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ORIGINAL ARTICLE

Suitability of GPS telemetry for studying the predation of Eurasian lynx on small- and medium-sized prey animals in the Northwestern Swiss Alps

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Abstract

Predator diet composition and kill rates have to be known in order to quantify predation pressure on prey populations. While ground-truthing of GPS location clusters (GLCs) is a reliable method for finding large- and medium-sized prey items, finding the remains of small prey is still considered a major difficulty. In this study, we searched GLCs of Eurasian lynx *Lynx lynx* in the Northwestern Swiss Alps in order to determine if GLC analysis is a suitable method for detecting kill sites of new-born ungulates and other small prey animals. Juvenile ungulates made up 26% of the prey spectrum and 17% total consumed biomass (TCB), while hares, marmots, and red foxes accounted for 25% of all found prey items (8% TCB). Lynx spent significantly more time in GLCs containing large prey, but no clear transition in GLC duration for distinguishing between large (≥ 10 kg; mean duration = 46.9 h, SD = 30.1 h) and small prey (< 10 kg; mean duration = 26.7 h, SD = 21.1 h) could be defined. We explored the influence of different cut-off values for GLC duration on lynx diet composition. GLCs with a duration of < 9 h had less than 25% detection success, but still contained 13% of all small prey items. We conclude that GLC analysis is a promising tool for exploring predation on new-born ungulates, mesopredators, and other smaller prey animals weighing between 2 and 10 kg. However, substantial field effort is mandatory to sufficiently detect prey remains in short-lasting GLCs.

Keywords GPS telemetry · *Lynx lynx* · Predation · Juvenile ungulates · GPS location clusters

Introduction

Predator diet composition and kill rates are two main factors that researchers have to take into account in order to quantify predation pressure on prey populations (Breitenmoser et al. 2010). In this regard, the advent of GPS telemetry as a new field technology has substantially advanced our understanding of movement and feeding behaviour of large carnivores and has improved systematic quantification of predation (Blecha and Alldredge 2015). Apart from information on predator kill rates and diet composition, sex and age structure of prey, prey preferences of individual predators, or habitat characteristics of kill sites can also be inferred from ground-truthing of GPS location clusters (GLCs) (e.g. Gervasi et al. 2013; Heurich et al. 2016; Krofel et al. 2014). In recent times, GPS telemetry has replaced VHF telemetry, scat analysis, and other methods for finding large- and medium-sized prey items in the field (Bacon et al. 2011). However, detecting the remains of small prey items (i.e. <

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10 kg, Bacon et al. 2011; <5 kg, Elbroch et al. 2017; < 8 kg, Knopff et al. 2009) is still considered a major difficulty, since less evidence of the predation event is left and the few remains may disappear fast because of different scavenger species (Krofel et al. 2013; Martins et al. 2011; Mattioli et al. 2011; Palacios and Mech 2011; Svoboda et al. 2013). Consequentially, both VHF and GPS telemetry studies are often biased towards medium- and large-sized prey items (Bacon et al. 2011; Webb et al. 2008). Scat analysis still remains the method most often applied for detection of small prey species in the diet of carnivores, even though the results from these analyses are subject to several sources of bias (Klare et al. 2011). As GPS technology advances, it allows obtaining movement data at previously unknown resolutions (Bacon et al. 2011; Martins et al. 2011; Matthews et al. 2013; Svoboda et al. 2013). However, for many types of GPS collars, limitations of battery weight still do not enable usage of high localisation rhythms over extended periods of time for small- to medium-sized predators. Therefore, to balance the number of GPS locations taken per day with the collar longevity needed to capture a representative period of the animal's lifetime (e.g. > 100 days for large carnivores like cougars; Knopff et al. 2009), a compromise between collecting data and saving battery life is usually sought (e.g. in Blecha and Alldredge 2015; Krofel et al. 2013; Martins et al. 2011; Ruth et al. 2010).

Since the effort and time invested in the field to ground-truth GPS locations and find prey remains may be considerable, models have been developed to predict predation events and reduce time and resources required to obtain reliable kill estimates. This has been attempted for example for leopards *Panthera pardus* (Martins et al. 2011), cougars *Puma concolor* (Blecha and Alldredge 2015; Knopff et al. 2010), wolves *Canis lupus* (Webb et al. 2008), bobcats *Lynx rufus* (Svoboda et al. 2013), and Eurasian lynx *Lynx lynx* (Krofel et al. 2013). Important factors allowing for discrimination between kill sites and non-kill sites in predictive models were GLC duration, the timespan between GLC formation (i.e. presumed time of predation) and investigation, and the distance from the kill site to the closest night location (for nocturnal predators, Krofel et al. 2013; Svoboda et al. 2013). For example, Krofel et al. (2013) found 99% of lynx kills in GLCs with a duration longer than 30 h and observed that the distances from the kill site to the closest night location were more than 3 times smaller than the distances to the closest day location. Svoboda et al. (2013) found that 82% of bobcat kill sites were detected less than 7 days after cluster formation and suggested that researchers should investigate GLCs within 7 days following GLC initiation whenever possible. Other factors, such as daytime of GLC formation, land cover, and ground-truthing error, have also been taken into account, but were of less significance (Blecha and Alldredge 2015; Svoboda et al. 2013). Generally, model algorithms designed to identify kill sites were more efficient in predicting kill sites of large prey than those of small prey (Elbroch et al. 2017; Knopff et al. 2010; Svoboda et al. 2013; Webb et al. 2008). For example, the top logistic regression models applied by Webb et al. (2008) to predict wolf kill sites correctly classified 100% of kills of large prey species, whereas in small prey species, 40% were classified as non-kills. Thus, predicting kill sites of small prey items, which have a shorter handling time, seems to be more difficult (Palacios and Mech 2011; Svoboda et al. 2013; Webb et al. 2008). When deciding on where to spend restricted resources, field technicians and practitioners are likely to choose the most promising GLCs to be visited based on characteristics such as GLC duration and accessibility. Especially, GLCs with duration of less than 24 h are often assumed to be non-predation events (Elbroch et al. 2017; Svoboda et al. 2013). However, selectively subsampling GLCs based on certain characteristics can lead to inaccurate results, such as over- or underestimation of predation events or reduced diversity of diets (Elbroch et al. 2017). In this study, we searched GLCs of Eurasian lynx in the Northwestern Swiss Alps, where lynx are efficient stalking predators of roe deer *Capreolus capreolus* and chamois *Rupicapra rupicapra* (Breitenmoser and Breitenmoser-Würsten 2008; Molinari-Jobin et al. 2002). Lynx usually feed for several days on adult ungulate kills, hiding during the day and returning to the carcass each evening (Krofel et al. 2013; Molinari-Jobin et al. 2002; Nilsen et al. 2009). This quite predictable pattern has made the Eurasian lynx a suitable species for the application of GLC analysis (Krofel et al. 2013; Mattisson et al. 2011). However, part of the lynx' diet is made up of small prey items weighing < 10 kg (e.g. brown and mountain hares *Lepus europaeus* and *L. timidus*, Alpine marmot *Marmota marmota*, red fox *Vulpes vulpes*, and new-born ungulates; Molinari-Jobin et al. 2004). Since previous studies on lynx diet conducted in Switzerland were mostly based on VHF telemetry (e.g. Breitenmoser et al. 2010; Jobin et al. 2000; Molinari-Jobin et al. 2002, 2004), their results were likely biased towards larger prey. If new-born ungulates and other small prey items are overlooked, this may lead to an underestimation of kill rates and to a bias in prey diversity towards certain prey types and age classes.

