Animal 17 (2023) 100719



Contents lists available at ScienceDirect

Animal The international journal of animal biosciences

Planning for wolf-livestock coexistence: landscape context predicts livestock depredation risk in agricultural landscapes



Hannes J. König^a, Christian Kiffner^a, Katrin Kuhls^b, Sandra Uthes^{a,*}, Verena Harms^c, Ralf Wieland^a

^a Leibniz Centre for Agricultural Landscape Research (ZALF), Eberswalder Straße 84, D 15374 Müncheberg, Germany

^b Technical University of Applied Sciences Wildau, Hochschulring 1, Haus 16, D 15745 Wildau, Germany

^c Brandenburg State Office for the Environment (LfU), Seeburger Chaussee 2, OT Groß Glienicke, D 14476 Potsdam, Germany

ARTICLE INFO

Article history: Received 7 July 2022 Revised 13 January 2023 Accepted 17 January 2023 Available online 25 January 2023

Keywords: Decision support Grazing-based livestock Human-wildlife coexistence Machine learning Risk map

ABSTRACT

Extensive pastoral livestock systems in Central Europe provide multiple ecosystem services and support biodiversity in agricultural landscapes but their viability is challenged by livestock depredation (LD) associated with the recovery of wolf populations. Variation in the spatial distribution of LD depends on a suite of factors, most of which are unavailable at the appropriate scales. To assess if LD patterns can be predicted sufficiently with land use data alone at the scale of one federal state in Germany, we employed a machine-learning-supported resource selection approach. The model used LD monitoring data, and publicly available land use data to describe the landscape configuration at LD and control sites (resolution 4 km * 4 km). We used SHapley Additive exPlanations to assess the importance and effects of landscape configuration and cross-validation to evaluate the model performance. Our model predicted the spatial distribution of LD events with a mean accuracy of 74%. The most influential land use features included grassland, farmland and forest. The risk of livestock depredation was high if these three landscape features co-occurred with a specific proportion. A high share of grassland, combined with a moderate proportion of forest and farmland, increased LD risk. We then used the model to predict the LD risk in five regions; the resulting risk maps showed high congruence with observed LD events. While of correlative nature and lacking specific information on wolf and livestock distribution and husbandry practices, our pragmatic modelling approach can guide spatial prioritisation of damage prevention or mitigation practices to improve livestock-wolf coexistence in agricultural landscapes.

© 2023 The Author(s). Published by Elsevier B.V. on behalf of The Animal Consortium. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

Implications

The recolonisation of wolves in Central Europe poses severe challenges to grazing livestock farmers. To identify the role of land use context on the occurrence of livestock depredation by wolves and develop risk maps, we used a machine-learning-based modelling approach. The trained model predicted wolf attacks with an accuracy of over 70%, showing that landscape context plays a considerable role for the occurrence of livestock depredation. Using readily available data, our modelling approach delivers risk maps that can assist in planning livestock husbandry practices and can help authorities to allocate preventative and compensatory measures in different areas.

Introduction

Pastoral livestock systems in Europe are valued for providing a suite of ecosystem services and supporting biodiversity (Dean et al., 2021), but their persistence and viability are challenged by the recolonisation and expansion of legally protected carnivores (König et al., 2020). This is particularly the case for wolves (*Canis lupus*), the most widespread large carnivore in Central Europe (Chapron et al., 2014). Livestock depredation (**LD**) by wolves includes mostly sheep but also other ruminants, such as goat, cattle and farmed deer (Pimenta et al., 2017) and causes animal stress (Janczarek et al., 2021) as well as serious concerns, economic costs, and negative attitudes among livestock herders and parts of the general public (Arbieu et al., 2019).

How sustainable coexistence of wolves and pastoral livestock system can be achieved is part of an ongoing societal learning and negotiation process (Kiffner et al., 2019). Reducing LD is arguably-one of the most important tasks for facilitating a more sustainable coexistence of people, livestock and wolves

* Corresponding author. *E-mail address:* uthes@zalf.de (S. Uthes).

https://doi.org/10.1016/j.animal.2023.100719

1751-7311/© 2023 The Author(s). Published by Elsevier B.V. on behalf of The Animal Consortium. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

(Van Eeden et al., 2018). To achieve this overarching goal, identifying the effect of land use characteristics on LD could yield valuable information for livestock herders, politics and administration (Marucco and McIntire, 2010). Identifying such spatial associations could support a more focussed planning and implementation of prevention, support and compensatory measures, and thus ensure a more cost-effective use of public funds.

Predicting the LD risk by large carnivores would ideally be based on mechanistic models, which focus on the causality of input-output relationships. However, their use is constrained by the scarcity of relevant data at the appropriate scale. On the one hand, such models require information on the spatial distribution of wolves (Marucco and McIntire, 2010), which could itself be influenced by the distribution and density of wild prey (Janeiro-Otero et al., 2020). Wolves typically occupy large home range sizes (200 km² territory size on average in Germany, https://www.dbbw. de) and have a wide habitat niche (Mancinelli et al., 2018). For example, habitat suitability models for wolves in Europe suggest that wolves mostly prefer forests, meadows and wetlands, and typically avoid anthropogenic landscape features such as roads, settlements and cropland (Jedrzejewski et al., 2008). Even though wolves seem to avoid anthropogenic structures, they clearly use these landscape features occasionally. Several studies reported that wolves use bridges, roads, pipelines, and other linear features as travel corridors (e.g. Plaschke et al., 2021). On the other hand, LD is conditional on the availability of different livestock species and this precondition is ideally incorporated in risk models (Kuiper et al., 2021). Additional factors to be considered in LD risk modelling include the presence and type of practices to prevent depredation, as well as landscape features that mediate hunting success by large carnivores (Gable et al., 2021).

