



Modeling Female Brown Bear Kill Rates on Moose Calves Using Global Positioning Satellite Data

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ABSTRACT The recent development in Global Positioning System (GPS) techniques has started a new era in predation studies. Estimates of kill rates based on animal movements and GPS relocation clusters have proven to be valid in several obligatory carnivores. The main focus has been to obtain accurate mean predation estimates for the management of wildlife populations. We present a model to estimate individual kill rates of moose calves by adult female brown bears in Sweden, based on spatiotemporal clustering of 30,889 bear GPS relocations and 71 moose calves verified killed during 714 field investigations in 2004–2006. In this virtually single-predator single large prey system, the omnivorous brown bear is an efficient predator on moose calves up to 4 weeks of age. The top model set only included models with cluster radii of 30 m or 50 m, indicating very high kill-site fidelity. The best model included a cluster radius of 30 m and number of periods of bear activity at the kill site as a single covariate. The mean estimated individual kill rate of 7.6 ± 0.71 ($n = 18$, $\bar{x} \pm SE$) moose calves per calving season is comparable to the estimate of 6.8 from a previous study of radio-tracked moose in our study area, though at a lower moose/bear ratio. The mean annual kill rates varied from 6.1 to 9.4 calves per bear. The estimated individual kill rates ranged from 2 to 15 calves per season, indicating a large individual variation in hunting skills and possibly effort. Predation and livestock depredation represent a core conflict between humans and carnivores in rural Scandinavia. Accurate predation estimates represent an important step in quantifying costs of carnivores and reducing human–carnivore conflicts. Our technique may be applied in the exploration of predation mechanisms and predator–prey interactions, and contribute to the old and global debate of problem individuals in livestock depredation. © 2012 The Wildlife Society.

KEY WORDS *Alces alces*, carnivore management, depredation, GPS, predation, predator–prey interactions, problem individuals, Scandinavia, *Ursus arctos*.

The introduction of Global Positioning System (GPS) technology started a new era in the monitoring of free-ranging wildlife species. Predation has received much attention in spatial analyses and modeling of carnivore behavior with GPS data, as the predators usually have long stays in the vicinity of large prey kills, which results in relatively easily detectable movement patterns. Traditional methods of studying predation on large-prey species include energy models (Laundré 2005), snow tracking (Swenson et al. 2001), aerial observations (Boertje et al. 1988), very high frequency (VHF) radio tracking of predators (Ballard et al. 1981, Boertje et al. 1988), and marking females and calves of the prey species (Swenson et al. 2007). Most of these methods involve intensive field work, which may depend on season, weather, or light, and thus tend to produce short

and fragmented monitoring intervals. In addition, some traditional methods do not enable the detection of small prey. Thus, these methods may produce unreliable estimates, lack error estimates, and not incorporate individual differences. In addition, Swenson et al. (1999b) recommended not marking moose (*Alces alces*) calves with ear transmitters, because of increased mortality rates.

After an initial study of kill rates in mountain lions (*Puma concolor*; Anderson and Lindzey 2003), predation studies based on GPS data and successive field verifications have been reported for several obligatory carnivores, including gray wolf (*Canis lupus*; Sand et al. 2005, Franke et al. 2006, Webb et al. 2008), mountain lion (Knopff et al. 2009, Ruth et al. 2010), lion (*Panthera leo*; Tambling et al. 2010), leopard (*P. pardus*; Martins et al. 2010), jaguar (*P. onca*; Cavalcanti and Gese 2010), and Eurasian lynx (*Lynx lynx*; Mattisson et al. 2011). The methods included carcass detection via location-cluster analysis (most studies), reducing field visits by targeting location clusters of high

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predation probability (Anderson and Lindzey 2003, Zimmermann et al. 2007, Webb et al. 2008, Knopff et al. 2009, Ruth et al. 2010, Tambling et al. 2010), modeling predation events by movement patterns (Franke et al. 2006, Merrill et al. 2010), and modeling time-to-kill (Merrill et al. 2010). Methods have been proposed to differentiate between prey sizes (Webb et al. 2008, Knopff et al. 2009), and estimating kill rates only from GPS data have been evaluated (Anderson and Lindzey 2003, Franke et al. 2006, Zimmermann et al. 2007, Webb et al. 2008, Merrill et al. 2010). Field-based predation data have been included in the analyses of diet composition (Anderson and Lindzey 2003, Sand et al. 2008, Cavalcanti and Gese 2010, Knopff et al. 2010, Martins et al. 2010) and factors associated with handling time (Cavalcanti and Gese 2010, Martins et al. 2010), time between kills (Sand et al. 2008, Cavalcanti and Gese 2010), and kill rates (Sand et al. 2008, Cavalcanti and Gese 2010, Knopff et al. 2010, Mattisson et al. 2011).