The objectives of our study were (i) to determine if GLC analysis is a suitable method for detecting kill sites of new-born ungulates and other small prey animals killed by Eurasian lynx, (ii) to characterise GLCs containing large prey items versus small prey items in order to understand when and where small prey items are found, and (iii) to investigate whether invested field effort could be balanced with the chances of missing (small) prey items using GLC duration as a criterion.

Methods

Study area

The study area is situated in the Northwestern Swiss Alps, expands over approximately 1500 km^2, and includes parts of the Bernese Oberland and the pre-Alps of the cantons Vaud and Fribourg (Vogt et al. 2016; Zimmermann et al. 2012a,b). The landscape is composed of a mixture of forests, fragmented by pastures and human settlements, with a human density of about 42/km^2 on average (Swiss Federal Statistical Office 2015). Altitudes range up to more than 2000 m a.s.l. The Eurasian lynx is the only widespread large carnivore species in the study area, with an estimated density of 2.05 (1.50–2.60, 95% confidence interval) independent (subadult and adult) lynx/100 km^2 of suitable habitat (95.3% of total study area; Zimmermann et al. 2014). Lynx main prey in the area are roe deer and chamois (Breitenmoser and Breitenmoser-Würsten 2008; Molinari-Jobin et al. 2002), whereas other possible prey species with an adult body weight of ≥ 1 kg are red fox, badger *Meles meles*, pine marten *Martes martes*, stone marten *M. foina*, brown and mountain hare, Alpine marmot, black grouse *Tetrao tetrix*, and hazel grouse *Tetrastes bonasia* (Molinari-Jobin et al. 2007). Red deer, Alpine ibex *Capra ibex*, wild boar *Sus scrofa*, and capercaillie *T. urogallus* occur only locally.

Lynx captures

Between 2012 and 2014, we captured and radio-collared 12 Eurasian lynx (7 males, 5 females) and recaptured 3 of them, following established standard protocols (described in Ryser-Degiorgis et al. 2002; Ryser et al. 2005; Vogt et al. 2016) and with all permits required according to Swiss legislation. We used two trapping techniques: double-door box traps (3 captures) and foot snares (12 captures). Unbaited double-door box traps made from solid wood were placed on forest roads used by lynx. They were equipped with a GSM-based alarm system allowing for 24-h monitoring. Any non-target species were directly released from the traps. Foot snares made from 3-mm wire cables were placed around fresh lynx kills and connected to an alarm system. The cables were passed through aluminium tubes equipped with long springs to avoid leg injuries. The capture team was always able to reach the capture site within less than 15 min and all lynx caught were examined by a veterinarian. After release, we tightly monitored the movements of all lynx and inspected GPS location clusters (GLCs) until we could confirm that they were hunting successfully.

Lynx were immobilised with 0.1–0.15 mg/kg medetomidine hydrochloride (Domitor®, Orion Corporation, Espoo, Finland) and 3.2–5.5 mg/kg ketamine hydrochloride (Ketasol®, Graeub, Switzerland). Atipamezole hydrochloride (0.56–0.77 mg/kg; 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 unit (GPS Plus Mini-1 C collars, Vectronic Aerospace GmbH, Berlin, Germany; 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 1–2 years. None of the captured lynx died due to capture procedures or problems with the collar or showed any skin abrasions caused by the collar.

Data collection

Similar as in other studies on wild felids (i.e. Blecha and Alldredge 2015; Krofel et al. 2013; Martins et al. 2011; Ruth et al. 2010), GPS collars were programmed to record 7–8 GPS fixes per day. In the first weeks after capture, collars were set to take a location every 3 h in order to monitor lynx activity throughout the day. From May onwards, collars were set to a rhythm with a higher resolution during twilight and night hours, when lynx are most likely to feed on their kills (02:00, 05:00, 14:00, 18:00, 20:00, 21:00, and 22:00 CET time).

Kill sites were located by searching GPS location clusters (GLCs), similar to the procedures described in Bartnick et al. (2013), Krofel et al. (2013), Lone et al. (2014), and Palacios and Mech (2011). GLCs were generated in R (version 3.1.0, R Core Team 2014) using an adaptation of the cluster algorithm developed by Svoboda et al. (2013). Fixes belonging to a GLC were visualised using Google Earth software (version 7.1.5.1557). We defined a GLC as a set of at least 2 GPS fixes within a maximum distance of 100 m. Lynx sometimes move up to several kilometres away from kill sites and interrupt use of their kills for 1 to several days (Breitenmoser and Breitenmoser-Würsten 2008). In order to reduce pseudoreplication caused by associating multiple GLCs with the same kill site, we considered a GPS fix as part of the same GLC if a lynx returned into this GLC within 72 h. This method was validated by double-checking exemplary kill sites after lynx had returned from an excursion and by calculating the mean duration of all excursions from GLCs (26.6 ± 53.0 h SD, $N = 732$). GLCs containing only 2 fixes with a time span of > 48 h between consecutive fixes were excluded from analysis, since they corresponded to areas repeatedly travelled through by lynx (e.g. ridges, forest roads) where locations may be taken in close spatial proximity without the lynx actually being stationary.

We attempted to search all GLCs from 1 January 2013 to 31 December 2014 for 4 focal lynx individuals (2 males, 2 females) in each year ($N = 7$, 1 female followed during both years). For 5 additional animals (2 females, 3 males), we searched at least one "large" (> 3 GPS fixes) and one "small" (2–3 GPS fixes) GLC per month. GLCs were not checked if they were inaccessible due to extreme steepness or high risk of avalanches. If time constraints did not allow us to check all GLCs of our focal lynx, we gave priority to those GLCs containing at least one night location (between 18:00 and 06:00 CET). Each selected GLC was examined as soon as possible with a mean timespan between GLC formation and control date of 5.6 days (± 5.0 days SD). We checked GLCs after the lynx had left the area whenever possible, although lynx in our study area live in close proximity to humans and are known to be tolerant to human activities near their kills from earlier studies (Breitenmoser and Breitenmoser-Würsten 2008; Molinari-Jobin et al. 2002). GPS locations within GLCs were searched using a handheld GPS (Etrex vista HCx, Garmin, Olathe, KS, USA) with a mean accuracy of 1.9 m (± 0.4 m SE, calculated from 71 test waypoints in our study area). We searched the area within a radius of 30 m of each fix and zigzagged the area between fixes until all accessible fixes were checked, when possible using a trained dog (in 38% of all checked GLCs). Kill sites were logged with a handheld GPS and distance to nearest fix, species, sex, age class, and found body parts were noted for each kill.

