Use of GPS location clusters analysis to study predation, feeding and maternal behavior of Eurasian lynx

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Abstract Analysis of global positioning system (GPS) location clusters (GLCs) is becoming increasingly popular in studies of carnivore ecology. While promising, this application of GPS technology is still poorly developed for most species. We applied this method to study predation and maternal behavior of the Eurasian lynx (*Lynx lynx*) in Dinaric Mountains. Low population densities, rugged terrain, dense vegetation, and administrative borders make studies of this endangered population using traditional methods and a limited budget very challenging. We used geographic information system (GIS) and linear mixed effects models to understand the movement of lynx during the consumption process and denning period and estimate lynx kill rates. 99% of kills were found at GLCs longer than 30 h and with minimum two locations within 300 m. We confirmed 86% of potential kills and all potential dens that were searched for in the field. High success in predicting kill and den sites showed that Eurasian lynx is a suitable species for application of the GLC analysis methods. Comparison of field-confirmed kills with model predictions showed the possibility for remote estimation of approximate kill

rates in Eurasian lynx. Movements of lynx were primarily affected by daytime period, time since the last kill/den translocation, lynx category and their interactions. Based on the empirical data we programmed simulations of lynx movements and elaborated recommendations for more efficient field procedures and study designs (GPS schedules) for future studies. We believe that our findings and approach will also benefit studies of other species with similar behavior.

Keywords global positioning system, kill rate, *Lynx lynx*, mixed-effects models, telemetry

Introduction

Elusive behavior and low population densities often make large carnivores difficult to study. Among the most important aspects of large carnivore ecology from the conservation and management perspective are predation and reproduction. Kill rates and feeding behavior were traditionally studied using techniques such as direct observations from ground or air (Mills 1992; Literak et al. 2000; Molinari and Molinari-Jobin 2001), tracking in snow or sand (Haglund 1966; Bothma and le Riche 1986), and VHF telemetry (Okarma et al. 1997; Jobin et al. 2000; Odden et al. 2006). Similar methods were used to study maternal behavior and reproduction (Schaller 1972; Bothma and le Riche 1984; Schmidt 1998; Boutros et al. 2007). While these techniques can provide desired results, they are labor-intensive and usually costly. In addition, they cannot be used in all environments, and can be biased e.g. by irregular sampling intervals, habitat variability,

45 unfavorable weather conditions, prey size, and displacements by dominant scavengers
46 (Merrill et al. 2010; Ruth et al. 2010).

47 New technological developments, especially telemetry with global positioning system
48 (GPS) and global system for mobile communications (GSM), have the potential to
49 radically change and improve the way such research is conducted (Tomkiewicz et al.
50 2010). Analysis of GPS location clusters (GLCs) is becoming increasingly popular in
51 studies that deal with locating prey remains of large carnivores. So far this method has
52 been tested for relatively small number of species, e.g. cougars (*Puma concolor*;
53 Anderson and Lindzey 2003; Knopff et al. 2009), African lions (*Panthera leo*; Tambling
54 and Belton 2009; Tambling et al. 2010), and gray wolves (*Canis lupus*; Sand et al. 2005;
55 Franke et al. 2006; Zimmermann et al. 2007; Palacios and Mech 2010; Metz et al. 2011).

56 It was met with variable success, as short feeding times, displacements by dominant
57 scavengers and pack splitting in social carnivores proved to be considerable obstacles for
58 successful detection of kill sites (Webb et al. 2008; Ruth et al. 2010). Although GLC
59 analysis is usually limited to kill rate estimation, it has occasionally been used also for
60 studying other aspects of carnivore ecology, for example detecting mating events (Krofel
61 et al. 2010), dens with offspring (Alfreden 2006), winter dens (pacapan 2012),
62 kleptoparasitism (Mattisson et al. 2011b; Krofel et al. 2012) and conflicts with humans
63 (Jerina et al. 2012).

64 Detailed analysis of prey use and maternal behavior enables successful strategy in
65 searching for prey remains or den sites, which is important for fast detection of prey
66 remains and offspring in the field. This minimizes disturbance to the animals and
67 researcher-related effects on the carcass consumption process and nursing. Better

68 knowledge of feeding behavior also improves efficiency of animal capture for research
69 purposes, which is often attempted at the kill sites in regions where darting from the air is
70 not possible. Battery life span of GPS collars is a common constraint in ecology studies,
71 especially for small and mid-sized carnivores (Mattisson et al. 2010). Therefore the
72 development of efficient GPS fix sampling schedule for given study objective is a crucial
73 part in study design and can strongly affect the amount of collected data.

74 We tested applicability of GLC analysis to study behavior and ecology of the Eurasian
75 lynx (*Lynx lynx*), a mid-sized (12-35 kg) solitary predator. The Eurasian lynx uses
76 denning sites for several weeks and, unlike other members of the *Lynx* genus, hunts
77 relatively large prey (predominantly small ungulates) and spends long periods of time
78 utilizing it (Kos et al. 2005; Breitenmoser and Breitenmoser-Würsten 2008). We
79 expected that these ecological characteristics provide enough time for detectable GLCs to
80 form, which should make the Eurasian lynx a suitable species to be studied using the
81 GLC analysis methods. The low population density, elusive behavior, crepuscular-
82 nocturnal activity, remote and rugged terrain, dense vegetation, and administrative
83 borders often make studies of Eurasian lynx using traditional methods and a limited
84 budget very challenging. Given endangered status of many lynx populations (von Arx et
85 al. 2004), there is a great need for new cost-effective approaches to studying its ecology,
86 especially predation and reproduction. That will provide solid data for conservation
87 management of this species, as misbeliefs about its reproductive rate and impact on wild
88 ungulates seem to be one of the main motives for poaching. Better understanding of GLC
89 analyses will also benefit ecological studies of other mammals with similar behavior that
90 are difficult to study using traditional methods.

In our study we explored usefulness of GLC analysis for locating kill and den sites and use of statistical modeling for gaining additional insights into predation, feeding and maternal behavior of Eurasian lynx. An additional objective of this study was to prepare recommendations for future ecological studies on this predator and other species with similar behavior.