However, the full suite of these data is typically not available at scales useful for planning livestock prevention methods, e.g. for an entire state or landscape of several thousand square kilometres. For example, ruminant livestock management (especially of sheep) often combines keeping animals in fixed paddocks during the winter time, and rotational grazing with movable fencing during the vegetation period. Particularly in the latter case, the distribution of small livestock is dynamic and thus difficult to monitor and predict. Similarly, while wolves are monitored in Germany, movement data of wolves are only available for a few individuals. Currently, the most widely available data sources originate from monitoring programs that focus on LD events (Khorozyan and Heurich, 2022). This monitoring typically includes systematic recording of the location of the lethal interactions between wolves and livestock. Although the data collected through these efforts are not covering all the above-described information, they are standardised, regularly updated and have a large spatio-temporal coverage.

In this paper, we make use of these readily available LD monitoring data, link them to open-source spatial datasets, and employ state-of-the art machine-learning models to predict the LD risk. Our intention is not to improve or reveal a clear mechanistic understanding of this risk (Kuiper et al., 2021), as it will be unclear whether the identified associations between LD and specific landscape features are primarily due to wolf-related or livestockrelated variables.

However, our data-driven approach can be used to plough through the available data of inputs and outputs and predict the LD risk without focusing on the underlying causalities. This allows us to explore which land use configuration is currently facilitating LD by wolves across wider areas. Finally, we use our model to develop risk maps, which in turn can inform decisions on appropriate livestock management actions, and thus can contribute to a more sustainable coexistence between wolves and ruminant livestock husbandry in central Europe.

Material and methods

Case study region

As a case study area for our research (Fig. 1), we chose the federal state of Brandenburg, Germany with a total area of 29 654 km², half of which is used for agriculture (48.6%), followed by cover of forests (34.8%), settlements, roads, water bodies and other vegetation (combined 16.6%) (Statistik, 2022).

Brandenburg is located in the centre of Europe, and until the Middle Ages, the wolf population was relatively large and stable. With the expansion of deforestation and livestock husbandry, LD by wolves was considered a major problem resulting in organised wolf eradication programmes, which eventually led to the local extinction of wolves by the end of the 18th century (Ludwig, 2017). During the 19th and 20th centuries, reports suggest occasional occurrences of wolves immigrating to Germany from Eastern Europe. However, these wolves were persecuted and typically killed. Since Germany's reunification in 1990, the wolf is under legal protection (EEC, 1992). In 2000, wolves started reproducing in Saxony, and in 2007, the first territorial wolves in Brandenburg were documented (Reinhardt et al., 2019; Schade, 2010). Since their recolonisation, Brandenburg's wolf population grew quickly and expanded along a South-East – North-West gradient. while some parts of Brandenburg are not vet colonised (DBBW, 2020). Concurrent with the expansion of the wolf population, the frequency of LD events increased (LfU, 2021), and state authorities initiated systematic monitoring of LD events, provided funding for livestock protection (e.g. for fencing, livestock guarding dogs and operating costs) and damage compensation. In 2020, annual expenditures in Germany for herd protection amounted to €9.5 million, while compensation payments for livestock losses amounted to €0.8 million (DBBW, 2020).

The increase in LD events caused by wolves (Khorozyan and Heurich, 2022), however, poses new challenges for grazing livestock farms in Brandenburg (particularly shepherds and suckler cow holders), thus potentially undermining political objectives linked to the support and expansion of grazing-based livestock systems. Poor soils in most regions of Brandenburg, in combination with low precipitation (on average 550 mm per year), provide rather less advantageous conditions for crop production compared to other German regions. Hence, livestock husbandry, particularly of bovines, equines and sheep, is an important component of the regional farm structure, the most important farm types are specialist grazing livestock (37.8%), specialist field crop (36.9%) and mixed farms (20.7%).

Lack of profitability and altered marketing and consumption patterns since Germany's reunification in 1990 caused a considerable decrease in livestock numbers (particularly bovines) with a current average ruminant livestock density of 0.3 units per ha (own calculation based on Integrated Administration and Control System data from 2017). The observed decline of grazing livestock is threatening the maintenance of extensive grasslands and its associated biodiversity (MLUL, 2014).