Brown bear (*Ursus arctos*) predation on several prey species is well documented. In North America, the brown bear can be a primary predator on moose (Ballard et al. 1981, Boertje et al. 1988, Bertram and Vivion 2002), caribou (*Rangifer tarandus*; Adams et al. 1995, Young and McCabe 1997, Valkenburg et al. 2004), and elk (*Cervus elaphus*; Singer et al. 1997, Barber-Meyer et al. 2008). In Scandinavia, brown bears prey on moose, semi-domesticated reindeer (*R. tarandus*), and free-ranging domestic sheep (Dahle et al. 1998, Persson et al. 2001), resulting in costly compensation arrangements and serious controversies (Sagør et al. 1997). The controversy around brown bear depredation of sheep is the single largest threat to a sustainable brown bear population in Norway today (Swenson and Andrén 2005). In south-central Sweden, the brown bear is a primary predator of moose calves, with an estimated predation rate (proportion of moose calves killed by brown bears) of 26%, and an individual kill rate (number of moose calves killed annually per brown bear) of 6.8 for bears ≥ 4 years old (Swenson et al. 2007). During summer (21 May to 31 Jul), moose calves constitute 36–44% of the seasonal dietary energy content of brown bears in the area (Opseth 1998). According to Swenson et al. (2001), the brown bear predation rates on moose calves in Scandinavia were comparable to predation rates reported from North America at corresponding relative moose/brown bear ratios.

We explore the possibility of predicting moose calf predation events and estimating individual kill rates of adult female brown bears, based on GPS records. We hypothesize that the individual kill rates within this demographic class is comparable to the average kill rates of adult bears reported by Swenson et al. (2007). We further analyze the variation between years and individuals within this single demographic class of bears.

STUDY AREA

We conducted our study in the counties of Dalarna, Gävleborg, and Jämtland, south-central Sweden (61°N, 15°E). The area is gently rolling with scattered hills and elevations of 200–700 m, all below tree line. It is in

the northern boreal forest zone, with coniferous forest and numerous lakes, rivers, and large bogs. The forest was intensely managed, with large clear cuts and tree monocultures intersected by a network of gravel roads. The forest was dominated by Scots pine (*Pinus silvestris*) mixed with Norway spruce (*Picea abies*) and various deciduous tree species. Understory vegetation included brown bear food sources such as bilberry (*Vaccinium myrtillus*), cowberry (*V. vitis-idea*), and crowberry (*Empetrum hermaphroditum*).

The study area was located in the southern core area of the Scandinavian brown bear population, with a brown bear density of approximately 30 bears/1,000 km (Bellemain et al. 2005). In the 750-km² Orsa Communal Forest, where we conducted most of the field work, the winter moose population was approximately 500 moose/1,000 km² with a harvest of roughly 100 subadult/adult moose and 50 moose calves/1,000 km² (S. Brunberg, Scandinavian Brown Bear Research Project, personal communication). Other potential large prey species of the brown bear were roe deer (*Capreolus capreolus*) and beaver (*Castor fiber*), but the brown bear is not considered to be an efficient predator of these species (Opseth 1998). Ants (*Formica* spp. and *Camponotus* spp.) were alternative small-sized prey (Swenson et al. 1999a). Eurasian lynx occurred in relatively low and stable numbers, approximately 1.0–1.5 family groups per 1,000 km² (Liberg and Andrén 2005). Single gray wolves wandered occasionally through the entire study area, and minor parts of the study area overlapped with territories of 2 different packs and 2 territorial pairs of wolves during the summers of 2004–2006 (Wabakken et al. 2006).

METHODS

GPS Data Collection

During 2004–2006 we studied 6, 5, and 7 sexually mature (3- to 13-yr-old) female brown bears, respectively. Fourteen were solitary and 4 were accompanied by yearlings during part of the study period. We studied 5 individuals in 2 of the 3 years. The procedures of capture, marking, and age determination followed pre-established protocols (Arnemo et al. 2011), reviewed and approved by Uppsala's Ethical Committee on Animal Experiments. We equipped the bears with GPS Plus-3 or GPS Pro-4 neck collars including dual-axis activity sensors and Global System for Mobile Communication (GSM) lateral modems (VECTRONIC Aerospace GmbH, Berlin, Germany). Location and activity data were stored in the GPS collars, and could be downloaded at collar removal. In addition, GPS locations were automatically transmitted by the GSM modem, 7 locations at a time, resulting in next-to-real-time GPS data. The process of transferring data by GSM relies on the GSM network coverage, and some rare communication failures resulted in the loss of 7 locations at a time. Thus the GPS records that we used for field work, model development, and estimating kill rates had a slightly reduced location success in relation to those later downloaded at collar removal. The GPS collars were programmed to fix intervals of 30 minutes, yielding a maximum of 48 locations per day.