We (1) explored the factors that best predicted the presence and location of a kill site and (2) modeled how different parameters affected distance of lynx to the prey during prey utilization. We (3) used these data to program simulations of lynx movement around the kill sites to explore how different GPS sampling regimes and GLC duration affect GLC analysis, and elaborated clear rules for kill site detection. We also (4) explored the possibility of estimating lynx kill rate with minimizing visits to the field (“remote predation monitoring”). In addition, we (5) used modeling approach to determine how different parameters predict den site locations and to better understand development of the nursing behavior. Based on this, we (6) provided recommendations to improve study design (GPS fix sampling schedules) in future studies and demonstrated applicability of GPS-GSM telemetry, GLC analysis and mixed-effects modeling approach for studying ecology of an elusive predator in an environment challenging for studies using traditional methods.

Study area

The study was conducted in the northern part of the Dinaric Mountain Range (Central and Southeastern Europe), in Snežnik-Javorniki and Kočevska regions of Slovenia and Gorski Kotar region of Croatia (45°24'–45°47'N and 14°15'–14°50'E). This study area is divided by the national (and European Union) border. The altitudes range from

114 approximately 150 m to the peak of Mount Snežnik at 1,796 m. Limestones and
115 dolomites are the prevailing geological foundation in the area, forming a characteristic
116 rugged relief with numerous karst phenomena (cliffs, dolines, collapse dolines, caves,
117 vertical shafts, steep canyons etc.). Surface water is rare, as water runoff is largely
118 underground. The climate is a mix of influences from the Alps, the Mediterranean sea
119 and the Pannonia basin with annual temperature averaging 5–8° C, ranging from average
120 maximum of 32° C to a minimum of –20° C, and average annual precipitation of 1400–
121 3500 mm. Most of the area is covered by Dinaric fir and beech forests (Omphalodo-
122 Fagetum s. lat.), with four dominant tree species: common beech (*Fagus sylvatica*), silver
123 fir (*Abies alba*), Norway spruce (*Picea abies*), and sycamore maple (*Acer*
124 *pseudoplatanus*). The area is mostly uninhabited, with scattered villages dotting the
125 valleys.

126 Dinaric lynx population is one of the most threatened populations of Eurasian lynx. It is
127 rapidly declining and today the Eurasian lynx is considered the most endangered mammal
128 in the region, with estimated 20–40 animals left in Slovenia and 40–60 in Croatia
129 (Sindičić et al. 2009). In this area lynx hunt mainly wild ungulates, which together
130 represent 88% of biomass consumed by lynx. Roe deer (*Capreolus capreolus*) is the main
131 prey species (79% of consumed biomass), and edible dormouse (*Glis glis*) and red deer
132 (*Cervus elaphus*) the most important alternative prey, each representing approximately
133 7% of consumed biomass (Krofel et al. 2011). Besides Eurasian lynx, brown bear (*Ursus*
134 *arctos*) and gray wolf are present in the area, as well as several species of smaller
135 carnivores. The most important scavenger in the area is brown bear, which lives here in
136 high population density (Skrbinšek et al. 2012) and displaces lynx from about one third
137 of its kills (Krofel et al. 2012).

138 **Methods**

139 *Lynx capture and telemetry*

140 We captured the lynx in box traps set at animal trails known to be used by lynx through
141 snow tracking. The traps were made of wire mesh, had double falling doors and were
142 triggered when an animal tripped the trigger thread crossing the middle of the trap. We
143 did not bait the traps with food to avoid trapping bears and other non-target species, but
144 occasionally sprinkled them with some lynx urine obtained during snow tracking. The
145 traps were equipped with alarm systems (PKN4 Nautilus, Pinkerton, Slovenia) that sent a
146 message through the GSM network when a trap was sprung, providing immediate
147 notification of a capture event. Trapping was done year-round between 2006 and 2010,
148 however lynx were captured only during winter and spring.

149 We immobilized the lynx using a combination of Medetomidine and Ketamine. A
150 veterinarian was present at each capture, and the animal was closely monitored
151 throughout the anesthesia. We fitted the captured lynx with GPS collars with remote
152 GSM download technology and a programmable drop-off system (3 collars from TVP
153 Positioning AB, Sweden on the two females and one male and 1 collar from Vectronic
154 Aerospace GmbH, Germany on the second male). We programmed the collars to attempt
155 7–8 GPS fixes per day: 1–2 during daytime, 1–2 at dusk, and 3–5 during the night. The
156 schedule was weighted towards the night as a trade-off to extend the battery life since our
157 previous studies (Krofel et al. 2006) showed that lynx tend to return to the prey mainly at
158 night.

159 *Locating prey remains*

160 We used a geographic information system (GIS – ArcGis Desktop, ESRI, Redlands, CA,
161 USA) to analyze GPS locations as they were received via GSM network and visually
162 identified all aggregations – GLCs (Merrill et al. 2010). Previous experiences from VHF
163 telemetry studies on Eurasian lynx (Jobin et al. 2000; Krofel et al. 2006) showed that a
164 GLC can be considered a potential ungulate kill site when a lynx remains within an
165 approximately 200 m radius for more than 6 h during the night. However, we also
166 explored several shorter and more dispersed GLCs in order to develop robust rules. We
167 defined a GLC as a potential ungulate kill site when at least two locations were detected
168 less than 300 m apart within the time frame between them of more than four hours and
169 less than three days (i.e. interval between locations of GLC could be more than three
170 days, but at least two of them should be recorded within three day time span). All
171 locations recorded in the time interval between the first and the last visit of the lynx to the
172 confirmed kill site were regarded as a part of the GLC, even if some of them were located
173 more than 300 m from the kill site.

174 When a potential kill site was detected, we field-checked the site looking for prey
175 remains (median 4.5 days after the kill). We used a handheld GPS to first search the area
176 around the center of the GLC, and continued in the areas within a 150 m radius of each
177 cluster location. Unless prey remains were found earlier, we searched for a minimum of
178 two man hours (i.e. one person searching for 2 h, 2 persons for 1 h and so forth). If the
179 area was particularly rugged or densely vegetated, the search was extended. Upon finding
180 the prey remains we recorded the GPS coordinates of the kill site. If we observed that the
181 lynx or scavengers had been moving the prey, we took the coordinates of the estimated
182 kill site – usually indicated by tracks, hair, blood, or a heap from the first covering of the

prey by the lynx. As scavenging is very rare among Eurasian lynx (Krofel et al. 2011), we regarded all carcasses detected at GLCs as lynx kills.

