Estimating individual kill rates on moose calves by brown bears based on GPS technology and GIS cluster analysis.

Estimering av brunbjørn sine individuelle predasjonstakter på elgkalv basert på GPS-teknologi og GIS-analyser.

Geir Rune Rauset

NORWEGIAN UNIVERSITY OF LIFE SCIENCES
DEPARTMENT OF ECOLOGY AND NATURAL RESOURCE MANAGEMENT
MASTER THESIS 60 CREDITS 2006

ABSTRACT

The brown bear *Ursus arctos* L. is an omnivorous species, utilising a range of different food sources. The Scandinavian brown bear is an efficient predator on moose calves *Alces alces* L. during the first four weeks after their birth in early summer. In south-central Sweden, we studied six and five GPS collared female brown bears during 2004 and 2005, respectively. During the predation season, 15 May – 30 June, a total of 17,885 GPS positions were transmitted, representing a mean location success of 76±2.8%. I performed a simple position simulation procedure, increasing the mean location success up to 86±2.8%. Based on a combination of GIS cluster analysis and a field study of 653 randomly selected GPS locations (including 20 verified moose calf carcasses) and 35 potential predation locations from a preliminary GIS-analysis (including 21 verified carcasses), I developed models to predict sites of predation. The best model consisted of a single predictor variable "active positions" (based on primary bear activity periods), a cluster radius of 50 m, and GPS data sets with no simulated positions. The predation model estimated a total of 78 moose calf predations, with a mean individual kill rate of 7.1±0.92 calves, ranging from 3.8 to 15. This estimate is supported by reported predation rates from Scandinavia and North America at corresponding relative moose densities (moose/bear). The mean individual kill rates differed between the years, possibly due to individual differences rather than year differences. Estimated date of predation ranged from 18 May to 24 June, with an even distribution throughout the predation season. Estimated time of predation exhibited a relatively uniform distribution throughout the day, with no differences among the different activity periods. Predation rates based on GIS analysis and GPS-data have been reported from studies of cougar *Puma concolor* L. and grey wolf *Canis lupus* L.. These are obligate predators, preying on relatively large species. However, no studies have yet reported on how to estimate predation rates for an omnivorous species with a relatively small prey based on GPS positions. This predation model is, with some modifications, applicable in studies of moose calf predation by other classes of bears, and the methods should be applicable in the studies of brown bear depredating free-ranging domestic sheep *Ovies aries* L. and semi-domesticated reindeer *Rangifer tarandus* L.. Individual-based predation studies provide new insight into predation mechanisms. This knowledge hopefully will result in improved management of bear populations and reduce the conflict levels in relation to moose hunting, sheep farming and reindeer herding.

Key words: *Alces*, brown bear, GIS, GPS, moose calf, predation, Scandinavia, *Ursus arctos*

SAMANDRAG

Brunbjørnen *Ursus arctos* L. er ein omnivor art som kan nytte seg av ei rekkje ulike matressursar. I ein periode på forsommaren er brunbjørnen i Skandinavia ein effektiv predator på elgkalv *Alces alces* L.. Dette fell saman med dei fire fyrste vekene etter fødsel av elgkalvane. I eit studieområde i sentrale Sør-Sverige følgde vi seks og fem binner med GPS-halsband i åra 2004 og 2005. I predasjonsperioden, avgrensa til 15. mai – 30. juni, sendte GPS-halsbanda tilsaman 17 885 posisjonar med eit snitt på 76±2,8% vellukka posisjonar. Eg introduserte ein enkel prosedyre for simulering av manglande GPS-posisjonar, og auka opp til 86±2,8% posisjonering. Basert på ein kombinasjon av GIS-analyser og eit feltstudie av 653 tilfeldig utvalde GPS-posisjonar (20 kadaver av elgkalv funne) og 35 potensielle predasjons-lokalitetar (21 kadaver funne) utvikla eg ein modell for å forutsjå predasjon på elgkalv på bakgrunn av GPS-data. Bjørn i Skandinavia føl i predasjonsperioden generelle aktivitetsmønster, og døgnet kan delast inn fire periodar - to aktive (morgon og kveld) og to passive (dag og natt). Eg fann at beste modellen for å forutsjå ein elgkalvpredasjon baserte seg på samlingar av posisjonar (cluster) frå bjørnen sine aktive periodar innanfor ein radius på 50 m. Det originale GPS-datasettet utan posisjonssimuleringar viste seg å gje tydlegare svar enn dei "utbetra" datasetta. Predasjonsmodellen gav eit estimat på tilsaman 78 drepte elgkalvar, noko som tilsvarar gjennomsnittleg predasjonstakt for einslege skandinaviske bjørnebinner på 7,1±0,92 elgkalvar per år. Dette stemmer godt overens med rapportar frå Skandinavia og Nord-Amerika ved tilsvarande relativ elgtettheit (elg/bjørn). Estimert predasjonstakt varierte frå 3,8 til 15,1 mellom ulike individ. Gjennomsnittleg predasjonstakt var ulik i dei to åra, og resultata indikerer at dette kan tilskrivast at vi nytta ulike individ. Estimerte predasjonsdatoar strekte seg frå 18. mai til 24 juni og var jamnt fordelt gjennom predasjonsperioden. Estimerte predasjonstidspunkt fordelte seg relativt jamnt utover døgnet, og var ikkje ulik i bjørnen sine fire døgnlege aktivitetsperiodar. Predasjonsrater basert på GPS-data og GIS-analyser er tidlegare rapportert nytta på puma *Puma concolor* L. og ulv *Canis Lupus* L. Dette er predatorar som tek relativt store bytte. At predasjonsrater hjå ein omnivor art med eit relativt lite bytte kan reknast ut på bakgrunn av GPS-data er imidlertid ny kunnskap. Denne predasjonsmodellen kan med modifiseringar nyttast for andre bjørneklasser sin predasjon på elgkalv, og metodikken vil kunne anvendast også på bjørn som drep sau *Ovies aries* L. og tamrein *Rangifer tarandus* L.. Individbaserte predasjonsstudier opnar for ny kunnskap og innsikt i predasjonsmekanismane. Håpet er at dette vil føre til ei betre framtidig forvaltning av bjørnestammen, og redusere konfliktnivået mot jegerar og primærnæringar.

INTRODUCTION

The brown bear *Ursus arctos L.* is an omnivorous species, utilising a broad range of different food sources throughout its geographical range (e.g. Clevenger, Purroy & Pelton, 1992; Krechmar, 1995; McLellan & Hovey, 1995; Sato, Mano & Takatsuki, 2005). Most studies on brown bear diet report seasonal changes according to the available food sources, but the diet is also reported to differ between individuals and age and sex classes (Jacoby et al., 1999), between females of different mating histories (having cubs of the year vs. not) (Ben-David, Titus & Beier, 2004), between subpopulations (Hilderbrand et al., 1996), and possibly due to different altitudes (Hobson, McLellan & Woods, 2000) and latitudes (climate) (Krechmar, 1995; Persson et al., 2001). Diet studies based on fecal samples of the brown bear in south-central Sweden reported berries *Vaccinium myrtilus* , *Empetrum* spp., moose *Alces alces* and ants *Formica* spp*., Camponotus* spp. to constitute the main food sources in terms of total assimilated energy (Dahle, 1996; Johansen, 1997; Opseth, 1998).

