European Journal of Wildlife Research (2024) 70:52
https://doi.org/10.1007/s10344-024-01804-4

RESEARCH

Estimating kill intervals for a specific prey species using location clusters from GPS-collared Eurasian lynx (*Lynx lynx*)

Kristina Vogt[1] · **Tobias Roth**[2] · **Sven Signer**[1] · **Christian Simon Willisch**[3] · **Valentin Amrhein**[2]

Received: 4 July 2023 / Revised: 19 April 2024 / Accepted: 25 April 2024

Abstract

An increasing number of GPS telemetry studies have helped to gain important insights into predator-prey relationships in recent years. However, considerable time and effort is needed to evaluate whether GPS location clusters (GLCs) reflect predation events. To reduce field effort, predictive models are being developed to calculate predator kill intervals, but few studies have attempted to do this for a specific species of prey. Between 2013 and 2018, we studied predation by 13 GPS-collared Eurasian lynx (*Lynx lynx*) on Alpine chamois (*Rupicapra rupicapra*) in the northwestern Swiss Alps. Our objectives were to predict the total number of killed chamois, including potential kills in unchecked GLCs, and to evaluate if model predictions were sufficiently accurate. We built a set of generalized linear models (GLM) predicting the occurrence of GLCs containing lynx-killed chamois (1) versus GLCs containing other prey types or no prey (0) and compared their predictive performance by means of k-fold cross-validation. We found that model performance was very similar for all candidate models, with the full model yielding the best cross-validation result (accuracy = 0.83, sensitivity = 0.43, specificity = 0.94). Female lynx killed on average one chamois every 11.9 days (10.6–13.0 days, 95% CI); male lynx killed one chamois every 7.2 days (6.7–7.6 days, 95% CI). Our model showed high specificity for detecting non-chamois GLCs, but sensitivity for detection of GLCs with actual chamois kills was low. We conclude that the sensitivity of the models should be further improved, but the results can be sufficient for practical application. Predictive modelling approaches do not replace extensive fieldwork but require large sets of field data, high individual variability and thorough knowledge of a predator's ecology and prey community. Our approach may provide useful results for binary classifications in rather simple predator-prey systems, but extrapolations from one study system to another might be difficult.

Keywords Ground-truthing · Classification accuracy · Ungulate · Capreolus capreolus · Kill rate

Introduction

Studies on predator kill rates help evaluate the impact of predation on populations of prey species (e.g., Breitenmoser et al. 2010; Vucetich et al. 2011). In recent decades, technical advances in GPS telemetry have substantially improved quantification of predation (Blecha and Alldredge 2015). However, considerable time and effort must be invested to ground-truth GPS location clusters in the field; that is, to search for possible prey remains and to evaluate whether an observed cluster of GPS locations reflects a predation event. Many researchers have, therefore, developed predictive models to supplement field work and thus to reduce time and resources required to obtain reliable kill rate estimates. Predictive models of predation events have been developed, for example, for leopards (*Panthera pardus*; Martins et al. 2011; Pitman et al. 2012), cougars (*Puma concolor*; Blecha and Alldredge 2015; Knopff et al. 2009), wolves (*Canis lupus*; Webb et al.2008, Irvine et al. 2022), bobcats (*Lynx rufus*; Svoboda et al. 2013), and Eurasian lynx (*Lynx lynx*; Krofel et al.2013). Large felids are especially well-suited for predation studies using GPS telemetry because they are usually solitary and tend to return to their prey items for several days until they have completely consumed the carcass,

✉ Valentin Amrhein
v.amrhein@unibas.ch

[1] KORA, Carnivore Ecology and Wildlife Management, Muri bei Bern 3074, Switzerland

[2] Department of Environmental Sciences, University of Basel, Basel 4051, Switzerland

[3] School of Agricultural, Forest and Food Sciences, Bern University of Applied Sciences, Zollikofen 3052, Switzerland

thereby generating GPS location clusters (hereafter GLCs; Merrill et al. 2010). Model algorithms can be designed to distinguish (1) kill sites from non-kill sites and (2) kill sites of different prey types. Generally, model algorithms designed to identify kill sites are more efficient in predicting kill sites of large prey than of small prey (Elbroch et al. 2018; Knopff et al. 2009; Svoboda et al. 2013; Webb et al.2008; Oliveira et al. 2022). An important factor allowing for discrimination between kill sites and non-kill sites in predictive models is GLC duration (i.e., time elapsed between the first and last location of a GLC; Irvine et al. 2022). While large prey items usually result in GLCs of a longer duration ($>$24 h), smaller prey items are associated with shorter GLC duration and are more difficult to distinguish from GLCs caused by other types of behaviour (e.g., resting sites; Oliveira et al. 2022).

Prediction of a specific prey species from GPS location cluster data has so far rarely been attempted and typically showed low classification accuracy for less common prey species (e.g., Knopff et al. 2009). Especially in complex predator-prey systems with a large predator guild and a wide diversity of prey species, prediction of prey species for individual kill sites may in fact be impossible. However, for management and conservation purposes, kill rates might need to be specific for a particular prey species, for example when the predation impact on one particular prey species is of special interest (e.g., for conservation of endangered prey species or management of hunted prey species).

The predator-prey system of the Eurasian lynx, the roe deer (*Capreolus capreolus*), and the Alpine chamois (*Rupicapra rupicapra*) in the Swiss Alps is suitable for studying the feasibility of prey species prediction from GLC data because the two prey species in this system differ in their habitat selection (Morellet et al. 2011; Nesti et al. 2010). Lynx return to their prey repeatedly, and GPS location clusters can be used to find kill sites (even of smaller prey such as neonate ungulates), as has been shown in several previous studies (Krofel et al. 2013; Vogt et al. 2018). Moreover, predation impact of lynx on ungulate species is often of strong interest for wildlife managers and conservationists, as conflicts with hunters over prey species are one reason for illegal killings of lynx, a major threat to lynx conservation in many populations (von Arx et al. 2021). In Switzerland, the Alpine chamois currently receives special attention, since both population sizes and hunting bags have been declining in several areas during the last decades (Breitenmoser et al. 2016). Culling of Eurasian lynx is a possible management measure that could be applied by responsible agencies to increase chamois numbers (BAFU 2016). However, the Alpine lynx population is also still small and isolated and considered endangered according to IUCN Red List criteria (von Arx et al. 2021).

