



Research Article

Improving predation risk modelling: prey-specific models matter

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Abstract

Globally, large carnivore livestock predations are major causes of conflicts with humans, thus identifying hotspots of carnivore attacks is fundamental to reduce the impact of these, and hence promote coexistence with humans. Species distribution models combining predictor variables with locations of predation events instead of species occurrences (also known as predation risk models) are increasingly used to predict livestock depredation by carnivores, but they are often developed pooling attacks on different livestock species.

We identified the main factors related to predation risk on livestock using an extensive dataset of 4604 locations of verified wolf predation events on livestock collected in northern and central Italy during 2008–2015 and assessed the importance of pooling versus splitting predation events by prey species.

We found the best predictors of predation events varied by prey species. Specifically, predation risk increased with altitude especially for cattle, with grasslands especially for cattle and sheep and with distance to human settlements, especially for goats and livestock but only slightly for cattle and sheep. However, predation risk decreased as human population density, human settlements and artificial night-time light brightness increased, especially for cattle. Finally, livestock density was positively related to predation risk when herd exceeds 500 heads for km². Moreover, prey-specific risk models are better tools to predict wolf predation risk on domestic ungulates.

We believe that our approach can be applied worldwide on different predator-prey systems and landscapes to promote human-carnivore coexistence. Actually, while pooling predation events could be primarily used by managers and personnel of wildlife agencies/offices in developing general policies, splitting predation events by prey species could be used at farm-level to better identify livestock owners at risk in high-priority areas and which prevention tools and deterrents (e.g. electric fences, guarding dogs, predator-proof enclosures) should be applied, as the most effective measures differ by species.

Introduction

One of the most important threats to the long-term conservation of large carnivore populations worldwide is illegal killing caused by conflicts with human activities (Ripple et al., 2014).

Attacks on livestock can cause extensive conflicts between humans and carnivores, even if the mitigation of conflicts is often addressed with compensation schemes to offset losses and preventing tools to reduce attacks of large carnivores (Bautista et al., 2017, 2019). The recent recovery of large carnivores in human dominated landscapes has increased the controversy and concern for livestock producers, especially where wild predator populations and farmlands overlap (Zingaro and Boitani, 2017). Therefore, the evaluation of conflicts with human activities is fundamental to design sound conservation strategies for both large carnivore populations and pastoral communities (Marino et al., 2016; Inskip and Zimmermann, 2009). However, the knowledge about the underlying mechanisms and factors associated with carnivore attacks on livestock are often limited.

In recent years, an increasing number of studies adopted species distribution models (SDMs; Guisan et al., 2013) to predict predation risk on livestock (also known as predation risk models, PRMs; Miller, 2015). While SDMs are widely used to predict species-environmental relationships (e.g. the extent of species invasions or species' range shifts due to climate and land use change; Brewer et al., 2016), PRMs are aimed to predict spatial distribution of predation risk and thus spatially identify livestock exposed to carnivores attacks. Specifically, PRMs use locations of carnivores' attacks, instead of species occurrences, in combination with environmental predictors to predict predation risk on livestock. Several carnivore species hunt in areas characterized by a combination of land cover, vegetation structure and human activities where they can easily access and kill prey (Gorini et al., 2012), often regardless prey abundance (also known as "landscape of fear"; Laundré et al., 2010). Identifying factors related to the sites where carnivores successfully kill livestock and quantifying their effects could reveal the spatial features associated to predation risk (Hebblewhite et al., 2005), thus offering much needed insights to understand and forecast spatial predation risk (Trainor and Schmitz, 2014). Actually, predation on livestock compromises the economic security of local farmers and increases negative attitude towards predators, leading to human-

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carnivore conflicts, which counteract the efforts made to promote large carnivore conservation (Pimenta et al., 2018). Thus, it is fundamental to accurately prevent attacks on livestock in areas where human-carnivore conflicts is likely to arise and focus interventions where the depredation risk is higher (Zingaro and Boitani, 2017).

However, depredation events on livestock species (e.g. cattle *Bos taurus*, goats *Capra hircus* and sheep *Ovis aries*) are often grouped in PRMs, without considering potential differences related to attacks on different species (Karanth et al., 2012; Abade et al., 2014; Behdarvand et al., 2014; Soh et al., 2014; Miller, 2015; Miller et al., 2015; Gese et al., 2016). The factors that best determine prey accessibility can vary over different domestic ungulates (Bradley and Pletscher, 2005; Kaartinen et al., 2009). Specifically, cattle, sheep and goats are among the main livestock species killed by large carnivores (Treves and Karanth, 2003; Nowak et al., 2005; Rigg et al., 2011) but there has been little research on the different factors that may affect predation risk on different domestic preys (Cascelli de Azevedo and Murray, 2007; Odden et al., 2008; Valeix et al., 2012; Pimenta et al., 2018).

