Discrepancies between wolf distribution estimates from opportunistic mortality records and probabilistic field-based surveys

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Abstract

The gray wolf (*Canis lupus*) has expanded its distribution in Europe, where some countries implemented population schemes through structured surveys. However, increasing wolf populations has also resulted in a growing number of wolves being found dead each year. Although these opportunistic reports are promising for population monitoring, their accuracy in reflecting wolf distribution is still unclear.

We compared the spatial distribution of the density of wolf carcasses found in Central Italy (n = 983), with robust occupancy estimates at a 100 km^2 resolution, obtained from a structured population monitoring based on spatially-balanced sampling over an area of 50,200 km^2. We fitted a zero inflated Bayesian GLM to estimate the density of carcasses, according to covariates explaining both wolf presence and detectability.

The density of carcasses was higher in cells with low landscape naturalness and a low density of deers, higher for cells with a low abundance of the wild boar and higher for cells with high landscape anthropization. Model estimates for the density of carcasses also differed from occupancy estimates from the national monitoring program, for most of our study area.

Conditional effects, overdispersion in model residuals, and discrepancy between occupancy estimates based on the national structured survey and the distribution of carcasses indicate that estimating the spatial distribution of wolves from the latter can be misleading. Bias can stem from the systematic persecution of wolves at particular hotspots, as well as from undetected or unreported collisions with vehicles.

Authorities responsible for wildlife monitoring should therefore improve the standardization and centralization of records of wolf carcasses and engage experts to understand the causes of their bias before using them for population monitoring in place of surveys adopting probabilistic sampling.

keywords: population monitoring; illegal killing; roadkill; large carnivore; multifarious data; Besag-York-Mollié model

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Introduction

In the last three decades, the gray wolf (*Canis lupus*) has expanded its distribution in Europe, due to legal protection and the increase in forest cover and large ungulates [1][2]. Wolves are now present in all mainland Europe [3] and in some countries they have recovered most of their historical range (e.g., Italy)[4]. This population increase poses new challenges for human-wolf co-existence [5][6][7], as wolves prey on wild ungulates, livestock [8][9], and pets such as dogs [10][11]. These interactions can worsen public attitudes and increase the risk of persecution. To establish baseline information, many environmental agencies have implemented monitoring schemes to map the spatial distribution, size, and genetic structure of national [4][12][13] or transboundary [14][15][16][17] wolf populations.

Increasing wolf populations also result in high numbers of opportunistic reports of individuals found dead and reported to local authorities [18][19][20][21]. These opportunistic reports can help identify movement corridors [22] and mortality hotspots [18][19]. Moreover, they can provide biological samples useful for assessing the sanitary status of wolf populations [23][24] or highlight the impact of landscape anthropization [25][26].

Thanks to the increasing availability of easy-to-use and flexible software for spatial modeling [27][28] and freely available environmental datasets [29], opportunistic reports are now widely used in population monitoring. For example, an increasing number of studies rely on opportunistic reports to reconstruct the occurrence [30][31][32][33], abundance [34][35], and demographic structure [36][37] of terrestrial mammal populations, as well as to assess their spatio-temporal changes [38][39][40][41]. In the case of wolves, this possibility is particularly appealing to wildlife agencies. Their large distribution across many European countries, territorial behavior and dispersal [42][43], capacity to colonize new environments and cope with disturbance [7][44][45][46][47], and the effort required for large-scale surveys [48] make field surveys both expensive and time-consuming. Therefore, analyzing opportunistic reports of dead wolves appears to offer a low-cost alternative for estimating wolf abundance and distribution, supporting more effective evidence-based conservation strategies.

However, while it is relatively easy to obtain unbiased estimates of ecological parameters (e.g. occupancy)[49] from surveys adopting probabilistic sampling [50][51], achieving the same with non-probabilistic samples, such as opportunistic reports, is far more demanding [52]. As for models aiming at reconstructing the spatial distribution of animal species, provided that records attain a satisfactory level of quality [53][54], models needs to adjust observations for accessibility [40][55][56], and factors influencing detectability of animals by humans [57][58]. Furthermore, even when modeling successfully accounts for spatial bias, estimates can still have considerable uncertainty [59]. Therefore, estimates obtained from opportunistic reports should be benchmarked against those from structured surveys before being used for management.