Here, we studied predation of GPS-collared lynx on Alpine chamois in the northwestern Swiss Alps. Previous studies on Eurasian lynx have attempted to distinguish between large and small prey but not between different ungulate prey species (e.g., Oliveira et al. 2022). The objectives of our study were (1) to predict the total number of chamois killed by lynx, including potential kills in GLCs that could not be ground-truthed due to extreme steepness or risk of avalanches, and (2) to evaluate if our model predictions were accurate enough for practical use by wildlife managers.

Methods

Study system

The study area covered approximately 1,300 km² and was mainly situated in the northwestern Swiss Alps, in the Canton of Bern, and comprised the main ridges and valleys from the Stockhorn to the Niesen mountain chains, as well as parts of the central Swiss Alps (Augstmatthorn mountain chain; Fig. 1). The landscape is composed of a mixture of forests, grazed pastures, and rocky ground, interspersed with human settlements. The area is intensively used for tourism year-round. Elevations range from 600 m a.s.l. up to 3,050 m a.s.l. at the highest peak.

The Eurasian lynx is the only widespread large carnivore in the study area, with an estimated density of 3.16 (2.54–3.78, 95% compatibility interval; Amrhein and Greenland 2022) independent lynx (i.e., subadults and adults) per 100 km^2 of suitable habitat (suitable habitat covers 95% of total study area; Zimmermann et al. 2018). The main prey of the lynx in the area are roe deer and Alpine chamois; alternative prey species include red fox (*Vulpes vulpes*), badger (*Meles meles*), European brown hare (*Lepus europaeus*), mountain hare (*Lepus timidus*), Alpine marmot (*Marmota marmota*), black grouse (*Tetrao tetrix*), and hazel grouse (*Tetrastes bonasia*; Molinari-Jobin et al. 2002; Vogt et al. 2018). Red deer (*Cervus elaphus*) began recolonizing the area in the 1970s and still occur in low densities in most parts of the study area. Alpine ibex (*Capra ibex*) occurs only locally. The area is sporadically visited by vagrant wild boar (*Sus scrofa*) and solitary wolves (*Canis lupus*), but no resident populations of these species occur. The vertebrate species most commonly observed scavenging at lynx kill sites include red foxes, common raven (*Corvus corax*), carrion crow (*Corvus corone*), common buzzard (*Buteo buteo*), and golden eagle (*Aquila chrysaetos*).

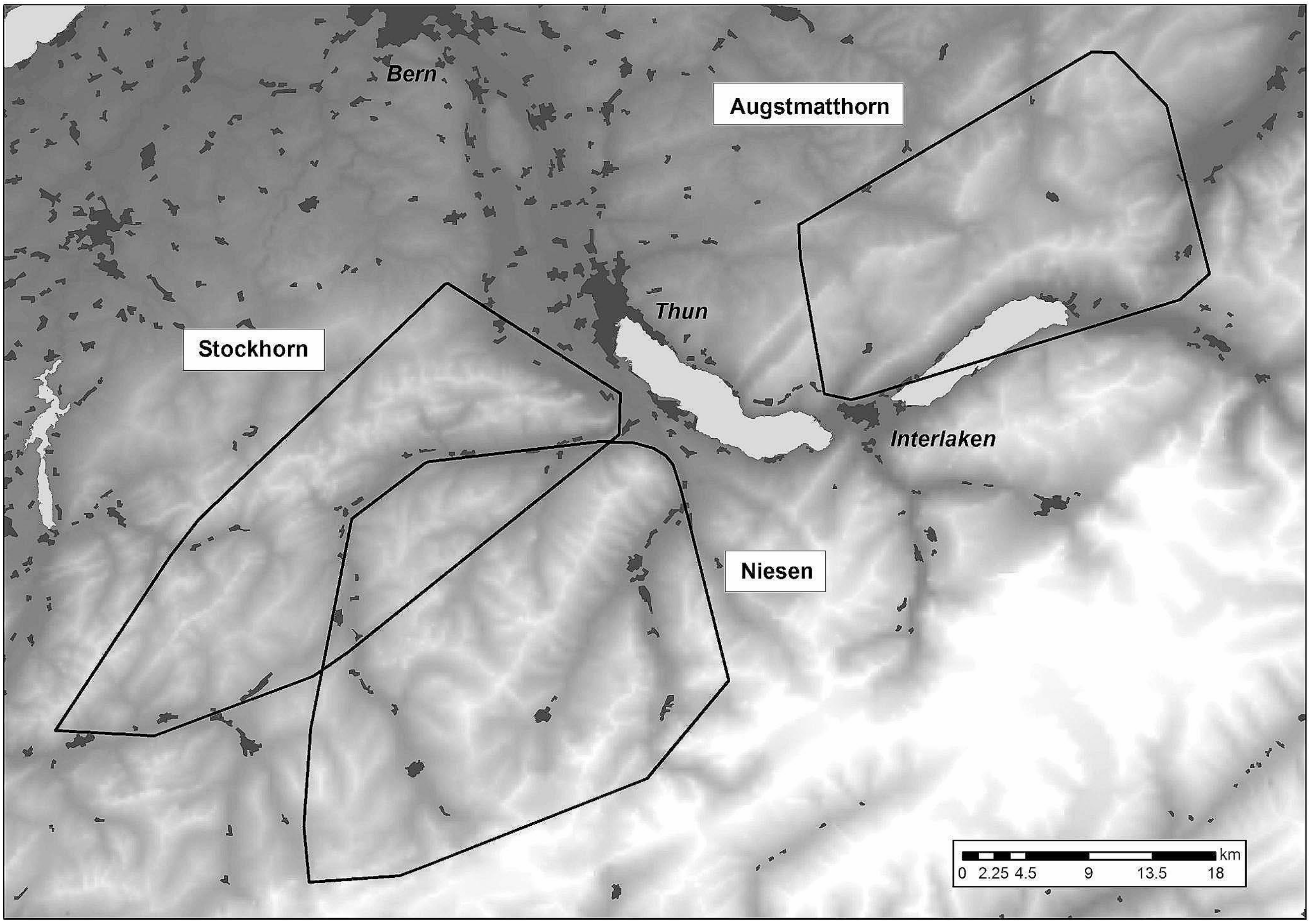

Fig. 1 Study area with the three regions. Polygons = 100% MCPs containing GPS data of all lynx observed in this region (Stockhorn: $n=5$; Niesen: $n=6$; Augstmatthorn: $n=2$). Dark grey features = settlements, light grey features = lakes. Shaded grey area = Digital Elevation Model for Switzerland (BFS GEOSTAT, http://www.geostat.admin.ch). Higher elevations are represented by lighter shades