Maintaining and restoring grassland biodiversity via supporting and expanding extensive grazing-based livestock systems is thus a key political priority in Brandenburg. Additional benefits are new farm income sources through meat production including novel value chains, such as direct marketing and improving sustainability through better linking meat production in rural and meat consumption in urban areas, and EU-wide promotion of the "Farm to Fork strategy". From a socioeconomic and circular economy perspective, the low supply of locally produced grazing-fed, and thus more sustainable, livestock is not desirable. For example, only ten percent of the organic meat consumed by residents of Germany's



Fig. 1. Map of the state of Brandenburg (bold grey lines), Germany, and its districts (grey lines), showing locations of confirmed livestock depredation by wolves. Each symbol indicates one livestock depredation event (n = 1 094) in the period from 2007 (the first appearance of wolves in Brandenburg) until April 2021. The five 50 km \times 50 km regions for which we created risk maps are indicated as numbered boxes. Region 1 includes the district Dahme-Spreewald and the southwestern part of the district Oder-Spree; region 2 is located in the district Potsdam-Mittelmark; region 3 coincides with the district Ostprignitz-Ruppin and a small part of Prignitz and Havelland; region 4 includes the district Uckermark, and region 5 is located in the district Märkisch-Oderland including the northern part of district Oder-Spree and a small part of southeastern Berlin.

capital Berlin, which is located in the centre of Brandenburg, is actually produced in Brandenburg, while the rest originates from other regions (Scholl, 2007). However, livestock owners, particularly shepherds, are questioning the future of their farming system given the extent of livestock losses due to wolves and a perceived lack of sufficient political action to address this issue (NABU, 2022).

As a consequence, the recovery of the wolf population and the desired expansion of grazing livestock systems are conflicting. In addition to other socio-ecological stressors, the impacts of LD may challenge the sustainability of this type of land use. Improved knowledge on where LD events are more likely to occur could help formulate more targeted measures and thus contribute to resolving this conflict and contribute to more sustainable wolf-livestock coexistence.

Modelling methodology

To predict the LD risk by wolves, we used a resource selection approach (i.e. comparing areas with LD and areas where no depredation occurred) and employed machine-learning algorithms (Wieland et al., 2021) to identify spatial correlates of the LD risk (for an overall illustration of the methodology, see Fig. 2).

This approach involves five main steps:

- Data provisioning and preparation for model training
- Model training: Training of a classification model (XGBoost) using LD events
- Evaluation of the training results using cross-validation (30% of the dataset)
- Determination of land use feature importance based on the (SHapley Additive explanations (**SHAP**)-Library (Lundberg and Lee, 2017)
- Prediction of model results for specific regions and visualisation through LD risk maps

Data provisioning and preparation

Geo-referenced monitoring data on livestock depredation events were provided by the Brandenburg State Office for the Environment. The dataset contained 1 100 LD events for the period October 2007 to April 2021. The dataset included information on the location (GPS coordinates), evidence for the cause of the event, and the livestock species. For our analyses, we only considered events where wolves were either confirmed or very likely to have caused the death of the livestock; additionally, we excluded six cases with missing or erroneous coordinates, resulting in 1 094 data points used for modelling. We obtained land use features from the OpenStreetMap (**OSM**) project. These data are freely available, have a high resolution (10 m * 10 m), and a high level of detail in terms of represented land use features. We defined the influence area of the landscape for an LD event with a cell size of 16 km² (4 km * 4 km). We chose this cell size to approximate the daily movement of wolves which average 16 km per day (Wrangham et al., 1993: 14.3 km/day; Bryce et al., 2022: 18 km/day). As our approach relates to an area extent, we took the square root of this average daily movement rate to define the cell size. The coordinates of the LD event determine the centre of the influence area. The definition of the influence area is a compromise: it should be large enough to include all important landscape elements, but not too large to include unnecessary elements.

The chosen modelling approach requires the presence and pseudo-absence sites for the training. The presence sites are the LD, and the pseudo-absence sites are sites without reported LD events. Approximately, the same number of presence and pseudo-absence sites should be provided for a training session.

The area of the state of Brandenburg (without the largest cities) is 28 922 km², thus containing 1 808 cells (28 922 km² divided by 16 km²). The cell size of 4 km * 4 km represents a compromise between important landscape elements and the bias caused by overlaps. We loaded 1 094 presence sites as images (png) from the OSM server. Subsequently, we randomly loaded pseudoabsence sites with a minimum (empirical) site centre distance of 2 500 m from each presence site. We chose this distance-based rule to minimise the likelihood that pseudo-absence sites coincide with LD events. Since we cannot exclude the possibility that some LD events were not reported, we refer to these sites as "pseudoabsence". For both, pseudo-absence and presence sites, we extracted the proportion of land use variables. Initially, we included all available land use features. However, during the course of modelling, we omitted some features (e.g. building or mining areas) as they were not influential. We based our final models on the proportion of ten features: (1) cropland and fallow crops: (2) grassland, meadow and paddock: (3) forest: (4) scrubland: (5) residential, industrial and commercial areas: (6) gardens. parks, cemeteries, and sports fields; (7) farmyard; (8) lake; (9) river; and (10) fallow areas.

We first created histograms showing the proportions of each land use feature for both positive and negative sites (Fig. 2). It is noticeable that the proportions of the various land use types differ substantially between the positive and negative example maps. In the positive examples, the embedding of field and grassland in the forest stands out, whereas on the negative ones, there appears to be no correlation and preponderance of specific land use features.

Model training, evaluation and validation

To compare land use characteristics of sites with LD to pseudoabsence sites, we employed XGBoost (https://xgboost.readthedocs. io/en/stable/index.html), a modern and powerful machinelearning algorithm suitable for solving classification tasks (Brownlee, 2016). Together with the scikit-learn library, which includes tools for data preprocessing tools and calculation of evaluation metrics, XGBoost can be used to train and validate a model.