Scavenging does occur in lynx (Ray et al. 2014) but is considered of minor importance (e.g. carrion made up 0.5% of all food items found in 6 different studies in Switzerland; von Arx et al. 2017). For our study, 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, no sign of trauma other than throat bite (e.g. broken bones). The mean distance of the found prey remains from the nearest GPS location was 10 m (± 12 m SD). We also recorded typical characteristics of lynx feeding activities: lynx kill ungulate prey with a throat bite and usually start feeding on the carcass at the hind legs. They cleanly gnaw the meat off the bones, thereby turning the skin on the prey animal's legs inside out. Eurasian lynx do not remove and cache parts of their kills. The skeleton remains in one piece, only the ribs are eaten, while the stomach and intestine are never consumed. The carcass is often loosely covered with leaves, moss, grass, or snow (von Arx et al. 2017). Small mammals weighing between 2 and 10 kg are consumed in a similar way, with only the front part of the skull, legs, tail, stomach, and intestines left in one place. In many cases, however, scavengers such as foxes or birds had already removed parts of the kill when we conducted our search. In these cases, parts of the carcass were missing and we found signs of presence of the scavengers as well as the lynx. Even so, the original feeding site of the lynx is marked by a dense patch of loose hair (often still partly covered with plant material) and the stomach content in the same place.

Statistical analysis

We calculated the number of prey items found in each prey category, as well as their frequency of occurrence and the percent of total estimated consumed biomass (% TCB). Roe deer and chamois were separated into four age classes (juveniles ≤ 5 months, juveniles > 5 months, ungulates ≥ 12 months, age class indetermined). Assumed mean live weights for chamois age categories were calculated from the hunting statistics of the Canton of Bern (unpublished data) and taken from Schnidrig-Petrig and Salm (2009). Data for roe deer were derived from Stubbe (1997). Weights for smaller mammals were taken from Hausser (1995). We assumed that lynx consumed 72% of the body mass of large wild ungulates on average, as was determined by Rühe et al. (2007) for roe deer eaten by captive lynx. For juveniles ≤ 5 months and small mammals (red fox, hares, marmot), we assumed a higher consumption rate of 85% which corresponded to our own field observations. For sheep and goats, we took the value given by Rühe et al. (2007) for mouflon. Consumption rates for birds and small rodents were taken from Sunde et al. (2000). For each prey category, we further calculated GLC duration in hours (Figure 4 in the Appendix) as well as the number of nights between 18:00 and 06:00 CET, where at least one GPS location was located within the GLC containing the kill site.

We tested how prey size correlated with environmental factors (serving as proxies for accessibility of the GLC) and the time a lynx spent in a given GLC in a generalized linear mixed model (GLMM) using the R package *lme4* (Bates et al. 2015). The GLMM was fitted to the data from 494 GLCs, assuming a binomial error distribution with a probit link function and using maximum likelihood (Laplace approximation). Prey size (small/large) was set as the binary response variable. GLCs containing prey of unknown size were excluded. Ungulates > 5 months of age were considered as large prey, and ungulates ≤ 5 months and non-ungulate species (e.g. red foxes, hares, marmots, birds, small rodents) were considered as small prey. Between May and September, the juveniles of both roe deer and chamois still weigh less than 10–15 kg (chamois (Canton of Bern, late autumn), < 11 kg, Wandeler and Huber 1969; roe deer (our study area, late August), mean = 10.6 ± 0.3 kg SE, *N* = 18, M. Pewsner, unpublished data). The following factors were included as fixed effects: elevation, terrain ruggedness, duration of the GLC and study period (1 = January to April, 2 = May to August, 3 = September to December). Elevation was calculated from a digital elevation model (DEM) for Switzerland with a grid cell size of 25 m (BFS GEOSTAT, http://www.geostat.admin.ch). To quantify terrain ruggedness, we calculated a Terrain Ruggedness Index (TRI, Riley et al. 1999) for each GLC centroid. Duration of each GLC in hours was log-transformed to match a normal distribution. Values of the factor ruggedness were divided by 10 and values of elevation were divided by 100 to fit the scale of the other parameters in the model. Lynx identity and GLC ID were included as random effects in order to account for individual variation in prey size selection and to avoid pseudoreplication (19 GLCs contained 2 prey items). All statistical analyses were conducted using R (version 3.1.0, R Development Core Team 2013) and ArcGIS (ArcGIS 10.1 SP for Desktop, ©1999–2012 Esri Inc.).

In order to optimise field effort, we compared the chance of finding prey items in GLCs of different duration categories. We further explored whether there was a breakpoint in the linear relationship between GLC duration and chance of finding prey remains for short-lasting GLCs (< 24 h) using the R package *segmented* (Muggeo 2017). Given a generalised linear regression model with detection success as binary response variable and duration as explanatory variable, the function *segmented* tries to estimate a new model with broken-line relationships defined by the slope parameters and the breakpoints where the linear relation changes. The number of breakpoints of each segmented relationship is fixed via the argument psi, where initial values for the breakpoints must be specified. The model yields estimates and relevant approximate standard errors of all the model parameters, including the breakpoints (Muggeo 2017). We ran the model with psi = 6 h as the initial value but also tested for changes in the estimate when psi was set to 3 h, 9 h, and 12 h. We also determined the influence of different cut-off values for GLC duration on the % of prey items found, on % TCB, and on two measures of diet diversity: Shannon's diversity index (*H*) and Evenness scores (Shannon 1948). High values in these measures indicate greater prey diversity that is evenly distributed across prey types (Elbroch et al. 2017).

Data availability The datasets generated and analysed during the current study are not publicly available, since they contain information on the exact localisations of living individuals of a threatened species, but are available from the corresponding author on reasonable request.