Brown bear predation on several prey species is well documented. In various studies in North America, the brown bear has been found to be an important predator on moose (Ballard, 1992; Bertram & Vivion, 2002; Gasaway et al., 1992), caribou *Rangifer tarandus* (Boertje et al., 1988; Young & McCabe, 1997) and elk *Cervus elaphus* (Singer et al., 1997). In different areas of Scandinavia, brown bear has been reported to predate on moose and depredate semi-domesticated reindeer *Rangifer tarandus* and free-ranging domestic sheep *Ovis aries* (Dahle et al., 1998; Persson et al., 2001). In south-central Sweden, the brown bear is reported to be an important predator on moose calves, with an estimated predation rate (proportion of moose calves killed by brown bear) of 26%, and a corresponding individual kill rate (number of moose calves killed annually per brown bear) of 6.8 for bears ≥ 4 years old (Busk, 1998; Swenson et al., Unpublished data). Ninety-three percent of predated moose calves were killed within 4 weeks after birth, the moose parturition period ranging from mid-May to early June (Busk, 1998). During summer (21 May to 31 July), moose calves constitute the most important food source of brown bears in this area, with an estimated dietary energy content of 36-44% (Opseth, 1998). According to Swenson et al. (unpublished data), the brown bear predation rates on moose calves in Scandinavia were comparable to predation rates reported from North America at corresponding relative moose densities (moose/brown bear).

The traditional methods of estimating brown bear predation rates involve intensive field work, and most of them do not include individual differences and error estimates. In addition, Swenson et al (1999) recommended not to mark moose calves with ear transmitters, because of the high mortality rates calves experienced. The introduction of GPS technology in the monitoring of free-ranging species started a new era in wildlife studies (Rempel, Rodgers & Abraham, 1995; Moen et al., 1996; Rodgers, Rempel & Abraham, 1996). The GPS technique provides an automatic position collection independent of location, time of day or weather conditions, with high accuracy and large data storage capacity. The GPS positioning records are easily processed into Geographical Information Systems (GIS), providing an important tool in animal movement investigations. Predation rates based on GIS analysis and GPS-data have been reported from studies of cougar *Puma concolor* and grey wolf *Canis lupus* (Anderson & Lindzey, 2003; Sand et al., 2005). The aim of this study is to explore the possibility of predicting moose calf predations by single female brown bears in south-central Sweden, and the estimation of corresponding individual kill rates, based on GPS records.

Study area

The study was conducted in the counties of Dalarna, Gävleborg, and Jämtland, south-central Sweeden (61°N, 15°E). The area is gently rolling with scattered hills, the elevation ranging from about 200 to 700m. No part of the study area is above treeline, which is at about 750 m above m.s.l. The area belongs to the northern boreal forest zone, comprising coniferous forest and numerous lakes, rivers, and large bogs. Human settlement is limited to a few scattered villages and cabins. The forest is intensely managed, and constitutes a mosaic of large clear cuts and tree monocultures. The landscape is intersected by a network of gravel roads. The coniferous forest is dominated by Scots pine *Pinus silvestris* L., with large fractions of Norway spruce *Picea abies* L. and the exotic lodgepole pine *Pinus contorta* Dougl. ex Loud. The forest also includes a minor fraction of deciduous tree species like birches *Betula pubescens* Ehrh., *B. pendula* Roth., aspen *Populus tremula* L., European mountain ash *Sorbus aucuparia* L., and grey alder *Alnus incana* (L.) Moench. Field vegetation includes bilberry *Vaccinium myrtillus* L., cowberry *V. vitis-idea* L., crowberry *Empetrum hermaphrodium* Hagerup, heather *Calluna vulgaris* (L.) Hull, common juniper *Juniperus communis* L., willows *Salix* spp., and different forbs, grasses and sedges. Most areas are covered by mosses and lichens.

The study area is located in the southern core area of the Scandinavian brown bear population (Fig. 1). Brown bear density in the area was estimated to be 30/1,000 km by a combination of a mark-recapture technique and fecal DNA sampling (Bellemain et al., 2005; Solberg et al., 2006). Bears are legally hunted; the bear hunting season lasts from 21 August to 15 October. In Orsa Besparingsskog, the 750 km^2 communally owned forest where most of the field work was conducted, the winter population of moose was estimated to be about 500/1,000 km^2 (Sven Brunberg pers com). The moose harvest is about 100 mature moose/1,000 km^2 and 50 moose calves/1,000 km^2, the moose hunting season lasts from 5 to 25 September and 8 October to 31 January (Sven Brunberg pers com; Swedish Environmental Protection agency, 2005.). Other potential large prey species of the brown bear are roe deer *Capreolus capreolus* L., which occur at low densities, the estimated summer density of about 300-600 individuals per 1000 km^2 (Liberg & Andrén, 2005) and beaver *Castor fiber* L., but the brown bear is not considered to be an efficient predator on these species (Dahle, 1996; Johansen, 1997; Opseth, 1998). Eurasian lynx *Lynx lynx* L. occur in relatively low and stable numbers, with yearly estimates ranging from about 1.0 to 1.5 family groups per 1,000 km^2 (Liberg & Andrén, 2005). Single grey wolves wander sporadically through the entire study area, and the south-eastern part of the study area included parts of the territories of two different wolf packs during the summers of 2004 and 2005 (Pedersen et al., 2005; Wabakken & Aronson, 2006).

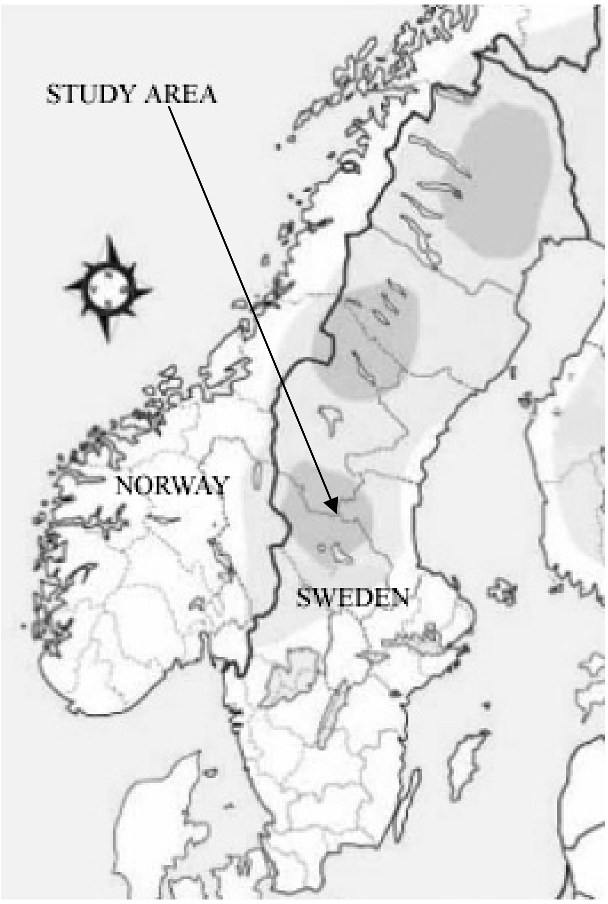

Figure 1. Study area and the distribution of brown bears *Ursus arctos* L. in Scandinavia; brown bear core areas in dark grey (After (Swenson et al., 2005)).