For this purpose, absence and pseudo-absence sites were randomly divided into a training set (70%) and a validation set (30%). Based on cross-validation and using specific validation scores (**TP** = True positive; **FP** = False positive; **TN** = True negative; **FN** = False negative), we calculated three key metrics to assess model performance.

These were

Accuracy:
$$AC = (TP + TN)/(TP + TN + FP + FN)$$
.

Precision: PR = TP/(TP + FP). Recall: RC = TP/(TP + FN).

To illustrate the calculation of these parameters, assume the following exemplary confusion matrix of one model run (Table 1):

Applying the above formulae yields the following parameter values:

Accuracy: 73.8%. Precision: 74.5%. Recall: 73.6%.

Accuracy is the most important parameter. Precision shows the influence of the FP results on the classification, and Recall describes the influence of the FN results on the classification. A decrease in FP is accompanied by an increase in FN scores above a certain training level.

Similar to other machine-learning algorithms, XGBoost models are complex models, which are different to interpret without additional tools. We use here the SHAP software (https://github.com/ slundberg/shap), developed on the basis of cooperative game theory (Lundberg and Lee, 2017), which allows for the quantification of the feature importance in the training data.

Results

We used the waterfall visualisation, as part of the SHAP library, to analyse the effect of each feature on the rating of the sites. The waterfall visualisation is read from bottom to top. The blue arrows point towards no LD risk, while the red arrows point towards LD risk. If the result (top) is >0, LD risk is assumed to be high; if it is <0, the LD risk is assumed to be low. Fig. 3 illustrates an example for a map with (Fig. 3A) and without LD (Fig. 3B).

The trained model was applied to predict the LD risk in five 50 km \times 50 km areas in Brandenburg (see Fig. 1). Region 1 includes the district Dahme-Spreewald and the southwestern part of the district Oder-Spree; region 2 covers the district Potsdam-Mittelmark; region 3 is located in the district Ostprignitz-Ruppin and a small part of Prignitz and Havelland; region 4 includes district Uckermark; and region 5 covers the district Märkisch-Oderland including the northern part of district Oder-Spree and a small part of southeastern Berlin (Fig. 1). These five areas represent different land use configurations and disparate wolf recolonisation histories.

We projected the predictions into high-resolution maps of these 50 km \times 50 km areas for visualisation. To contrast the model predictions with observed data, we also plotted the recorded locations of LD events.

Fig. 4 summarises the mean impact of the included land use parameters on the model output in descending order. Farmland, grassland and forests had the highest impact on the magnitude of the model output (>0.38), while lakes, residential areas and farmstead-related features (farmyard, garden) as well as scrub and fallow land had lower impacts (<0.2) (Fig. 4).

To evaluate the importance of land use features on the model output magnitude, while also showing the original feature values, SHAP uses a beeswarm summary plot (Fig. 5). Each instance of the given model is represented by a single dot on each feature. The x position of the dot is determined by the SHAP value of that feature, and dots "pile up" along each feature row to show density. Colour is used to display the original value of a feature, with red dots indicating high feature values (e.g. a high grassland share), and blue dots indicating low feature values (e.g. a low grassland share). In our case, grassland, farmland and forest are the most important

Animal 17 (2023) 100719



Fig. 2. Graphical overview of the methodology to model livestock depredation risk due to wolves in Brandenburg. The XGBoost algorithm compares the proportion of ten main land use features between livestock depredation areas (three example sites out of the 1 094 cases in the top part) and randomly selected areas without livestock depredation cases (three example sites in the bottom part). Land use features are colour-coded as follows: yellow – farmland and fallow crops, dark green – forest, light green – meadows and grassland, grey – residential, industrial and commercial areas, blue – lake, lightblue – river, brown – farmyard.

Table 1

Exemplary confusion matrix of one model run for predicting depredation risk by wolves.

Item	Predicted Positive (PP)	Predicted Negative (PN)
Actual Positive (P)	True positive (TP) 245	False negative (FN) 88
Actual Negative (N)	False positive (FP) 84	True negative (TN) 240

features and high grassland values (red) are more likely associated with LD events.

We tested dispersion of the key metrics of the models using the feature set described in Fig. 2 for 30 runs (Table 2). Accuracy values ranged from 0.70 to 0.79, with a mean value of 0.74. Based on the statistics of key metrics as well as of the SHAP analysis, we chose one model for validation in the five sub-regions of Brandenburg

H.J. König, C. Kiffner, K. Kuhls et al.

Animal 17 (2023) 100719



А



В

Fig. 3. Waterfall graph from SHapley Additive exPlanations (SHAP), visualising the importance of land use features on the model for (A) selected positive sites (i.e. maps with recorded livestock depredation) and (B) negative sites (i.e. sites without reported livestock depredation). The values beside the feature names are the proportions of each feature. The size of the region shown in the sites is 4 km * 4 km.



Fig. 4. Average impact of the ten included land use features on a model to predict livestock depredation by wolves in Brandenburg, Germany as inferred by the SHapley Additive exPlanations (SHAP) approach.