Results

The mean collar accuracy calculated from 46 test fixes taken by 4 GPS collars was 8.8 m (± 1.3 m SE) in our study area and there were only few missing GPS locations (mean percentage of successful GPS fixes for all collars = 90%). The collars of the 12 study animals recorded a total of 23,952 GPS fixes and we automatically generated 2597 GLCs (males, $N = 1597$; females, $N = 1000$). We checked 931 GLCs (males, $N = 527$; females, $N = 404$; Fig. 1), 11 of which were checked twice by different observers, and found a total of 492 kills. Nineteen GLCs (checked once or twice) contained 2 kills, while 9 kills were attributed to 2 GLCs, respectively.

Suitability for finding new-born ungulates and other small prey animals

Seventy-two percent of the found prey items were wild ungulates which amounted to 88% of the TCB (Table 1). Prey weighing < 15 kg accounted for more than half of the found prey items. If all juvenile ungulates were included, they made up 26% of the prey spectrum (17% TCB), while hares, marmots, and red foxes accounted for 25% of all found prey items (8% TCB). Juvenile ungulates ≤ 5 months made up 17% of the prey spectrum (8.5% TCB). The duration of GLCs with detection of prey ranged from 2.5 h (red squirrel *Sciurus vulgaris*) to 174 h (adult male chamois) and there was considerable overlap in GLC duration between different prey types (Table 1). Lynx returned to ungulate prey weighing > 10 kg during between 2.5 and 4 different nights on average. Neonate ungulates and other small mammals (hares, red foxes, and marmots) were usually consumed within 1–2 nights but still seemed to represent food enough for one up to three separate feeding bouts.

Characterising GLCs containing small prey items and optimising field effort

The GLMM revealed that lynx spent significantly more time in GLCs containing large prey (Table 2). However, no clear transition in GLC duration for distinguishing between large (mean = 46.9 h, SD = 30.1 h) and small prey (mean = 26.7 h, SD = 21.1 h) could be defined. Ruggedness of the terrain was not related to prey size, but GLCs with large prey items were located at significantly lower elevations than GLCs containing small prey items. Juvenile chamois and marmots were found at higher elevations than other prey items (Fig. 2). We also found a higher proportion of small prey items in the time period from May to August compared to the rest of the year.

The proportion of GLCs in which we found prey remains ranged from < 10% for GLCs lasting < 6 h to 100% for GLCs lasting between 60 and 72 h (Fig. 3). While the chances of finding prey remains strongly increased with GLC duration during the first 39 h, GLCs lasting for ≥ 39 h had consistently high chances of containing prey remains (mean = 92%). In order to find an optimal method to balance invested field effort with the chances of missing (small) prey items and thereby biasing results of feeding studies, we explored whether there was a breakpoint in the linear relationship between GLC duration and the chance of finding prey remains for short-lasting GLCs (< 24 h). The breakpoint identified by the segmented regression model was 8 h (± 1.5 h SE) and was robust to changing starting values (psi) for breakpoint parameters between 3 and 12 h (estimate ± 0.023 h). We investigated the number of found prey items in GLCs shorter than the breakpoint value and we explored other possible GLC cut-off values (Table 3). Sixty percent of the kills (69% TCB) were found in GLCs lasting ≥ 24 h. However, 58% of the small ungulates and other small prey items would have been lost, if GLCs with a shorter duration had not been checked. Applying this cut-off value to GLCs would also have caused a loss of one third of TCB and a reduction in the diversity and in the evenness of the lynx' diet composition (Table 3). Diversity *H* and evenness were less sensitive to cut-offs < 12 h; however,

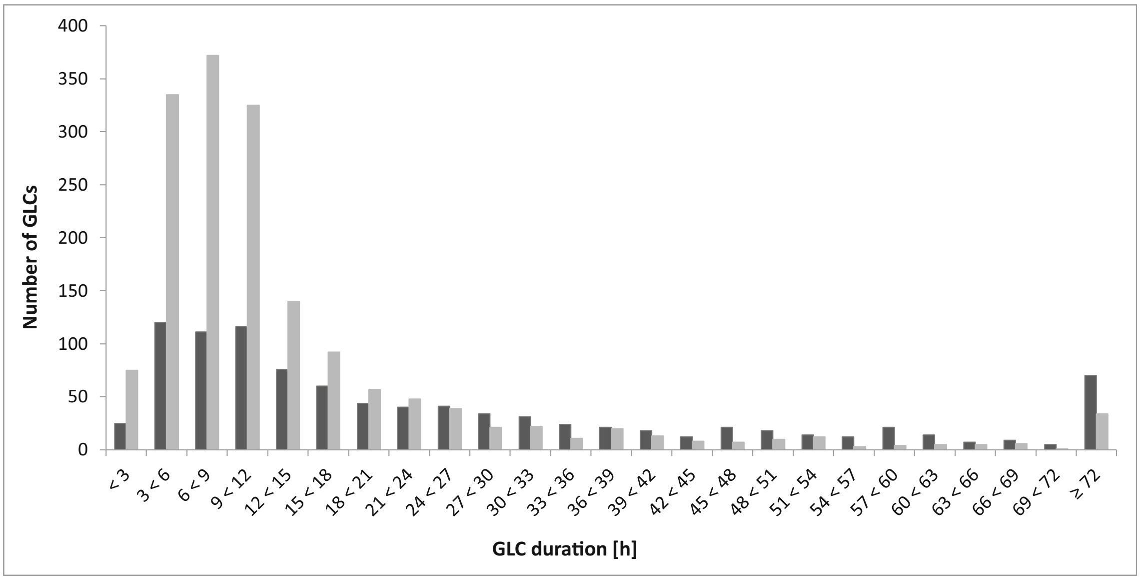

Fig. 1 Number of GLCs checked (dark grey bars) and unchecked (light grey bars) per GLC duration category ($N = 2597$)

setting the cut-off value at < 12 h would still have led to missing 26% and at < 9 h to missing 13% of the small ungulates and other small prey items. Even applying the breakpoint value identified by segmented regression would still have led to a loss of 9% of small prey items.