We investigated wolf predation risk on livestock in Italy where, after a human-driven decline in the last two centuries, this large carnivore experienced a recovery following conservation efforts, recolonizing the entire Apennine chain and the Alps, thanks to the protection by laws, its adaptability to habitat changes and the marked recovery of wild prey populations (Boitani, 2000; boitani, 2003; Valiere et al., 2003; Fabbri et al., 2007; Galaverni et al., 2016). This positive trend also raised public negative attitudes due to the perceived high impact on human activities and caused concern of livestock breeders because of its predatory behaviour (Fritts et al., 2003; Marucco and McIntire, 2010; Dondina et al., 2015).

Our aims were (i) predict the spatial patterns of wolf (*Canis lupus*) predation risk on livestock in the Northern-Central Apennines, Italy, in order to identify hotspots of livestock depredation where adoption of prevention tools should be prioritized and (ii) to identify the main environmental and anthropogenic factors related to wolf predation on livestock assessing the importance of pooling versus splitting predation events by prey species.

Materials and methods

Study area

Our study area is located in the southern part of the European wolf range, covering a large portion (48882 km²) of the Northern-Central Apennines, Italy (7°49'-13°91' E; 45°-42°39' N; Fig. 1). Elevation ranges from 0 to 2476 m a.s.l. and there is a climatic gradient, from temperate to continental to alpine, resulting in high habitat diversity. Forests are mainly composed of broadleaf or mixed woods and, to a lesser extent, by coniferous forests. As a result of human population abandonment experienced during the last 40–50 years in the hilly and mountainous parts of study areas, shrub-lands and grasslands are mainly used only for livestock grazing. Thus, our study area results in a patchy landscape pattern of forests and open-areas across large zones where livestock, mostly cattle, sheep and goats, are commonly free-ranging (with births on pastures) and unguarded in pastures from April to October. Some wild ungulates used as main prey by the wolf are also present (i.e. wild boar, *Sus scrofa*, roe deer, *Capreolus capreolus*, fallow deer, *Dama dama* and red deer, *Cervus elaphus*; Milanese et al., 2015). While livestock breeders seemed to be technically and culturally prepared to interact with the wolf in areas of its historical occurrence, this is no longer true in many areas of its recent recolonization (Ciucci and Boitani, 1998). In Italy, the system of compensations paid annually to owners for damages has proved to be not very effective, producing dissatisfaction among livestock breeders (Dondina et al., 2015; Marino et al., 2016). In our study area, public administrations (Regions, Provinces and Parks) have distributed electrified fences and provided livestock guarding dogs over the past 20 years to promote coexistence by the adoption of preventive measures. However, this is often perceived as difficult and economically disadvantageous, involving additional workload often not applicable or functional (Ciucci and Boitani, 2005).

Table 1 – Predictor variables considered in the analysis. Variables with a variance inflation factor (VIF) >3 were removed from further analysis (*) due to multi-collinearity.

Predictor variable	VIF
Altitude (m a.s.l.)	2.739
Slope (°)	2.240
Landscape roughness (ratio of isoipses' average length in a cell over the cell side)*	>3.000
Croplands (%) *	>3.000
Coniferous forests (%)	1.108
Deciduous forests (%)	2.322
Mixed forests (%)	1.182
Grasslands (%)	1.454
Shrub-lands (%)	1.302
Water courses (%)	1.072
Distance to forests (m)	1.641
Shannon' habitat diversity index ($H' = -\sum(\pi * \ln(\pi))$)	1.666
Human settlements (%)	1.939
Distance to human settlements (m)	1.895
Distance to roads (m)	1.172
Artificial night-time light brightness (nw/cm ² /sr)	2.419
Human population density (number/km ²)	1.673
Livestock density (number/km ²)	1.082

Data collection

We collected a total of 4604 verified depredation events on livestock (1273 on cattle, 2906 on sheep and 425 on goats) caused by wolves across our study area in the period 2008–2015 from Regional and Provincial wildlife and veterinary Agencies. The data collected contained information on the location (X and Y coordinate in the WGS 84 / UTM zone 32N system), date and prey species depredated by wolves. Data were verified by the staff of the public veterinary service and State Forestry Corps or Provincial Police, often in collaboration with Regional and Provincial wildlife staff, 24–48 hours after the predation event reported by owners. While we are aware that local management practices (e.g. surveillance and protection) may dramatically affect livestock vulnerability (Pimenta et al., 2017), we could not consider such information in our analysis because, similar to Pimenta et al. (2018), of the lack of standardized data over our study.

Predictor variables

Considering previous published papers on livestock depredation risk modelling (Miller, 2015; Gese et al., 2016), we selected 18 predictor variables available for the entire study area (Tab. 1). We chose three topographic variables (altitude, slope and landscape roughness), derived from a digital elevation model of Italy with a spatial resolution of 20 m (<http://www.sinanet.isprambiente.it>), nine land cover variables (percentage of coniferous, deciduous and mixed forests, croplands, grasslands, shrub-lands, water courses as well as distance to forests and habitat diversity) derived from CORINE Land Cover vector data (ISPRA, 2019). Moreover, we considered anthropogenic features such as the percentage and distance to human settlements (i.e. urban areas and villages also derived from the CORINE Land Cover 2012), distance to roads (OpenStreetMap; <http://www.openstreetmap.org>), human population density (GEOSTAT 2011 1×1 km grid dataset – Eurostat – European Commission; ec.europa.eu/eurostat/web/gisco/geodata/reference-data/population-distribution-demography; Tab. 1) and artificial night-time light brightness (NOAA, NPP VIIRS – NASA 2012 with a spatial resolution of 350 m; https://ngdc.noaa.gov/eog/viirs/download_dnb_composites.html). Finally, we calculated livestock density (pooling cattle, sheep and goats; FAO's Gridded Livestock of the World v.2.0 with a spatial resolution of 1 km; <http://livestock.geo-wiki.org/home-2/>).