Fig. 5. Feature importance of the included land use parameters (as inferred by the SHapley Additive exPlanations (SHAP) approach) for the model to predict livestock depredation by wolves in Brandenburg, Germany. The beeswarm plot shows the impact of each feature including its values.

Table 2

Summary statistics of models predicting depredation risk by wolves in Brandenburg, Germany; statistics were averaged over 30 model runs; size of data (number of livestock predation points): n = 1 094.

Item	Accuracy	Precision	Recall
Number of runs	30	30	30
Mean	0.74	0.72	0.78
SD	0.02	0.04	0.03
Min	0.7	0.65	0.72
Max	0.79	0.79	0.83

(Fig. 1). The validation scores of the trained model were as follows: accuracy = 75.8, precision = 74.2 and recall = 77.7.

Results of the fifth step (prediction), in which we applied the trained model to the five sub-regions in Brandenburg (Fig. 1), are shown in Fig. 6. The likelihood of LD is shown on the left side in a raster of 1 km * 1 km (Fig. 6) on a scale from 0 (no risk) to 1 (highest risk).

The underlying OSM map of each area is shown in the central panel. On the right panel, this map is overlaid with a heatmap (bicubic interpolation from 1 km * 1 km to 30 m * 30 m). Light (dark) areas indicate a high (low) LD risk. LD events are marked as blue dots (middle and right panel). Simulation and observed data showed a high degree of correspondence, thus confirming the potential usefulness of our approach for the prediction of the LD risk.

Discussion

Interpreting land use configuration – livestock depredation associations

Given the suite of factors that can potentially influence LD by wolves, the central question of the presented work was whether there are patterns in these events that can be explained exclusively by the surrounding land use features. Our study showed that the LD risk by wolves was strongly associated with the cooccurrence of distinct land use proportions of grassland, forest and farmland. The identified strong influence of forest is in line with expectations, as wolves prefer forests as key habitat (e.g. Jędrzejewski et al., 2008); similarly, the presence of grasslands and farmsteads in a landscape patch implies a higher availability of livestock as potential prey. Consequently, LD appears to primarily occur at the landscape interface, where suitable wolf habitat borders or overlaps with areas where livestock is kept. These results suggest that the occurrence of LD is driven by land uses that influence both resource selection decisions by wolves (i.e. positive association with forests) as well as the distribution of livestock (i.e. grassland and farmland). This aligns well with research on other humanwildlife conflict scenarios, suggesting that damage occurrence is fundamentally influenced by principles of resource selection decisions by both wildlife and humans (Bautista et al., 2021).

However, a more nuanced, functional interpretation of the identified co-occurrence is not possible given the interrelatedness of livestock presence and wolf habitat use, which cannot be disentangled with the currently used data. Considering that predictive ability does not imply causality, the importance of grasslands and farmland in our models does necessarily suggest that wolves have a tendency to hunt in the proximity of these land uses. In fact, farmland or human infrastructure such as buildings are generally avoided by wolves, as more detailed studies on wolf movement have clearly demonstrated (e.g. Mancinelli et al., 2019).

Simulation results for the five sub-areas confirmed the strong impact of the co-occurrence of these three key land use variables. In the region "Uckermark" (region 4), LD was less likely to occur. This region is dominated by large agricultural fields and features little forest cover and little grassland. Therefore, from its structural characteristics, it appears less suitable for animal husbandry. From the wolf's perspective, the landscape appears also less suitable due to the relative scarcity of forest cover (e.g. Jędrzejewski et al., 2008). In tandem, this landscape configuration results in a comparatively low LD risk. In contrast, region 3 ("Havelland") is a diverse, structural rich landscape with a large share of grassland and forests. Consequently, both observed and simulated data indicate high depredation risk (Fig. 6).

In sum, the modelling results suggest that LD is more likely to occur in diverse landscapes with a minimum of three cooccurring landscape elements (forest, grassland, and farmsteads),



Fig. 6. Models of livestock depredation risk as applied for regions 1–5 (top to bottom) of 50 km \times 50 km (Brandenburg state, Germany. Left panel: yellow (blue) areas are areas with high (low) livestock depredation risk. Middle panel: OpenStreetMap (OSM)-map of each region. Right panel: simulation results shown as heatmaps overlaid with the OSM map. Light areas mark regions of high livestock depredation risk. Livestock depredation events are marked by blue dots (middle and right panel).

transboundary areas and smaller fields, while in croplanddominated landscapes with little grassland and forest cover, depredation events are unlikely to occur.

Methodological aspects

Our approach used only a few, yet readily available input data and achieved a moderate accuracy for predicting LD by wolves. However, the obtained accuracy also means that every fourth prediction is incorrect. Thus, landscape features are important, but other factors which could not be considered here due to the mentioned data availability constraints are perhaps required for predicting depredation by wolves. The key advantages of the presented methodology are that it makes use of available data, and it is exclusively based on machine learning without requiring the involvement of experts or other potentially costly work steps. It can be efficiently applied and transferred to other regions if training data (i.e. systematically collected LD data) are available.