Discussion

Large carnivores may not only affect mortality of different ungulate sex and age classes by direct predation (Linnell et al. 1995; Molinari et al. 2004) but may also generate indirect

Table 1 Diet composition and feeding behaviour of Eurasian lynx in the Northwestern Swiss Alps 2013–2014 (5 males, 4 females). Means are presented ± standard deviations

Prey category	No. of prey items	% of total	Weight range (kg)	% TCB	GLC duration (h)[a]	No. of nights at kill[b]
Chamois (≥ 12 months)	86	17.5	15–50	26.8	58.4 ± 33.7	4.0 ± 1.6
Chamois kid (≤ 5 months)	63	12.8	2–11	6.3	22.7 ± 13.5	1.7 ± 1.3
Chamois kid (> 5 months)	23	4.7	11–15	4.6	30.4 ± 13.1	2.4 ± 0.9
Chamois (age indet)	28	5.7	11–50	8.9	40.3 ± 19.1	2.5 ± 0.9
Roe deer (≥ 12 months)	81	16.5	15–36	26.3	47.9 ± 32.5	3.7 ± 1.5
Roe deer fawn (≤ 5 months)	22	4.5	1–11	2.2	30.9 ± 16.2	2.4 ± 0.8
Roe deer fawn (> 5 months)	20	4.1	11–15	4.2	38.8 ± 16.2	3.2 ± 0.7
Roe deer (age indet)	29	5.9	11–36	7.8	29.9 ± 19.8	2.6 ± 1.1
Indet wild ungulates	3	0.6	5–50	1.2	19.7 ± 12.1	2.0 ± 0.0
Hare spp.[c]	53	10.8	2–5	2.9	13.8 ± 7.3	1.3 ± 0.5
Alpine marmot	40	8.1	3–6	2.2	35.0 ± 25.5	2.2 ± 1.7
Red fox	29	5.9	5–7	2.7	30.6 ± 16.7	2.1 ± 1.1
Domestic animals[d]	5	1.0	45–100	3.9	49.0 ± 34.7	4.8 ± 2.5
Grouse spp.	3	0.6	0.75–1.75	0.0	15.0 ± 3.5	1.5 ± 0.7
Other birds	3	0.6	< 1	0.0	10.8 ± 3.3	2.0 ± 1.0
Small rodents	3	0.6	< 0.5	0.0	12.5 ± 8.9	1.0 ± 0.0
Total[e]	491					

[a] Cases with more than one kill per cluster are excluded

[b] Number of nights between 18:00 and 06:00 CET, where at least one GPS location was located near the kill site. Cases with more than one kill per cluster are excluded

[c] Hare spp. include European brown hare and mountain hare

[d] Domestic animals include 4 sheep and 1 goat

[e] One European badger was killed but was not consumed and is excluded

Table 2 Generalized linear mixed model (GLMM) on the factors affecting the probability of finding small (ungulates ≤ 5 months, non-ungulate prey) instead of large prey items (ungulates > 5 months) in searched GLCs

Fixed effects	Estimate	*SE*	z-value	*p*
Intercept	0.711	0.540	1.316	0.188
Ruggedness index (TRI)	0.006	0.006	1.110	0.267
Elevation	0.069	0.031	2.218	*0.027*
log(GLC duration)	− 0.807	0.127	− 6.331	*< 0.001*
Study period 2	1.198	0.222	5.386	*< 0.001*
Study period 3	0.383	0.205	1.869	0.062

Prey size (small/large) was set as binary response variable. Ungulate prey includes roe deer, chamois, and livestock. Non-ungulate prey includes red foxes, hares, marmots, birds, rodents, and one badger. *SE* standard error. Study period 1 = January to April, 2 = May to August, 3 = September to December. Study period levels are compared against study period 1. The analysis was conducted on 494 GLCs which could be attributed to kills with known prey size. Lynx identity ($\sigma = 0.539$) and GLC ID ($\sigma = 0.115$) were included as random effects. Significant *p* values are indicated in italic script

effects by predation on mesopredators (i.e. mesopredator-release hypothesis, Soulé et al. 1988). Studies on diet composition and kill rates of large carnivores are one piece in the puzzle of understanding complex predator-prey systems. However, finding remains of small prey items such as neonate ungulates or other small mammals is often considered as a major difficulty (Krofel et al. 2013; Martins et al. 2011; Mattioli et al. 2011; Palacios and Mech 2011; Svoboda et al. 2013). As a consequence, most predation studies based on VHF and GPS telemetry are biased towards medium- and large-sized prey items (Bacon et al. 2011; Webb et al. 2008). Scat analysis is considered to be better suited for detection of small prey items in the diet of carnivores, although other problems may arise using this method, such as difficulties in finding scats during summer, incorrect identification of the predator species leaving the scat, as well as bias arising from the use of conversion factors (Bacon et al. 2011; Foran et al. 1997; Marucco et al. 2008; Rühe et al. 2008).

Suitability for finding new-born ungulates and other small mammals

Our first objective was to determine whether GLC analysis can be a suitable method for detecting kill sites of new-born ungulates and other small prey animals. In our study, wild ungulates accounted for 72% of the found prey items. Somewhat higher percentages of occurrence were reported in two earlier studies on Eurasian lynx in Switzerland using VHF telemetry (83%, Breitenmoser and Breitenmoser-Würsten et al. 2008; 91%, Jobin et al. 2000). In south-central Sweden, roe deer accounted for 83% of prey items found by means of VHF telemetry and snow tracking (Andrén and Liberg 2015). Gervasi et al. (2013) used GPS telemetry to locate lynx kills in southern Norway and found variable proportions of wild ungulates in lynx diet, depending on the intensity of predation on domestic sheep and goats. However, wild ungulates and livestock together made up between 68 and 94% of all found prey items. Krofel et al. (2011) combined results from GPS telemetry and scat analysis in their study on the diet of Eurasian lynx in the Dinaric Mountains. They found that wild ungulates made up 88.4% of TCB, while small mammals and birds accounted for 8.5% of TCB (88.3% and 7.8% in our study). Also in the study conducted by Sunde et al. (2000) in central Norway, wild ungulates made up 72–91% of TCB calculated from faecal analysis. Mountain hares accounted for 7–28% of TCB, while small rodents and birds were of less importance.

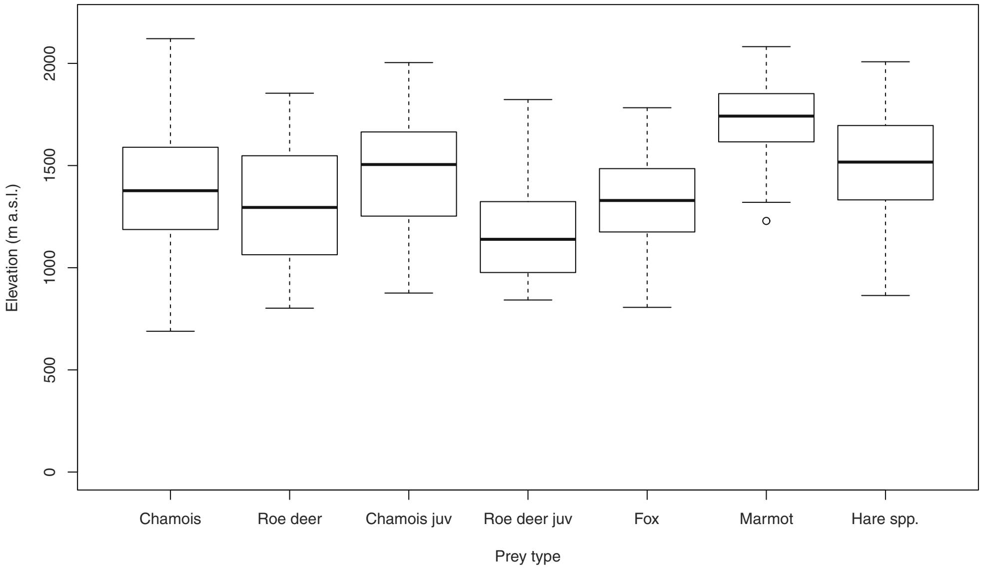

Fig. 2 Elevation at GLC centroids for different prey types ($N = 480$). Chamois/roe deer = animals ≥ 1 year, chamois juv/roe deer juv = animals < 1 year, and hare spp. = European brown hare and mountain hare. Each box encompasses the 25th through 75th percentiles, with the median represented by an interior line. Whiskers denote maximum values or in case of outliers 1.5 times the interquartile range. Circles denote outliers

