effects(mod)
```



From what we can see, the marginal effect is positive but relatively low. The probability of having recorded at least a dead wolf in a certain municipality, between 2015 and 2021 increased by about 10% for a 1-unit increase in the standardized and centered logarithm of the number of predation events in that municipality.

Entire study area

Now consider the whole dataset about the Tuscany and Emilia-Romagna regions, which contains the following variables of interest:

- "illegal.ever" - a dichotomous variable indicating if any illegally killed wolf was found at a certain municipality, between 2005 and 2021. Municipalities with more illegally killed wolves are nevertheless coded in this binary way, because those with 2 or 3 wolves were few.
- "farm.density" - the total number of farms in each municipality, divided per its total surface in hectares.
- "human density" - the total number of residents in each municipality, divided per its total surface in hectares.
- "wolf.presence" - a dummy variable indicating whether wolves had been recorded on a certain municipality on some consecutive monitoring initiatives, between 2006 and 2016 (see Apollonio et al., 2016, reference n. 45).
- "marginal.area" - a dummy variable indicating if a certain municipality was considered to be marginal for agriculture. Based on the National Agricultural Network (https://www.reterurale.it/flex/cm/pages/ServeBLOB.php/L/IT/IDPagina/1)
- "wolf.found offset" - a variable indicating the number of wolves that were found, between 2005 and 2021 on a certain municipality. Used as an offset.

Let's calculate the VIF on an analogous frequentist logistic regression, before fitting the full model (without BYM structure):

```
vif(glm(illegal.ever ~ farm.density + human.density + wolf.presence +
        marginal.area + wolf.found,
        family=binomial(link="logit"), data=d))
```

```
##  farm.density human.density wolf.presence marginal.area    wolf.found
##      1.100959      1.187683      1.336548      1.342534      1.299716
```

VIF looks good and there is no sign of strong collinearity between predictors:

```
#mod.a.tot <- brm(illegal.ever ~ farm.density.std + human.density.std + wolf.presence +
#                  marginal.area,
#                  family=bernoulli(link = "logit"), data=d,
#                  chains=4, cores=4, iter=5000, warmup=1000, thin = 10,
#                  control = list(adapt_delta = 0.99, max_treedepth = 10),
#                  prior=c(prior(normal(0, 1), class=b, coef = farm.density.std),
#                          prior(normal(0, 1), class=b, coef = human.density.std),
#                          prior(normal(0, 1), class=b, coef = wolf.presence1),
#                          prior(normal(0, 1), class=b, coef = marginal.area1)))
#
#mod.b.tot <- brm(illegal.ever ~ farm.density.std + human.density.std + wolf.presence +
#                  marginal.area +
#                  offset(log(wolf.found.offset)), family=bernoulli(link = "logit"),
#                  data=d,
#                  chains=4, cores=4, iter=5000, warmup=1000, thin = 10,
#                  control = list(adapt_delta = 0.99, max_treedepth = 10),
#                  prior=c(prior(normal(0, 1), class=b, coef = farm.density.std),
#                          prior(normal(0, 1), class=b, coef = human.density.std),
#                          prior(normal(0, 1), class=b, coef = wolf.presence1),
#                          prior(normal(0, 1), class=b, coef = marginal.area1)))
#
#mod.c.tot <- brm(illegal.ever ~ farm.density.std + human.density.std + wolf.presence +
#                  marginal.area +
#                  offset(log(wolf.found.offset)) + car(W, type = "bym2"),
#                  family=bernoulli(link = "logit"),
#                  data=d, data2 = list(W = m),
#                  chains=4, cores=4, iter=5000, warmup=1000, thin = 10,
#                  control = list(adapt_delta = 0.99, max_treedepth = 10),
#                  prior=c(prior(normal(0, 1), class=b, coef = farm.density.std),
#                          prior(normal(0, 1), class=b, coef = human.density.std),
#                          prior(normal(0, 1), class=b, coef = wolf.presence1),
#                          prior(normal(0, 1), class=b, coef = marginal.area1)))
#
#mod.d.tot <- brm(illegal.ever ~ human.density.std + wolf.presence +
#                  offset(log(wolf.found.offset)) + car(W, type = "bym2"),
#                  family=bernoulli(link = "logit"),
#                  data=d, data2 = list(W = m),
#                 chains=4, cores=4, iter=5000, warmup=1000, thin = 10,
#                  control = list(adapt_delta = 0.99, max_treedepth = 10),
#                  prior=c(prior(normal(0, 1), class=b, coef = human.density.std),
#                          prior(normal(0, 1), class=b, coef = wolf.presence1)))
#
#mod.e.tot <- brm(illegal.ever ~ human.density.std +
#                  offset(log(wolf.found.offset)) + car(W, type = "bym2"),
#                  family=bernoulli(link = "logit"),
#                  data=d, data2 = list(W = m),
```

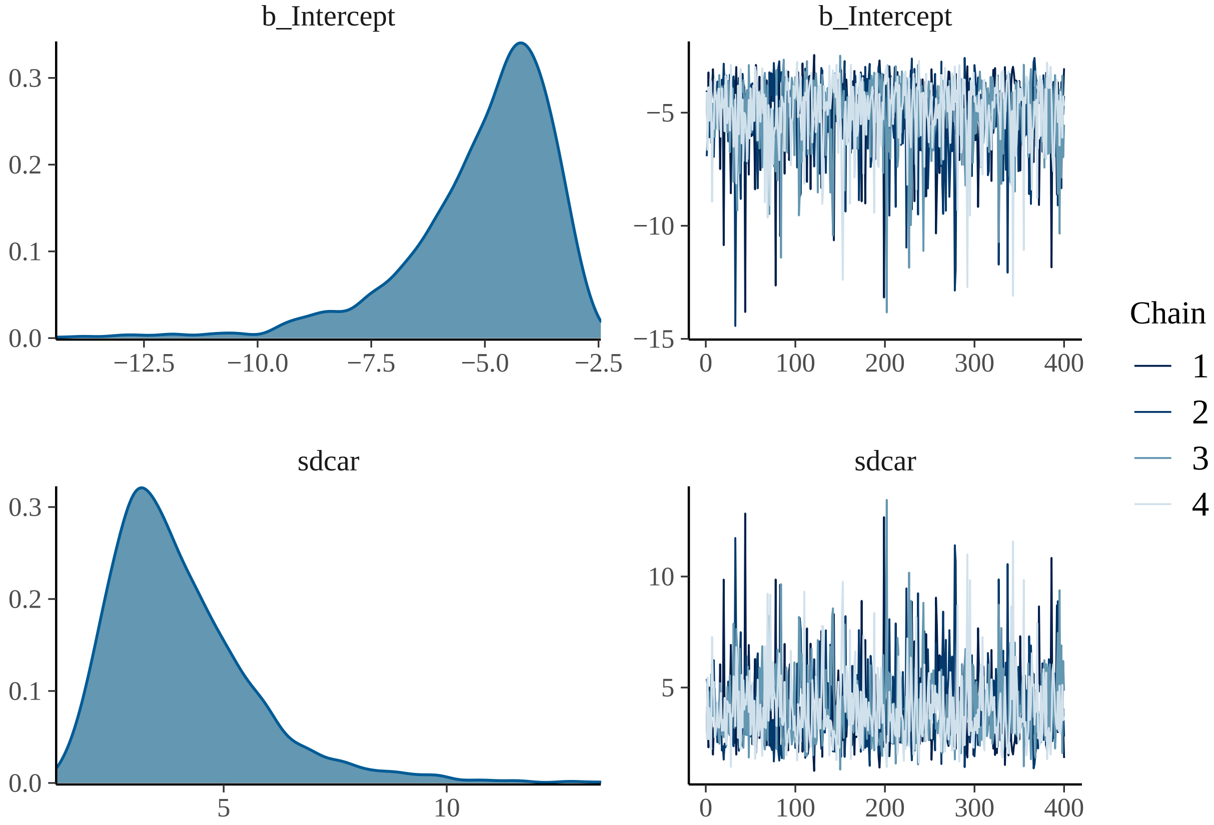
```
#                   chains=4, cores=4, iter=5000, warmup=1000, thin = 10,
#                   control = list(adapt_delta = 0.99, max_treedepth = 10),
#                   prior=c(prior(normal(0, 1), class=b, coef = human.density.std)))
#
#mod.f.tot <- brm(illegal.ever ~ 1 +
#                   offset(log(wolf.found.offset)) + car(W, type = "bym2"),
#                   family=bernoulli(link = "logit"),
#                   data=d, data2 = list(W = m),
#                   chains=4, cores=4, iter=5000, warmup=1000, thin = 10,
#                   control = list(adapt_delta = 0.99, max_treedepth = 10))
#
#mod.g.tot <- brm(illegal.ever ~ 1 + car(W, type = "bym2"),
#                   family=bernoulli(link = "logit"),
#                   data=d, data2 = list(W = m),
#                   chains=4, cores=4, iter=5000, warmup=1000, thin = 10,
#                   control = list(adapt_delta = 0.99, max_treedepth = 10))
```

From Table 1 we can see that a model with only the offset variable and the BYM correlations structure is probably the best one. Let‘s keep it as the best candidate model. But did it converge?