Field Verification

We investigated random samples of the 2004 and 2005 bear GPS locations, using the randomization function in Microsoft[®] Excel (Microsoft Corporation, Redmond, WA) to select locations from the data records to visit. We did not discriminate between locations that were single points or in a cluster of locations. When 2 or more of the selected locations were within 30 m of each other, we used the first selected point as the starting point of the investigation. As a general rule, we investigated 3-day-old locations as a compromise between observing relatively fresh bear sign and avoiding possible disturbances. We investigated the area within a radius of 30 m of the location by walking in circles at 5-m radii intervals. We performed this procedure independently of whether we observed a moose calf carcass or not. We documented all sign of bear activity, bear foods, and various additional observations, such as sign of other species. Moose calf predations were verified by 1) moose calf remains, 2) the age of these remains matched the time of the GPS locations, 3) the age of the bear sign at the location all matched the time of the GPS locations, and 4) no sign of other large carnivores. The moose calf remains were usually easy to detect, because of the bears' habit of covering carcasses with large amounts of vegetation. Because little remained of the moose calf carcasses in all cases, we had no possibility to observe sign of trauma (e.g., bite or claw marks, bleeding), or to perform necropsies. We estimated the time since death based on the degree of decomposition, and by the state of the vegetation above and underneath the remains. We located the sites with handheld GPS receivers. The GPS location error was approximately 10 m (Moe et al. 2007), therefore our 30-m radius procedure included most of the true bear locations.

We plotted GPS locations from 2005 in ArcView[®] GIS 3.2 (Environmental Systems Research Institute, Inc., Redlands, CA). An investigation of verified moose calf predation sites revealed patterns of clustered GPS locations close to the kill sites and a distinct increase in missing GPS locations among these locations. We hypothesized that location clusters with high numbers of locations and long total time spans indicated potential predation sites. We used the Spatial Analyst 2.0 Neighborhood Statistics function to retrieve location density maps, and manually selected an additional 33 potential kill sites and investigated them in the field. In 2006, we performed targeted field work at sites with location clusters of modeled predation probability >0.1. We chose this threshold to ensure that we observed all predation events. Thus, we set it below the 95% confidence interval for the receiver operating characteristic (ROC) cut-off level of the predation model (Fig. 2a), and substantially lower than the probability of predation for any kill site observed among the random locations. On the other hand, this threshold left us with a manageable amount of sites to visit in the field.

GPS Data Processing

Ungulates may synchronize births in a birth pulse, perhaps to reduce the exposure of offspring to predation (Rutberg

1987). The moose parturition period in the study area ranges from mid-May to early June, and 93% of the bear-killed moose calves were killed within the first 4 weeks after birth (Swenson et al. 2007); 20 May was the first observed predation event (Busk 1998). We defined the predation season as 15 May to 30 June, and excluded all GPS locations outside this period. We later evaluated the adequacy of this time frame by estimating date of kill for all the verified moose calf kills by defining time of kill as corresponding with the first bear GPS location within the model buffer distance of a verified kill. We excluded locations diverging in time from the other cluster locations, ensuring both spatial and temporal clustering. We further tested whether the distribution of kills differed among the weeks of the predation season. All statistics otherwise not specified were performed in program R (R Development Core Team 2011).

The omnivorous brown bear often uses anthropogenic foods, such as deposits of slaughter remains from hunter-killed moose, livestock, and photo baits on our study area (Sahlén 2006). We removed GPS locations <200 m from known sites containing such foods from the GPS records.

One of the main problems with the use of GPS telemetry is fix-rate bias, due to lack of contact between the satellites and the GPS collar. Fix rate may depend on species-specific behavior (Mattisson et al. 2010) and fix rates for bears follow circadian activity patterns (Moe et al. 2007, Heard et al. 2008), and correlate with movements and body size (Graves and Waller 2006). Moe et al. (2007) reported that 78% of the GPS data loss occurs when bears are inactive, strongly suggesting behavior-induced data loss from failed location attempts. To improve GPS data location success, we introduced a simple distance- and time-difference location simulation procedure, bearing similarities to the first step of the iterative simulations proposed by Frair et al. (2004). For every missing location, we calculated the time difference and distance between the surrounding valid GPS locations. We set the maximum time difference to perform simulations to 4 hours, equaling the loss of 7 locations in a failed GSM communication attempt. We varied the maximum distance to allow simulations (30 m, 50 m, 100 m, and 200 m) to create different data sets. We assigned the missing locations meeting these time and distance criteria a random location (using the randomization function in Microsoft[®] Excel) between the preceding and later valid location. We tested the data sets in a pair-wise manner to evaluate whether an increase in maximum simulation distance resulted in a significant increase in location success.

Based on the results of Moe et al. (2007), we categorized the GPS locations into 4 daily activity periods, 2 active and 2 inactive periods. We further defined a location as active when belonging to the early-day or late-day activity periods (Moe et al. 2007).

Predation Model

We used the 33 investigated potential predation sites from the preliminary Global Information System (GIS) analysis and added 35 randomly selected and investigated locations from 2005 to develop a general predation model. The inves-

tigated locations were joined spatially to the GPS locations with buffer distances of 30 m, 50 m, 100 m, and 200 m. We classified the verified moose calf predation locations and 1 unspecified (either moose calf or roe deer) predation location as predation events. We used generalized linear models (GLMs) with binomial error distribution and the logit link function (i.e., logistic regression; Hosmer and Lemeshow 2000) to model the probability of predation. The model covariates were number of locations, number of locations in active periods, number of activity periods, and number of days within buffer distances of 30 m, 50 m, 100 m, and 200 m. The GPS data used in the models included both the original records and simulated locations. As we wanted the model to be general and its application not only restricted to our study area, we did not include site-specific covariates (e.g., bear and moose calving habitats). As all model covariates are parameters describing the time span at the location cluster (i.e., handling time), they were in general highly correlated. We did not include predictor variables correlated at $r^2 > 0.7$ in the same model. We examined pair-wise interactions. We based the model selection on small sample size correction for Akaike's Information Criterion (AIC_c; Burnham and Anderson 2002), tested the models for overdispersion and goodness-of-fit, and visually explored model diagnostic plots. We assessed correct model classification by estimating the area under the curve (AUC) of ROC curves (Fielding and Bell 1997), and set cut-off probability thresholds for kill or non-kill to balance false positives and false negatives (i.e., the intersection between the sensitivity and [1-specificity] curves).