Moreover, the results can be used in many ways. Not an obvious, but in our eyes, important use is the analysis of waterfall diagrams. In Fig. 3A, the model shows an LD site. The landscape elements (grassland, farmland, forest, river) add up to values >0. It is interesting to note that the first three of them occupy a large proportion of the area, while the (positive) river accounts only for a small proportion of the area. The landscape elements (fallow and garden) add up to values <0. However, their area shares are 0, i.e. their absence has a negative effect. Fig. 3B, shows a pseudoabsence site. Here, the small area of forest has a negative effect on LD risk. These different effects show that the model can reproduce nonlinear relationships. This nonlinear relationship is also shown in Fig. 5 with respect to the training data. The waterfall diagrams, which can be created for any location, are suitable for relating the model output to the expert's expectations. This allows modellers to check and possibly correct their ideas against the data.

A key prerequisite of a good model is a solid database of livestock predation events. Monitoring livestock predation events has considerably improved over the years and represents a robust database for the analyses presented in this paper. The available monitoring protocol, however, is currently wolf-centred, e.g. it does not, or not systematically, include additional variables that might affect LD, such as herd size and composition or the type and quality, of livestock protection and husbandry measures applied by herders. Data on fine-scaled wolf and livestock distribution are also not available at the scale of a federal state.

Despite the lack of such data, our model provided reasonable prediction accuracy. The achieved accuracy of 74% is likely sufficient for the simulation shown, yet not ideal. Possibly, achieving a higher accuracy is affected by the choice of pseudo-absence data, which were generated by a random selection process. Especially since the wolf population in Brandenburg was still expanding during the time period of the study (DBBW, 2020), some of the pseudo-unaffected sites would in reality be risky. In addition to accuracy, precision and recall should also be considered. Precision also includes the false positives and recall the false negatives. Looking at both precision (72%) and recall (78%) indicates that there are more false positives than false negatives (Beattie et al., 2020). Thus, more risky areas are falsely identified as low-risk areas than low-risk areas are falsely predicted as high risk. Again, this can be explained by the expanding wolf population, and the fact that not all areas of the state had been occupied by wolves during the entire study period.

A possible source of bias is that land use may change over time, yet we used maps from a single time step, which may not adequately describe the land use at each time step. In particular, this applies to earlier recorded depredation events. Potentially, this could have contributed to a lower accuracy, yet the influence of this factor is likely to be small.

The inclusion of additional factors in our model, such as more detailed data regarding livestock densities (Kuiper et al., 2021), e.g. from the Integrated Administration and Control System (Uthes et al., 2020), data on wolf distribution or proxy data for key wolf habitat such as protected areas or military training areas (Reinhardt et al., 2019), barriers limiting wolf expansion such as motorways without green bridges, or the type of forest and wildlife management, could further improve the accuracy of the model. For example, one could assume that the intensity of hunting activities differs between privately and state-owned forests, resulting in heterogeneous wild ungulate densities. In turn, changes in ungulate densities, the main prey for wolves in Germany, could influence LD patterns.

However, these additional data sources are either not available at all or more difficult to obtain compared to the OSM maps used in our approach. Including them in our model would cause higher costs and divert from our initial intention to base our modelling on publicly available data.

Use for decision support

Our model produced risk maps illustrating the LD risk based on available land use parameters, a useful tool for the rapid classification of areas with high and low depredation risk. This information can assist zonation-planning projects and help authorities decide on the degree of preventative and compensatory measures required in different areas. For example, livestock herders with permanent grazing areas located in high-risk landscapes (dark areas in Fig. 6) could be encouraged to adopt more effective prevention measures (e.g. electric fence and livestock guarding dogs) while in low-risk areas (white areas in Fig. 6), less cost-intensive prevention measures (e.g. electric fence only) could suffice. Similarly, livestock herders could be encouraged to move livestock, especially mobile small stock such as sheep, to suitable and available pastures in low-risk areas. Such evidence-based, spatiotemporal avoidance by livestock herders has been effective in reducing carnivore depredation on livestock in other parts of the world (Melzheimer et al., 2020). Coexisting with large carnivores requires substantial learning and adaptations among key stakeholders (König et al., 2021) and an integrated perspective rooted in a socio-ecological-systems understanding and aimed at winwin solutions (Gordon, 2018). To overcome the implementation gap between knowledge of effective prevention methods and relevant action, dedicated farm coaching workshops in areas with high LD risk may be an effective means to increase the adoption of effective livestock prevention methods.

Ethics approval

Not applicable.

Data and model availability statement

None of the data or models were deposited in an official repository. The data are not publicly available as they include sensitive information.

Author ORCIDs

Hannes J. König: https://orcid.org/0000-0002-4980-7388. Christian Kiffner: https://orcid.org/0000-0002-7475-9023. Katrin Kuhls: https://orcid.org/0000-0003-4168-8684. Sandra Uthes: https://orcid.org/0000-0002-2527-7052. Verena Harms: no ORCID. Ralf Wieland: https://orcid.org/0000-0002-2278-610X.

Author contributions

Hannes J. König: Conceptualisation, Investigation, Writing, Supervision, Project administration, Funding acquisition.

Christian Kiffner: Conceptualisation, Writing, Supervision.

Katrin Kuhls: Conceptualisation, Methodology, Writing, Visualisation.

Sandra Uthes: Conceptualisation, Investigation, Writing.

Verena Harms: Investigation, Resources.

Ralf Wieland: Conceptualisation, Methodology, Data Curation, Writing, Supervision, Visualisation.

Declaration of interest

None.