Lynx GPS collar data

Between 2013 and 2018, we captured and radio-collared 13 Eurasian lynx (6 males, 7 females) and recaptured 2 of them, following established standard protocols (described in Ryser-Degiorgis et al. 2002; Ryser et al. 2005; Vogt et al. 2016) and with all animal experimentation permits required according to Swiss legislation. We used two trapping techniques: unbaited double-door box traps made from solid wood (5 captures) and foot snares made from 3-mm wire cables (10 captures). Box traps and foot snares were equipped with an alarm system allowing for constant monitoring. Non-target species were immediately released from the traps. Lynx were immobilized with medetomidine hydrochloride (Domitor®, Orion Corporation, Espoo, Finland) and ketamine hydrochloride (Ketasol®, Graeub, Switzerland). Atipamezole hydrochloride (Antisedan®, Orion Corporation, Espoo, Finland) was used as an antagonist for medetomidine (Ryser-Degiorgis et al. 2002). Each individual was equipped with a GPS/GSM tracking collar (Wild Cell SL/SD GPS-GSM collars, Lotek Wireless, Ontario, Canada) weighing 250–300 g. Collars contained a break-off device (a seam stitched with 1.2–1.5 mm corrodible annealed wire), allowing the unit to drop off after 1–4 years. All lynx caught were examined by a veterinarian and monitored after release until we could confirm that they were hunting successfully.

As in other studies on wild felids (i.e., Blecha and Alldredge 2015; Krofel et al. 2013), GPS collars were programmed to record 7 GPS fixes per day with one location taken at noon and the others between 18:00 and 06:00 CET, with hourly intervals around dusk—the time when lynx are most likely to feed on their kills (Krofel et al. 2013, 2019; Mattisson et al. 2011). GPS location clusters (GLCs) were generated in R (version 4.0.2, R Development Core Team 2020) using the cluster algorithm developed by Svoboda et al. (2013). We defined a GLC as a set of at least 2 GPS fixes obtained within 72 h and within a maximum distance of 100 m.

Kill sites were identified by ground-truthing GLCs in the field as described by Vogt et al. (2018). The coordinates of kill sites, along with the prey species and the distance to the nearest GPS location within the GLC were recorded for each kill. Scavenging occurs rarely in Eurasian lynx (von Arx et al. 2017). We classified animal remains as kills if they matched the following criteria: found within 150 m of the GLC centroid, state of decay corresponds to date of GLC initiation, typical characteristics of lynx feeding activities (e.g., throat bite, kill covered with plant material, stomach and intestine not eaten, skin around legs turned inside out), and no sign of other trauma. Prey remains were found a mean of 8 ± 10 m (SD) from the nearest GPS location within a GLC. If kills were completely consumed, prey species could usually still be identified from skulls, horns and antlers, legs and hooves, as well as by comparison against hair reference samples.

All GPS collared lynx were resident adults (≥ 2 years old). All but one of the seven females had young. The mean observation duration was 12 months (range = 7.5 to 21 months). For one male lynx, we had only six months of data before his collar failed. He was, however, the direct successor of another GPS collared male lynx whose home range he had taken over. In this case, we combined data from both males to cover a full year. The 13 GPS-collared lynx provided a total of 3,144 GLCs, of which 1,457 could be ground-truthed in the field (46%). We attempted to reduce bias towards larger prey and more accessible areas as much as possible (as explained in Vogt et al. 2018), with the help of experienced field workers checking GLCs in steep terrain whenever snow conditions permitted access. However, 14% of GLCs could not be ground-truthed because access was too dangerous due to extreme steepness or high risk of avalanches. If time constraints did not allow us to check all newly formed GLCs, we gave priority to those GLCs with a duration of at least 6 h and containing at least one night location (between 18:00 and 06:00 CET). In this way, we reduced the likelihood of checking GLCs containing only daybeds while reducing the chance of systematically missing small prey items (e.g., neonate ungulates) as much as possible (Krofel et al. 2013; Vogt et al. 2018).

Selection of predictors for chamois occurrence

We built a set of generalized linear models (GLM) predicting the occurrence of GLCs containing killed chamois (1) versus GLCs containing other prey types or no prey (0). To find predictors for the presence of chamois killed by lynx within a GLC, we selected a set of variables from the literature that were associated either with the prediction of kill sites from GPS location data (Krofel et al. 2013; Svoboda et al. 2013) or with different habitat selection of the two most common prey species, chamois and roe deer (Baumann and Struch 2000, Fankhauser and Enggist 2004; Darmon et al. 2012; Gehr et al. 2018; Morellet et al. 2011; Nesti et al. 2010). We selected a total of seven predictors: GLC duration and proportion of night locations as GLC characteristics, and elevation, slope, aspect, distance to rocks, and forest (yes, no) as habitat characteristics. GLC duration was calculated as the time spent within a given GLC (excluding the time spent outside the GLC; details in Vogt et al. 2018). Elevation, slope and aspect were calculated from a digital elevation model (DEM) for Switzerland with a grid cell size of 25 m (BFS GEOSTAT, http://www.geostat.admin.ch). Rocky areas and forest were extracted as vector data from the SwissTLM3D geodatabase of the Swiss Federal Office of Topography (ESRI File Geodatabase 10.1, http://www.swisstopo.admin.ch). We included the sex of lynx in all our models, since male lynx kill chamois more frequently than females (Molinari et al. 2002). All statistical analyses were conducted using R (version 4.2.0, R Development Core Team 2022) and ArcGIS (ArcGIS 10.1 SP for Desktop, Esri Inc.).