Predicting kill sites and modeling lynx movement during the feeding period

We used GIS to analyze movement of the tracked lynx while they were using prey remains confirmed in the field. We analyzed several parameters of GPS locations during the prey consumption process (i.e. within defined GLC) to gain detailed insights into lynx feeding behavior and determine if any of these parameters could be used for predicting whether certain locations are more likely to be present at the actual kill site than the others. For each location recorded during the consumption process we measured the time elapsed since the estimated time of the kill, as well as the distance, the difference in elevation (GIS data with 5 m contour lines were used), and the closest cardinal or intermediate direction (W, NW, N, NE, E, SE, S, SW) in relation to the kill site. Locations were classified with regard to the lighting conditions as night, twilight, and day. Day was defined as the time between sunrise and sunset, twilight as the time between sunrise or sunset and the beginning or end of nautical twilight, and night as the time between the end and the beginning of nautical twilight. Times for sunrise, sunset, beginning, and end of nautical twilight were calculated for our study area for each day of the study using the tools available from the Naval Oceanography Portal (<http://www.usno.navy.mil>).

All statistical analyses were done in R statistical environment (R Development Core Team 2011). We used Wilcoxon paired samples test to compare minimum and maximum distances between GPS locations in a GLC and the actual kill site. We used linear mixed effects models (R package nlme; Pinheiro et al. 2011) to understand how different

parameters predicted lynx distance from the prey while it was utilizing it. The unit of replication was a single distance from the actual prey location calculated for each GPS location of the animal. A set of biologically feasible hypotheses and corresponding models was constructed to form an a priori model set (Burnham and Anderson 2002). Lighting conditions (day, night or twilight), time elapsed since the kill, category of the animal (adult female or subadult male), individual lynx, whether the lynx had kittens and if the kittens were immobile at the time of the kill were used as explanatory variables. Kittens were identified as immobile while the female was returning to a den site – until 1 August 1 or 14 July, respectively for each of the two females. To keep the number of parameters in the models manageable, the levels in these categorical variables (category of the animal, presence and mobility of kittens) were grouped in different manners to form biologically feasible hypotheses with regard to the effect on movement around prey (group 1: single female or mobile family, immobile family, subadult male; group 2: adult female, immobile family, mobile family, subadult male), and these groupings were used to construct different sets of models. Similarly to the animal category, the models were also constructed with lighting conditions levels grouped, with twilight modeled as day or night, respectively. We used scatter plots and Cleveland dot plots paneled by levels of categorical variables to detect outliers. Extreme data points with high leverage were closely inspected and corrected (in case of data manipulation or entry errors) or removed after careful consideration if they seemed to be genuine outliers (possibly incorrect GPS fixes or solitary “excursions” that considerably deviated from the general pattern). As locations in a GLC around an individual kill are not independent, individual kill was used as a categorical random effect variable fitted into the intercept. We checked for independence assumption using temporal auto-correlation function (ACF) as suggested

by Zuur et al. (2009) and included error structure in the model. We checked for heterogeneity in the data by plotting residuals against fixed effects variables and included correction in the model error structure (Zuur et al. 2009). Second-order Information Criterion (AICc) with restricted maximum likelihood (REML) for parameter estimation and the maximum fixed effects model were used to select optimal random effects structure. We also compared the models that included random effects with a generalized least squares model without random effects and the same fixed effects structure. Inference was based on model selection using the information theoretic approach (Burnham and Anderson 2002). AICc with maximum likelihood parameter estimation was used for model selection. Difference in AICc was used to compare the competing hypotheses or models and select the model that was best supported by the data. Sets of models structured with different groupings of categorical variables were compared according to their AICc rankings, and the model set with the highest ranking models was selected. Within that set the models with $\Delta AICc < 4$ were averaged according to Akaike weights (Burnham and Anderson 2002) using the R package MuMIn (Bartoń 2010) to estimate average parameters and their relative importance. The average model was used for plotting of model predictions and effect sizes.

GPS location clusters simulations and rules for detection of kill sites

We tried to understand how the number of locations available in a GLC (function of sampling rate and duration of prey utilization) and the threshold distance between the locations (at what distance are two locations defined as a GLC) affect detectability of a kill site in order to produce the most efficient GPS fix sampling schedules for future predation studies using GPS telemetry.

We simulated movement of lynx around a kill site using the empirical data from the monitored lynx. All simulations were programmed in R statistical environment. To construct a simulated GLC, we bootstrap re-sampled locations belonging to real GLCs around detected kill sites. We simulated two days of lynx utilizing the prey with different numbers of locations per day and two sampling schedules – one when sampling was uniformly distributed throughout the 24-hour period, and one when sampling done was only at night. For the simulated day period the locations were re-sampled from the actual locations of lynx around each prey collected during the day, and for the simulated night period from the locations collected during night and twilight. The time of each location was taken uniformly from the 24-hour period or only from the 12-hour simulated night period, respectively. We calculated pairwise distances for each pair of locations in a simulated GLC. We varied the maximum threshold distance between two points that still assigns them to the same GLC and the number of locations per day, and calculated the proportion of simulated kill sites that would be detected under each sampling regime. Increasing the distance threshold increases the possibility of creating the error of commission – calling a GLC when there is actually no prey. On the other hand, decreasing this threshold increases the probability of missing an actual GLC (error of omission). The idea of the simulation was to find the minimum distance threshold that would still reliably detect a GLC given a certain number of locations per day. We made 1000 iterations for each combination of these two parameters, and used the observed GLC duration (30 h) above which we found 99% of prey remains as a minimum duration of a GLC that would still be considered a kill site.

We programmed a similar simulation to understand how the sampling rate affects detectability of kill sites with regard to the duration of the lynx using the prey. Instead of

using the locations around each prey to produce simulated GLCs, we re-sampled the observed distances of lynx to prey, also taking into account the different movement of lynx with regard to the daylight period. For each re-sampled distance we selected a random point on a circle that had a center in the simulated “kill site” and the observed distance to the prey as the circle’s radius. We used the distance and time thresholds observed in the real data for two GPS locations to be considered to belong to the same GPS cluster. We varied the number of GPS locations per day (sampling rate) and the duration of lynx’s feeding on the prey with 1000 iterations for each combination of these two parameters, and observed the proportion of detected kill sites.