All predictor variables were resampled at a 1×1 km grid cell size and we calculated the Variance Inflation Factor (VIF; Zuur et al., 2010) to check for multicollinearity among predictors. Thus, we removed

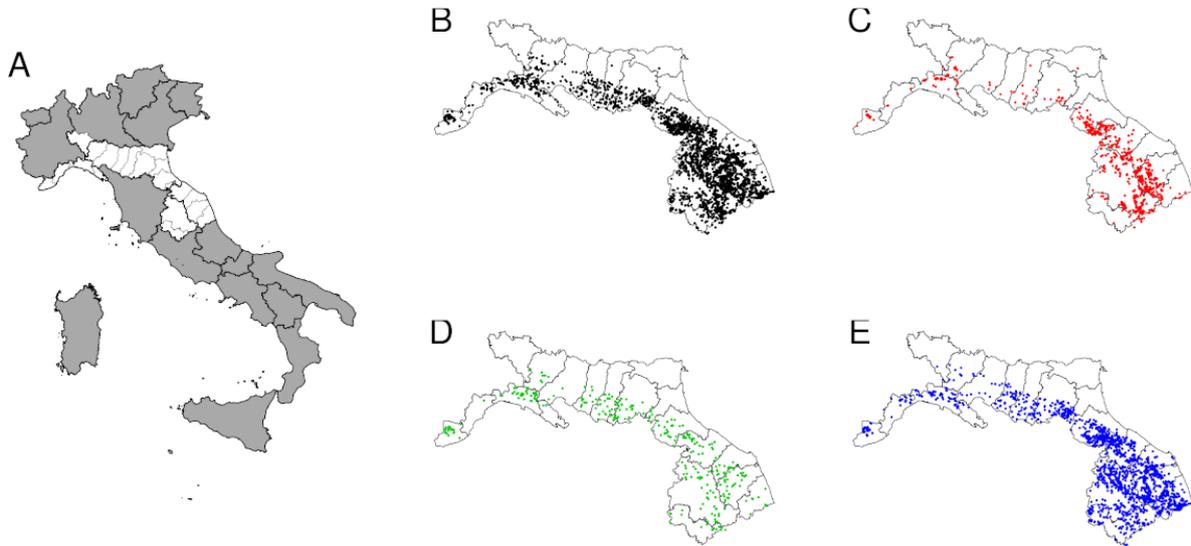


Figure 1 – A: study area (in white) in Italy (in dark grey). Thin and thick black lines indicate provincial and regional borders, respectively. B: locations of wolf predations on livestock (black dots); C: locations of wolf predations on cattle (in red); D: locations of wolf predations on goats (in green); E: locations of wolf predations on sheep (in blue).

landscape roughness and croplands because $VIF > 3$ (highly related to other predictors; Zuur et al., 2010; Tab. 1).

Predation risk models

To fit PRMs avoiding biased estimation due to single model uncertainty (Thuiller et al., 2009), we calculated the weighted ensemble prediction (wEP, weighted by the true skills statistic, TSS; see below) averaging 12 different SDMs namely (1) artificial neural networks (ANN; Ripley, 2007), (2) boosted regression trees (BRT; (Friedman, 2001)), (3) classification tree analyses (CTA; Breiman et al., 1984), (4) flexible discriminant analyses (FDA; Hastie et al., 1994), (5) generalized additive models (GAM; Hastie and Tibshirani, 1990), (6) generalized linear models (GLM; McCullagh and Nelder, 1989), (7) factorial decomposition of Mahalanobis distances (MADIFA; Calenge et al., 2008), (8) multivariate adaptive regression splines (MARS; Friedman, 1991), (9) maximum entropy algorithm (MAXENT; Phillips et al., 2006), (10) maximum-likelihood model (MAXLIKE; Royle et al., 2012), (11) MAXENT model using the `glmnet` package (Friedman et al., 2010) for regularized generalized linear models (MAXNET; Phillips et al., 2017) and (12) random forests (RF; Breiman, 2001). We developed SDMs through the packages `adehabitat` (Calenge, 2006), `biomod` (Thuiller et al., 2016), `maxlike` (Chandler and Royle, 2013) and `maxnet` (Phillips et al., 2017) in R (R Core Team, 2019; <https://www.R-project.org/>). To develop the above mentioned PRMs, we randomly sampled a total of 10000 pseudo-absences distributed proportionally to the accumulated percentage of grasslands and shrublands (Fig. S1). Here, we assume that livestock is available to wolves in our sampled pseudo-absences as these areas mainly correspond to pastures where livestock graze.