Model selection and cross-validation

The full model contained all predictors and those interactions that were considered biologically meaningful. We compared the performance of the full model to the performance of six simpler candidate models (built from combinations of the selected predictors; Table 1) by means of 10-fold cross-validation with three repeats using the function train() of the R package *caret* (Kuhn 2019). The GLMs were fitted

Table 1 Structure of the 7 candidate GLMs to predict the probability of a GLC containing a killed chamois. GLC duration and lynx sex were included in all models. * denote interaction terms

Model	Fixed factors
Full model	duration + $(\text{duration})^2$ + proportion of night locations + slope*elevation + distance to rocks*elevation + distance to rocks*forest + slope*forest + aspect + sex
model1	duration + proportion of night locations + slope + elevation + distance to rocks + forest + aspect + sex
model2	duration + proportion of night locations + slope + distance to rocks + elevation*forest + aspect + sex
model3	duration + proportion of night locations + slope + elevation + distance to rocks*forest + aspect + sex
model4	duration + proportion of night locations + slope + elevation + distance to rocks + sex
model5	duration + $(\text{duration})^2$ + slope + elevation + distance to rocks + sex
model6	duration + $(\text{duration})^2$ + slope + distance to rocks*forest + sex

to the data from 1,457 ground-truthed GLCs, assuming a binomial error distribution. The response variable was occurrence of killed chamois (1 = GLC contains a killed chamois, 0 = GLC contains other prey species or no kill). GLC duration and sex of lynx were included in all candidate models. Some models contained GLC duration as quadratic term to allow for very long-lasting clusters (e.g., den sites of female lynx) to be classified as non-kills. Numeric variables were rescaled as follows to make them more comparable: elevation = (elevation-1,000)/100; slope = (slope-30)/10; aspect = aspect/10; GLC duration = log(GLC duration); distance to rocks = log(distance to rocks + 1). Factors (forest, sex) were transformed into dummy variables for analysis. We applied the function confusionMatrix() of the package *caret* to the dataset of all ground-truthed clusters to calculate confusion matrices and several metrics for measuring model performance (accuracy, sensitivity, specificity). Accuracy was defined as the number of correct predictions divided by the total number of predictions. Sensitivity was the true positive rate (i.e., the number of GLCs correctly classified as chamois divided by the true number of GLCs containing chamois [true positives + false negatives]). Conversely, specificity was the true negative rate (i.e., the number of GLCs correctly classified as non-chamois divided by the true number of GLCs not containing chamois [true negatives + false positives]).

Prediction of kill intervals for chamois

We fitted the best model to the data of all ground-truthed GLCs and then made predictions for unchecked GLCs. We simulated fitted values (5,000 simulations) and Bayesian compatibility intervals (Amrhein and Greenland 2022; "credible intervals") for the unchecked GLCs using the function sim() of the package *arm* (Gelman et al. 2021). The fitted values (probabilities) were converted into binary values using the function rbinom(). To estimate the total number of chamois killed by each individual lynx, we added the number of verified chamois from the dataset of the ground-truthed GLCs to the number of predicted chamois from the dataset of the unchecked GLCs (mean of the 5,000 simulations). We then calculated predicted kill intervals as the number of days between two killed chamois and reported means together with Bayesian compatibility intervals.

Accuracy of kill-interval predictions

To evaluate whether our predicted kill intervals for chamois were realistic and of practical use, we compared the number of predicted chamois to the number of true chamois in the dataset of the ground-truthed clusters and discuss the width of the Bayesian compatibility intervals for kill rate predictions (estimated with the output of the predictive model plus the field data). We also compared predicted kill intervals (days between consecutively killed chamois), with kill intervals calculated from field data (kill series). A kill series consisted of at least two consecutive kills from the same lynx individual that were found by ground-truthing of GLCs in the field, under the condition that all GLCs with a duration of ≥ 6 h formed in between the GLCs containing these two kills had been ground-truthed as well. GLCs with a duration of < 6 h have a low probability of containing a kill ($< 10\%$; Vogt et al. 2018) and were not considered. We then estimated the kill intervals for chamois based on field data from the number of kills found per year (extrapolated from kill-series data including all prey species) and the proportion of chamois in the prey spectrum for male and female lynx separately.

Regional extrapolation

To test how well model predictions could be extrapolated to other areas, we split our dataset into three regions that differed topographically (Fig. 1) and with respect to chamois density (LANAT 2018; Vogt et al. 2019). Five lynx (452 GLCs) were tracked in the Stockhorn region, six (762 GLCs) in the Niesen region and two (243 GLCs) in the Augstmatthorn region. For this analysis, we only used the model yielding the best overall performance for the whole dataset. We used data from two regions to train the model and then used the data from the third region as test dataset. Model performance was compared by means of 10-fold cross-validation with three repeats using the function train() of the R package *caret* (Kuhn 2019). To evaluate how well one region could be predicted with data from the other two, we applied the function confusionMatrix() to the test datasets. We also compared deviance between predicted and ground-truthed number of chamois between the three regions using the same approach as explained in section "Prediction of kill intervals for chamois".

Results

Model selection and cross-validation

Model performance was very similar for all candidate models, with the full model yielding the best cross-validation result (accuracy = 0.83, sensitivity = 0.43, specificity = 0.94; Table 2). The model output of the full model is presented in Table 3.