Estimating feeding time, searching time and kill rate

The feeding time at each prey (rounded to the closest 12 hour period) was calculated as the time period between the estimated time of killing and until the lynx left the carcass without returning (time of departure). If there was a time gap with no successful GPS fixes between the last on-kill location and the first location after departure, we used the mean time between these two locations as the time of departure. If this gap was longer than 24 h, the data were excluded from further analysis. The same approach was used for the time of killing. We excluded the data for certain kills when it seemed that the lynx left the carcass as a result of human disturbance (e.g. during recapture attempts to change the collar). Similar to the feeding time, we estimated the searching time defined as the time between leaving one prey and killing the next one. It was calculated using only the data for confirmed consecutive prey remains between which there was no potential kill site. We calculated kill rate (the number of ungulates killed per time unit) from the average time interval between the two consecutive killings (feeding time + searching time). If

there was a GLC indicating potential kill site, but no prey was found or the GLC was not inspected in the field, we terminated the kill series and started from the beginning after the next confirmed kill (similar to Okarma et al. 1997 and Molinari-Jobin et al. 2002). The calculated kill rate refers only to killed ungulates, as smaller prey was difficult to detect and because it is predation of ungulates that is usually considered most important from management and conservation perspective. We grouped the data from the monitored lynx into three categories: family groups (females with mobile kittens), single females (females without offspring or with immobile kittens), and subadult male lynx. Kruskal-Wallis rank sum test was used for testing differences in feeding and searching times and kill rates between different lynx categories.

To explore the possibility of calculating the kill rate based only on the GPS location data without field-checking, we produced a simple rule-based model for detecting GPS location clusters from the empirical data. We compared the kill rates obtained using “remote” kill site detection with the kill rate calculated only from the data confirmed in the field.

Monitoring of nursing behavior

During the time of parturition (May–June; Kos et al. 2005) and in the following months we defined the GLCs in radius of 200 m to which female lynx were returning for more than five days as potential den sites, according to previous experiences from VHF telemetry studies (Schmidt 1998; Boutros et al. 2007). As a rule, we waited until we estimated that the kittens were at least three weeks old before we tried locating them in the field. To minimize disturbance, we visited each litter only once. Other den sites of the same litter were not visited and were identified on basis of GLCs alone. Based on GPS

locations we estimated the time period during which each den site was used and the distances between consecutive den sites.

To improve predictions of den site locations and to explore possibilities of studying maternal behavior in Eurasian lynx, we modeled the effects of various parameters on the distance of the females to the den site during the denning period (the time period between birth and until the kittens started to follow their mother) using a similar approach to the one we used for modeling lynx behavior during prey utilization (linear mixed effects models and information-theoretic approach to model selection and inference). The unit of replication was a single distance from the den location calculated for each GPS location of the animal. The response variable was the distance to the den site, and fixed effects were time since birth, time at the current den site (i.e. time since birth for the first den site or the time since the last change of den site), lighting conditions and individual lynx. Individual den sites were fitted into the intercept as a categorical random effect variable. Corrections for heterogeneity of variance and violations of the independence assumption were included in the error structure using the same procedure that was used to model lynx movements around kill sites.

Results

Between 2006 and 2010 we captured and radio-collared 4 lynx, 2 adult females and 2 subadult males. We monitored each lynx for an average of 219 days (range 108-285 days). In total 2730 successful GPS fixes were obtained (380-979 per lynx) with average GPS fix success rate of 56%. GPS fix success rate was 24% lower during the denning period of females and 22% higher for the Vectronic collar.

Success rate of finding lynx kills in the field

We searched for lynx prey remains in the field at 101 GLCs with time spans between the first and the last location of the cluster from 3 to 170 h ($\bar{x}$ =65.6 h, SD=39.2 h, median=60.0 h). We found ungulate prey remains (n=72) at GLCs almost exclusively when the time span was 30 h or more. Only in one case we found prey remains at a GLC where lynx spent 12 h. There was evidence at this kill site suggesting that the scavengers (probably brown bear) removed the carcass soon after the kill. Success rate of searching for lynx prey remains at GLCs with time span of 30 h or longer (n=83) was 86%. For GLCs with locations >30 h apart, the time span of the cluster had little effect on prey finding success rate, which was the highest at the time interval 80–99 h (Fig. 1).

Actual locations of prey within the GLCs

We analyzed 818 GPS locations of lynx while they were feeding on prey remains that were confirmed in the field. Nineteen locations were removed as outliers after initial data exploration. We measured the distances of the actual location where the prey was found to individual GPS locations in the GLC around that prey, and to the mean center points of all locations and all night locations in the GLC. The median distance to the mean center of all points in each cluster was 67 m (interquartile range[IQR]=240 m, range 4–954 m), larger than the median distance for night locations (48 m, IQR=49 m, range 6–771 m, paired-samples Wilcoxon test, n=64, V=1490, P<0.001). The distances from the kill site to the closest night location (n=64) were more than 3-times smaller than the distances to the closest day location (n=58, V=206, P<0.001) and similar to the distances to the closest twilight location (n=39, V=308, P=0.26; Table 1). The same pattern was observed for farthest locations within the GLC to the kill site (night vs. day: V=341, P<0.001; night vs. twilight: V=352, P=0.6; Table 1).

For locations when lynx was not present at prey (>30 m from the kill site), we did not observe any trend regarding the elevation (median difference to the kill site=0 m; n=544). However, during day lynx did tend to move to locations that were somewhat higher, on average for 52.2 m (median=10 m) above the kill site. Daytime locations were also on average 39.2 m higher than night locations (n=450, Wilcoxon rank sum test, W=27720, P<0.001) and 39.4 m higher than twilight locations (n=250, W=8218, P=0.02). Compared to random locations, lynx preferred to move toward the northern directions (N, NW, NE) from the kill site (n=539, $\chi^2=21.66$, df=7, P=0.003; Fig. 2). The selection was even stronger at individual kill sites, as lynx often moved away into the same direction, so that in 56% of kills more than half of all locations were in the same direction from the kill site.