We included models with most support from AIC_c ($\Delta AIC_c < 4$) in further model validation. We compared modeled kills from the best predation models to the corresponding number of verified kills in 2 different data sets: 1) all the randomly selected and investigated locations in 2004 and those from 2005 that were not used in building the predation models, and 2) clusters with a modeled predation probability >0.1 investigated in 2006. We analyzed the relationship between verified kills at visited GPS clusters and the corresponding number of modeled kills. We tested the influence of individual GPS collar location success, bear age and reproductive status, and number of kills on the difference between modeled individual kills and verified kills (i.e., the residuals to the theoretical curve of $y = x$) by simple linear regression ($n = 18$). As an earlier test of distribution of kills throughout the predation season revealed a decline through the chosen calving season, and our predation period was relatively short, we chose to quantify predation estimates as seasonal kill rates rather than time between kills (also see Knopff et al. 2010 for a thorough discussion).

We estimated individual seasonal kill rates for the years 2004–2006 and tested the influence of individual GPS collar location success, bear age, and reproductive status on these estimates by simple linear regression ($n = 18$). To test for annual differences in kill rate estimates, we applied a generalized linear mixed model (GLMM; Bolker et al. 2009) with individual as a random intercept effect and year as a fixed effect, a Poisson error distribution, and the log link function.

Because of the small sample (i.e., the average number of counts per group = 6), we applied restricted maximum likelihood (REML) estimation and a Laplace approximation of model parameters (Bolker et al. 2009). We compared this model's AIC_c value to the intercept-only model, and tested the year effect by a chi-square test.

RESULTS

We obtained 30,889 valid GPS relocations with a mean location success rate of $77 \pm 1.9\%$ ($n = 18$, $\bar{x} \pm SE$) in 2004–2006 when restricting the data sets to the predation season only. Each increase in simulation distance resulted in a significant increase in mean location success (Wilcoxon signed rank test, $P < 0.01$ for all tests). At best, mean location success was $86 \pm 2.8\%$. We removed 228 GPS relocations <200 m from known anthropogenic foods. We investigated 1,587 GPS randomly selected locations in the field during 2004 and 2005; 583 during the predation seasons. We searched the 30-m radius surrounding the location for 42 minutes on average. Bear sign was present at 77% of the locations; signs of foraging (57% of the sites), bed sites (30%), scats (30%), and tree or ground scratches (25%) were observed most frequently. We verified 23 moose calf kill sites and several other bear foods items (Table 1). Based on field observations, we categorized 2 of the investigated potential kill sites in 2005 as no predation, as we considered these moose calves to have been killed and consumed by other bears. In the first case, the moose calf carcass was discovered 14 days before bear W0209's first appearance at the location. In the second case, bear W0210 had only 1 GPS location within a 50-m radius of the carcass, but spent some time in the neighboring area. In the same period, this bear was observed with a larger and older bear that was not included in this study. The average time from the bears' stay at a site and our subsequent field work was 3.5 days (range: 1–10 days, 97% of the observations within

Table 1. Food items consumed by female brown bears in Sweden at 829 locations (both randomly selected bear locations and modeled predation locations) during the predation season 15 May to 30 June, 2004–2006.

Food item	Fresh foods or signs	Older foods
Moose (calf)	84	4
Moose (≥ 1 yr)	2	6
Slaughter remains	1	6
Small game ^a	2	
Ants (<i>Formica</i> spp.)	302 ^b	
Ants (<i>Camponotus</i> spp.)	799 ^c	
Cowberry	NA ^d	
Herbs or ferns	$>15^e$	
Fish ^f	1	

^a European mountain hare (*Lepus timidus*) and capercaillie (*Tetrao urogallus*), possibly scavenging.

^b Excavated ant hills, turned stones and digging in the ground.

^c Opened tree branches and stumps.

^d Not possible to verify berry consumption directly. However, bears often stayed in locations rich in cowberrys from last fall for a long time, and we observed large quantities of berries in bear scats.

^e Hard to verify sign of bear grazing (e.g., to separate between bear and moose foraging).

^f Remains of pike (*Esox lucius*), probably left by fishermen.