While some recent studies have used opportunistic data to map the spatial distribution of wolves [60][61][62], to the best of our knowledge no study compared spatial distribution estimates of wolves obtained from opportunistic reports with those derived from a structured survey. Although Karppinen et al. (2022)[63] developed a statistical model to estimate wolf territories from citizen science data, they relied on auxiliary information about previously known territories, derived from long-term monitoring programs.

This study aims to address this gap by benchmarking the estimated density of individuals found dead and reported to local authorities across a large area of Central and Northern Italy, corrected through a spatial-explicit model, against robust occupancy estimates from a population survey based on a spatially-balanced sampling [64]. Findings highlight the limitations of opportunistic reports as indicators of wolf presence and call for increased standardization of their collection.

Materials and methods

Study area

The study area covers an area in Northern and Central Italy, shared between the Lombardy, Emilia-Romagna, Tuscany, Marche and Umbria regions (Fig. 1a,b). In Lombardy, we considered the provinces of Pavia, Lodi and Cremona, as occupancy estimates were available exclusively for these areas [4][64]. In Tuscany, we excluded the provinces of Arezzo, Siena and Grosseto because data on wolf carcasses, collected by local authorities, were unavailable at the time of the study.

The study area hosts a variety of ecosystems, ranging from the Mediterranean maquis along the Tuscany coast to temperate forests and sub-alpine grasslands in the Apennines. Over recent decades, rural abandonment has significantly altered the landscape, leading to increased forest cover and a reduction of croplands in mountainous areas [65]. At the same time, the study area faced the large-scale recovery of wild ungulates [66], which became the basis of wolf diet.