Modeling lynx movement during the feeding period

We used the maximal fixed effects model to explore the impact of different random effects variables and variance covariates on the model fit. When modeling distance of the lynx to the kill site as the response variable, including individual GLC in the model as a random effect variable considerably improved the model fit ($\Delta\text{AIC}=40.5$). The variance in distance to the kill site was not constant, as the lynx made further and further excursions from the kill as the time passed, and we included the variance structure with time elapsed since the kill ($\Delta\text{AIC}=38.4$), daylight period ($\Delta\text{AIC}=537.4$), and lynx category ($\Delta\text{AIC}=310.4$) as variance covariates. The ACF plots showed temporal autocorrelation in the data, and we included the residual correlation structure with time since the kill as a covariate ($\Delta\text{AIC}=50.6$). We included 73 models in the a priori model set. All models within $\Delta\text{AICc}<10$ from the best model included the time elapsed from the

kill and daylight period (day, night or twilight). The best supported group of models were the models that included the category of the lynx as group 1 (adult female with mobile or no young, adult female with immobile young, subadult male) as the overall best model and 3 out of 5 models with $\Delta AICc < 4$ belonged to this group. We constructed an average model using Akaike weights (Burnham and Anderson 2002) using the three best models ($\Delta AICc < 4$), which had together 99% of support in the data. There was no observable pattern in the model residuals plotted against explanatory variables. The fixed effects included in the average model were the category of the lynx, the daylight period, the time elapsed since the kill, and 2-way interactions daylight period $\times$ lynx category (the differences in the lynx response, distance to the kill site, between lynx of different categories with regard to the specific lighting conditions), daylight period $\times$ time since the kill (the differences in the lynx response to different lighting conditions with regard to the time passed since the kill) and lynx category $\times$ time since the kill (the differences in response of different category of lynx to the time passed since the kill) (Table 2).

The daylight period variable had a 1.0 relative variable importance (proportion of models that include this variable weighted by Akaike weights; Burnham and Anderson 2002).

Likewise were the models that included twilight much better supported than models that had twilight modeled as either a part of the day ($\Delta AICc \geq 29.0$) or the night

($\Delta AICc \geq 20.09$). The lynx tended to return to the prey at night, and stayed further away

during the day, with twilight somewhere in between (Fig. 3). Category of the lynx also

had considerable explanatory value (relative variable importance 1.0), as had the

interaction between daylight period and lynx category (relative variable importance 1.0).

The females with immobile kittens tended to move further away from the prey than

females with mobile kittens or solitary females. The daylight period had more effect on

the females, especially while they had immobile young, than on the subadult males. The subadult male lynx generally kept close to the prey for the entire duration of feeding (Fig. 3). Other important explanatory variables were the time elapsed since the kill (relative variable importance 0.87), the interactions of this variable with the daylight period (relative variable importance 0.56), and the lynx category (relative variable importance 0.55). The lynx tended to stay closer to the prey immediately after the kill, but were found increasingly further away, especially during the day, as the time progressed (Fig. 3). This effect was especially pronounced in the females with immobile kittens, but practically non-existent in the subadult male (Fig. 3).

Simulations and rules for detection of kill sites

We used the 30-hours GLC duration threshold, as was observed in the studied lynx, as a minimum for a GLC to be considered a ungulate kill site, and simulated lynx using the prey for 48 h. Fig. 4 shows the probability of detection of a GLC with regard to maximum distance threshold between two locations below which they were considered to belong to the same GLC and the number of successful GPS fixes per day. The probability of detecting a GLC did not change much if the maximum distance threshold between two locations was higher than approximately 200–300 m. There was a difference in the number of successful GPS fixes per day required to detect the GLC if sampling was done through the entire day versus the sampling scheduled only during night and twilight. While two successful locations per day were required to detect a 48-hour cluster with 95% probability at the 300 m cluster threshold using only night and twilight locations, the same result required almost four successful locations if the GPS locations were taken throughout the day.

We used the 300 m / 30 h thresholds to detect the simulated lynx kill sites and calculated the proportion of them that would be detected with regard to the GPS schedule and the time the lynx is utilizing its prey (Fig. 5). A GPS schedule with two night GPS locations or four locations spread through the entire day will detect kill sites that are visited for at least two consecutive days (cluster duration 45 h or 50 h for day or night locations, respectively) with 95% probability.

Feeding time, searching time and kill rate

The lynx on average stayed with the prey for 3.15 days (SD=1.39, range=0.5–6 days, n=68). Feeding times were the shortest for family groups ($\bar{x}$ =2.43 days, SD=0.95 days, n=22), intermediate for single females ($\bar{x}$ =3.16 days, SD=1.42 days, n=31) and longest for subadult males ($\bar{x}$ =4.70 days, SD=1.25 days, n=10; Kruskal-Wallis χ^2 =14.58, P<0.001).

Mean searching time lasted 3.68 days (SD=2.82, range: 0–12.5 days, n=57). Similar to feeding times, we also observed differences between different categories of lynx in the searching times, although we were not able to show statistical significance. The searching times were the shortest for family groups ($\bar{x}$ =2.71 days, SD=1.64 days, n=21), intermediate for single females ($\bar{x}$ =4.08 days, SD=3.19 days, n=26) and the longest for subadult males ($\bar{x}$ =4.65 days, SD=3.40 days, n=10, Kruskal-Wallis χ^2 =2.99, P=0.22).

To calculate lynx kill rates, we used 72 confirmed kills. They formed 16 kill series, which lasted between 2 and 64 days ($\bar{x}$ =23.5 days, SD=17.1 days) and were composed of 2–10 consecutive kills ($\bar{x}$ =4.5, SD=2.4). The mean kill rate was 1 ungulate killed every 6.63 days (SD=3.20 days). This corresponds to 55.1 ungulates killed per year per lynx. Kill rates were the highest for family groups ($\bar{x}$ =1 ungulate killed every 5.00 days, SD=1.94

days), intermediate for single females ($\bar{x}$ = 1 ungulate killed every 6.80 days, SD=3.00 days) and the lowest for subadult males ($\bar{x}$ = 1 ungulate killed every 9.10 days, SD=3.99 days, Kruskal-Wallis $\chi^2_2 = 8.07$, $P=0.018$).