We found evidence of spatial autocorrelation among models' residuals through Moran's I correlogram and thus, similarly to Pasinelli et al. (2016), we included x- and y-coordinates of species locations and their interaction in SDMs (then, the model residuals were no longer spatially autocorrelated).

By using a random subsample of 90% of the locations to calibrate the models and the remnant 10% to validate them (Thuiller et al., 2009), we carried out 10-fold cross-validations to evaluate the predictive accuracy of SDMs. Since there is actually no consensus about the most accurate way to evaluate model prediction, we considered three widely used indices to evaluate model performance: (i) the area under the receiver operating characteristic curve (AUC), (ii) the true skills statistic (TSS) and (iii) the Boyce index (BI). Thus, we converted the resulting wEP continuous maps into binary ones, considering threshold values estimated by maximizing TSS (Allouche et al., 2006; Thuiller et al.,

2016). Values higher and lower than these thresholds represent sites where wolf kills are likely to occur or not, respectively.

Comparison of predation risk models and factors related to predation risk on livestock

We develop two sets of PRMs, (i) pooling locations related to predation events on livestock (P-PRMs) and (ii) splitting predation events by prey species (S-PRMs; resulting in cattle-, sheep- and goats-PRM). To avoid that P-PRMs could be affected by the different sample size of locations of predations on sheep (2906), cattle (1273) and goats (425), we randomly selected a total of 425 locations (equal to the number of goats depredations) for both sheep and cattle (we repeated this procedure 10 times to verify consistency of the results). Moreover, for both sheep and cattle we used the unselected locations as independent datasets for model evaluations.

Thus, we carried out pairwise Spearman correlation tests between the resulting wEPs of both P-PRMs and three S-PRMs and finally estimated response curves plotting predation risk on P- and each S-PRMs vs. each predictor variables.

Results

Our random selection of 425 locations of depredations events on both sheep and cattle provided consistent results in the 10 runs carried out.

The 10-fold cross-validations showed high predictive accuracy of both P-PRMs and S-PRMs, ranging between 0.786 and 0.998 for AUC, 0.751 and 0.998 for TSS and from 0.988 to 0.998 for BI and the S-PRMs showed higher values than those of P-PRMs (Tab. 2). Similarly, validating the models of both sheep and cattle with the, independent, randomly non-selected data showed high predictive accuracy of the relative S-PRMs (Tab. S1).

Considering the resulting threshold values (maximizing TSS) of 56, 58, 55 and 61 for livestock, cattle, goats and sheep, respectively, we estimated depredation risk in 26.29% (12852 km²), 12.84% (6276 km²), 21.45% (10484 km²) and 21.14% (10335 km²) of the study area, respectively.

Comparing the resulting risk maps of P-PRMs and S-PRMs, we found the lowest correlation between cattle and goats ($\rho=0.37$) and the highest between livestock and sheep ($\rho=0.76$; Fig. 2).

Response curves derived by P-PRMs and S-PRMs highlighted a direct relation between predation risk and grasslands, except for goats that showed a steep decrease after 75% of grassland coverage (Fig. 3). A similar pattern was found also in relation to coniferous forest coverage, except for cattle that showed a decrease after 25% of coniferous forest coverage (Fig. 3). While predation risk increased with altitude, slope,

Table 2 – Ten-fold cross-validations of the 12 species distribution models (artificial neural network, ANN; boosted regression trees, BRT; classification tree analyses, CTA; flexible discriminant analyses, FDA; generalized additive models, GAM; generalized linear models, GLM; factorial decomposition of Mahalanobis distances, MADIFA; multivariate adaptive regression splines, MARS; maximum entropy algorithm, MAXENT; maximum-likelihood model, MAXLIKE; MAXENT model using the glmnet package for regularized generalized linear models, MAXNET; random forests, RF) and their weighted ensemble prediction (wEP) used to estimate predation risk on livestock pooling and splitting by species predation risk models (P-PRM and S-PRM, respectively). Area Under the Curve (AUC) ranges between 0 and 1 (worse than a random model and best discriminating model, respectively). True Skill Statistic (TSS) and Boyce's Index (BI) ranges between -1 and 1 (higher values indicate a good predictive accuracy, while 0 indicates random prediction). Average values are shown.