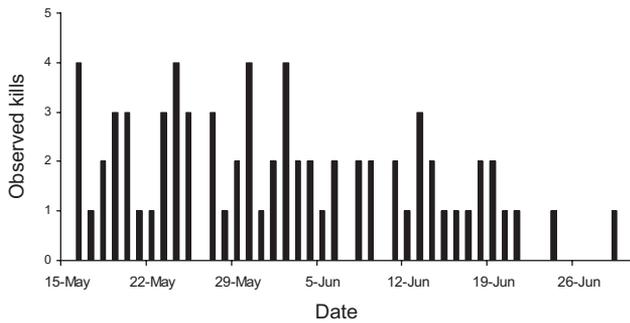


Figure 1. Date of brown bear predation on moose calves in Sweden in 2004–2006 ($n = 71$), defined as the first date with GPS relocations within a 30-m buffer from verified carcasses.

≤ 5 days). The estimated date of all verified predations ($n = 71$; Fig. 1) ranged from 16 May to 29 June. The distribution of the predation dates differed throughout the study period ($\chi^2_6 = 15.7$, $P = 0.013$).

Predation Model

We detected 21 kills at the 33 potential kill sites that were determined from the initial GIS analysis. None of the additional 35 randomly selected locations used for model development included kills. Thus, the predation model data set contained 21 locations classified as predation, and 47 as no predation. Based on AIC_c , we selected a suite of 3 top models with the most support from the total of 44 models (Table 2). The ROC area under the curve (Table 2) showed excellent model fit to the data for all 3 models and we did not need to adjust for overdispersion. The model that included a buffer distance of 30 m, a simulation distance of 30 m, and number of activity periods as a single covariate appeared to be the best model, based on AIC_c , and its ROC cut-off suggested that all clusters including 4 separate activity periods would be kill sites.

When we applied the top 3 models to 548 investigated bear locations during the 2004 and 2005 predation seasons (not used in model building) with 23 verified predation events, the number of predicted predations ranged from 18 to 51 (Table 2). Though all 3 top models had some support by Akaike weights (Table 2), we finally chose 1 best model. This simple model, included a buffer distance of 30 m, a simulation distance of 30 m, and number of activity periods as a single covariate predicted kills very well (Table 2).

In the 2006 field season, we used the best model to predict predation events. The model predicted 39 predation events at 98 sites and we detected 37 moose calf kills at those 98 sites we investigated. When evaluating the relation between verified and modeled number of kills per individual bear, the modeled kill rates explained 83% of the variation in verified kills (Fig. 3; intercept set to null, $y = 1.04x$, $r^2 = 0.825$, $P < 0.001$). Collar location success ($r^2 = 0.051$, $P = 0.37$), bear age ($r^2 = 0.016$, $P = 0.62$), reproductive status (Wilcoxon rank sum test, $W = 36$, $P = 0.42$), and number of modeled kills ($r^2 = 0.0048$, $P = 0.78$) did not influence the difference between modeled individual kills and verified kills.

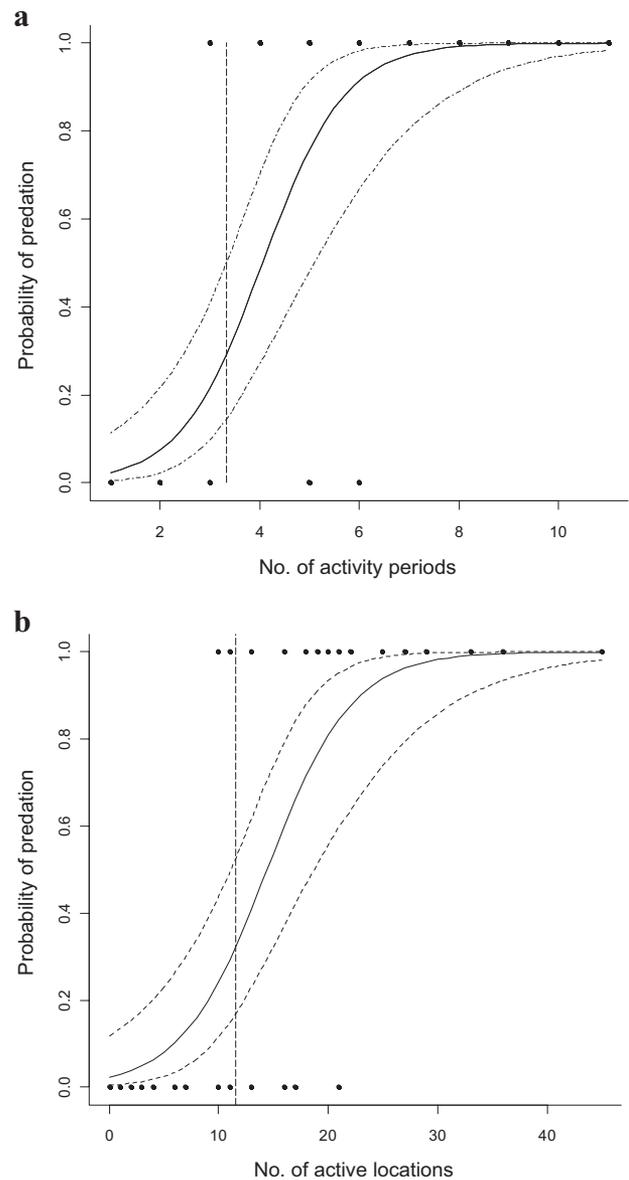


Figure 2. Model of moose calf predation by brown bears with a buffer distance of 30 m, a location simulation distance of 30 m, and number of activity periods as a single covariate (a) and with a buffer distance of 50 m, original data set, and number of active locations (i.e., locations belonging to the periods early-day and late-day activity) as a single covariate (b). Points represent observations of predation or no predation by brown bears, and dotted lines represent 95% confidence intervals. The receiver operating characteristic (ROC) cut-off values (vertical dashed lines) suggest location clusters with ≥ 4 activity periods or ≥ 12 active locations to be classified as kill sites.