We used the model proposed above (min. 2 locations closer than 300 m within minimum of 30 h) to produce a GPS-only kill rate without taking into account whether kills were confirmed in the field or not. The GPS-only kill rate was calculated from 12 kill series during 558 monitoring days with 102 potential kills (i.e. 42% more kills than the kills confirmed in the field). This kill rate for all lynx was 1 ungulate killed every 6.34 days (SD=3.32 days), 4.4% higher than the kill rate estimated using only the field-confirmed data, and the difference did not show statistical significance (Wilcoxon rank sum test, $W=2190.5$, $P=0.55$). Looking only at kills that were not confirmed in the field ($n=36$), which can be considered independent data, the kill rate was 1 ungulate killed every 5.83 days or 12.0% higher than for the field-confirmed kills, and also not showing statistical significance ($W=804.5$, $P=0.21$).

Monitoring of nursing behavior

We located six potential den sites from GLCs, three for each female. One site for each female was visited and on both occasions we found lynx kittens. One female gave birth to two kittens, one male and one female probably on 10 June 2007. The second female also gave birth to two kittens (gender unknown) on 11 May 2008. All visited den sites were located under large boulders in rugged, karstic terrain.

GPS locations showed that each female used three different dens in a season. Consecutive den sites were 110–2313 m apart (median=645 m; six den sites, four translocations). For both females the distance of the first translocation was smaller than the second

translocation. Individual den site was used for 5–39 days ($\bar{x}$ = 19.8 days, n=6). The females stopped returning to permanent dens when kittens were 53 or 66 days old, respectively.

During the denning period the median distance of females to the den site was 627 m (IQR=1853 m, range 0–5799 m, n=284) and 27.8% of all GPS locations (n=284) were located at the den site. This percentage was higher for day locations (53.3%, n=75) than for twilight (24.0%, n=75) and night locations (15.7%, n=134). The situation was similar with distance to the den site, and the lynx were closer to the den site during the day (median=63 m, IQR=922 m, range 0–5799 m, n=75) compared to twilight (median=679 m, IQR=1295 m, range 0–5609 m, n=75, Wilcoxon rank sum test, W=1974, P=0.002) or night locations (median=1048 m, IQR= 1838 m, range 0–5772 m, n=134, W=2891, P<0.001).

In modeling movement of females during the denning period (distance of the female to the current den), the models that included individual den as a random factor were much better supported by the data (ΔAIC =24.1) than the maximal model that included only the fixed effects. Nine outliers were removed from the data. The time since establishment of a den (date of translocation to a new den or parturition date for the first den) was used as a covariate to describe variance and correlation structure, which considerably improved the models (ΔAIC_c =143.5 or ΔAIC_c =14.5, respectively). An a priori set of 26 models was constructed (Table 3).

The models that used the time since establishment of a den to explain the distance of a female to the den site were considerably better supported than the models that used only the time since birth instead ($\Delta AIC_c \geq 12.1$). The time since birth parameter was included

in a model with some support in the data ($\Delta AICc=1.31$, Table 3) besides the time since establishment of a den, but was not present in the best model. All models with $\Delta AICc<10$ included the time since establishment of a den parameter and the daylight period. The best model also included the interaction between these two parameters. Females tended to stay closer to the den site during the day than during the night or twilight. Also, the distances of excursions from the den increased with the time passed since the den was established (Fig. 6). The model that had the individual lynx included as a fixed effect had some support in the data ($\Delta AICc=1.7$), but this parameter also wasn't included in the best model.

Discussion

Our study demonstrated usefulness of GPS locations cluster analysis and mixed-effects modeling approach for studying of foraging and maternal behavior of Eurasian lynx, even in difficult to access areas, across national borders and with small research budgets. Our results also indicated that once the basic parameters that define a GLC indicating a kill site are known, remote predation monitoring can be used to calculate approximate kill rates for large prey even without searching for further prey remains in the field. Lynx, similar to many other felids, follows a relatively simple and predictable pattern of moving, killing prey, staying close to the kill site for several days, and then moving on in search for the next prey. This pattern is clearly observable from GPS telemetry data, and such remote monitoring can be important when opportunities for intensive field work are limited. Nevertheless, similar to the conclusions of researchers studying cougars (Knopff et al. 2009; Ruth et al. 2010), we recommend that at least a sample of potential kill sites

is visited in the field, especially if field data is not available for the specific population, habitat, or animal category and when precise kill rate values are needed.

We were able to find ungulate prey remains at 86% of GLCs defined as potential kill sites. The success rate of finding prey remains could possibly be further increased with use of dogs, which has been proven useful in some previous studies (e.g. Jobin et al. 2000; Krofel et al. 2006). We believe that a kill was also made in the majority of other cases where the prey remains were not found. Even after hours of searching it is easy to miss some of the prey remains in the rugged terrain with dense vegetation, especially if they were consumed or removed by scavengers. Since it is impossible to confirm with absolute certainty that a given location does not contain a kill, the errors of commission (i.e. incorrectly identifying a non-kill cluster as a kill) can be a problem when using the GLC method for detecting kills, especially in species with short feeding times (Webb et al. 2008; Knopff et al. 2009; Merrill et al. 2010). However, for the Eurasian lynx the time threshold defining a GLC as a kill (30 h) was high enough to minimize this kind of error, since it is difficult to expect a lynx to remain stationary for such a long time without either having a prey, kittens, or a major injury (in the latter two cases this should become visible in the subsequent movement pattern). During several years of our studies of the Eurasian lynx (including intensive snow tracking and VHF telemetry) we have never observed any other reason that would cause a lynx to remain stationary for so long, and we are not aware of such a case from the literature. If GLCs without a confirmed prey were coincidental and not connected with kills, dens or injury, the success of finding prey remains should increase with the duration of the GLC, as proportion of such chance GLCs should decrease. Our data did not show this pattern, as the success rate of finding the prey was approximately the same for all GLCs that lasted more than 30 h regardless

of the duration of the cluster, even for GLCs lasting more than five days (Fig. 1). We conclude that the probability of commission errors appears to be very low for Eurasian lynx and should not importantly affect the results.