Table 2 Cross-validation performance of the 7 candidate models (GLMs, Table 1) to predict the probability of a GLC containing a killed chamois. Performance metrics were calculated using the function confusionMatrix() of the R package caret. Models were fitted to data of 1,457 ground-truthed GLCs using repeated k-fold cross-validation with 10 folds and 3 repeats. The confusion matrix for the full model is shown in the supplementary materials (Tab. S1). The true number of chamois in the training dataset was 318. Predictions are the mean of the 5,000 simulations. CI = 95% Bayesian compatibility intervals (Amrhein and Greenland 2022)

Candidate model	Accuracy (CI)	Sensitivity	Specificity	chamois predicted (CI)
model0 (full model)	0.83 (0.81–0.84)	0.43	0.94	320 (295–348)
model1	0.82 (0.80–0.83)	0.38	0.94	320 (294–347)
model2	0.82 (0.81–0.83)	0.40	0.94	320 (294–346)
model3	0.82 (0.81–0.83)	0.40	0.94	320 (295–345)
model4	0.82 (0.80–0.83)	0.39	0.93	319 (293–346)
model5	0.82 (0.81–0.83)	0.41	0.94	319 (293–346)
model6	0.82 (0.81–0.83)	0.42	0.93	319 (293–346)

Table 3 Model parameters of the best GLM (model0, Table 1) predicting the probability of a GLC containing a killed chamois (1) versus no chamois (0)

Predictor	Estimate	*SE*	*p*-value
Intercept	-11.313	1.402	< 0.001
GLC duration	5.04	0.698	< 0.001
(GLC duration)2	-0.553	0.102	< 0.001
aspect	0.011	0.008	0.143
proportion of night locations in GLC	1.42	0.521	0.006
slope	0.663	0.209	0.002
elevation	0.058	0.073	0.429
forest	1.239	0.476	0.009
distance to rocks	-0.142	0.104	0.172
lynx sex	-1.101	0.158	< 0.001
distance to rocks*forest	-0.372	0.103	< 0.001
distance to rocks*elevation	0.001	0.016	0.964
forest*slope	-0.234	0.184	0.202
elevation*slope	-0.039	0.028	0.162

The model was fitted to the data of 1,457 ground-truthed GLCs by maximum likelihood. Factors were transformed to dummy variables (lynx sex: 1 = female, 0 = male; forest: 1 = forest, 0 = open area). The estimates show the effect of factor level = 1 (forest/female). Numeric factors were transformed to fit the scale of the other variables as described in the methods section. * denote interaction terms

Prediction of kill intervals for chamois

The number of predicted chamois (mean of the 5,000 simulations: 320 [295–348, 95% Bayesian compatibility interval]) was close to the true number of chamois ($n = 318$) in the dataset of the ground-truthed GLCs. Predicted kill intervals for chamois inferred from the total number of chamois killed during the observation period of each lynx (output of the predictive model plus field data) differed between the sexes. Female lynx killed on average one chamois every 11.9 days (10.6–13.0 days), while male lynx killed one chamois every 7.2 days (6.7–7.6 days). This calculation included chamois of all age classes. There was regional variation, with female lynx in the Niesen region killing less chamois than in the other two regions (Table 4).

Comparison with kill intervals calculated from kill series

When we extrapolated from the subsample of consecutive kills found in the field (number of prey found within kill series, $n = 155$), female lynx killed on average one prey every 3.7 days. We found that 27.5% of all kills from female lynx ($n = 403$) were chamois. This would lead to a calculation of one chamois killed every 13.4 days for females. Male lynx killed on average one prey every 4.2 days (number of prey found within kill series, $n = 155$), while 43.7% of all kills found from males ($n = 320$) were chamois. This would lead to a calculation of one chamois killed every 9.6 days for males.

Regional extrapolation

Predicting data from one region with the full model trained on data of the other two regions showed that our model could not be generalized to all regions with the same success. Accuracy was lowest for predictions for the Augstmatthorn region made from the model trained on data from the other two regions. Predictions for the Niesen region had the highest accuracy, but the number of chamois in the dataset was overestimated by 20% (Table 5).

Table 4 Predicted kill intervals for chamois (days between consecutive kills). Total chamois = number of chamois found in ground-truthed GLCs + number of predicted chamois in unchecked GLCs (mean over 5,000 simulations). CI = 95% Bayesian compatibility intervals

Lynx individual	Chamois found	Total chamois	CI	Days observed	Predicted kill interval	CI
Stockhorn region						
NEVE	32	60	55–65	510	8.5	7.8–9.3
CATO	25	47	43–51	384	8.2	7.5–8.9
EYWA	25	40	37–43	345	8.6	8.0–9.3
LUPO/MISO	28	60	56–65	365	6.1	5.6–6.5
Niesen region						
GIRO	33	44	42–46	278	6.3	6.0–6.6
LARY	42	73	69–77	538	7.4	7.0–7.8
ISIS	26	40	38–44	479	12.0	10.9–12.6
WEGA	13	21	19–24	313	14.9	13.0–16.5
LYRA	14	25	22–31	398	15.9	12.8–18.1
LELA	12	21	19–23	284	13.5	12.3–14.9
Augstmatthorn region						
AMOR	53	80	75–87	631	7.9	7.3–8.4
CARA	15	22	21–24	219	10.0	9.1–10.4

Table 5 Performance of models trained on data from the other two regions for predicting the number of chamois killed by lynx in the third region. Performance metrics were calculated using the confusionMatrix() function of the R package caret. The confusion matrices are shown in the supplementary materials (Tab. S2–S4). Predictions are the mean of the 5,000 simulations. CI = 95% Bayesian compatibility intervals

Region	Accuracy (CI)	Sensitivity	Specificity	chamois predicted (CI)	true number of chamois	difference
Stockhorn	0.80 (0.76–0.83)	0.35	0.94	102 (90–115)	110	-7%
Niesen	0.86 (0.83–0.88)	0.49	0.94	168 (146–192)	140	+ 20%
Augstmatthorn	0.74 (0.68–0.79)	0.35	0.89	62 (55–69)	68	-9%

Discussion

Accuracy of kill interval predictions

Classification accuracy was high in all of our models (83% in the best model) and was comparable to other studies using different modelling approaches (kills versus non-kills: 74–77%, Franke et al. 2006; 72%, Webb et al. 2008; 67%, Svoboda et al. 2013) or prey types based on prey size or species (88%, Webb et al. 2008; 75%, Knopff et al. 2009; 66–75%, Oliveira et al. 2022). Our approach of classifying two categories (chamois versus no chamois) provided higher accuracies than the multi-class model generated by Knopff et al. (2009) for classification of several prey species. More in-depth analyses of confusion matrices showed that our models were more successful in correctly predicting GLCs that did not contain chamois (specificity, 93–94% in all models) than in correctly predicting GLCs containing chamois (sensitivity, 38–43% in all models, similar to Irvine et al. 2022). However, since non-chamois GLCs make up the largest part of our dataset (78%), wrongly classifying them would lead to a strong overestimation of killed chamois. A high specificity is, therefore, essential for useable kill-interval estimates (Knopff et al. 2009).