Individual Kill Rate Estimates

Using the best model, we estimated 136 moose calves killed by radio-marked bears during 2004–2006, with a mean individual kill rate of 7.6 ± 0.71 moose calves per season ($n = 18$, $\bar{x} \pm SE$), ranging from 2 to 15 (Table 3). The estimated individual kill rates did not depend on the GPS collar location success ($r^2 = 0.095$, $P = 0.21$), age ($r^2 = 0.0058$, $P = 0.76$), or reproductive status ($P = 0.97$). The mean annual kill rates were 7.7, 9.4, and 6.1 moose calves per bear per season in the years 2004, 2005, and

Table 2. The 3 top models to predict sites of female brown bear predation on moose calves in Sweden, 2004–2006, applied to 548 randomly selected and investigated bear locations with 23 verified predated moose calves. Models are shown in order of decreasing rank with model log-likelihood (LL), number of model parameters (K), small sample corrected Akaike's Information Criterion (AIC_c), AIC_c differences (Δ_i), AIC_c weights (w_i), receiver operating characteristics area under the curve (AUC_{ROC}), and threshold probability for separating kills from non-kills (ROC cut-off). All other models were $>4 \Delta AIC_c$ from the highest ranked model.

Model	LL	K	AIC_c	Δ_i	w_i	AUC_{ROC}	ROC cut-off	Estimated kills
B30_sdist30_periods ^a	-21.8	2	39.7	0.0	0.56	0.96	0.29	22
B30_original_periods	-22.9	2	41.8	2.1	0.19	0.97	0.21	51
B50_original_active	-23.1	2	42.1	2.4	0.16	0.95	0.32	18

^a B30, buffer distance of 30 m; sdist30, includes simulated locations when the distance between the former and later valid location <30 m and time span <4 hr; periods, no. of activity periods; original, no. simulated locations; active, no. of active locations; B50, buffer distance of 50 m.

2006, respectively. The GLMM with year as a fixed effect and individual as a random effect did not perform better than the intercept-only model ($\Delta AIC = -0.3$; $\chi^2_2 = 3.7$, $P = 0.15$); so when accounting for individual variation, the mean kill rates did not differ among years. The removal of GPS locations close to known anthropogenic food sources removed 5 modeled kills and reduced the mean individual kill rate by 2.5%.

DISCUSSION

Predation Model

Our best model with a buffer distance of 30 m, a simulation distance of 30 m, and number of activity periods as a single covariate performed very well in both predicting the total numbers of killed moose calves and accounting for variation in kill rates among individual brown bears. The general conclusion of GPS-based predation studies is that successful modeling of predation probabilities works best for solitary predators preying on relatively large prey, displaying a high fidelity to kill site, and having long handling time (Knopff et al. 2009). Models tend to be less predictive for pack-living

species with less predictable movement patterns and where not all pack members are collared (Zimmermann et al. 2007, Webb et al. 2008). All of our top models indicated that bears display a very high fidelity to kill sites, although the prey in our study was smaller than in most other studies. For example, Cavalcanti and Gese (2010) classified jaguar kills <15 kg as “very small,” and reported their inference to be most applicable to prey >45 kg. Adult female Scandinavian brown bears weigh 60–200 kg (Zedrosser et al. 2006) and a newborn moose calf weighs approximately 13 kg, growing >1 kg daily (Sand et al. 2008). Our top models' cluster radii of 30 m and 50 m might be sensitive to observational error (e.g., when bears or other scavengers remove a carcass from the kill site). However we believe our method of visiting many random locations and clusters only a few days after the bears had been at the site, combined with the habit of bears of covering carcasses with vegetation and producing distinct signs, counteracted this potential error and that most kill sites therefore were classified correctly.

Our methods relied on GSM-transferred GPS data, and an intensive and constant sampling regime of half-hourly relocations. Despite the possible presence of behaviorally in-

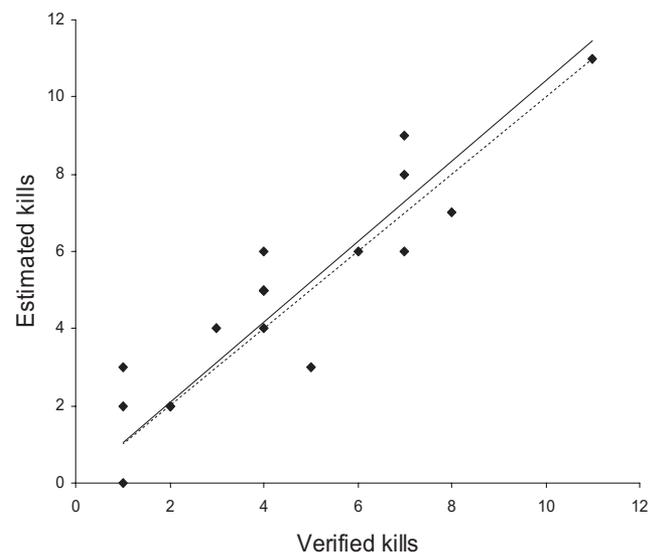


Figure 3. Linear regression model of the relationship between modeled number of predations on moose calves and field-verified predations for individual female brown bears in Sweden during 2004–2006. The dotted line illustrates the optimal line ($y = x$).