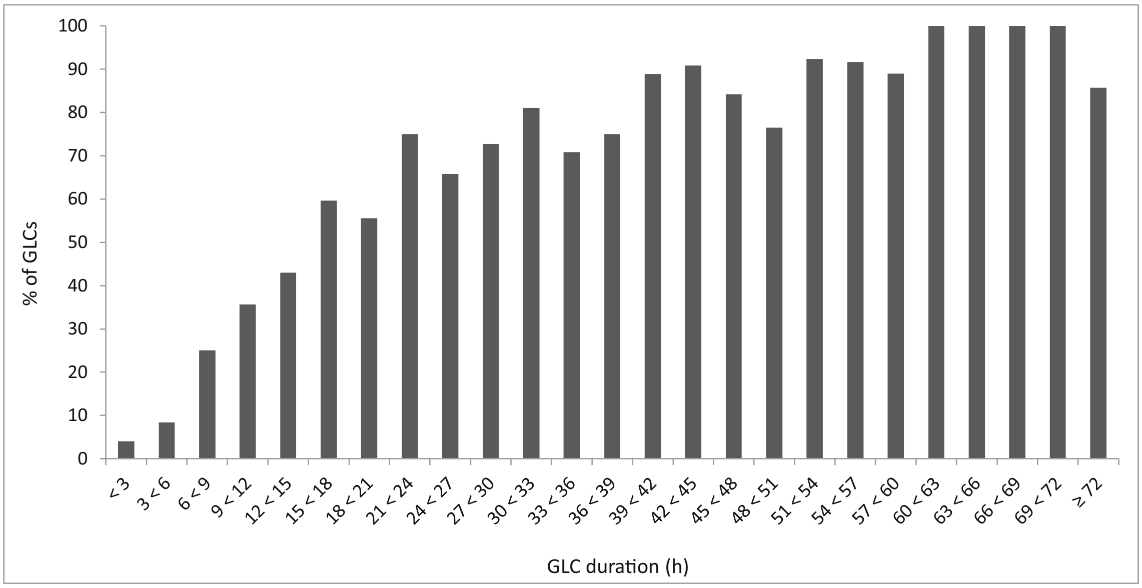

Fig. 3 Proportion of GLCs containing prey remains in relation to GLC duration ($N = 931$)

In our study, we very rarely found prey items weighing ≤ 1 kg such as black grouse *Tetrao tetrix*, hazel grouse *Tetrastes bonasia*, or red squirrels *Sciurus vulgaris*. Of these animals, there were also very few remains left, making identification as lynx kills more ambiguous. Even smaller prey items like mice or voles are probably completely consumed in most cases, which makes scat analysis the only method to reliably detect their occurrence in lynx diet (Bacon et al. 2011; Krofel et al. 2011). We therefore focused on juvenile ungulates and small mammals weighing between 2 and 10 kg, i.e. new-born roe deer and chamois, red foxes, hares (European brown hare, mountain hare), and marmots. These prey categories made up a substantial part of the lynx' diet in our study: 42% of all the found prey items and 16.5% of TCB. In a feeding trial, Rühe et al. (2007) found that captive lynx consumed 1.6 kg of prey per day on average. Jobin et al. (2000) weighed prey of radio-collared wild lynx in the Swiss Jura Mountains during consecutive days and determined that single female lynx consumed 3.2 kg and male lynx 3.4 kg of meat per night on average. However, meat lost to scavenging birds or invertebrates is included in this measure. Lynx normally return to their kills until all the edible parts are completely consumed. Our data on GLC duration and number of nights at the kill suggests that prey weighing between 2 and 10 kg will last a lynx for about 1–3 nights. Even if the actual feeding time at each occasion is less than 1 h, lynx may stay in the vicinity of their prey and return to it more than once, thereby generating a GLC. Our chosen localisation rhythm with 7 locations per day and hourly localisations during dusk enabled us to find these prey items. As opposed to scat analysis, ground-truthing of

Table 3 Influence of applying different GLC duration cut-offs on lynx diet composition and diversity

GLC duration cut-off	No. of detections	Large ungulates[a]	Small ungulates[b]	Other small prey[c]	Prey size indet[d]	% of all prey items missed	% of small prey items missed	% TCB missed	*H*	Evenness
< 3 h	1	0	0	1	0	0.2	0.5	0.0	2.39	0.86
< 6 h	11	4	2	5	0	2.2	3.2	1.7	2.38	0.86
< 8 h	29	9	6	14	0	5.8	9.1	4.1	2.39	0.86
< 9 h	39	10	9	20	0	7.8	13.2	5.1	2.39	0.86
< 12 h	81	21	21	37	2	16.2	26.4	11.3	2.38	0.86
< 24 h	204	66	47	81	7	40.7	58.2	31.3	2.25	0.81
Full dataset	501[e]	264	86	134	17				2.39	0.86

[a] Chamois, roe deer, and livestock > 5 months

[b] Chamois, roe deer, and livestock ≤ 5 months

[c] Red fox, marmot, European brown hare, mountain hare, and other rare small prey items (i.e. rodents, birds, badger)

[d] Ungulate prey where age class could not be determined

[e] 9 kills were attributed to two GLCs

GLCs additionally provides information on sex and age structure or even condition of ungulates killed by predators. This information is crucial for a better understanding of the impact lynx predation may have on prey population dynamics. Future improvements in battery performance of GPS collars will allow for even tighter monitoring rhythms and surely enhance the suitability of this method for studies on predation of neonate ungulates or mesopredators. As technology for activity sensors advances, studies applying GLC analysis in combination with activity data, as was already done for cougars by Williams et al. (2014) and Wang et al. (2015), could further help to better distinguish true predation events from scavenging and to shed more light on energy requirements and kill rates of Eurasian lynx living in different habitats with different prey communities.