In our predator-prey system, chamois killed by lynx could potentially be confused with roe deer or Alpine ibex killed by lynx. While Alpine ibex ($n = 5$) made up only 0.7% of all lynx kills ($n = 722$) found in our study area, roe deer ($n = 263$) killed by lynx were observed nearly as often as chamois ($n = 318$). GLCs containing chamois show similarities to GLCs containing roe deer and the latter were contained in the non-chamois category within our model. There is an overlap in body weight between chamois and roe deer of different age classes, leading to overlapping handling times by lynx (Vimercati 2014). Additionally, chamois tend to prefer steeper, rockier areas at higher elevations than roe deer, but both species can also be found in mountain forests, especially in winter when chamois migrate to lower altitudes for feeding (Lovari et al. 2006; Unterthiner et al. 2012). When comparing GLCs that were erroneously classified as non-chamois (false-negatives) with the correctly classified chamois (true-positives), we found that false-negatives were on average found at lower elevations, in less steep terrain and further from rocky areas than true-positives (Table S5, Supplementary Materials). To compensate for this problem, at least partially, we calculated the total number of chamois killed by lynx as the sum of chamois found in the field (for ground-truthed GLCs) and the number of predicted chamois (for unchecked GLCs). We assumed that easily accessible GLCs in less steep and rocky areas were more likely to be ground-truthed.

Of course, the ability of our model to correctly predict chamois occurrence in very steep and rocky areas would depend on such GLCs being part of the training dataset, to avoid projections outside the data range. With the help of experienced field workers, we went to great lengths to also include a subsample of the most “extreme” GLCs in our dataset. Nevertheless, further studies on the potential effects of biased field sampling on model classification accuracy would be useful. The low sensitivity of our models remains somewhat unsatisfying at the level of individual GLCs, for example if one envisions an analysis of habitat parameters associated with predicted chamois kill sites. Sensitivity could potentially be further improved by restricting the dataset only to chamois of a certain age, because many model algorithms are less successful in distinguishing kill sites of small prey (such as juvenile chamois) from non-kill sites, due to brief handling times resembling other behaviours such as resting (Elbroch et al. 2018; Knopff et al. 2009; Svoboda et al. 2013; Webb et al. 2008; Oliveira et al. 2022). Also, the use of more advanced machine-learning methods such as multi-class random forest (Oliveira et al. 2022) or the inclusion of activity inferred from accelerometer data (Blecha and Alldredge 2015; Petroelje et al. 2020) might further improve predictions not only of small-bodied prey but potentially also of prey species.

While some classification error at the level of individual GLCs could not be removed, the overall number of chamois predicted by our models closely matched the actual number of found chamois in our training dataset. Our model was, therefore, useful for estimating the total number of killed chamois but less so for estimating their spatial distribution. Nonetheless, spatial plots of our model predictions showed plausible patterns, and areas with high predicted probability of killed chamois overlapped well with empirical data (Fig. S1, Supplementary Materials) and with knowledge of chamois distribution in the study area, based on our personal observations and those of local game wardens. The width of Bayesian compatibility intervals for the number of chamois predicted by our models were reasonably narrow, so we conclude that estimates of the overall number of chamois killed within our study area were accurate enough for practical use for wildlife management purposes.

Kill intervals for chamois calculated with the approach presented here (number of verified chamois from the dataset of the ground-truthed GLCs + number of predicted chamois from the dataset of the unchecked GLCs) were 1.5 to 2 days shorter than kill intervals calculated only from field data (combining information from consecutive kills found in the field and proportion of chamois in the prey spectrum). This probably reflects an underrepresentation of chamois in the total number of verified kills found in the field and highlights how the inclusion of “virtual kills” can help to reduce potential bias in field work, if the limitations of the modelling approach are critically discussed as well.

Regional extrapolation

Biologists not only seek to complement datasets and reduce field work effort by including information from GLCs that were not ground-truthed (e.g., Webb et al. 2008; Svoboda et al. 2013; Irvine et al. 2022; Oliveira et al. 2022), but there is also the intention to extrapolate from well-studied individuals or areas to situations where less fieldwork was conducted. Irvine et al. (2022) suggest that predictive models are system-specific and emphasize the need for field visits to GLCs. In our study, predicting data from one region with the model trained on data from the other two regions showed that predictions could not be generalized to all regions with the same success. In the Niesen region, for example, female lynx killed less chamois than in the other two regions, and even though model accuracy was highest, predicting the Niesen region from the other two regions resulted in a 20% overestimation of chamois in the dataset. Part of these differences could be due to low sample size and sampling variation (the Niesen area contained more data than the other two regions). Regional differences could also arise from differences in behaviour of individual lynx or in environmental conditions such as prey availability or prey community structure. In the Niesen region, the prey community seems the same as in the other two regions, but the density of chamois compared to roe deer is lower (Vogt et al. 2019). However, ungulate census data were available only at a very coarse spatial resolution for our study area (LANAT 2018), so that we were not able to include this parameter in our models. If regional variation is unknown or cannot be accounted for, extrapolations from one study area to another can result in substantial bias and should be critically discussed.

Concluding remarks

It is possible, with some reservations, to calculate species-specific kill intervals from GPS location cluster data of Eurasian lynx. The sensitivity of the models should be further improved, but the results can be sufficient for practical application. However, predictive modelling approaches do not replace extensive fieldwork but require large sets of field data, high individual variability, and thorough knowledge of a predator’s ecology and prey community. They may provide useful results only for binary classifications in rather simple predator-prey systems, and results cannot easily be extrapolated from one study area to another. Use of more complex machine-learning approaches combining data from different study areas to increase sample size may help to further improve classification results and expand knowledge in this field.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10344-024-01804-4.