We observed that large scavengers, like brown bears and wild boars (*Sus scrofa*), often consumed the entire carcass or dragged it several hundred meters away. Although in such cases there were usually some traces remaining, like bone fragments, blood, hair or heaps of litter made from covering of the prey by lynx, these kill sites were more difficult to find. Therefore lower proportion of kills removed by dominant scavengers is probably found in the field compared to the kills that were not usurped by scavengers. Because predator's average feeding time and interval between the kills can be considerably shorter for kills usurped by dominant scavengers (Krofel et al. 2012), analysis of GLCs based only on GPS data might give even less biased estimate of kill rate compared to approach when only kill intervals between GLCs with confirmed kill sites in the field are taken into account. In our case, this might be indicated by the somewhat lower kill rate estimates when only the data from the kills confirmed in the field were used. However, the kill rate calculated only from GPS data might also be underestimated when dominant scavengers displace the predator from the kill in the early stages of the consumption process, so that the predator abandons the kill before detectable GLC can be established. This potential bias must be taken into account when using GLC analysis to study predation, especially in areas with presence of large scavengers, like ursids. Ruth et al. (2010) proposed collaring all potential competing carnivores in the area or direct observations of kill sites to record displacement frequency and reduce biases due to scavengers. Unfortunately, this is usually impossible for studies with limited budget, especially in areas with high density of dominant scavengers (e.g. up to >20 bears/100 km² in Slovenia; Jerina et al.,

unpublished data) and high vegetation cover that prevents direct observations. In such cases we recommend that additional study is made (e.g. with the use of automatic video monitoring of simulated kills; Smole 2012) that will provide data to calculate probability of carcass removal in early stages of prey consumption and accordingly correct the kill rate estimates.

Field visits are important to collect data about the species spectrum, demographic structure, condition of killed prey, etc. (Knopff et al. 2009). However, for such studies attention must be paid that smaller prey is more difficult to find with the use of GLCs compared to large prey (Palacios and Mech 2010; Mattisson et al. 2011a). Therefore we recommend a combination of GLC analysis with diet study using scat and/or stomach content analysis to determine relative importance of small and large prey (e.g. see Krofel et al. 2011).

Using modeling approach to determine the thresholds defining whether a GLC represents a kill site or not, we were able to increase success rate of finding ungulate kills compared to the study of lynx predation on semi-domestic prey in Scandinavia (Mattisson et al. 2011a), thus reducing time and costs needed for the field work. Success rate of locating lynx kills in our study was similar to the success reported for cougars (Anderson and Lindzey 2003; Knopff et al. 2009) and higher than that reported for social carnivores like grey wolves (Sand et al. 2005; Webb et al. 2008; Palacios and Mech 2010) and African lions (Tambling et al. 2010). It should, however, be taken into account that the definition of a cluster as well as the interval between consecutive GPS fix attempts varied considerably between the studies. Lower success in some of these studies can probably also be attributed to the considerable time that passed between the kill and the search for

prey in the field, which was in our case short because of the near real time data transfer via GSM (in contrast to store on board or remote download), and to the shorter feeding times of gray wolves and African lionesses compared to the Eurasian lynx and cougars. Our study together with previous works on cougars (Anderson and Lindzey 2003; Knopff et al. 2009) indicates that the GLC analysis method seems to be most suitable for studies of solitary predators (typically felids) that hunt large prey which is then being utilized for several days.

GPS telemetry data collection enables many opportunities to gain detailed insights into several aspects of foraging behavior of monitored animals. For example, we observed that lynx tended to be closer to the kill during the night and in twilight and moved further away during the day, frequently in the same direction in consecutive days and to higher ground. The distance from the kill also increased with the time elapsed since the kill, which may be attributed to increasing motivation for hunting as the prey was getting consumed.

The GLC analysis proved to be very effective also for finding den sites with immobile kittens, as the return pattern of female lynx during that time is very clear. Although we were able to work only with a small number of animals and den sites, the patterns observed were very similar for both individuals. There was a notable difference in movement of female lynx during consumption process in time of denning (Fig. 3). While their kittens were immobile, the females were frequently found further away from the kill compared to when they were alone or had mobile kittens, as they kept regularly returning to the den site. This was particularly the case during daytime, when the females spent a lot of time at the den site (53% of successful GPS locations). Similar to observations in

Scandinavia (Krofel et al. 2007; Mattisson et al. 2010), we noted that GPS positioning success rate decreased during the denning period, probably because of the poorer satellite visibility while the females were inside the den. This makes it quite possible that the proportion of time spent with cubs is underestimated when GPS locations alone are used. Intensive VHF telemetry monitoring of den site attendance (e.g. Schmidt 1998) should possibly give less biased data.

All ungulate kills detected in our study during denning period were located between 1 and 2.5 km from the den. It is difficult to assess from our data whether this was a coincidence, but such behavior made it possible for the females to feed without abandoning kittens for too long and at the same time avoid attracting potentially dangerous scavengers too close to the kittens. With time, the females' locations and the kill sites were found increasingly further away from the den. This could be partly explained by the kittens becoming increasingly independent and able to be left alone for longer periods. However, the analysis showed that the movement of the tracked females is better explained by the time since the last change of the den than by the date of parturition. A tempting explanation would be that prey depletion around the den might be a more important stimulus for a change of the den site, but this can't be confirmed from our data and further studies are needed to test this hypothesis.

As the Dinaric lynx population is small and possibly heading towards extinction, these animals were very difficult to capture. Consequently, our study included a small number of animals. As such, the results should be used with caution and cannot be generalized to all Eurasian lynx in the Dinaric landscapes.

Recommendations for future studies

We have observed that four successful GPS locations per day, or two per night, are enough to reliably detect a GLC at the kill site in Eurasian lynx. The GPS positioning success rate should however be taken into account (in our case 56%) when programming the collars. If detection of prey remains is critical for the main goal of the study, the GPS schedule can be adjusted to collect the majority of locations at night, which increases the chances of detecting a GLC representing the kill site, makes looking for prey remains easier and increases the life span of the collar battery. On the contrary, the day locations seem to be more useful for detection of den sites, as females tend to keep closer to the den during the day, so it may be useful to modify the location schedule during the denning period. When scheduling the collar in order to estimate kill rates, we also recommend higher frequency of GPS fix attempts during the denning period due to lower GPS positioning success rate and less time spent near prey. Because of longer feeding times, lower GPS sampling frequency is generally needed for single lynx compared to family groups.