Characterising GLCs containing small prey items and optimising field effort

The second objective of this study was to characterise GLCs containing small prey items. We wanted to investigate whether GLC duration was a good predictor of prey size and whether small prey items were possibly found in less accessible terrain. Although the time a lynx spent in a GLC was correlated with prey size, large prey items were occasionally found in short-lasting GLCs and there was great overlap in GLC duration among prey of different sizes. This may be explained by the fact that lynx family groups utilise prey much faster than single individuals (Jobin et al. 2000). Lynx will also sometimes abandon prey before it is completely consumed or they may lose portions of their prey to scavengers. Small prey was not found in more rugged terrain but at higher elevations than large prey. This correlation was mainly caused by juvenile chamois and marmots, which were found at the highest elevations. The higher proportion of small prey items in the time period from May to August also corresponded to the availability of new-born chamois and marmots during this period. In our Alpine study area, there are many forest roads allowing easy access to high elevations in summer, which enabled us to track the lynx' utilisation of juvenile chamois and marmots. In winter, however, accessing higher GLCs gets extremely time-consuming. Even with a randomised sampling procedure, some GLCs still have to be discarded because they are inaccessible due to the risk of avalanches. Depending on the habitat requirements of potential prey species, prioritising GLCs with certain characteristics may lead to an underestimation of kill rates. For example, killed chamois in our study area were found in more rugged terrain than roe deer (Welch two-sample *T* test, $t = 11.556$, $df = 364.74$, p value < 0.001) and extensive training of field personnel was necessary to ensure that such GLCs could be checked while safety requirements were met.

Our last objective was to find an optimal method to balance invested field effort with the chances of missing (small) prey items using GLC duration as a criterion. Application of the common cut-off value of < 24 h proved to lead to a loss of almost two thirds of small prey animals and a reduction in diet diversity. GLCs with a duration of < 9 h had a detection success of ≤ 25% but still contained 13% of the small ungulates and other small prey items. Short-lasting GLCs are generated by GPS-collared lynx in very high numbers (Fig. 1) and predation events in these clusters are predicted incorrectly by many computer models (Elbroch et al. 2017; Webb et al. 2008). Especially in remote study areas, short-lasting GLCs at high elevations may be the first to be discarded as they require a huge effort while yielding a low detection success. Our results suggest that discarding GLCs shorter than 12 h, 9 h or even 8 h may potentially bias the results of predation studies, while discarding GLCs shorter than 6 h seemed to have less impact on lynx diet composition. However, this cut-off value could be different depending on localisation rhythm, predator type, and prey community and should be revaluated for new studies.

Conclusion

In our study, a resolution of 7 GPS fixes per day with hourly intervals at dusk was sufficient to find prey items weighing between 2 and 10 kg, but also allowed thrifty use of the limited battery resources available. Therefore, GPS location cluster analysis is a very promising tool for exploring predation on new-born ungulates and can help shed more light on energy requirements of large carnivores as well as on predation on mesopredators and other smaller prey animals. However, since detection success in short-lasting GLCs is not easy to predict, substantial field effort has to be invested and unsuccessful GLC searches may also have to be accepted. Discarding short-lasting GLCs in inaccessible terrain (i.e. GLCs formed at high elevations without road access) out of logistic reasons may indeed lead to an underestimation of small prey items in the diet of carnivores.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

References

Andrén H, Liberg O (2015) Large impact of Eurasian lynx predation on roe deer population dynamics. PLoS One 10(3):e0120570. https://doi.org/10.1371/journal.pone.0120570

Von Arx M, Breitenmoser-Würsten C, Zimmermann F, Kunz F, Vogt K, Ryser A, Breitenmoser U (2017) Der Luchs im Jura- unter besonderer Berücksichtigung des Solothurner Juras. Mitteilungen/ Naturforschende Gesellschaft des Kantons Solothurn, 43. https://www.e-periodica.ch/digbib/volumes?UID=ngs-004 (In German)

Bacon MM, Becic GM, Epp MT, Boyce MS (2011) Do GPS clusters really work? Carnivore diet from scat analysis and GPS telemetry methods. Wildlife Soc B 35:409–415

Bartnick TD, Van Deelen TR, Craighead D (2013) Variation in cougar (*Puma concolor*) predation habits during wolf (*Canis lupus*) recovery in the southern Greater Yellowstone Ecosystem. Can J Zoolog 91:82–93

Bates D, Maechler M, Bolker B, Walker S (2015) lme4: linear mixed-effects models using Eigen and S4. R package version 1.1–9, <URL: https://CRAN.R-project.org/package=lme4>. (05/10/2018)

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(9):e0138915. doi: https://doi.org/10.1371/journal.pone.0138915

Breitenmoser U, Breitenmoser-Würsten C (2008) Der Luchs. Ein Grossraubtier in der Kulturlandschaft. Salm Verlag, Bern (In German)

Breitenmoser U, Ryser A, Molinari-Jobin A, Zimmermann F, Haller H, Molinari P, Breitenmoser-Würsten C (2010) The changing impact of predation 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, Oxford, pp 493–505

Elbroch LM, Lowrey B, Wittmer HU (2017) The importance of fieldwork over predictive modelling in quantifying predation events of carnivores marked with GPS technology. J Mammal 99:223–232

Foran DR, Crooks KR, Minta SC (1997) Species identification from scat: an unambiguous genetic method. Wildl Soc Bull 25:835–839

Gervasi V, Nilsen EB, Odden J, Bouyer Y, Linnell JDC (2013) The spatio-temporal distribution of wild and domestic ungulates modulates lynx kill rates in a multi-use landscape. J Zool 292:175–183

Hausser J (1995) Säugetiere der Schweiz. Denkschriften der Schweizerischen Akademie der Naturwissenschaften, Band 103, Birkhäuser Verlag, Basel, pp 203-461 (In German)

Heurich M, Zeis K, Küchenhoff H, Müller J, Belotti E, Bufka L, Woelfing B (2016) Selective predation of a stalking predator on ungulate prey. PLoS One 11:e0158449. https://doi.org/10.1371/journal.pone.0158449

Jobin A, Molinari P, Breitenmoser U (2000) Prey spectrum, prey preference and consumption rates of Eurasian lynx in the Swiss Jura Mountains. Acta Theriol 45:243–252

Klare U, Kamler JF, Macdonald DW (2011) A comparison and critique of different scat-analysis methods for determining carnivore diet. Mammal Rev 41:294–312

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

Knopff KH, Knopff AA, Kortello A, Boyce MS (2010) Cougar kill rate and prey composition in a multiprey system. J Wildlife Manage 74: 1435–1447

Krofel M, Huber D, Kos I (2011) Diet of Eurasian lynx *Lynx lynx* in the northern Dinaric Mountains (Slovenia and Croatia). Importance of edible dormouse *Glis glis* as alternative prey. Acta Theriol 56:315–322