Methods

Data collection

In the years of 2004 and 2005, we studied the habitat selection of female brown bears based on GPS positioning records of 6 and 5 brown bears, respectively. The process of capture, age determination, and marking of bears was described by Swenson et al. (2001). The bears were all sexually mature females, ranging from 3 to 10 years old. They were all solitary, except one who was accompanied by her yearlings. Three of the bears were studied in both years; one of the 2004 bears was shot during the legal bear hunt, and two gave birth to cubs and thus were excluded from the studies to avoid possible disturbance. The bears were all equipped with GPS Plus-3 and GPS Pro-4 neck collars including dual-axis activity sensors and GSM lateral modems (VECTRONIC Aerospace GmbH, Berlin, Germany). Position and activity data were stored in the GPS collar, and could be downloaded by collar removal or by bilateral UVH communication to a hand-held receiver. In addition, data packages of seven stored GPS positions were automatically transmitted by the GSM modem. The GPS collars were programmed to position intervals of 30 min yielding a maximum of 48 positions per day. Activity levels were stored every five min, representing the mean of activity levels measured 7 times per second. A single GPS position was assigned the activity levels of the 30-minute interval surrounding the time of the GPS fix. Active and passive bear behaviours could be separated, based on GPS collar activity levels (Gervasi, Brunberg & Swenson, In press).

We investigated a random sample of the downloaded GPS positions, chosen by the randomisation-function in Microsoft® Excel. As a general rule, we investigated three-day old locations as a compromise between relatively fresh signs and avoiding possible disturbances. We investigated the area within a radius of 30 m, registering all bear signs (e.g. beds, scats, and scratch marks) and a wide range of habitat parameters. Moose calf predations were verified by the presence of remains of the moose calf (usually sparse). The predation sites were usually easy to detect due to the brown bear's habit of covering carcasses with mosses and other vegetation. We located the sites with handheld GPS-receivers (MAGELLAN Spor Track Pro [Thales, Santa Clara, California, USA] and MAGELLAN GPS315 [Thales]). We commonly used the "GO TO" function on the handheld GPS-receivers, thus adding an extra location error source. GPS location error is reported to be ≤ 31 m 95% of the time (D'Eon et al. 2002). Still, we believe that the 30-m radius procedure covered most of the true bear locations.

I plotted the GPS locations from the year 2005 in ArcView® GIS 3.2 (Environmental Systems Research Institute 1999). An investigation of GPS positions neighbouring verified moose calf predation sites revealed a distinct pattern of clustering. I hypothesized that clusters with a high number of positions (including missing or non-valid positions in the time span between positions in cluster) and a long duration indicated a potential predation site. I used the Spatial Analyst 2.0 (ESRI, 1999) Neighbourhood Statistics function with a moving window search radius of 200 m to detect position clusters. Based on a subjective evaluation of GPS position clustering and some knowledge of the individual bear's movement patterns, I detected 35 potential kill sites, which I investigated in the field. These were not included in the random sampling.

GPS data processing

A previous study showed that 93% of the bear-killed moose calves in the study area are killed within the first four weeks after birth (Busk, 1998). The moose parturition period in the study area ranges from mid-May to early June (Busk, 1998). Thus, I defined the predation season as 15 May to 30 June. I excluded all GPS locations outside this period from the GPS positioning data set. The available 2004 data set started on 20 May; hence the 2004 predation season was set ad hoc to 20 May to 30 June.

One of the main problems with the use of GPS telemetry is the fix rate bias, as a result of a lack of contact between the satellites and the GPS collar. Location success is reported to depend on forest characteristics (Rempel, Rodgers & Abraham, 1995; Moen et al., 1996; Moen, Pastor & Cohen, 1997; Rempel & Rodgers, 1997; Dussault et al., 1999; D'Eon et al., 2002), topography (D'Eon et al., 2002; Cain et al., 2005), satellite constellation (Moen, Pastor & Cohen, 1997), radio collar position (D'Eon & Delparte, 2005), collar brand (Frair et al., 2004), and animal behaviour (Moen et al., 1996; Bowman et al., 2000). The GPS-GSM collars introduce an additional source of data loss, because data packages of seven GPS locations may be lost due to GSM communication malfunction. Jansson (2005) reported that 83±3.6% of the GPS data loss occurred when bears are inactive, strongly suggesting behaviour-induced data loss. I introduced a simplified version of location simulation procedure proposed by Frair et al. (2004) to improve GPS data location success. For every missing location, I calculated the time difference and distance between the surrounding valid GPS positions. I set the maximum time difference to perform simulations to 4 hours, equalling the loss of one GSM data package. I varied the maximum simulation distance (30, 50, 100, and 200 m) to create several different data sets. The missing locations meeting the time-difference and distance criteria were assigned a random position (using the random function in Microsoft® Excel) between the preceding and later valid position. I 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 (Wilcoxon signed rank test).

Based on the results of Moe (2005), I categorized the GPS positions as belonging to one of the Scandinavian brown bear's four daily activity periods (Table 1). I defined a position as "active" based on primary activity level, i.e. when belonging to the activity periods Early-Day Activity (EDA) or Late-Day Activity (LDA).

Table 1. Daily activity periods of Scandinavian brown bears during the mating season (20 May – 6 July), based on half-hour mean activity levels (after Moe 2005)

Period	Primary Activity Level	Time of day (Central European summer time, i.e. GMT + 2 h)
Night rest (NR)	Inactive	00:30-02:59
Early-Day Activity (EDA)	Active	03:00-08:29
Day Rest (DR)	Inactive	08:30-17:59
Late-Day Activity (LDA)	Active	18:00-00:29

Predation model development

I used the 35 investigated potential predation sites resulting from the GIS analysis and added 35 randomly selected and investigated locations from the 2005 field season to develop a general predation model. Using the investigated potential predation locations, I tested whether the time lapse between the estimated predation time and the field observation influenced predation verification (Mann-Whitney U-test). All statistics described were performed in SPSS® 13.0 [SPSS Inc., Chicago, Illinois, USA]. I plotted the investigated locations, and the 2005 GPS position data sets (including GPS position simulations) in ArcView® GIS 3.2. The observed locations were spatially joined to the GPS positions with buffer distances of 30, 50, 100 and 200 m. I thus described the observed locations by the parameters "no. of positions", "no. of active positions" (See Table 1), "no. of periods", and "no. of days" within buffer distances of 30, 50, 100, and 200 m, both with original predation season GPS data set and with simulated locations within radii of 30, 50, 100 and 200 m. This resulted in 20 different data sets of observed locations described by four variables.