Acknowledgements

None.

Financial support statement

This work was supported by the Marianne and Dr. Fritz Walter Fischer-Stiftung for the Junior Research Group "LandSTRAT: Landnutzungskonflikte zwischen Menschen und Wildtieren auf landwirtschaftlich genutzten Flächen in UNESCO-Biosphärenreservaten" (Recipient: Dr. Hannes J. König).

The publication of this article was funded by the Open Access Fund of the Leibniz Association.

References

- Arbieu, U., Mehring, M., Bunnefeld, N., Kaczensky, P., Reinhardt, I., Ansorge, H., Böhning-Gaese, K., Glikman, J.A., Kluth, G., Nowak, C., 2019. Attitudes towards returning wolves (Canis lupus) in Germany: Exposure, information sources and trust matter. Biological Conservation 234, 202–210.
- Bautista, C., Revilla, E., Berezowska-Cnota, T., Fernández, N., Naves, J., Selva, N., 2021. Spatial ecology of conflicts: unravelling patterns of wildlife damage at multiple scales. Proceedings of the Royal Society B 288, 20211394.
- Beattie, K., Olson, E., Kissui, B., Kirschbaum, A., Kiffner, C., 2020. Predicting livestock depredation risk by African lions (Panthera leo) in a multi-use area of northern Tanzania. European Journal of Wildlife Research 66, 1–14.
- Brownlee, J., 2016. XGBoost With python: Gradient boosted trees with XGBoost and scikit-learn. Machine Learning Mastery. Pty. Ltd., Vermut Victoria, Australia.
- Bryce, C.M., Dunford, C.E., Pagano, A.M., Wang, Y., Borg, B.L., Arthur, S.M., Williams, T.M., 2022. Environmental correlates of activity and energetics in a wideranging social carnivore. Animal Biotelemetry 10, 1.
- Chapron, G., Kaczensky, P., Linnell, J.D., Von Arx, M., Huber, D., Andrén, H., López-Bao, J.V., Adamec, M., Álvares, F., Anders, O., 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346, 1517–1519.
 DBBW, 2020. Wölfe in Deutschland: Statusbericht 2019/2020. Dokumentations-
- DBBW, 2020. Wölfe in Deutschland: Statusbericht 2019/2020. Dokumentationsund Beratungsstelle des Bundes zum Thema Wolf (DBBW). Retrieved on 12 January 2023 from https://www.dbb-wolf.de/mehr/literatur-download/ statusberichte?file=files/publisher/downloads/Statusbericht%20_W%C3%B6lfe% 20in%20DE%2020192020_DBBW_20201217.pdf.
- Dean, G., Rivera-Ferre, M.G., Rosas-Casals, M., Lopez-i-Gelats, F., 2021. Nature's contribution to people as a framework for examining socioecological systems: The case of pastoral systems. Ecosystem Services 49, 101265.
- EEC, 1992. Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. Retrieved on 12 January 2023 from https://eur-lex.europa.eu/legal-content/EN/TXT/HTML/?uri=CELEX: 31992L0043&from=DE.
- Gable, T.D., Homkes, A.T., Johnson-Bice, S.M., Windels, S.K., Bump, J.K., 2021. Wolves choose ambushing locations to counter and capitalize on the sensory abilities of their prey. Behavioral Ecology 32, 339–348.

Gordon, I.J., 2018. Review: Livestock production increasingly influences wildlife across the globe. Animal 12, s372–s382.

Janczarek, I., Stachurska, A., Kędzierski, W., Pawlak, E.W., Wilk, I., Zyglewska, K., Paszkowska, A., Ryżak, M., Wiśniewska, A., 2021. Heart rate variability in Konik and purebred Arabian horses in response to different predator vocalisations. Animal 15, 100045.