The actual locations of the kill site were in the majority of cases close to the mean center of GPS locations obtained during the night. However, we do not recommend routinely calculating the center of all GPS locations defining the GLC. We observed that when the lynx were not present at the kill, they were not located randomly, but often moved away in the same direction, which would shift the mean center away from the actual kill site. The best way in our opinion is to use GIS software to plot and visually define the nucleus (concentration of GPS locations) within a GLC, keeping in mind that the day locations with higher elevation usually indicate the area the lynx is moving to when it is not feeding. We also observed that in the majority of cases at least one GPS location in a GLC was very close to the actual kill site – median of just 11 m, with a narrow spread

(IQR=10 m). We recommend that if the prey is not found at the center of the nucleus, the areas around individual locations in the nucleus should be searched first, and then to continue working outward towards the locations that are further away. This will improve the time efficiency of field personnel, minimize disturbance and researcher-related effects on the carcass consumption process, as well as improve efficiency of animal capture for research purposes.

In conclusion, the Eurasian lynx appears to be a perfect species to apply the GLC analysis methods and we can recommend this method for future studies of ungulate predation and reproduction of Eurasian lynx and other carnivores with similar behavior and foraging strategy. Before applying GLC analysis to a new species we recommend a preliminary study that will provide data to simulate success of different GPS fix sampling regimes for reaching study goals and enable elaboration of efficient and cost-effective study designs.

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animals and current laws of the country in which they were performed. Procedures involving handling of lynx were according to the permission issued on 1 June 2006 by the Slovenian Environmental Agency (permission no. 35601-45/2006-6).

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Figures

Fig. 1 Proportion of GPS location clusters (GLCs; n=101) where prey remains of Eurasian lynx were found as a function of the time a lynx remained at a certain GLC in Dinaric Mountains, Slovenia and Croatia. The numbers above columns indicate sample sizes for each time interval. Note that the time intervals are increasing after 60 h (indicated by the width of the column) in order to retain sensible sample sizes.

Fig. 2 Spatial distribution of lynx GPS locations (n=539) during the consumption of prey remains in relation to direction from the kill site. Only locations when lynx was not present at prey (>30 m from the kill site) were included.

Fig. 3 Model-predicted and actual lynx distances from the kill site with regard to the category of the lynx, the time elapsed since the kill and the daylight period for females with immobile young (a), females with mobile or no young (b) and subadult male Eurasian lynx (c) in Dinaric Mountains, Slovenia and Croatia. Lines show model predictions, points show the empirical data.

Fig. 4 Proportion of correctly detected simulated GPS location clusters (GLCs) with regard to the number of successful GPS fixes per day and the maximum distance threshold between 2 locations below which they are considered to belong to the same GLC, based on the data from Eurasian lynx in Dinaric Mountains, Slovenia and Croatia. Sampling was simulated either during the entire 24 hour period (a) or only during the night (b).

Fig. 5 Proportion of correctly detected simulated GPS location clusters (GLCs) with regard to the number of GPS fixes per day and the time the lynx is visiting the prey. Distance of maximum 300 m between points and time difference of minimum 30 h were

847 considered to define a GLC, based on the data from Eurasian lynx in Dinaric Mountains,
848 Slovenia and Croatia. Probability contours are spaced at 0.1, with the exception of the
849 0.95 line. Sampling was simulated either during the entire 24 hour period (a) or only
850 during the night (b).

851 **Fig. 6** Distance from the den site with regard to time since the establishment of the last
852 den and daylight period in female Eurasian lynx in Dinaric Mountains, Slovenia and
853 Croatia. Lines show model predictions, points show the empirical data.

854

Table 1. Spatial distribution of lynx GPS locations (n=818) during the consumption of prey remains. Distances (in meters) of the closest and the farthest lynx GPS location to each kill site location are shown. IQR = interquartile range.

	closest location			farthest location		
	median	IQR	min-max	median	IQR	min-max
day	42	94	4-2873	422	1093	4-4577
night	13	14	0-106	133	205	5-3424
twilight	19	28	1-928	96	354	14-3478
all locations	10	11	0-60	396	1163	25-4577

Table 2 The four top-ranked models (covering nearly 100% of the support in the data) and relative importance of variables from modelling of distance of Eurasian lynx to the kill site during prey utilization as the response variable. w_i = Akaike weight.

Model	ΔAIC_c	w_i
LIGHT + CAT + T + LIGHT×CAT + LIGHT×T + CAT×T *	0.00	0.55
LIGHT + CAT + T + LIGHT×CAT *	1.18	0.31
LIGHT + CAT + LIGHT×CAT	0.88	0.13
LIGHT + CAT + LIGHT×CAT + LIGHT×T	7.85	0.01
Variable	Relative var. importance	
LIGHT	1.00	
CAT	1.00	
LIGHT×CAT	1.00	
T	0.87	
LIGHT×T	0.56	
CAT×T	0.55	

LIGHT: effect of daylight period; CAT: effect of lynx category; T: effect of time since the kill; LIGHT × CAT: differences in response of different lynx categories to different light conditions (modelled as interaction); LIGHT×T: differences in lynx response to time passed since the kill with regard to light conditions (modelled as interaction); CAT×T: differences in response of different lynx categories to the time passed since the kill.

* models included in the confidence set and used to construct the average model

Table 3 The five top-ranked models (covering nearly 100% of the support in the data) and relative variable importance from modelling of distance of Eurasian lynx females to a den site as the response variable. The best model (*) was used for plotting of effects and interpretation. w_i = Akaike weight.

Model	ΔAIC_c	w_i
LIGHT + TD + LIGHT×TD *	0.00	0.43
LIGHT + LYNX + TB + TD + LIGHT×TD	1.31	0.23
LIGHT + LYNX + TD + LIGHT×TD	1.72	0.18
LIGHT + LYNX + TB + TD + LIGHT×TD + LYNX×TD	3.24	0.09
LIGHT + LYNX + TD + LIGHT×TD + LYNX×TD	3.62	0.07
Variable	Relative var. importance	
LIGHT	1.00	
TD	1.00	
LIGHT×TD	1.00	
LYNX	0.57	
TB	0.31	
LYNX×TD	0.16	

LIGHT: daylight period; TD: time since establishment of a den; LYNX: individual lynx; TB: time since birth; LIGHT×TD: difference in response of the females to the time passed since establishment of the den with regard to the lighting conditions; LYNX×TD: difference in response of different individual female to the time passed since establishment of a den.