Table 3. Estimated individual seasonal moose calf kill rates for mature female brown bears in Sweden, 2004–2006.

Year	Bear	Age	GPS location success ^a	Estimated number of calves killed
2004 ^b	W0004	9	0.89	11
2004	W0109	10	0.89	5
2004	W0208	3	0.92	11
2004	W0209	3	0.68	7
2004	W0229	6	0.89	5
2004	W0323	4	0.85	7
2005	W0208	4	0.73	8
2005	W0209	4	0.74	7
2005	W0212	4	0.88	15
2005	W0323	4	0.70	6
2005	W0427	4	0.89	11
2006 ^b	W0004	11	0.91	8
2006	W0212	5	0.85	9
2006	W0410	3	0.70	7
2006	W0411	3	0.84	6
2006	W0422	3	0.86	2
2006 ^b	W0425	6	0.81	5
2006 ^b	W9403	13	0.76	6

^a Includes simulated Global Positioning System (GPS) locations when the distance between the former and later valid GPS location <30 m and time span <4 hr.

^b Accompanied by yearlings for a part of the season.

duced fix-rate bias (Moe et al. 2007), we obtained good location successes, which was further improved by our location simulations. The simple and conservative GPS data simulation procedure significantly improved location success rate at a simulation distance of only 30 m, which corresponds very well with the behavior-induced GPS location data loss in inactive periods. The inclusion of simulated locations in the best model is in contrast to Knopff et al. (2009), who reported that at a fix interval of 3 hours, the kill rate or prey composition estimates for mountain lions were not biased until the fix rate was less than 45%. We did not explore the influence of the GPS sampling regime to model performances, but in general, our study relied on an intense GPS location sampling, because of the relative small prey size.

To our knowledge we are the first to include activity periods in predation models, though some studies have included time of day at the start of a cluster as a model covariate (Zimmermann et al. 2007, Tambling et al. 2010). Including data from activity loggers in predation models may further improve our understanding of predatory behavior. However, when developing predation models, activity data were only available for the 2004 season, including only 13 verified predation locations, so we were not able to investigate this supposition. Still, we documented an average of 5.2 bear beds at 66 of the 71 verified kill sites, indicating extensive resting behavior associated with moose calf predation sites. Our results correspond well with the general pattern of predation models, that length of time at the cluster alone is not enough to predict presence or absence of a kill. The 2 best model covariates both represent behavior expected to distinguish between kill sites and other location clusters. The active locations covariate represented a clustering of locations in periods when bears otherwise are active, whereas number of activity periods was able to represent both long stays and repeated returns to a kill site.

Our study period was designed to encompass the food pulse of vulnerable neonatal moose, with study period kill rates representing virtual annual kill rates. The estimated predation dates all fell within the predefined predation season. However, in 2006 we estimated that 4 kills took place on 16 May, which indicates a tight frame of the study period. We explain our choice by an observed shift in bear behavior around 15 May, based on activity data patterns and the length of resting periods, possibly induced by changing day lengths, the moose calf food pulse, or the beginning of the mating season. We visited 1,166 clusters and random locations outside the time frames of the study period without observing any moose calf kills, which gave us confidence in our choice of study period.

Individual Kill Rate Estimates

Several studies emphasize the importance of long, continuous in-field study periods to produce reliable kill rates (Sand et al. 2008, Knopff et al. 2009). Our study included periods of in-field verifications of clusters with high predation probabilities for 7 individuals and a high number of visited random locations for 11 individuals. The individual seasonal kill rates were later estimated based on GPS data. Because of the

complexity of brown bear foraging and mating behavior, their plasticity in diet composition, and the difference in size and availability of alternative protein-rich food sources (ants vs. moose), we stressed exploring the individual variation in moose calf predation. To our knowledge, this is the first study to test the influence of factors affecting individual differences in model classification success. However, none of the tested factors affected this relationship; variation in kill rate estimates explained 83% of the variation in verified kills. As some of the individual records included only a few verified kills, this method was sensitive to chance events.