Acknowledgements We thank the game wardens of the Canton of Bern for their essential help with capturing and monitoring of lynx and for monitoring of prey species in our study area. We also thank the game wardens of the Cantons of Luzern, Obwalden, Fribourg and Vaud for their help with monitoring transboundary lynx. We further thank the following wildlife veterinarians of the Institute for Fish and Wildlife Health (FIWI), Bern for their participation in lynx captures: Marie-Pierre Ryser-Degiorgis, Mirjam Pewsner, Roman Meier, Iris Marti, and Simone Pisano. We also thank all involved KORA personnel, interns, civil servants, and students for their help with field work, Fränzi Korner-Nievergelt for statistical advice, and Brent Patterson, an anonymous reviewer, and Thomas Jung for providing suggestions for improving the manuscript.

Author contributions KV designed the study, conducted field work, performed data analyses, and wrote the draft of the manuscript. TR helped with developing the modelling approach and with data analysis. SS collected field data and performed analyses of kill intervals. CW helped with study design and project planning. VA provided general support and helped revising the manuscript. All authors reviewed the manuscript.

Funding This study could be realized thanks to a grant from a charity foundation from Liechtenstein and financial support from the hunting inspectorate of the canton of Bern as well as from the following foundations: Stotzer-Kästli Stiftung, Zigerli-Hegi Stiftung, MAVA foundation and Fondation de bienfaisance Jeanne Lovioz.
Open access funding provided by University of Basel

Data availability Data can be obtained from the authors upon reasonable request.

Declarations

Ethics approval Lynx were captured with all permits required according to Swiss legislation for capturing, immobilizing, and radio tagging lynx (capture permits from the Federal Office for the Environment: Bewilligung_KORA_Luchsfang_Kompartimente I, III und IV_2011–2015, Bewilligung_KORA_Luchsfang_Schweiz_2017–2020/Q342-1667; animal experimentation permit from the Animal Welfare Commission of the Office for Agriculture and Nature of the Canton of Bern: 111/13 and BE3/17+).

Competing interests The authors declare no competing interests.

References

Amrhein V, Greenland S (2022) Discuss practical importance of results based on interval estimates and *p*-value functions, not only on point estimates and null *p*-values. J Inform Technol 37:316–320

BAFU (2016) Konzept Luchs Schweiz – Vollzugshilfe des BAFU zum Luchsmanagement in der Schweiz. Bundesamt für Umwelt, Abteilung Arten, Ökosysteme, Landschaften. Bern, Switzerland

Baumann M, Struch M, Jäggi C, Schnidrig-Petrig R (2000) Habitatspezifisches Überleben von Gemsgeissen: Leben Waldgemsen bei sympathrischem Vorkommen des Luchses riskanter als Alpingemsen? In: Bauman M, Struch M (2000) Waldgemsen – Neue Erscheinung der Kulturlandschaft oder alte Variante der Naturlandschaft? WildARK. Bern, Switzerland

Blecha KA, Alldredge MW (2015) Improvements on GPS location cluster analysis for the prediction of large Carnivore feeding activities: ground-truth detection probability and inclusion of activity sensor measures. PLoS ONE 10:1–19

Breitenmoser U, Ryser A, Molinari-Jobin A, Zimmermann F, Haller H, Molinari P, Breitenmoser-Würsten C (2010) The changing impact of prédation as a source of conflict between hunters and reintroduced lynx in Switzerland. In: MacDonald DW, Loveridge AJ (eds) Biology and Conservation of Wild Felids. Oxford University Press, pp 493–505

Breitenmoser U, Bürki R, Lanz T, Pittet M, von Arx M, Breitenmoser-Würsten C (2016) The recovery of wolf *Canis lupus* and lynx *Lynx lynx* in the Alps: Biological and ecological parameters and wildlife management systems. RowAlps Report Objective 1. KORA Bericht Nr. 70. KORA, Muri bei Bern, Switzerland

R Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org

Darmon G, Calenge C, Loison A, Jullien J-M, Maillard D, Lopez J-F (2012) Spatial distribution and habitat selection in coexisting species of mountain ungulates. Ecography 35:44–53

Elbroch LM, Lowrey B, Wittmer HU (2018) The importance of fieldwork over predictive modeling in quantifying predation events of carnivores marked with GPS technology. J Mammal 99:223–232

Fankhauser R, Enggist P (2004) Simulation of alpine chamois *Rupicapra r. rupicapra* habitat use. Ecol Modelling 175:291–302

Franke A, Caelli T, Kuzyk G, Hudson RJ (2006) Prediction of wolf (*Canis lupus*) kill-sites using hidden Markov models. Ecol Modelling 197:237–246

Gehr B, Hofer EJ, Pewsner M, Ryser A, Vimercati E, Vogt K, Keller L (2018) Hunting-mediated predator facilitation and superadditive mortality in a European ungulate. Ecol Evol 8:109–119

Gelman A, Su Y-S, Yajima M, Hill J, Pittau MG, Kerman J, Zheng T, Dorie V (2021) Package 'arm'. Data Analysis Using Regression and Multilevel/Hierarchical Models. https://CRAN.R-project.org/package=arm

Irvine CC, Cherry SG, Patterson BR (2022) Discriminating grey wolf kill sites using GPS clusters. J Wildl Manage 86:e22163

Knopff KH, Knopff AA, Warren MB, Boyce MS (2009) Evaluating global positioning system telemetry techniques for estimating cougar predation parameters. J Wildl Manage 73:586–597

Krofel M, Skrbinšek T, Kos I (2013) Use of GPS location clusters analysis to study predation, feeding, and maternal behavior of the eurasian lynx. Ecol Res 28:103–116

Krofel M, Skrbinšek T, Mohorović M (2019) Using video surveillance to monitor feeding behaviour and kleptoparasitism at eurasian lynx kill sites. Folia Zool 68:274–284

Kuhn M (2019) The caret Package. https://topepo.github.io/caret/index.html. Accessed 16 August 2022

LANAT (2018) Jagdinspektorat des Kantons Bern. Jahresbericht 2017. https://docplayer.