I classified the verified moose calf predation locations, one unspecified (either moose calf or roe deer) predation location, and two locations containing a substantial amount of old slaughter remains as predation events. I coded a 'predation' event as 1 and 'no predation' as 0, and used a binary logistic regression analysis (Hosmer & Lemeshow, 2000) to estimate the probability of a predation event. I used forward-stepwise logistic regression, based on a model likelihood ratio test to screen the large number of data sets and covariates. I set the entry probability to 0.01. This differs from the default 0.05 value, and even more from the general advice of Hosmer & Lemeshow (2000) of including covariates at a probability level of 15-20%. I chose 0.01, because all of the four possible covariates are in essence different descriptions of the same phenomenon, i.e. the duration of the time bears stayed at a location. A best model of one or two covariates should be sufficiently precise to predict the predation probabilities, thus minimizing model variance and avoiding the problem of overfitting the model. All pair-wise interactions were examined. I tested the models for overdispersal (Residual Deviance/ DF), and applied Hosmer-Lemeshow deciles of risk test to assess goodness-of-fit.

I based the model selection on Bayesian Information Criterion (BIC). This criterion penalises the number of model covariates more than the Aikaike's Information Criterion (AIC) (Burnham & Anderson, 2002; Johnson & Omland, 2004), depending on sample size. I chose to include several of the best models from this process in the field tests. I applied the best predation models to the randomly selected investigated locations in 2004 and the 2005 investigated locations that were not used in building the predation model. Based on field observations, I chose to categorize two of the verified predation locations of 2005 as "no predation", as I evaluated these moose calves to have been killed and consumed by other bears (In the first case, the moose calf carcass was discovered 14 days ahead of bear W0209's first appearance at the location. In the second case, bear W0210 only had one GPS position within a 50 m radius of the carcass, but spent some time in the neighbouring area. In the same periode, this bear was observed accompanied by a larger, older and more dominant female bear). I estimated the number of predations by adding the model predation probabilities of all inspected clusters (≥ 2 positions within a given buffer distance), and compared the estimate with the verified number of predations. I calculated the models' standard error manually based on covariance matrixes, and used the standard error to obtain 95% confidence intervals (CI) of each individual cluster's predation probability. The 95% CI of the predation estimates were calculated by summing the 95% CI values of the individual clusters. Based on the criteria of a simple, precise and easily applicable model, I chose one final model. Based on the classification tables of the final model (Hosmer & Lemeshow, 2000), I calculated model sensitivity (correctly classified kills / total kills) and specificity (correctly classified non-kills / total non-kills), using three different decision rules (i.e. choose to inspect all clusters with a kill probability more than a set value) with probabilities of 0.1, 0.2, and 0.3.

Ignoring the previous field work and its verification of predations, I applied the final model on the 2004 and 2005 GPS position records to estimate individual kill rates. The individual kill rates (moose calves killed per bear) were estimated as the sum of predation probabilities of each cluster (≥ 2 positions within a given buffer distance). I tested whether the mean estimated kill rates of the years of 2004 and 2005 differed, using a two-tailed Mann Whitney U test, and whether the estimated individual kill rates depended on each individual GPS collar location success, using linear regression.

Investigating date and time of predation.

I defined the time of predation to correspond to the first GPS location within the model buffer distance of a verified kill. I excluded positions diverging in time to the other cluster positions, ensuring both spatial and temporal clustering. I estimated time of kill for all the verified kills, except those two which I evaluated to be killed by other bears. I tested whether the distribution of kills differed among the weeks of the predation season 2005, using a χ^2 test. I also tested whether the time of kill was evenly distributed among the four daily activity periods (χ^2 test, $p<0.05$).

RESULTS

The GPS radio collar records consisted of 19,209 valid GPS positions with activity levels in 2004 and 19,658 GPS positions in 2005, but with no activity recordings. The mean overall location success rate was 69±4.4% (LSR±SE). After removing two cases of serious collar malfunction, the mean overall location success rate was improved to 75±1.6%. Restricting the data sets to predation seasons only resulted in 9,617 and 8,268 valid GPS positions in 2004 and 2005, respectively, with a mean location success of 76±2.8% during the predation season. After including simulated positions (Table 2), each increase in the maximum distance allowed between the preceding and later valid GPS positions to perform simulations resulted in a significant increase in location success (Wilcoxon signed rank test, $p<0.01$ for all tests). At best, mean location success was 86±2.8%.

Table 2. Mean location success rate (LSR±SE) of predation-season GPS positioning records of six female Scandinavian brown bears in south-central Sweden in 2004 and five in 2005. The original data sets were transmitted directly from the GPS radio collars by GSM. A GPS position simulation procedure was applied when missing positions were within a maximum time lapse of four hours, and when the distance between preceding and later valid GPS positions were less than the given values in the table (Simdist, in meters).

Year	LS_original	LS_simdist30	LS_simdist50	LS_simdist100	LS_simdist200
2004	0.80 ± 0.033	0.86 ± 0.036	0.87 ± 0.037	0.88 ± 0.037	0.89 ± 0.038
2005	0.73 ± 0.044	0.79 ± 0.040	0.80 ± 0.039	0.81 ± 0.037	0.82 ± 0.035

Predation model

A total of 653 locations were randomly selected and investigated during the 2004 and 2005 predation seasons, resulting in the detection of 20 moose calf kill sites. Of the 35 potential kill sites investigated, 21 kills were detected. Basing the model on the 35 potential kill sites and an additional number of 35 randomly selected locations, the predation model data sets contained 23 locations classified as predation, and 47 as no predation. The forward stepwise logistic regression screening process resulted in a set of 5 best models (Table 3).

Table 3. The 5 best logistic regression models to predict locations of brown bear predation on moose calves in soth-central Sweden based on GPS positions within buffer distances of 70 investigated locations (23 predations, 47 non- predations). "B" refers to the buffer distance, e.g. B30 means a buffer of 30 m. "simdist" refers to the maximum distance (in meters) between preceding and later valid GPS position to allow position simulations. The covariate "periods" describes the number of different activity periods (see Table 1) the bear stayed within the buffer. The covariate "activepos" is the number of positions belonging to the activity periods "Early day activity" and "Late day activity" (See Table 1). Model selection was based on the Bayesian Information Criteria weights (w_{BIC}). The BIC weights (w_{BIC}) do not sum up to one, as only the best models are included.