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, Klemen J, Kljun F, Kos I, Potočnik H, Ražen N, Zor P, Žagar A (2014) Comparing patterns of human harvest and predation by Eurasian lynx *Lynx lynx* on Eurpoean roe deer Capreolus capreolus in a temperate forest. Eur J Wildl Res 60:11–21

Linnell JDC, Aanes R, Andersen R (1995) Who killed Bambi? The role of predation in the neonatal mortality of temperate ungulates. Wildl Biol 1:209–223

Lone K, Loe LE, Gobakken T, Linnell JDC, Odden J, Remmen J, Mysterud A (2014) Living and dying in a multi-predator landscape of fear: roe deer are squeezed by contrasting pattern of predation risk imposed by lynx and humans. Oikos 123:641–651

Marucco F, Pletscher DH, Boitani L (2008) Accuracy of scat sampling for carnivore diet analysis: wolves in the Alps as a case study. J Mammal 89(3):665–673

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

Matthews A, Ruykys L, Ellis B, Fitzgibbon S, Lunney D, Crowther MS, Glen AS, Purcell B, Moseby K, Stott J, Fletcher D, Wimpenny C, Allen BL, Van Bommel L, Roberts M, Davies N, Green K, Newsome T, Ballard G, Fleming P, Dickman CR, Eberhart A, Troy S, McMahon C, Wiggins N (2013) The success of GPS collar deployments on mammals in Australia. Aust Mammal 35:65–83

Mattioli L, Capitani C, Gazzola A, Scandura M, Apollonio M (2011) Prey selection and dietary response by wolves in a high-density multi-species ungulate community. Eur J Wildl Res 57:909–922

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

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

Molinari-Jobin A, Molinari P, Loison A, Gaillard J-M, Breitenmoser U (2004) Life cycle period and activity of prey influence their susceptibility to predators. Ecography 27:323–329

Molinari-Jobin A, Zimmermann F, Ryser A, Breitenmoser-Würsten C, Capt S, Breitenmoser U, Molinari P, Haller H, Eyholzer R (2007) Variation in diet, prey selectivity and home-range size of Eurasian lynx Lynx lynx in Switzerland. Wildl Biol 13(4):393–405

Muggeo VMR (2017) Regression models with break-points/ change-points estimation (Version 0.5–3.0). https://cran.r-project.org/web/packages/segmented/segmented.pdf (05/10/2018)

Nilsen EB, Linnell JDC, Odden J, Anderson R (2009) Climate, season, and social status modulate the functional response of an efficient stalking predator: the Eurasian lynx. J Anim Ecol 78:741–751

Palacios V, Mech LD (2011) Problems with studying wolf predation on small prey in summer via global positioning system collars. Eur J Wildl Res 57(1):149–156

R Core Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/. Accessed 14 Nov 2018

Ray R-R, Seibold H, Heurich M (2014) Invertebrates outcompete vertebrate facultative scavengers in simulated lynx kills in the Bavarian Forest National Park, Germany. Anim Biodivers Conserv 37:77–88

Riley SJ, DeGloria SD, Elliot R (1999) A terrain ruggedness index that quantifies topographic heterogeneity. Intermt J Sci 5:23–27

Rühe F, Burmester T, Ksinsik M (2007) Data for estimating eaten prey masses from Eurasian lynx *Lynx lynx* scats in Central and East Europe. Acta Theriol 52:317–322

Rühe F, Ksinsik M, Kiffner C (2008) Conversion factors in carnivore scat analysis: sources of bias. Wildl Biol 14:500–506

Ruth TK, Buotte PC, Quigley HB (2010) Comparing ground telemetry and global positioning system methods to determine cougar kill rates. J Wildlife Manage 74:1122–1133

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. Wildlife 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. 147–153

Schnidrig-Petrig R, Salm UP (2009) Die Gemse- Biologie und Jagd. Salm Verlag, Bern, pp 22 (In German)

Shannon CE (1948) A mathematical theory of communication. Bell Syst Tech J 27:379–423

Soulé ME, Bolger DT, Alberts AC, Wright J, Sorice M, Hill S (1988) Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. Conserv Biol 2:75–92

Stubbe C (1997) Rehwild: Biologie, Ökologie, Bewirtschaftung. Parey Buchverlag, Berlin, pp 44–52 (In German)

Sunde P, Kvam T, Bolstad JP, Bronndal M (2000) Foraging of lynxes in a managed boreal-alpine environment. Ecography 23:291–298

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

Swiss Federal Statistical Office (2015) STAT-TAB: Die interaktive Statistikdatenbank. Ständige und Nichtständige Wohnbevölkerung nach Region, Nationalität und Geburtsort http://wwwbfsadminch Accessed 12 November 2015 (In German)

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

Wandeler A, Huber W (1969) Gewichtswachstum und jahreszeitliche Gewichtsschwankungen bei Reh und Gemse. Revue suisse de zoologie: annales de la Société suisse de zoologie et du Muséum d'histoire naturelle de Genève, 1969/76/3/686 (In German)

Wang Y, Nickel B, Rutishauser M, Bryce CM, Williams TM, Elkaim GH, Wilmers CC (2015) Movement, resting, and attack behaviors of wild pumas are revealed by tri-axial accelerometer measurements. Mov Ecol 3:2. https://doi.org/10.1186/s40462-015-0030-0

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

Williams TM, Wolfe L, Davis T, Kendall T, Richter B, Wang Y, Bryce CM, Elkaim GH, Wilmers CC (2014) Instantaneous energetics of puma kills reveal advantage of felid sneak attacks. Science 346:81–85

Zimmermann F, Pesenti E, Breitenmoser U (2012a) Fotofallen-Einsatz im Aufsichtsgebiet von Erich Peissard im Kanton Freiburg im Winter 2011/12. KORA Bericht zu handen des Kantons Freiburg. http://www.kora.ch/index.php?id=134 (In German)

Zimmermann F, Pesenti E, Mini L, Lanz T, Breitenmoser-Würsten C, Breitenmoser U (2012b) Abundanz und Dichte des Luchses in den Nordwestalpen: Fang-Wiederfang-Schätzung mittels Fotofallen im K-VI im Winter 2011/12. KORA Bericht, 57. http://www.kora.ch/index.php?id=135&L=0. (In German)

Zimmermann F, Foresti D, Bach J, Dulex N, Breitenmoser-Würsten C, Breitenmoser U (2014) Abundanz und Dichte des Luchses in den Nordwest-alpen: Fang-Wiederfang-Schätzung mittels Fotofallen im K-VI im Winter 2013/14. KORA Bericht, 64. http://www.kora.ch/index.php?id=135 (In German)