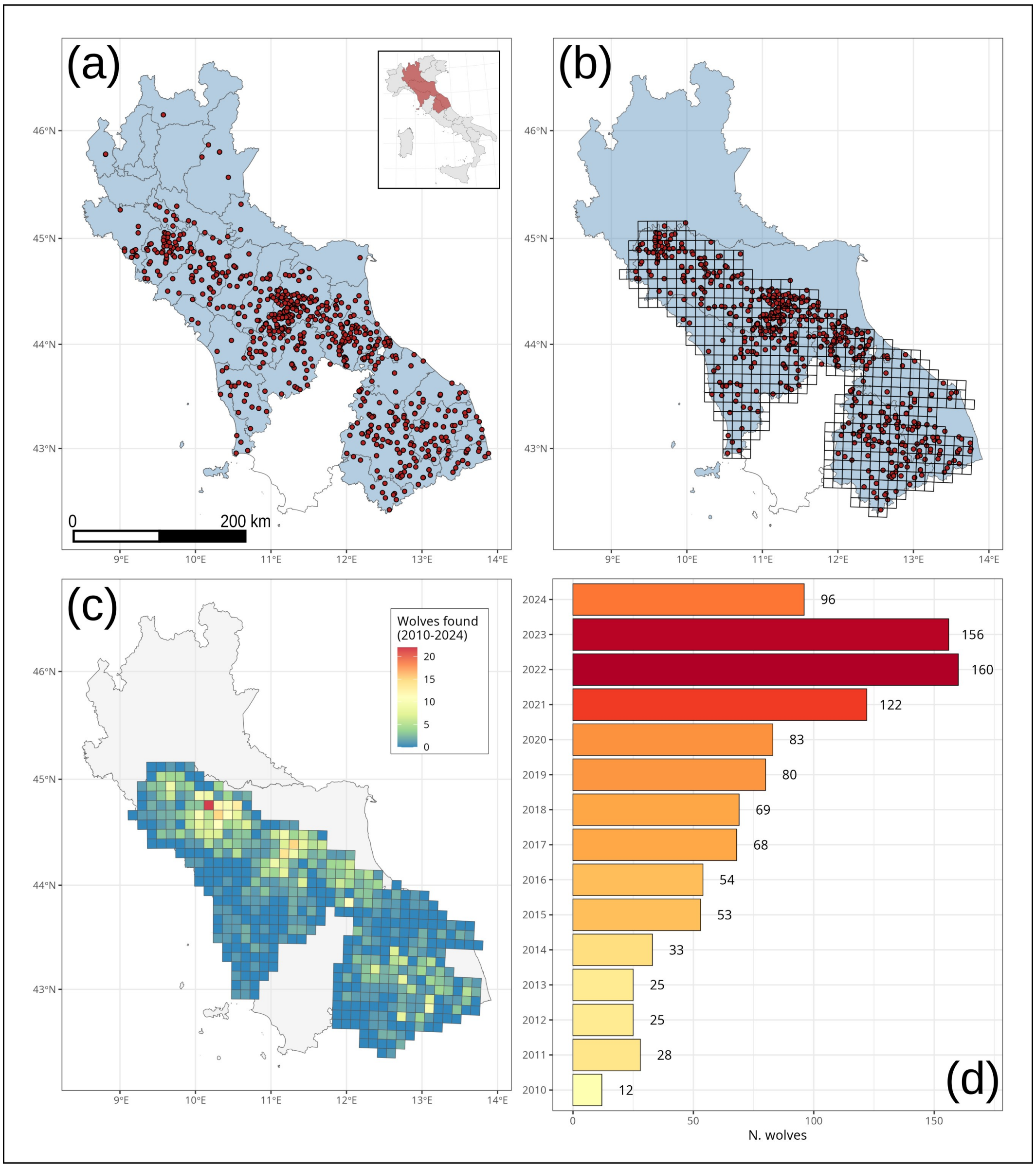

Figure 1: Map of the study area, representing the regions and provinces where wolves were collected (a), the 10km^2 grid used for modeling (b), the total number of wolves found dead between 2010 and 2024 in each cell of the grid (c) and each year (d). The locations of wolves that were found dead are shown on the map as points. Data from the Tuscany region does not include wolves that were recovered after May 2023.

Wolf presence in the study area has changed considerably over time, although tracing a large-scale picture is difficult due to the lack of synchronized monitoring schemes across different regions. Overall, the Apennines have served as a stronghold for wolves since at least the 1990s, harboring most wolf packs until the early 2000s. Wolves then progressively expanded and saturated the most suitable habitats by the early 2010s [67]. Over the last 15 years, wolves have dispersed and established their territories into more disturbed areas and are now commonly found near human settlements [47]. This expansion has increased the number of collisions between wolves and vehicles, diversified conflicts with human activities [19], and exposed wolves to toxic compounds [24].

Data collection

Wolf records

Between 2010 and 2024, 1,081 wolves were found dead and reported to local authorities as shown in Fig. 1 (a). The majority of these individuals (n = 664, 61.4%) died in collisions with vehicles or trains, and for most of them (93.7%) the coordinates of the recovery site were recorded. Out of 1,081 wolves, 108 were discarded due to missing coordinates. All individuals were sexed, aged, and subjected to different forms of biometric measurements and the collection of genetic material[19][24].

The final sample of individuals included 973 wolves with available coordinates, collected between 2010 and 2024 (Fig. 1a). The wolf record data were overlaid onto a 100 km^2 grid (Fig. 1b), used for the Habitat Directive reporting and the national wolf survey. This grid, provided by the Italian Institute for Environmental Research and Protection (ISPRA), also included occupancy estimates obtained from the spatially-balanced sampling of the national wolf survey. The total number of dead wolf records was aggregated within each grid cell, resulting in 502 cells covering a total area of 50,200 km^2. These cells served as the observational units for statistical modeling.

Environmental and Anthropogenic Covariates

For each grid cell, we also quantified 9 nine potentially relevant covariates to explain both wolf presence and detection. These reflected: (*i*) the abundance of wild ungulates (roe deer, red deer, fallow deer and wild boar); (*ii*) terrain roughness; (*iii*) forest cover in 2000, at the onset of wolf expansion; (*iv*) the proportional increase in forest cover between 2000 and 2023; (*v*) human density; and (*vi*) the total length of the road network.

We included wild ungulate abundance was included as evidence from the study area indicates that roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), wild boar (*Sus scrofa*) and fallow deer (*Dama dama*) are main prey of wolves [68][69][70][71][72][73][74]. We therefore assumed that cells with a higher abundance of wild ungulates could support a greater number of wolves and/or more wolf packs. We quantified abundance through estimates developed by the ENETWILD consortium at a 100 km^2 scale, consistent with the study grid, that were developed from hunting bags statistics after having been calibrated against densities [75].