Data set	g(x) =	w_{BIC}	H&L[a]
B30_original	-4.717±1.007 + 1.202±0.274 periods	0.138	0.068
B30_original	-4.793±1.128 + 0.734±0.334 periods + 0.182±0.091 activepos	0.137	0.85
B30_simdist30	-5.016±1.097 + 1.251±0.286 periods	0.388	0.097
B50_original	-3.754±0.858 + 0.264±0,059 activepos	0.109	0.61
B50_simdist30	-3.705±0.849 + 0.230±0.051 activepos	0.043	0.56

[a]Hosmer and Lemeshow deciles of risk test ($p<0.05$ suggests significant lack-of-fit)

No overdisperal adjustments were needed. Two models, both with "periods" as the only covariate, tended to have poor model fit (Hosmer and Lemeshow deciles of risk test, 0.05<p<0.10, Table 3), however based on the BIC model weight, the model of "B30_simdist30" with "periods" as single covariate appeared to be the single best model (Table 3). Based on BIC weight, I included 4 models in the next test (Table 4). When applied to 618 investigated bear locations during the predation season (not used in model creation), the number of predicted predations ranged from 19 to 42 (Table 4). Ninety-five % confidence intervals of only two of the models included the true number of 20 predations. Based on the criteria of obtaining a simple, precise and easily applied model, I chose "B50_original" as the final model (Fig. 1).

Table 4. Estimated number of brown bear predations on moose calves in south-central Sweden when the 4 best models were applied to a set of randomly selected and investigated locations (n=618) with 20 verified moose calf kill sites. The estimated numbers of predations were calculated as the sum of predation probabilities for all clusters' (≥ 2 positions within a given buffer distance) predation probabilities.

Data set	$\hat{g}$ (x) =	Est. predations	95% CI
B30_original	-4.717±1.007 + 1.202±0.274 periods	42	[25, 71]
B30_original	-4.793±1.128 + 0.734±0.334 per + 0.182±0.091 activepos	31	[15, 67]
B30_simdist30	-5.016± + 1.251± per	40	[25, 67]
B50_original	-3.754±0.858 + 0.264±0.059 activepos	19	[10, 39]

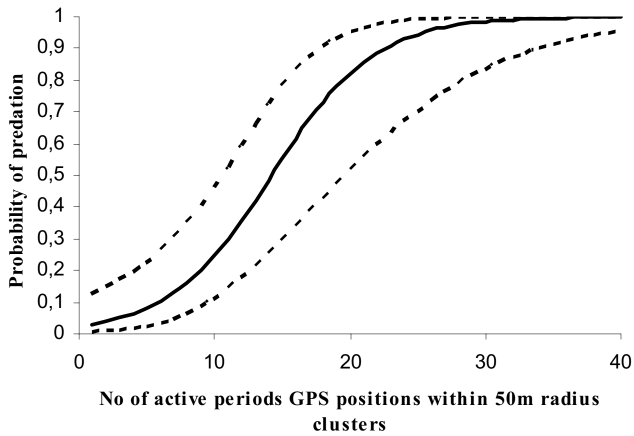

Fig. 1. The probability of predation on a moose calf for a single female Scandinavian brown bear, based on the number of active positions (i.e. belonging to the periods "Early day activity" or "Late day activity") within 50 m radius clusters. The GPS data-set consist of the original data transferred from the GPS radio collars by GSM. The predation model was based on 70 investigated locations (23 predations and 47 no predations). The solid line represents the logistic regression model $\pi(x) = e^{g(x)} / (1+ e^{g(x)})$, g(x) = -3.754±0.858 + 0.264±0.059*x, x = "active positions". Dotted lines represent the 95% confidence intervals of the model.

The final model classification tables, using different classification probability levels (p = 0.1, 0.2, and 0.3), reveal that the predation sites were detected in relation to model probabilities (Table 5) in this probability interval. When predation probabilities of the clusters exceeded 0.3, all the clusters included a verified kill site (Specificity=1.00, Table 5).

Table 5. Final model sensitivity (correctly classified predations / total predations) and specificity (correctly classified non-predations / total non-predations) of three different decision rules (i.e. choose to inspect all potential predation sites of more than a set probability level), when tested on random selected and inspected brown bear locations (n=618, with 20 verified moose calf predations) in south-central Sweden.

Sensitivity, p=0.1	Specificity, p=0.1	Sensitivity, p=0.2	Specificity, p=0.2	Sensitivity, p=0.3	Specificity, p=0.3
0.85	0.99	0.80	0.99	0.70	1.00

Individual kill rate estimates

Table 6. Estimated individual kill rates (number of moose calves killed in the spring predation periode) for single female brown bears in south-central Sweden based on the final model (Fig. 1) of cluster radius 50 m and original downloaded GPS data set. Predation estimates were calculated as the sum of cluster (≥ 2 positions within a 50 m radius) predation probabilities. The numbers of verified kills are from the investigation of randomly selected GPS positions (n=653, 20 verified kills) and investigation of potential predation sites detected in a preliminary GIS analysis (n=35, 21 verified kills). The number of verified kills detected by GIS analysis in parenthesis.

Year	Bear	Age of bear	Estimated individual kill rate	95 % CI	GPS Location Success rate	Verified kills
2004	W0004[a]	9	5.1	[2.5, 8.5]	0.85	3
2004	W0109	10	3.8	[2.9, 7.1]	0.83	0
2004	W0208	3	7.3	[4.8, 11]	0.86	1
2004	W0209	3	5.3	[2.9, 7.1]	0.64	1
2004	W0229	6	5.2	[2.3, 8.1]	0.82	1
2004	W0323	4	6.2	[3.3, 7.8]	0.78	4
2005	W0208	4	6.9	[3.3, 11]	0.64	4 (4)
2005	W0209	4	7.5	[4.0, 10]	0.69	4 (2)
2005	W0212	4	15	[8.2, 19]	0.81	11 (6)
2005	W0323	5	6.2	[3.2, 11]	0.63	5 (2)
2005	W0427	4	9.3	[4.4, 13]	0.85	7 (6)

[a]Accompanied by two yearlings

Applied to the 2004 and 2005 data sets, the final model estimated a total of 78 killed moose calves, with a mean individual kill rate of 7.1±0.92 during the predation season, ranging from 3.8 to 15 (Table 6). The estimated kill rates did not depend on the GPS radio collar location success (Linear regression, $r^2 = 0.20$, p=0.67). The estimated individual kill rates differed significantly between years (Mann-Whitney U test, p=0.022), with mean values of 5.5±0.48 and 9.0±1.6 for 2004 and 2005, respectively.