Model	P-PRM			S-PRM _{cattle}			S-PRM _{sheep}			S-PRM _{goats}		
	AUC	TSS	BI	AUC	TSS	BI	AUC	TSS	BI	AUC	TSS	BI
ANN	0.827	0.753	0.959	0.871	0.816	0.988	0.881	0.824	0.998	0.881	0.823	0.988
BRT	0.837	0.756	0.976	0.933	0.825	0.988	0.893	0.859	0.988	0.884	0.856	0.989
CTA	0.841	0.781	0.988	0.881	0.814	0.998	0.899	0.858	0.998	0.966	0.894	0.998
FDA	0.786	0.751	0.988	0.871	0.807	0.998	0.881	0.842	0.998	0.878	0.824	0.998
GAM	0.891	0.777	0.975	0.924	0.825	0.985	0.934	0.853	0.981	0.943	0.859	0.987
GLM	0.889	0.757	0.988	0.987	0.863	0.995	0.981	0.844	0.998	0.983	0.839	0.988
MADIFA	0.862	0.782	0.958	0.923	0.842	0.982	0.914	0.821	0.987	0.987	0.814	0.985
MARS	0.849	0.752	0.988	0.892	0.864	0.988	0.894	0.846	0.998	0.894	0.844	0.988
MAXENT	0.815	0.768	0.988	0.918	0.867	0.998	0.928	0.857	0.998	0.924	0.848	0.988
MAXLIKE	0.857	0.784	0.975	0.921	0.858	0.987	0.904	0.848	0.982	0.921	0.835	0.983
MAXNET	0.891	0.762	0.985	0.918	0.865	0.996	0.927	0.851	0.998	0.908	0.847	0.989
RF	0.958	0.898	0.983	0.988	0.981	0.998	0.998	0.989	0.988	0.998	0.998	0.998
wEP	0.878	0.789	0.988	0.936	0.876	0.998	0.931	0.862	0.997	0.927	0.897	0.998

habitat diversity and distance to human settlements, we found differences in the response curves of P-PRMs and S-PRMs, mainly due to a higher increase in the P-PRMs (Fig. 3). On the other side, both P-PRMs and S-PRMs showed a peak around 10% of shrublands, deciduous and mixed forests while for livestock density we found, after an initial peak, a decrease up to 300 heads km², but a strong increase at higher densities (Fig. 3). Finally, predation risk generally decreased as distance to forests and roads, increased. The same hold true for percentage of water courses and human settlements, human population density and artificial night-time light brightness.

Discussion

In this study, we found differences in the relation between environmental predictors and predation risk resulting from pooling and splitting predation events by prey species. Specifically, we developed and compared predation risk maps derived by pooling locations of predation

events on livestock to those estimated for each prey species separately in the Northern-Central Apennines, Italy and found differences among the resulting predation risk maps. Moreover, S-PRMs had a higher predictive accuracy than P-PRMs, showing that the former could be more accurate tools in predicting prey-specific predation risk. Thus, we strongly encourage researchers and managers to develop and apply prey-specific PRMs, when data on individual prey species are available, to predict more accurately hotspots of livestock predation risk. Finally, while sampling pseudo-absences proportionally to the accumulated percentage of grasslands and shrub-lands let us accurately estimate predation risk, we suggest collecting also data relative to availability of pastures in which livestock graze, in order to inform PRMs on true-absence data and thus potentially provide more accurate estimate of predation risk.

Effect of splitting vs pooling livestock species in PRMs

We found different patterns of predation risk for livestock, cattle, goats and sheep in our study area. Actually, the correlation between predation risk maps derived by P-PRM and S-PRMs for cattle and goats was relatively low ($\rho=0.59$ and $\rho=0.57$, respectively; Fig. 2) and even lower considering the three resulting maps of S-PRMs ($\rho=0.47$ between sheep and goats, $\rho=0.42$ between cattle and sheep and $\rho=0.37$ between cattle and goats; Fig. 2) with different surfaces in which wolf depredations are likely to occur in our study area. Thus, our results suggested that the predictor variables considered in this study quantitatively differ in relating predation risk on different prey species.

We found that predation risk increased directly with altitude, especially for cattle (up to the maximum elevation in our study area, 2,476 m a.s.l.) while it reached a plateau for sheep, goats and livestock approximately at 300, 400 and 1,750 m a.s.l., respectively (Fig. 3), mainly because alpine pasture at medium-high altitudes makes livestock more vulnerable to wolves attacks (Ciucci and Boitani, 2005); calves born on pastures at medium-high altitudes are often taken by wolves (Dondina et al., 2015). Actually, studies on the daily activities of cattle showed differences at different altitudes, i.e. high grazing rates at low altitudes while long resting periods at higher altitudes (Aldezabal et al., 1999). However, Alexander et al. (2006) found that in the Rocky Mountains wolves occurred at low altitudes probably because of the good conditions in those areas, such as occurrence of high biomass, good foraging sites and shelter for preys.

Considering slope, predation risk reached an asymptote approximately after 20 degrees for both cattle and goats while for sheep it firstly reached a peak around nine and then increased up to 50 degrees (the maximum slope in our study area; Fig. 3). In general, cat-