We quantified the overall terrain roughness of each cell by calculating the variance in the terrain roughness of all the 250 m cells from a Digital Elevation Model provided by Amazon AWS. This approach allowed us to distinguish between areas that were more or less homogeneous in terms of terrain roughness, and therefore between lowlands, hills, and mountainous regions. We accounted for terrain roughness in the statistical model, based on the assumption that mountainous and remote areas are less accessible to people and have a lower human density. Therefore, more likely to have fewer wolf records than the lowlands.

We also controlled for forest cover in 2000, as evidence indicates that forested areas in the late 1990s were strongholds of wolf presence [47]. Therefore, we predicted that grid cells with a higher forest cover would produce more wolf records of wolves in the study period, due to a systematically higher presence of wolves resulting from long-term population dynamics. We used the MODIS/Terra vegetation continuous field (`https://ladsweb.modaps.eosdis.nasa.gov/missions-and-measurements/products/MOD44B`) at a 250 m resolution to quantify the percentage of forested areas in each grid cell. Moreover, we also used MODIS/Terra data to quantify relative changes in forest cover between 2000 and 2023, as forest expansion was deemed to have favored the presence of wolves by providing them with suitable habitat to shelter from disturbance [76][77]. Both variables were scaled at a 100 km^2 resolution by calculating their median value. A visual comparison with the study area map confirmed that using the median aggregation effectively captured undisturbed forest areas and regions undergoing rural abandonment and forest expansion.

We also quantified landscape anthropization by using human density estimates at a 1 km resolution from the Global Human Settlement Layer (`https://human-settlement.emergency.copernicus.eu/`

ghs_pop.php). We accounted for human density, as we believed that it could simultaneously decrease wolf presence, by increasing disturbance, and increase the detection of dead wolves, by increasing the number of observers in the landscape. To quantify human density at a 100 km^2 resolution, we computed the Gini index of 1 km estimates. The Gini index ranges from 0 to 1, with higher values indicating a more concentrated distribution: cells with higher values of the index were therefore areas with more concentrated human settlements, such as mountains with small villages, whereas cells with lower values of the index corresponded to highly anthropized lowlands.

Finally, we also quantified the total density of the road network within each cell. Adjusting for this value was crucial, as a denser road network was expected to increase the frequency of wolf-vehicle collisions and thus the number of recorded wolf mortalities. We downloaded the shapefile of the road network from OpenStreetMap (https://www.geofabrik.de/), and excluded road types unlikely to result in roadkills (e.g., hiking trails, cycling lanes, pedestrian zones).

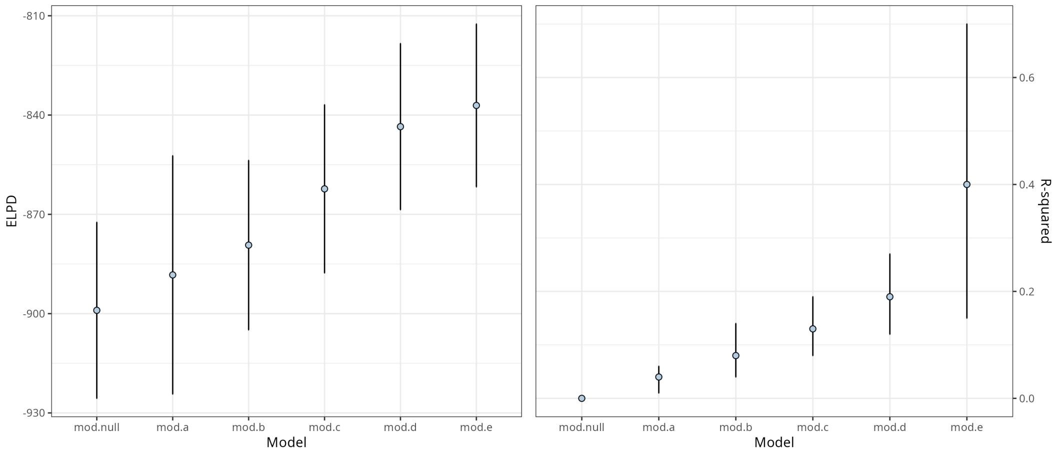

Figure 2: Expected Log-Pointwise Density (ELPD) and the Bayesian R2 of the different candidate models (higher values indicate a better model fit, see https://rdrr.io/cran/brms/man/loo.brmsfit.html).