org/114543902-Jagdinspektorat-des-kantons-bern-jahresbericht-2017.html. Accessed 16 August 2022

Lovari S, Sacconi F, Trivellini G (2006) Do alternative strategies of space use occur in male Alpine chamois? Ethol Ecol Evol 18:221–231

Martins Q, Horsnell WGC, Titus W, Rautenbach T, Harris S (2011) Diet determination of the Cape Mountain leopards using global positioning system location clusters and scat analysis. J Zool 283:81–87

Mattisson J, Odden J, Nilsen EB, Linnell JDC, Persson J, Andrén H (2011) Factors affecting eurasian lynx kill rates on semi-domestic reindeer in northern Scandinavia: can ecological research contribute to the development of a fair compensation system? Biol Conserv 144:3009–3017

Merrill E, Sand H, Zimmermann B, McPhee H, Webb N, Hebblewhite M, Wabakken P, Frair JL (2010) Building a mechanistic understanding of predation with GPS-based movement data. Philos Trans R Soc B Biol Sci 365:2279–2288

Molinari-Jobin A, Molinari P, Breitenmoser-Würsten C, Breitenmoser U (2002) Significance of lynx *Lynx lynx* predation on roe deer *Capreolus capreolus* and chamois *Rupicapra rupicapra* mortality in the Swiss Jura Mountains. Wildl Biol 8:109–115

Morellet N, Van Moorter B, Cargnelutti B, Angibault J-M, Lourtet B, Merlet J, Ladet S, Hewison AJM (2011) Landscape composition influences roe deer habitat selection at both home range and landscape scales. Landsc Ecol 26:999–1010

Nesti I, Posillico M, Lovari S (2010) Ranging behaviour and habitat selection of Alpine Chamois. Ethol Ecol Evol 22:215–231

Oliveira T, Carricondo-Sanchez D, Mattisson J, Vogt K, Corradini A, Linnell JDC, Odden J, Heurich M, Rodríguez-Recio M, Krofel M (2022) Predicting kill sites of an apex predator from GPS data in different multiprey systems. Ecol Appl 33:e2778

Petroelje TR, Belant JL, Beyer DE, Svoboda NJ (2020) Identification of Carnivore kill sites is improved by verified accelerometer data. Anim Biotelemetry 8:18

Pitman RT, Swanepoel LH, Ramsay PM (2012) Predictive modelling of leopard predation using contextual global positioning system cluster analysis. J Zool 288:222–230

Ryser A, Scholl M, Zwahlen M, Oetliker M, Ryser-Degiorgis M-P, Breitenmoser U (2005) A remote-controlled teleinjection system for the low-stress capture of large mammals. Wildl Soc B 33:721–730

Ryser-Degiorgis M-P, Lutz H, Bauer K, Sager H, Ryser A, Zimmermann F, Breitenmoser-Wuersten C, Breitenmoser U (2002) Veterinary supervision of lynx translocation within the Swiss Alps. European Association of Zoo- and Wildlife Veterinarians (EAZWV), 4th scientific meeting, joint with the annual meeting of the European Wildlife Disease Association (EWDA), May 8–12, Heidelberg, Germany, pp 147–153

Svoboda NJ, Belant JL, Beyer DE, Duquette JF, Martin JA (2013) Identifying bobcat *Lynx rufus* kill sites using a global positioning system. Wildl Biol 19:78–86

Unterthiner S, Ferretti F, Rossi L, Lovari S (2012) Sexual and seasonal differences of space use in Alpine Chamois. Ethol Ecol Evol 24:257–274

Vimercati E (2014) Predation of Eurasian lynx on roe deer fawns and chamois kids in the Northwestern Swiss Alps. Master Thesis. Zurich University of Applied Sciences ZHAW, Wädenswil, Switzerland

Vogt K, Hofer E, Ryser A, Kölliker M, Breitenmoser U (2016) Is there a trade-off between scent marking and hunting behaviour in a stalking predator, the eurasian lynx, *Lynx lynx*? Anim Behav 117:59–68

Vogt K, Vimercati E, Ryser A, Hofer E, Signer S, Signer C, Breitenmoser U (2018) Suitability of GPS telemetry for studying the predation of eurasian lynx on small-and medium-sized prey animals in the Northwestern Swiss Alps. Eur J Wildl Res 64:73

Vogt K, Signer S, Ryser A, Schaufelberger L, Nagl D, Breitenmoser U, Willisch C (2019) Einfluss Von Luchsprädation und Jagd Auf die Gämse – teil 1 und 2. Bericht in Zusammenarbeit Mit dem Jagdinspektorat Des Kantons Bern. KORA Bericht Nr. 84. KORA, Muri bei Bern, Switzerland

von Arx M, Breitenmoser-Würsten C, Zimmermann F, Kunz F, Vogt K, Ryser A, Struch M, Breitenmoser U (2017) Der Luchs Im Jura - Unter Besonderer Berücksichtigung Des Solothurner Juras. Naturforschende Gesellschaft Des Kantons Solothurn Mitteilungen 2017:43–177

von Arx M, Kaczensky P, Linnell J, Lanz T, Breitenmoser-Würsten C, Breitenmoser U, Boitani L (2021) Conservation status of the eurasian lynx in West and Central Europe. Cat News Special Issue 14:5–9

Vucetich JA, Hebblewhite M, Smith DW, Peterson RO (2011) Predicting prey population dynamics from kill rate, predation rate and predator–prey ratios in three wolf-ungulate systems. J Anim Ecol 80:1236–1245

Webb NF, Hebblewhite M, Merrill EH (2008) Statistical methods for identifying wolf kill sites using global positioning system locations. J Wildl Manage 72:798–807

Zimmermann F, Zoss R, Ryser J, Breitenmoser-Würsten C, Breitenmoser U, Kunz F (2018) Abundanz Und Dichte Des Luchses in den Westschweizer Alpen: Fang-Wiederfang-Schätzung mittels Fotofallen in den Referenzgebieten Simme-Saane (IVa) und teilweise Rhone-Nord (IVc) Im Winter 2017/18. KORA Bericht Nr. 82d. KORA, Muri bei Bern, Switzerland