Predation date and time

The estimated predation date of the verified predations (n=41) ranged from 18 May to 24 June. The distribution the of estimated 2005 predation dates did not differ between the periods (week one to five + the last 12 days) of the predation season ($\chi^2 = 9.40$, DF=5, p=0.94, Fig. 2). Also, the estimated time of day of predation on moose calves did not differ significantly among the 4 different activity periods (χ^2=2.43, DF=3, p=0.49, Fig.3)

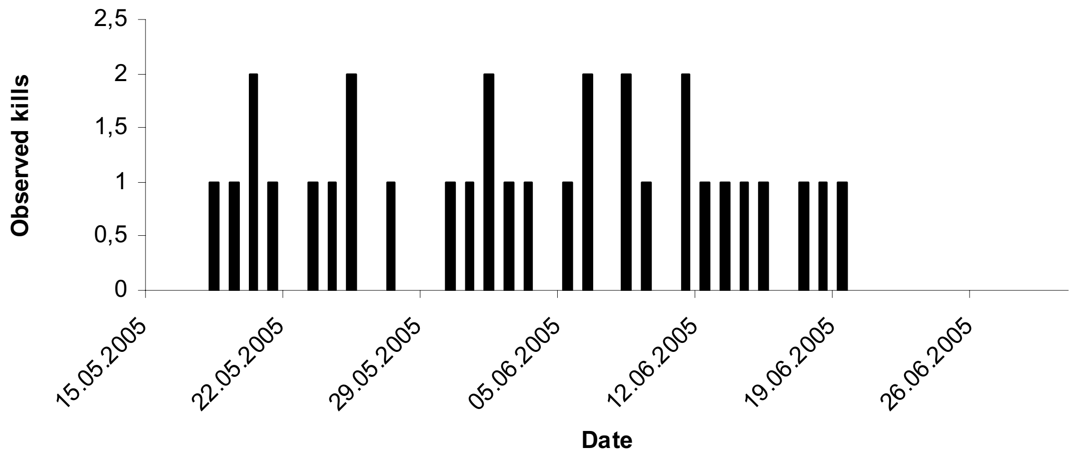

Fig. 2. The distribution of estimated brown bear predation dates for verified moose calf predations in south-central Sweden in 2005 (n=31). The predation season was defined as 15 May to 30 June.

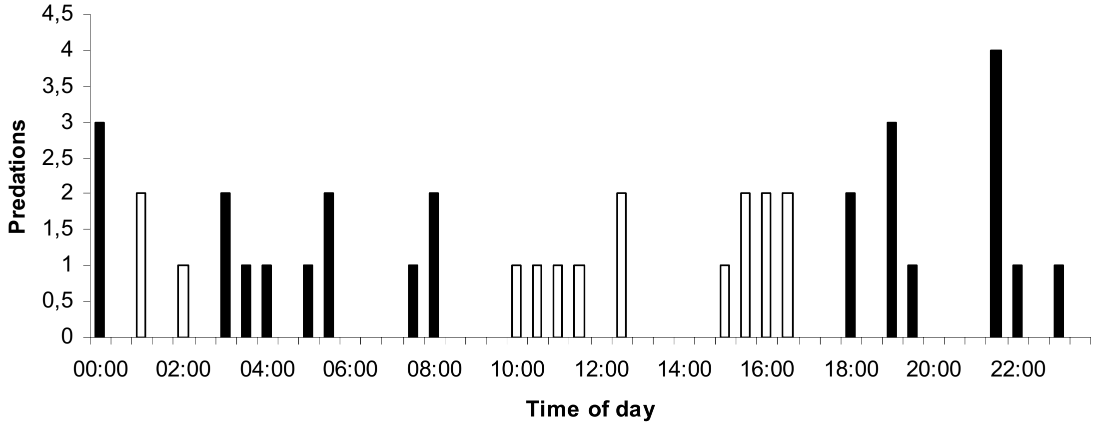

Fig. 3. Estimated time of predation for verified predations by brown bears on moose calves in south-central Sweden in 2004 and 2005 (n=41). White bars represent inactive periods, black bars represent active periods.

DISCUSSION

The mean location success rate during the predation season for this study was significantly lower than the mean value at a corresponding fix interval reported in a recent literature review of GPS collar performance (Cain et al., 2005). This is not surprising, because the results of Jansson (2005) strongly suggest behaviour-induced GPS data loss in brown bears. The mechanism behind this data loss may partly be habitat selection when inactive, but is most likely due to collar position (D'Eon & Delparte, 2005) or the obstruction of signal transmission by the bear's body while resting. I expected most of the bear behaviour at a long duration kill site to be inactive, i.e. resting and digesting, thus causing a bias towards data loss at kill sites. However, activity data was only available for the 2004 season and only 10 verified predation locations, so I was not able to investigate this supposition. Still, I detected bear beds at 36 of the 41 verified kill sites, and usually several beds (the mean no. 3.8±3.3), indicating extensive resting behaviour associated with moose calf predation sites. The simple and conservative GPS data simulation procedure improved location success rate at a maximum simulation distance of only 30 m, which corresponds very well with a behaviour-induced GPS data loss of inactive periods. The logistic regression model using a cluster radius of 30 m, a maximum simulation distance of 30 m, and with "periods" as the only covariate also performed best when ranked by Bayesian Information Criterion (BIC). Models with the single covariate "periods", however, tended to result in the same predation probability for very different durations of stay at a location, and were not applicable to estimating kill rate by adding all cluster predation probabilities of a GPS data set. The covariate "active positions" is better suited to discriminate different durations at bear locations into different predation probabilities.

The estimated mean individual kill rate of single female brown bears (3-10 years old) in south-central Sweden preying on moose calves was 7.1±0.92. The reported kill rate in the same study area, based on an earlier study using radio-marked moose calves and density estimates for moose and bears, was an average of 6.8 moose calves killed by each brown bear ≥ 4 years (Busk, 1998; Swenson et al., Unpublished data). This is well within the mean individual kill rate 95% CI of this model. However, the relative moose density at this time was higher than today (920 moose/30 bears vs. 500 moose/30 bears), and the brown bear kill rates on moose calves reported from Scandinavia and North America positively depend on relative moose density (Swenson et al., Unpublished data). As one also might expect different classes of bears (males, single females, females with cubs) to exhibit different predatory behaviour, the numbers are not directly comparable. Even though this estimate is slightly higher than those reported at a corresponding relative moose density, I still evaluate it to be strongly supported by the other studies in Scandinavia and North America.

One source of error of the predation verification process is the lack of discrimination between true bear predation and possible scavenging on moose calves that died from other reasons. Another obvious source of error of this model is the presence of other food sources, at which the bears exhibit behaviour similar to that at a moose calf predation site, e.g. carcasses, remains of slaughtered big game, baits, and consentrations of other foods. The two cases when slaughter remains were classified as predations in the model development were deposits containing substantial amounts of bones, and the duration bears spent there corresponded well with a moose calf predation. Of the total 688 bear locations inspected during predation season, 9 were sites with slaughter remains. But at only these two locations were the slaughter remains a sufficient food source to be predicted as a predation site by the model, resulting in a slight overestimation of the kill rates. This underlines the fact that the predation model is only a model, and proper use of it includes detailed in-field knowledge of the study area.