Data analysis

Covariates were spatially correlated in space, in line with large-scale and long-term landscape dynamics that affected forest distribution in the late 20th century, their subsequent recovery in the early 2000s, the presence of ungulates, and the distribution of human settlements in the study area. Therefore, to address this multicollinearity, we used a Principal Component Analysis (PCA) to identify a limited number of components explaining the highest proportion of variation in our data, which could then subsequently be used as covariates in our models. Environmental covariates were all continuous and were standardized and centered before being included in the PCA. PCA identified three main axes, which corresponded to three main large-scale attributes of the landscape, easily interpretable from an ecological point of view, and which collectively explained 76% of variation in the data. The first Principal Component (PC1) represented the level of habitat naturalness, with higher values indicating those areas, mostly in the northwest Apennines, that were forested in 2000, had few human settlements, a limited road network, and high densities of deer species. The second Principal Component (PC2) instead represented landscape anthropization, with higher values indicating urbanized areas with a diffused road network and a limited forest expansion in the 2000s. The third Principal Component (PC3) represented lowlands in the southernmost portion of the study area, which were characterized by high densities of the wild boar (see Appendix 1).

We also included a dichotomous covariate to indicate whether a certain cell belonged to the Umbria and Marche regions, or the Lombardia, Emilia-Romagna, or Tuscany regions. This distinction was necessary because wolves in the Umbria and Marche regions were collected by the Istituto Zooprofilattico Sperimentale dell'Umbria e delle Marche, which implemented harmonized protocols at a later stage and consequently had a higher proportion of wolves that were discarded due to missing coordinates (22.2% against 4.5%).

We fitted Bayesian Generalized Linear Models (GLMs) to quantify the effect of these three covariates on the number of wolf records per cell. Compared to conventional GLMs, distributional GLMs could model the effect of covariates over the mean value of the response, but also on the other distribution parameters,, such as scale, that quantify data variability [78]. Moreover we used a zero-inflated negative binomial distribution to quantify the effect of covariates on the probability that each cell had zero counts of wolves, accounting for structural and sampling zeroes [79]. We used stepwise-forward model selection by adding each covariate sequentially, and testing its impact on the median number of wolves, on the variability in the number of wolves, and on the probability of zero observations. We used leave-one-out cross validation to quantify improvements in model performances [80] and examined model residuals to detect non-linearity, which we addressed through Gaussian Processes [81]. We used a Besag-York-Mollié structure to account for residual spatial correlation among adjacent cells [82], due to different ecological and observational processes.

Finally we compared model predictions with occupancy estimates from the national wolf survey, carried out by the Italian Institute for Environmental Protection and Research (`https://www.isprambiente.gov.it/it/attivita/biodiversita/monitoraggio-nazionale-del-lupo/risultati`). The survey was based on different signs of presence and adopted a Generalized Random Tessellation Stratified survey design to ensure robust spatial estimates. For further details, please see Gervasi et al. (2024)[64] and La Morgia et al. (2022)[4]. Statistical analyses were carried out in STAN [83] through the brms package [84] in R [85].

Results

Model selection (see Appendix 2 for a complete overview) retained a model in which the total number of wolves found dead between 2010 and 2024 in each grid cell was predicted by the three principal components, as well as by a dichotomous covariate indicating whether wolves came from the Umbria/Marche regions.

Stepwise forward model selection improved the model residuals (Fig. S6 in Appendix 2), the Expected Log Pointwise Density (ELPD), and the Bayesian R^2 of each model (Fig. 2). The best candidate model demonstrated a good fit, in terms of posterior predictive checks (Fig. S5) and when residuals were plotted against covariates (Fig. S8). However, the best candidate model still had some pattern in its residuals when plotted against predicted values, indicating that some potentially relevant covariates had not been identified (Fig. S8).