The estimated mean individual kill rate for mature female brown bears (3–13 years old) in south-central Sweden was 7.6 ± 0.71 ($\bar{x} \pm SE$) moose calves per calving season. An earlier reported kill rate in the same study area, based on predation rates of radio-marked moose calves and density estimates for moose and bears, was 6.8 moose calves killed by each brown bear ≥ 4 years old (Swenson et al. 2007). This is well within the mean individual kill rate 95% confidence intervals of our model. However, the relative moose density at that time was higher than in 2004–2006 (920 moose/30 bears vs. 500 moose/30 bears), and the reported brown bear kill rates on moose calves from Scandinavia and North America correlate positively with relative moose density (Swenson et al. 2001). As one also might expect different demographic classes of bears (males, single females, females with cubs) to exhibit different predatory behavior, the numbers are not directly comparable. Nevertheless, our estimates are supported by the other studies in Scandinavia and North America. Another interpretation is that mature female bears, not accompanied by cubs of the year, are just as predatory as other demographic classes. The relatively high kill rates are further supported by the results from scat analysis in our study area, which showed that moose calves are a primary food resource for bears during late May–June (Opseth 1998).

Most GPS-based predation studies consider reported kill rates to represent an underestimation of true kill rates, especially for medium- and small-sized prey (e.g., Sand et al. 2005). This assumption is due to their study design, only visiting clusters of GPS locations. With some exceptions (Sand et al. 2008, Knopff et al. 2009, Ruth et al. 2010), most studies have failed to assess prey not detected at cluster sites. We believe that our method of visiting a high number of random locations only a few days after the bears were at the site makes our study less prone to an underestimation of kill rates. On the contrary, the omnivorous diet of brown bears and their lack of defined territories may result in an overestimation of kill rates, because of scavenging, carcass usurpation, and the utilization of anthropogenic food sources. We have tried to reduce this error source by excluding GPS locations close to known anthropogenic food sources, which only reduced the mean individual kill rate by 2.5%. Nevertheless, we believe this is an important principle when modeling kill rates in scavenging species. An influential and related source of error is the presence of other efficient predators within the study area. Wolves were occasionally present within our study area, but we do not believe they

affected our results significantly, although we were not able to quantify this effect. In a recent study of brown bear scavenging of wolf-killed moose carcasses in our study area (Milleret 2011), the average time from estimated date of death of adult moose to bears visiting the carcass was 13 days (range: 8–22). Though this study season was just before the appearance of newborn moose calves, this supplementary study provides further confidence about the robustness of our study design regarding the ability to separate kills from scavenging events. In the dense forests of our study area, we suspect brown bears to primarily rely on olfaction to locate carrion, and the time it takes to discover carcasses depends on carcass decomposition. This situation might differ from more open and easily visible landscapes, where other wolf–bear studies have been conducted (e.g., Ruth et al. 2010). Nonetheless, in more complex multiple-carnivore, multiple-prey systems, this source of error must be addressed parallel with the studies on bear predation (e.g., by radio-tracking other predators; Ruth et al. 2010).

The mean individual kill rates did not differ among years when we accounted for individual contribution to overall predation. The estimated individual kill rates ranged from 2 to 15 moose calves per season among individual bears of same sex and reproductive status, and within a geographically limited area, indicating a large variation in hunting skills and possibly diverging foraging strategies within a single demographic class of bears. Even though these are the extremes, the interval constituting 89% of the estimates ranged from 5 to 11, representing more than a 2-fold difference in seasonal kill rates among individuals. This illustrates a major advantage of this procedure compared to traditional study designs; individual-based predation models enable insight into predation mechanisms and foraging strategies. Our results correspond well with other studies reporting high individual variability in individual kill rates and prey composition (e.g., Cavalcanti and Gese 2010). The concept of livestock-killing “problem individuals” (Linnell et al. 1999) is a common underlying assumption in present carnivore management (Linnell 2011), that yet suffers from a lack of empirical evidence. Understanding the functional mechanisms behind variance in kill rates is a prerequisite for any preventive measure targeting so-called problem individuals.

Predation modeling is not a complete alternative to field-based methods. However, predation model accuracy and their potential applications are evolving as the development of GPS techniques continues and animal movements and time-to-kill models are included. At this stage, we see the potential of an automated cluster-identifying scanning of individual brown bear GPS records (Webb et al. 2008, Knopff et al. 2009), combined with the modeling of individual kill rates and geographic distribution of kill sites, for example, to model landscapes of risk, or link bear predation success to life history traits and fitness.

MANAGEMENT IMPLICATIONS

Haglund (1974) concluded that brown bear predation was not an influential factor in the population dynamics of moose in Sweden. However, the brown bear population has been

expanding in size and range (Kindberg et al. 2009), with a 2008 national population estimate of 3,298 (2,968–3,667) individuals (Kindberg et al. 2011). Swenson et al. (2007) advised Swedish wildlife managers to include the effects of brown bear predation in their moose population models, at least where bears are common. The results of this study, with similar predation numbers at a much lower moose/bear ratio, strengthen these conclusions. When quantifying the demographic impact of brown bear predation on moose, managers must also acknowledge the influence of the age composition of killed moose (Gervasi et al. 2012), and both the variation in kill rate and the portion of adults among bear-killed moose will alter the per capita bear impact on the moose population. Estimates of variance in kill rates and prey composition are crucial for measures of precision in population and harvest models, and thus represent an important step forwards for decision makers when managing carnivore and prey species.

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