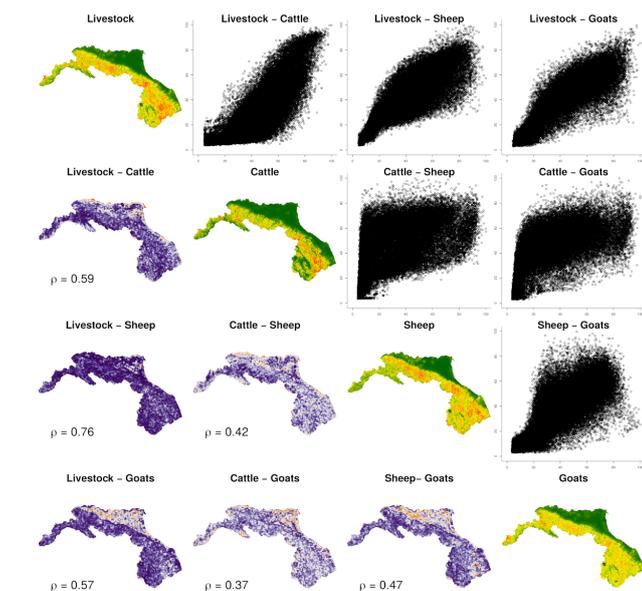


Figure 2 – Maps of pairwise Spearman' correlation coefficients between predation risk probability of wolves on livestock, cattle, sheep and goats (derived by weighted ensemble predictions) in each grid cell of our study area are shown below the diagonal. Purple-white-orange scale indicates positive, null or negative correlation, respectively (average values are shown on the bottom left corner of each map). Predation risk probability maps for livestock, cattle, sheep and goats are shown in diagonal (red-greenscale indicates high-low probability of predation risk) and their relative values are plotted above the diagonal.

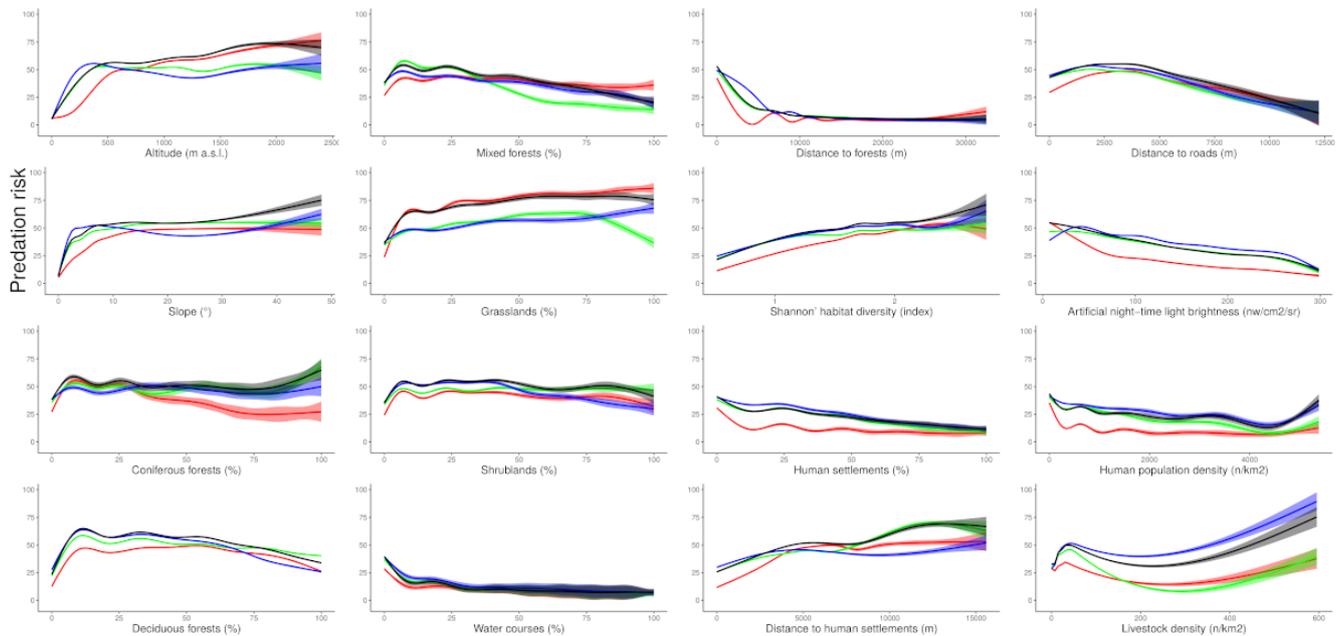


Figure 3 – Response curves and relative 95% confidence intervals (in gray) of predation risk probability of wolves on livestock (in black), cattle (in red), sheep (in blue) and goats (in green) derived by weighted ensemble predictions in relation to predictor variables.

to avoid slopes higher than 20% (~11-12 degrees; Gillen et al., 1984; Bailey, 2005) while goats are more agile than sheep and able to graze even in hardly accessible areas (Bartolomé et al., 1998), although their management and protection in mountain pastures is thus more difficult (Ciucci and Boitani, 2005; Iliopoulos et al., 2009). While, sheep mainly graze on pastures at medium-high slopes in our study area, their small body size and large rumen volume could represent a disadvantage when a predator attacks (Hanley, 1982). The response curves of predation risk on livestock increased directly with slope but without reaching a plateau, with an increase in predation risk above 30 degrees. Thus, in contrast to other studies (Abade et al., 2014; Miller, 2015; Carvalho et al., 2015), we found that slope is directly related to predation risk, probably because, in our study area, wolf attacks on domestic ungulates occur on pastures on steep slopes and thus are difficult to prevent, both by shepherds and guardian dogs (Ciucci and Boitani, 2005; Falcucci, 2007).