The mean individual kill rates differed between years. The estimated individual kill rates ranges from 3.8 (95% CI = [2.9, 7.1]) to 15 (95% CI = [8.2, 19]), indicating diverging foraging strategies also within the bear class of single females. Thus the difference between years may be due to mostly different individuals observed in the two years. This illustrates a major advantage of this procedure compared to traditional study designs. An individual-based predation model enables insight into the predation mechanisms and foraging strategies.

The biological interpretation of the different cluster radii tested in the predation model is the cautiousness bears exhibit at a kill site. A cluster radius of 30 m would indicate that the bears in general stay very close to the kill during the consumption period, whereas a larger radius could indicate a withdrawal to bed sites in the vicinity of the moose calf carcass. All the best models included a cluster radius of 30 or 50 m, indicating that the bears stayed very close to the kill site until the moose calves were consumed. It is obvious that diverging individual behaviour at a predation site influences the model's predation probabilities, and thus the estimated individual kill rates.

The estimated predation dates all fell within the predefined predation season, corresponding to the results of Busk (1998). The procedure of estimating predation time relies heavily on cluster radius. A small radius procedure is vulnerable to a scenario where the bear moves parts of the moose calf carcass to a location outside the kill site radius, where it later is observed. A larger radius will include locations where a bear is lurking at the outskirts of the presence of a defending moose cow, waiting for an opportunity to kill a moose calf. The estimated predation times did not differ between the activity periods of the day, contradicting my hypothesis of a relation between activity period and predation. This illustrates that the activity periods do not categorically describe the true activity levels, and that the possibility of killing a moose calf overrules the bears' general behavioural patterns.

MANAGEMENT IMPLICATIONS

This predation model based on GPS positioning data provides a simple tool to estimate kill rates of single female brown bears. The predation model represents several benefits compared to traditional designs. First of all, marking moose calves with radio transmitters can cause high mortality rates (Swenson et al., 1999). Second, as the GPS technique provides an automatic position collection, and the model does not depend on predation verification, the cost and effort of field work is dramatically reduced. As the price of GPS collars decreases and collar reliability improves, the technical costs will also be reduced.

With some parameter modifications, similar predation models can be developed for other classes of bears (females with cubs, males, juvenile bears), enabling an individual-based approach to bear predation studies. This technique is especially promising for predation studies of females with cubs of the year, as it enables predation estimates with no disturbance of the bears. However, this requires thoroughly testing, as females with cubs of the year display different movement and activity patterns (Dahle & Swenson, 2003). All together, this technique opens up new possibilities to study the mechanisms of predation, e.g. the kill rates of different bear classes and also individual differences within bear classes. Individual kill rates may be related to parameters as sex, age, and body mass, but may also be a result of learning. Obviously, the numbers of calves killed may depend on the number of moose calves available, i.e. related to moose habitat within the bears home range. As GPS collars provide large amounts of position data, I suggest studies of predation related to the predation process, e.g. habitat selection and bear movement patterns.

The individual-based predation estimates may have important implications to bear management and hunting policies for bear and moose. As the estimated kill rates indicate large differences in the number of moose calves killed within the home ranges of the different bears, the hunting teams might, for example, get compensation through differentiated prize systems. Bear management may also be adjusted as our knowledge into the predatory mechanisms of the brown bear is expanding.

With some further modifications, a predation model can be developed to fit brown bear predation on other species. In other parts of Scandinavia brown bear depredation on semi-domestic reindeer and free-ranging sheep represents an important part of the bear diet (Dahle et al., 1998), resulting in costly compensation arrangements and serious controversies (Sagør, Swenson & Røskaft, 1997). The controversy around brown bear depredation of sheep is the single largest threat against obtaining a sustainable brown bear population in Norway today (Swenson & Andrén, 2005). Individual-based insight into the depredation processes may result in better depredation estimates and the detection of potential “problem bears” (Linnell et al., 1999). Such knowledge would provide better premises to both brown bear management and compensation policies, and hopefully reduce conflict levels.

AKNOWLEDGEMENTS

I would like to express my deepest gratitude to the entire Scandinavian Brown Bear Project “family”, I feel proud and priviledged to be given the opportunity to conduct my thesis in such an inspiring environment.

First of all I would like to thank project leader and supervisor Prof. Dr. Jon Swenson and field work cordinator Sven Brunberg. Their support, knowledge and “ever-lasting” dedication and commitment to the brown bear research has been both a tremendous help and a great source of inspiration for me during my work

Thank you Ph.D. student Jonas Kindberg, SLU, for initiating this study and for valuable support in the methods development.

Thank you Inger Marie Yri, Jee-Yun Hyun, and Lisbeth Baklid for companionship and friendship during the field season 2005.

Thank you Ingela Jansson and Therese Fosholt Moe for introducing me to the field work and the 2004 data respectively.

And finally – thank you Gunhild for your support and your patience with me

LITERATURE CITED

Anderson, C.R. & Lindzey, F.G. (2003) Estimating cougar predation rates from GPS location clusters. *Journal of Wildlife Management*, 67, 307-16.

Ballard, W.B. (1992) Bear predation on moose: A review of recent North American studies and their management implications *Alces Supplement*, 1, 162-76.

Bellemain, E., Swenson, J.E., Tallmon, O., Brunberg, S. & Taberlet, P. (2005) Estimating population size of elusive animals with DNA from hunter-collected feces: four methods for brown bears. *Conservation Biology*, 19, 150-61.

Ben-David, M., Titus, K. & Beier, L.R. (2004) Consumption of salmon by Alaskan brown bears: a trade-off between nutritional requirements and the risk of infanticide? *Oecologia*, 138, 465-74.

Bertram, M.R. & Vivion, M.T. (2002) Moose mortality in eastern interior Alaska. *Journal of Wildlife Management*, 66, 747-56.

Boertje, R.D., Gasaway, W.C., Grangaard, D.V. & Kelleyhouse, D.G. (1988) Predation on moose and caribou by radio-collared grizzly bears in east central Alaska. *Canadian Journal of Zoology*, 66, 2492-99.

Bowman, J.L., Kochanny, C.O., Demarais, S. & Leopold, B.D. (2000) Evaluation of a GPS collar for white-tailed deer. *Wildlife Society Bulletin*(1), 141-45.

Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference*, 2nd edn. Springer-Verlag New York, Inc, New York.

Busk, H. (1998) *Brown bear (Ursus arctos) predation on moose calves in Swedish boreal forest*. Thesis, Swedish Agricultural University, SLU, Uppsala.

Cain, J.W., Krausman, P.R., Jansen, B.D. & Morgart, J.R. (2005) Influence of topography and GPS fix interval on GPS collar performance. *Wildlife Society Bulletin*, 33, 926-34.