```
mod.tot <- mod.g.tot
summary(mod.tot)
```

```
##  Family: bernoulli
##   Links: mu = logit
## Formula: illegal.ever ~ 1 + car(W, type = "bym2")
##    Data: d (Number of observations: 494)
## Samples: 4 chains, each with iter = 5000; warmup = 1000; thin = 10;
##          total post-warmup samples = 1600
##
## Correlation Structures:
##       Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sdcar     4.05      1.64     1.88     8.27 1.00     1197     1461
##
## Population-Level Effects:
##           Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## Intercept    -5.06      1.65    -9.17    -2.98 1.00     1246     1411
##
## Samples were drawn using sampling(NUTS). For each parameter, Bulk_ESS
## and Tail_ESS are effective sample size measures, and Rhat is the potential
## scale reduction factor on split chains (at convergence, Rhat = 1).
```

```
plot(mod.tot)
```

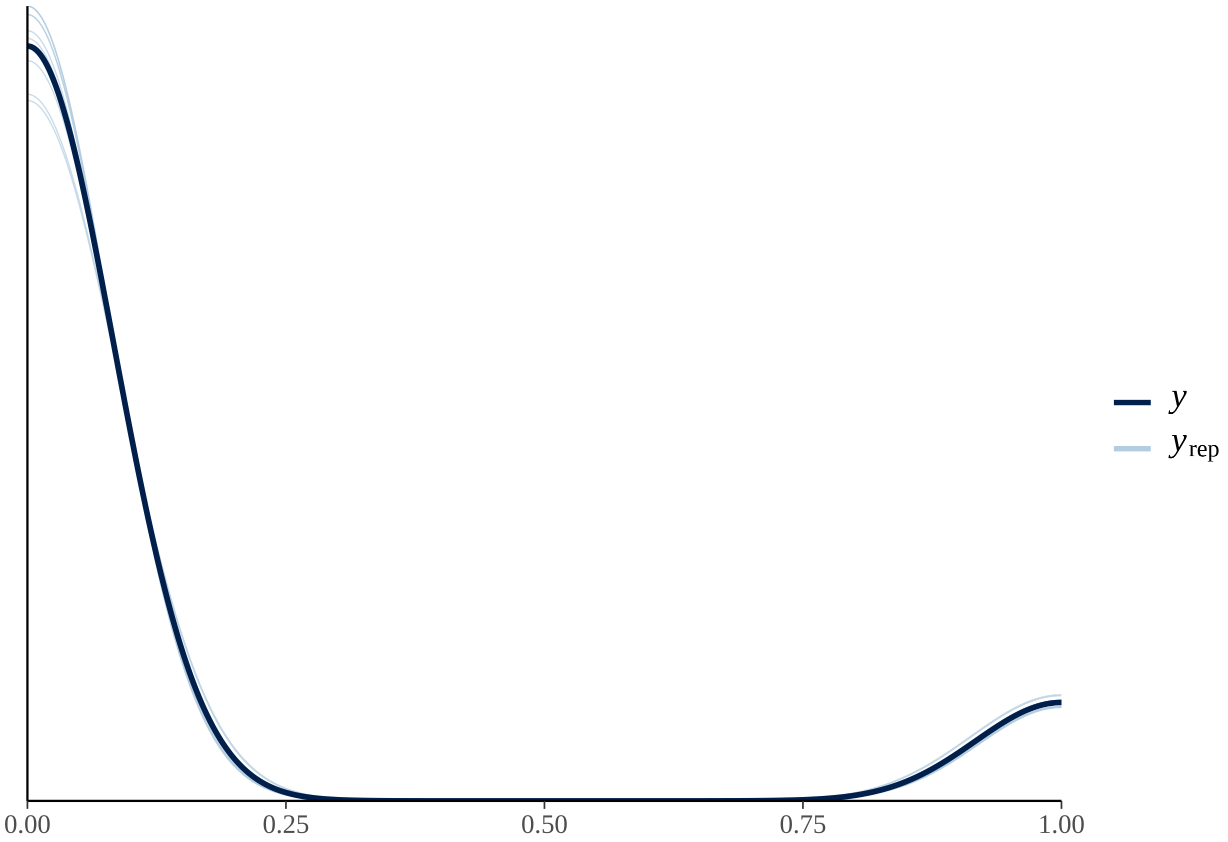


Yest, MCMC have mixed well and model parameters seem to have a nice posterior distribution. But will the model fit the data? Let's compare the observed response variable with simulated datasets from the posterior predictive distribution:

```
brms::pp_check(mod.tot)
```

```
## Using 10 posterior samples for ppc type 'dens_overlay' by default.
```

```
## Warning: Using CAR terms without a grouping factor is deprecated. Please use
## argument 'gr' even if each observation represents its own location.
```



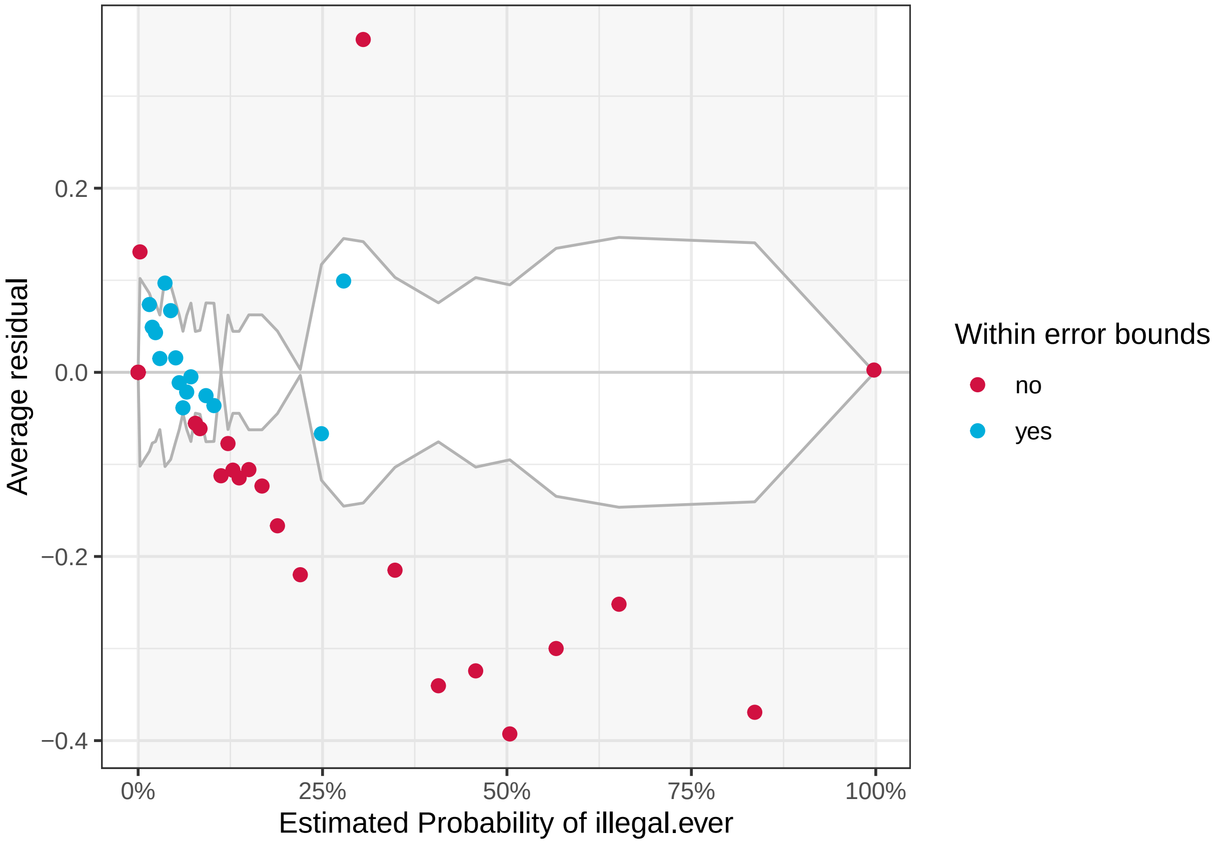
Now, let try to make model binned residuals plot. In this plot, data are partitioned into categories based on their fitted values and then average residuals are plotted against the average fitted value. In case of a good fit, one would expect 95% of residuals to fall within the error bounds:

```
binned_residuals(mod.tot)
```

```
## Warning: Using CAR terms without a grouping factor is deprecated. Please use
## argument 'gr' even if each observation represents its own location.
```

```
## Warning: Following potential variables could not be found in the data: W
```

```
## Warning: Probably bad model fit. Only about 34% of the residuals are inside the error bounds.
```



This result confirm the low predictive validity of the model, which not surprisingly did not identify any particular covariate for predicting the presence of one or more killed wolves in a municipality.