- Janeiro-Otero, A., Newsome, T.M., Van Eeden, L.M., Ripple, W.J., Dormann, C.F., 2020. Grey wolf (Canis lupus) predation on livestock in relation to prey availability. Biological conservation 243, 108433.
- Jędrzejewski, W., Jędrzejewska, B., Zawadzka, B., Borowik, T., Nowak, S., Mysłajek, R., 2008. Habitat suitability model for Polish wolves based on long-term national census. Animal Conservation 11, 377–390.
- Khorozyan, I., Heurich, M., 2022. Large-Scale Sheep Losses to Wolves (Canis lupus) in Germany Are Related to the Expansion of the Wolf Population but Not to Increasing Wolf Numbers. Frontiers in Ecology and Evolution 10, 78917.
- Kiffner, C., Chapron, G., König, H.J., 2019. Germany's wolves in the crosshairs. Science 365, 1089.
- König, H.J., Kiffner, C., Kramer-Schadt, S., Fürst, C., Keuling, O., Ford, A.T., 2020. Human-wildlife coexistence in a changing world. Conservation Biology 34, 786–794.
- König, H.J., Ceauşu, S., Reed, M., Kendall, H., Hemminger, K., Reinke, H., Ostermann-Miyashita, E.F., Wenz, E., Eufemia, L., Hermanns, T., 2021. Integrated framework for stakeholder participation: Methods and tools for identifying and addressing human–wildlife conflicts. Conservation Science and Practice 3, e399.
- Kuiper, T., Loveridge, A.J., Macdonald, D.W., 2021. Robust mapping of humanwildlife conflict: controlling for livestock distribution in carnivore depredation models. Animal Conservation 25, 195–207.
- LfU, 2021. Gemeldete Nutztierschäden und Rissstatistik im Land Brandenburg. Retrieved on 12 January 2023 from https://lfu.brandenburg.de/lfu/de/ aufgaben/natur/tiere-und-pflanzen/saeugetiere/woelfe-in-brandenburg/ schadensmanagement/gemeldete-nutztierschaeden-und-rissstatistik/.
- Ludwig, V., 2017. Geschichte Wolf und Mensch. Retrieved on 12 January 2023 from https://web.archive.org/web/20171215032504/http://www.wolf-sachsen.de/ de/allgemeines-woelfe-und-menschen.
- Lundberg, S.M., Lee, S.-I., 2017. A unified approach to interpreting model predictions. In: Proceedings of the 30th international conference on neural information processing systems, 4–9 December 2017, Long Beach, CA, USA, pp. 4768–4777.
- Mancinelli, S., Boitani, L., Ciucci, P., 2018. Determinants of home range size and space use patterns in a protected wolf (*Canis lupus*) population in the central Apennines, Italy. Canadian Journal of Zoology 96, 828–838.
- Mancinelli, S., Falco, M., Boitani, L., Ciucci, P., 2019. Social, behavioural and temporal components of wolf (*Canis lupus*) responses to anthropogenic landscape features in the central Apennines, Italy. Journal of Zoology 309, 114–124.
- Marucco, F., McIntire, E., 2010. Predicting spatio-temporal recolonization of large carnivore populations and livestock depredation risk: wolves in the Italian Alps. Journal of Applied Ecology 47, 789–798.
- Melzheimer, J., Heinrich, S.K., Wasiolka, B., Mueller, R., Thalwitzer, S., Palmegiani, I., Weigold, A., Portas, R., Roeder, R., Krofel, M., 2020. Communication hubs of an asocial cat are the source of a human-carnivore conflict and key to its solution. Proc. Natl. Acad. Sci. 117, 33325–33333.
- MLUL, 2014. Maßnahmenprogramm Biologische Vielfalt Brandenburg. Retrieved on 12 January from https://mluk.brandenburg.de/sixcms/media.php/ 9/masznahmenprogramm_biovielfalt.pdf.
- NABU, 2022. Weidetierhalter sind Partner des Naturschutzes: Mit der Rückkehr des Wolfes muss der Schutz ihrer Tiere erhöht werden. Die bisherige Förderung reicht nicht aus! Retrieved on 12 January from https://brandenburg.nabu.de/tiere-und-pflanzen/saeugetiere/wolf/herdenschutz/index.html.
- Pimenta, V., Barroso, I., Boitani, L., Beja, P., 2017. Wolf predation on cattle in Portugal: Assessing the effects of husbandry systems. Biological Conservation 207, 17–26.
- Plaschke, M., Bhardwaj, M., König, H.J., Wenz, E., Dobiáš, K., Ford, A.T., 2021. Green bridges in a re-colonizing landscape: Wolves (Canis lupus) in Brandenburg. Germany. Conservation Science and Practice 3, e364.
- Reinhardt, I., Kluth, G., Nowak, C., Szentiks, C.A., Krone, O., Ansorge, H., Mueller, T., 2019. Military training areas facilitate the recolonization of wolves in Germany. Conservation Letters 12, e12635.
- Schade, J.-U., 2010. Wölfe in Brandenburg: eine Spurensuche im märkischen Sand. Ministerium für Umwelt, Gesundheit und Verbraucherschutz des Landes Brandenburgs. Retrieved on 12 January 2023 from https://mluk.brandenburg. de/sixcms/media.php/9/woelfe.pdf.
- Scholl, G., 2007. Regionale Bio-Vermarktung in Berlin-Brandenburg: Potenziale und Perspektiven im selbständigen Lebensmitteleinzelhandel (SEH). Institut für ökologische Wirtschaftsforschung (IÖW) gGmbH. Retrieved on 12 January 2023 from https://orgprints.org/id/eprint/11107/4/11107-040E046-ioew-scholl-2007-broschuere.pdf.
- Statistik, 2022. Flächennutzung. Retrieved on 12 January 2023 from https://www. statistik-berlin-brandenburg.de/flaechennutzung.
- Uthes, S., Kelly, E., König, H.J., 2020. Farm-level indicators for crop and landscape diversity derived from agricultural beneficiaries data. Ecological Indicators 108, 105725.
- Van Eeden, L.M., Crowther, M.S., Dickman, C.R., Macdonald, D.W., Ripple, W.J., Ritchie, E.G., Newsome, T.M., 2018. Managing conflict between large carnivores and livestock. Conservation Biology 32, 26–34.
- Wieland, R., Kuhls, K., Lentz, H.H., Conraths, F., Kampen, H., Werner, D., 2021. Combined climate and regional mosquito habitat model based on machine learning. Ecological Modelling 452, 109594.
- Wrangham, R.W., Gittleman, J.L., Chapman, C.A., 1993. Constraints on group size in primates and carnivores: population density and day-range as assays of exploitation competition. Behavioral Ecology and Sociobiology 32, 199–209.