Conditional effect plots (Fig. 3) indicated that the number of wolf records was higher in grid cells with low values of PC1, namely in areas with low presence of natural habitats and low abundance of deer species (roe deer, red deer, fallow deer). Estimates were also higher in grid cells of the grid with medium-high values of PC2, corresponding to urbanized areas with a diffused road network and a limited forest expansion. They were also higher in cells with low values of PC3 or abundance of wild boar (Fig. 3).

Although the best candidate model smoothed the spatial distribution of wolf records (Fig. 1), showed a good fit to the data and explained a reasonable percentage of variability in the data (see Fig. 2 and Table S4), its predictions still differed significantly from occupancy values predicted by the national wolf survey carried out by ISPRA (Fig. 4).

Discussion

To the best of our knowledge this is the first study in which the spatial distribution of wolves, obtained from opportunistic reports of dead individuals, has been benchmarked against occupancy estimates from a field survey based on spatially-balanced sampling.

Our findings indicate that estimating the spatial distribution of wolves from records of dead individuals is nontrivial, at least when using models for areal data at a 100 km^2 resolution. Even after accounting for relevant covariates that explain both detection probability and the presence of wolves in each grid cell, and which should have reduced bias in our predictions, the resulting model exhibited low predictive power. It estimated a density of records that was both biased and characterized by considerable uncertainty.

Bias was clear when our estimated density of wolf records was compared against occupancy estimates from the national wolf monitoring [4][64]. Although our Bayesian model was somewhat effective at smoothing spatial differences in wolf records, it still predicted high densities around the area with the highest number of records, in the anthropized landscapes of the Emilia-Romagna region. Moreover, the model did not address the issue of missing data in the Umbria and Marche regions, where 22.2% of records were discarded due to missing coordinates. In these areas, the easternmost portion of our study area, our findings systematically diverged from national survey results. This widespread bias and the resulting discrepancies with the national survey may stem from three main underlying causes. The first cause is that identifying covariates explaining wolf presence in space is non trivial, due to their ecological flexibility [86] and broad dietary niche [8] throughout their distribution range. Conventional covariates quantifying land cover and landscape complexity may therefore be inadequate for predicting wolf distribution. Similar limitations apply to covariates accounting for the detection of wolves. Although many models based on non-probabilistic data incorporate metrics related to the distance from human settlements, human population density, or the presence of roads, these variables proved ineffective in predicting the probability of wolves being found within our 100 km^2 grid cells..

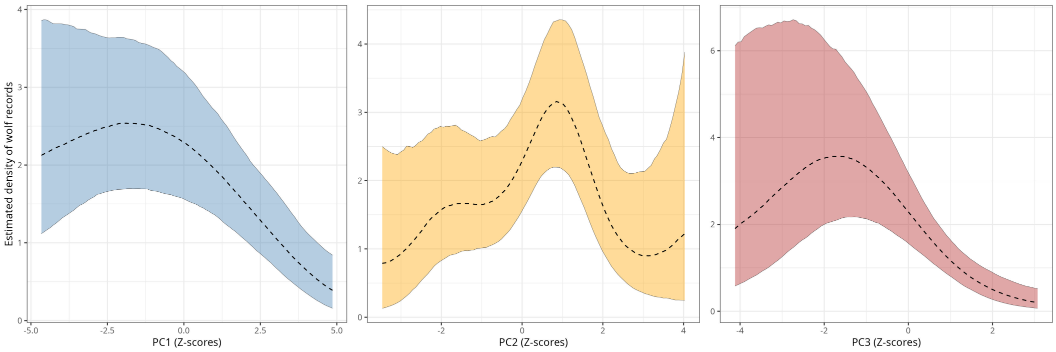

Figure 3: Conditional effect plots, showing the effect of the first principal component (PC1), the second principal component (PC2), and the third principal component (PC3PC2) over the density of wolf records. PC scores are expressed as Z-scores, in terms of standard deviations from the mean. For a complete description of PC1, PC2, and PC3 and their biological meaning, please see the Methods section. To compare model predictions against real data, please see Appendix 2.