Predation risk was negatively related to the occurrence of water courses, consistent with previous studies (Treves et al., 2004, 2011), because water courses prevent livestock from moving too far and thus being exposed to attacks, although not in all cases (Ripple and Beschta, 2003; Ciucci and Boitani, 2005; Abade et al., 2014).

Moreover, we found that predation risk was positively related to habitat diversity, mainly because wolves use different kinds of habitat for different activities (e.g. hunting, breeding; Houle et al., 2010) and because environmental heterogeneity attracts wolves as it promotes the abundance of the main wild prey of the wolf. However, while the response curve of livestock was consistent with the predation risk expected for goats or sheep, it has a slightly different shape considering cattle, decreasing after a peak habitat diversity index value of 2.5. Sheep and goats can forage in very different environmental conditions characterized by heterogeneous and complex landscapes, such as those occurring in our study area, where they could also try to escape from wolves (Leiber et al., 2009). On the other side, cattle do not respond selecting habitat different than pastures (e.g. forest cover) when wolves attack (Muhly et al., 2010).

In contrast to other studies, we found that shrublands (Davie et al., 2014; Miller et al., 2015; Pimenta et al., 2018), coniferous (Treves et al., 2004, 2011; Kaartinen et al., 2009), deciduous (Treves et al., 2004; Dondina et al., 2015) and mixed forests (Treves et al., 2004; Dondina et al., 2015) had a slight, even negative, relationship with predation risk. However, this is not surprising as wolves' attacks on domestic ungulates mainly occurred in pastures, where tree coverage is often very low by

definition (Abade et al., 2014; Imbert et al., 2016), mainly at the borders of pastures. Actually, our response curves showed a peak of predation risk on livestock around 10% of coniferous, deciduous and mixed forest coverage, those of cattle showed a marked decrease over 25% of coniferous forest cover, while goats and sheep showed a decrement over 30% of mixed forest cover. On the other side, grasslands showed a positive correlation with predation risk on cattle and sheep, because they often occur at high densities on pastures, with few or no refuges during the grazing season (Ciucci and Boitani, 2005). Conversely, predation risk on goats showed a negative relation to grasslands increase (after 75%) probably because goats avoid areas with too high percentage of grasslands as their diet contains larger amounts of browse and lignin than that of cattle and sheep (Bartolomé et al., 1998; Osoro et al., 2017).

Considering anthropogenic variables, we found a negative relation between predation risk and human population density as well as human settlements, confirming that human disturbance is a limiting factor for wolves (Jędrzejewski et al., 2005). However, the negative effect of both these anthropogenic variables is stronger for predation risk on cattle, as grazing close to human activities could represent safe areas for this domestic prey species (Muhly et al., 2010; Amirkhiz et al., 2018). Moreover, these patterns could also be related to wolf habitat use and selection, as high road and human densities can decrease habitat suitability for this large carnivore (Wydeven et al., 2002; Oakleaf et al., 2006; Amirkhiz et al., 2018; Mancinelli et al., 2019).

Distance to human settlements was positively related to predation risk, with a strong increase for goats and livestock but only a slight increase for cattle and sheep, as attacks often occur far from human settlements (Kaartinen et al., 2005; Davie et al., 2014; Miller, 2015). However, Behdarvand et al. (2014) found that in Iran, where the natural environment is strongly modified and wild preys are scarce, the proximity of human settlements is an important factor in wolf attack to livestock.

In contrast to Treves et al. (2011) and Behdarvand et al. (2014), we found that distance to roads and forests were negatively related to predation risk, in agreement with previous studies (Kissling et al., 2009; Miller et al., 2015) showing the highest risk of large carnivores attack on domestic ungulates around 5 km–8 km and 3 km from forests and roads, respectively. Thus, additional interesting aspects of our results are the threshold distances at which the large carnivore can access livestock despite of human activities (Miller et al., 2015). Actually, the location of the home-range, habitat use, activity patterns and movements of wolves are highly integrated to make the best functional compromise

between finding the main food resources available while avoiding human disturbance (Kaartinen et al., 2005; Mancinelli et al., 2018, 2019).

Accordingly, we also found that artificial night-time light brightness seems to be a disturbance factor for wolves, as it was negatively correlated with predation risk, especially for cattle. Thus, our results highlighted the importance of artificial night-time light in disrupting a predator's attack. This is probably related to the risk of conflicts with humans in urbanized areas or close to roads generally equipped with night lighting and thus artificial lights can also be exploited as a non-lethal preventing method to reduce livestock depredation (Darrow and Shivik, 2009). However, wolves can quickly become accustomed and habituated to passive disruptive stimuli (Shivik, 2004) but moving the object or light around intermittently and randomly may slow the habituation process (Shivik and Martin, 2001).

Finally, livestock density was positively related to predation risk when the herd exceeds 500 heads per km², as shown in the response curve that decreased until 300 heads and then increased over 500 heads. Indeed, large free-grazing livestock herds could attract wolves due to high availability of vulnerable individuals and relatively low human control (Cozza et al., 1996; Bradley and Pletscher, 2005; Kaartinen et al., 2009). The increase is more pronounced for sheep and livestock than goats and cattle, in agreement with Cozza et al. (1996) and Mech (2000) which showed that large sheep herds are highly attractive for wolves. However, our results are in contrast to those of Zarco-González et al. (2013), which found that in Mexico, livestock predation by puma (*Puma concolor*) is negatively related to livestock density.