A second potential cause of bias might be due to cryptic wolf persecution, which can result in wolves being systematically killed and removed from the environment without being recorded, particularly in certain hotspots [87][88]. Unreported collisions between wolves and vehicles may also contribute to under-reporting. In particular, when wolves are hit by large vehicles, some drivers may choose not to report to avoid dealing with insurance companies and/or local authorities. In such cases, the animal may be moved away from the road by the collision and remain undetected [89]. We suggest that expert elicitation could be used to better understand and map the spatial distribution of wolf persecution [90], while specialized questioning techniques [91] may help estimate the incidence of unreported wildlife-vehicle collisions. Future studies should also quantify the extent to which including/how including data on wolf persecution, considered a form of "anthropogenic resistance" [92], and vehicle collisions could improve the predictive power of models based on opportunistic reports.

A third plausible source of bias may stem from our modeling approach and the spatial resolution we adopted. In this study, we used a model for areal data (grid cells) to quantify the presence of wolves at a 100 km^2 resolution, to enable direct comparison with occupancy estimates from a structured survey. However, alternative approaches that operate at higher spatial resolutions, such as point process models [93] or species distribution models [94], have the potential to yield more accurate predictions. However, fine-scale predictions of wolf distribution from PPMs/SDMs should have been benchmarked against fine-scale estimates of wolf occupancy (e.g., from camera trapping schemes)[95], which were not available for the study area at the time of the study. Moreover, as 61.4% of our records resulted from vehicle collisions, we would have violated the assumption of PPMs or SDMs that points occur continuously in space, in response to a latent process such as animal distribution in space. Another alternative approach would have been occupancy modeling, which has already been used for roadkill data [35]. We did not adopt this method due to the fact that occupancy models have been originally conceived for ecological surveys with repeated sampling sessions. Due to the relatively low number of wolf records in our dataset and the size of our study area dividing counts of wolf carcasses in grid cells, through time, was impossible. Occupancy models could become more appealing in the near future, with the development of extensions for continuous-time data [96] and increased flexibility (e.g. spatial random effects)[97]. Nevertheless, it is important to emphasize that even these promising alternatives for opportunistic data should be compared against surveys adopting probabilistic sampling before being taken as valid. A praxis that is seldom implemented in ecology and conservation.

We believe our findings also provided valuable guidance about potential ways to improve the collection and use of records of dead wolves for population monitoring. First, the greater bias was observed in the Umbria and Marche regions, where a larger proportion of records were discarded due to missing coordinates, emphasizes the need for harmonized data collection protocols and better communications among different stakeholders, such as citizens, police officers, and environmental agencies. The introduction and the adoption of universal standards for the collection and sharing (e.g., FAIR)[98] of opportunistic reports of dead wolves is a priority for scaling-up our research to larger spatial scales in

Europe, while counteracting bias. Moreover, the adoption of standards for data collection and sharing would promote collaborative research, allowing researchers to pool mortality data across regions. Increased sample size would in turn reduce the uncertainty in estimated density of wolf carcasses, which in our model remained high. Even though reducing variance is of secondary importance, with respect to reducing bias, this would still be a meaningful improvement. Finally, our findings call for the need to integrate records of dead wolves with information from structured ecological surveys. Data integration is an emerging field in ecology. In the next few years, advances in statistical models for data integration will probably open new possibilities to use opportunistic reports as a complement to more structured information from ecological surveys[99].

Conclusion

This study represents a first attempt to benchmark the performances of opportunistic reports of wolf carcasses against a structured survey in terms of their capacity of reflecting the spatial distribution of wolves. Even after having accounted for relevant environmental covariates through a spatially-explicit model, we found that the density of wolf carcasses does not reflect the spatial distribution of wolves, obtained from a robust field survey. Although using opportunistic reports is cost-effective and appealing, it can result in seriously biased estimates of wolf distribution and it is far from replacing more robust methods, such as population monitoring schemes based on probabilistic sampling. Therefore, wildlife agencies should improve the standardization and centralization of opportunistic reports of wolves, and also engage experts to understand their potential limitations (e.g. cryptic persecution, unreported roadkills), before using them for population monitoring.