Prey selectivity is also dependent on their anti-predatory behaviour. For instance, goats tend to spread inside the forest in case of wolf attacks on pastures, which in turn increases the encounter rate of wolves with isolated individuals (Iliopoulos et al., 2009) while cattle giving birth on pastures could experience high predation risk by wolves on new-born calves (Dondina et al., 2015). Actually, wolves prey almost exclusively on calves born on pastures, whereas adults are rarely attacked (Milanesi et al., 2015) because new born are brought into the herd (as an anti-predatory strategy) only a few days or weeks after the birth (Lidfors and Jensen, 1988; Finger et al., 2014).

Other predictors not considered in our study may also have affected variation in wolf predation risk on livestock species. For example, previous studies showed that wolf predation on livestock may relate to husbandry practices (which can be difficult to quantify and so include in PRMs; Pimenta et al., 2018), wolf densities and availability of alternative wild preys (Mech, 2000; Treves et al., 2004, 2011; Kaartinen et al., 2009; Imbert et al., 2016; Pimenta et al., 2017). Pimenta et al. (2018) suggested that local variations in wolf densities and activity patterns may have affected predation intensity, as well as variables describing wild prey abundance (unavailable in both their and our studies). However, the same authors (Pimenta et al., 2018) found that PRMs developed considering predation intensity (i.e. considering the number of individuals killed per prey species as response variable) had low explanatory power and that heavy predation on livestock occurred also in areas where wild ungulates occurred (Llaneza et al., 1996, 2000; Casimiro, 2017), suggesting that livestock density (considered in our study but not in Pimenta et al., 2018 rather than wild prey densities may be the main driver of livestock predation patterns).

Predation risk models and management implications

Carnivore attacks on livestock are the main cause of conflicts with human activities and thus it is fundamental to develop accurate PRMs to identify areas where carnivores could successfully kill livestock. Recent studies showed the usefulness of PRMs in supporting effective conservation and management actions at multiple stages of decision-making (i.e. from farm management to region-level policies; Miller, 2015). Thus, validation of PRMs is particularly relevant as they potentially represent a basis for management actions (Grimm and Railsback, 2005; Marucco and McIntire, 2010) and, given the high values of the validation statistics, we have confidence in our PRMs as decision support tools for implementing efforts to prevent livestock depredations.

Currently, while most of the studies applying PRMs pool attacks on different livestock species (when available), our results highlighted that drivers of predation risk are prey species-specific and thus different livestock species may require different management prescriptions to reduce such risk (Pimenta et al., 2018). Accordingly, we provided more accurate estimates of prey-specific predation risk models, S-PRMs than pooling together attacks to all livestock species, P-PRMs, avoiding biased estimation of predation risk.

Hence, we suggest developing P- and S-PRM in an hierarchical decision process in which the former could provide a general overview of predation risk patterns when data on individual prey attacks are scarce (e.g. during initial colonization of a carnivore in a given area), averaging predation risk among different prey-species, while the latter could provide much insight to estimate prey-specific predation risk when data on individual prey attacks are widely available. Otherwise, P-PRMs could be primarily used by managers and personnel of wildlife agencies/offices in developing general policies, while S-PRMs could be used at farm-level to identify livestock owners in high-priority areas (with high predation risk) where prevention tools and deterrents (e.g. electric fences, guarding dogs, predator-proof enclosures; Miller, 2015) should be applied.

However, even if the availability and the correct use of prevention tools (i.e., electric fences, guarding dogs) is a prominent way to limit attacks on livestock, they cannot be efficiently used in all environments (Milanesi et al., 2015) and thus, a time- and cost-efficient method for reducing livestock losses is to avoid grazing domestic animals in areas where they are highly vulnerable to carnivore attacks (Treves et al., 2011), such as in those identified by PRMs. Developing effective PRMs (on a prey-species basis), therefore, has the potential to greatly reduce these human-wildlife conflicts.

Final remarks

In conclusion, it is clear that collecting detailed data on conflicts between wolves and humans is fundamental to determine the risk factors predisposing farms to wolf depredation to enable more effective defence against wolf attacks (Kaartinen et al., 2009). Mitigating human-carnivore conflict requires identifying the landscape features that reduce livestock accessibility and risk of death (Miller, 2015). While a more standardized data collection (e.g. collecting information related to husbandry practices) could have improved our predictions, our results showed that P- and S-PRM models, in addition to predicting and mapping hotspots of livestock depredation, can offer further important information on how predation risk changes in relation to a specific livestock species (i.e. cattle, goats, sheep) and to the predictor variables considered. Thus, we believe that our approach could be applied worldwide on different predator-prey systems and landscapes to promote human-carnivore coexistence. ☞

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

- Figure S1** Map of accumulated percentage of grasslands and shrub-lands coverage.
- Table S2** Independent validations carried out 10 times with occurrences of depredation events on cattle and sheep not used to develop 12 species distribution models.