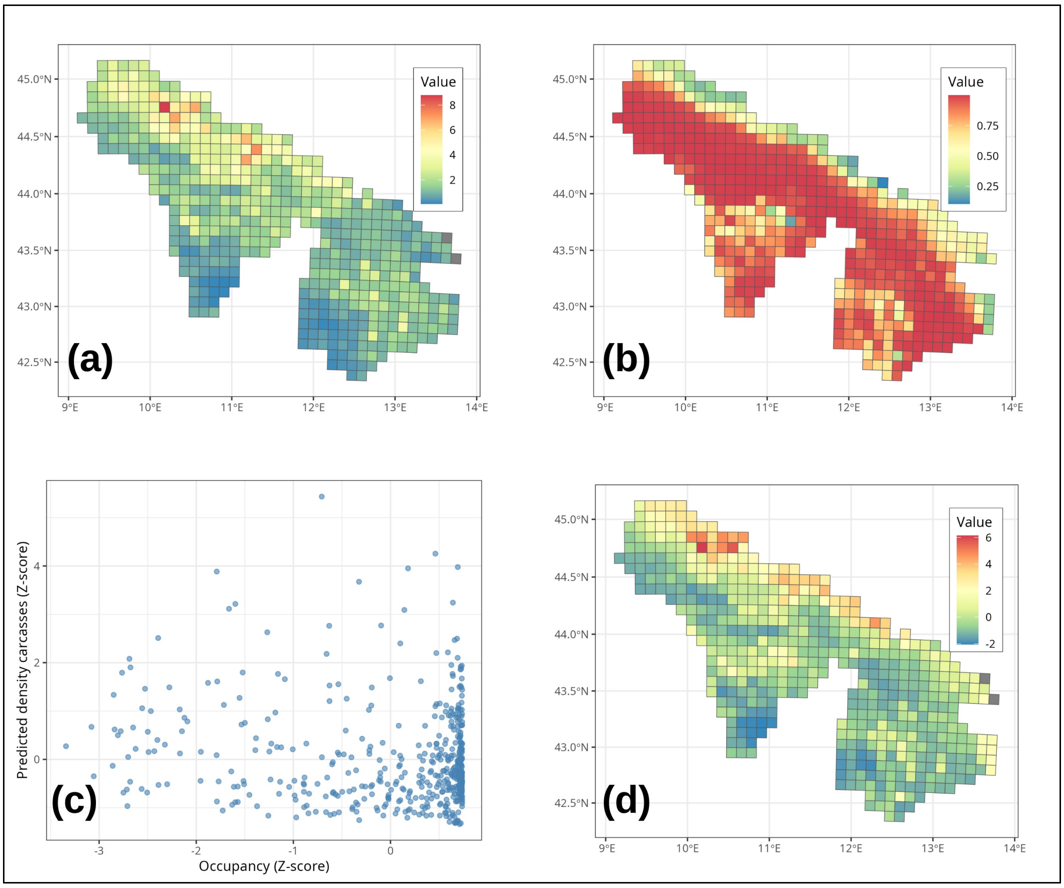

Figure 4: Density of wolf carcasses, estimated by the best candidate model (a), occupancy estimates from the national wolf survey (b, as a probability), association between predicted density of wolf carcasses and occupancy estimates (c, both converted to Z-scores) and difference between the predicted density of wolf carcasses and occupancy (both converted as Z-scores).

Acknowledgements

We are grateful to the Institute for Environmental Protection and Research (ISPRA), who kindly provided us with occupancy data from the first population assessment of wolves in Italy.

Data availability statement

Reproducible data and software code are available at: https://osf.io/2xpsq/

Funding

Carmela Musto was partially supported by a research grant funded by the Vienna Science and Technology Fund (WWTF) [https://doi.org/10.47379/ESR20009]. Pegah Mohammadpour was funded by the Portuguese Foundation for Science and Technology (FCT) under Grant No. 2021.05971.BD (FUNDREF: https://dx.doi.org/10.13039/501100001871). Matilde Martini was funded by the University of Florence, Department of Agriculture, Food, Environment, and Forestry (DAGRI), under Postgraduate research grant No. 5040, Prot. 86591.

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- Jacopo Cerri - Conceptualization, Formal Analysis, Methodology, Project administration, Software, Validation, Visualization, Writing - original draft, Writing- review and editing
- Carmela Musto - Conceptualization, Data curation, Investigation, Project administration, Resources, Validation, Writing - original draft, Writing- review and editing
- Mario Andreani - Data curation, Investigation, Resources
- Patrizia Bassi - Data curation, Investigation, Resources, Writing - original draft
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Conflict of interest

The authors declare no conflict of interest.

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