Clevenger, A.P., Purroy, F.J. & Pelton, M.R. (1992) Food-habits of brown bears (Ursus arctos) in the Cantabrian Mountains, Spain. *Journal of Mammalogy*, 73, 415-21.

D'Eon, R.G. & Delparte, D. (2005) Effects of radio-collar position and orientation on GPS radio-collar performance, and the implications of PDOP in data screening. *Journal of Applied Ecology*, 42, 383-88.

D'Eon, R.G., Serrouya, R., Smith, G. & Kochanny, C.O. (2002) GPS radiotelemetry error and bias in mountainous terrain. *Wildlife Society Bulletin*, 30, 430-39.

Dahle, B. (1996) *Nutritional ecology of brown bears (Ursus arctos) in Scandinavia with special reference to moose*. Thesis, Norwegian University of Science and Technology, NTNU Trondheim.

Dahle, B. & Swenson, J.E. (2003) Seasonal range size in relation to reproductive strategies in brown bears *Ursus arctos*. *Journal of Animal Ecology*, 72, 660-67.

Dahle, B., Sørensen, O.J., Wedul, E.H., Swenson, J.E. & Sandegren, F. (1998) The diet of brown bears *Ursus arctos* in central Scandinavia; effect of access to free-ranging domestic sheep *Ovies aries*. *Wildlife Biology*, 4, 147-58.

Dussault, C., Courtois, R., Ouellet, J.P. & Huot, J. (1999) Evaluation of GPS telemetry collar performance for habitat studies in the boreal forest. *Wildlife Society Bulletin*, 27, 965-72.

ESRI. (1999). Introduction to ArcView® GIS, version 3.2. In. ESRI, Redlands, Califorrnia, USA.

Frair, J.L., Nielsen, S.E., Merrill, E.H., Lele, S.R., Boyce, M.S., Munro, R.H.M., Stenhouse, G.B. & Beyer, H.L. (2004) Removing GPS collar bias in habitat selection studies. *Journal of Applied Ecology*, 41, 201-12.

Gasaway, W.C., Boertje, R.D., Grangaard, D.V., Kelleyhouse, D.G., Stephenson, R.O. & Larsen, D.G. (1992) The role of predation in limiting moose at low-densities in Alaska and Yukon and implications for conservation. *Wildlife Monographs*, 120, 1-59.

Gervasi, V., Brunberg, S. & Swenson, J.E. (In press) An individual-based method to measure activity levels in brown bears. *Wildlife Society Bulletin*.

Hilderbrand, G.V., Farley, S.D., Robbins, C.T., Hanley, T.A., Titus, K. & Servheen, C. (1996) Use of stable isotopes to determine diets of living and extinct bears. *Canadian Journal of Zoology*, 74, 2080-88.

Hobson, K.A., McLellan, B.N. & Woods, J.G. (2000) Using stable carbon (delta C-13) and nitrogen (delta N-15) isotopes to infer trophic relationships among black and grizzly bears in the upper Columbia River basin, British Columbia. *Canadian Journal of Zoology*, 78, 1332-39.

Hosmer, D.W. & Lemeshow, S. (2000) *Applied logistic regression*, 2nd edn. John Wiley and Sons, Inc., New York.

Jacoby, M.E., Hilderbrand, G.V., Servheen, C., Schwartz, C.C., Arthur, S.M., Hanley, T.A., Robbins, C.T. & Michener, R. (1999) Trophic relations of brown and black bears in several western North American ecosystems. *Journal of Wildlife Management*, 63, 921-29.

Jansson, I. (2005) *A pilot study of brown bear (Ursus arctos) habitat use in central Sweden at two temporal scales using GPS*. Thesis, Swedish University of Agricultural Sciences, Umeå.

Johansen, T. (1997) *The diet of brown bear (Ursus arctos) in central Sweden*. Thesis, Norwegian University of Science and Technology, NTNU, Trondheim.

Johnson, J.B. & Omland, K.S. (2004) Model selection in ecology and evolution. *Trends in Ecology and Evolution*, 19, 101-08.

Krechmar, M.A. (1995) Geographical aspects of the feeding of the brown bear (*Ursus arctos L*) in the extreme northeast of Siberia. *Russian Journal of Ecology*, 26, 436-43. - In Russian (English abstract).

Liberg, O. & Andrén, H. (2005). Lodjurstammen i Sverige 1994-2004. -Eurasian lynx population in Sweden 1994-2004. (In Swedish). In. Grimsö Wildlife Research station, Swedish University of Agricultural Sciences, Ryddarhyttan, Sweden.

Linnell, J.D.C., Odden, J., Smith, M.E., Aanes, R. & Swenson, J.E. (1999) Large carnivores that kill livestock: do "problem individuals" really exist? *Wildlife Society Bulletin*, 27, 698-705.

McLellan, B.N. & Hovey, F.W. (1995) The diet of grizzly bears in the Flathead River Drainage of southeastern British-Columbia. *Canadian Journal of Zoology*, 73, 704-12.

Moe, T.F. (2005) *Diel variation in habitat selection of female Scandinavian brown bears (Ursus arctos) in relation to resting and foraging behavior*. Thesis, Norwegian University of Life Sciences, Ås.

Moen, R., Pastor, J. & Cohen, Y. (1997) Accuracy of GPS telemetry collar locations with differential correction. *Journal of Wildlife Management*, 61, 530-39.

Moen, R., Pastor, J., Cohen, Y. & Schwartz, C.C. (1996) Effects of moose movement and habitat use on GPS collar performance. *Journal of Wildlife Management*, 60, 659-68.

Opseth, O. (1998) *Brown bear (Ursus arctos) diet and predation on moose (Alces alces) calves in the southern taiga zone in Sweden*. Thesis, Norwegian University of Science and Technology, NTNU, Trondheim.

Pedersen, H.C., Wabakken, P., Arnemo, J.M., Brainerd, S.M., Brøseth, H., Gundersen, H., Hjeljord, O., Liberg, O., Sand, H., Solberg, E.J., Storaas, T., Strømseth, T.H., H, W. & Zimmermann, B. (2005). Rovvilt og Samfunn (RoSa). Det skandinaviske ulveprosjektet. -SKANDULV. Oversikt over gjennomførte aktiviteter i 2000-2004. -Carnivores and Society (RoSa). The Scandinavian wolf research project SKANDULV. Activities carried out during 2000-2004 (In Norwegian, Abstract in English). In *NINA Rapport*, Vol. 117, p 78. Norwegian Institute for Nature Research, Trondheim, Norway.

Persson, I.L., Wikan, S., Swenson, J.E. & Mysterud, I. (2001) The diet of the brown bear *Ursus arctos* in the Pasvik Valley, northeastern Norway. *Wildlife Biology*, 7, 27-37.

Rempel, R.S. & Rodgers, A.R. (1997) Effects of differential correction on accuracy of a GPS animal location system. *Journal of Wildlife Management*, 61, 525-30.

Rempel, R.S., Rodgers, A.R. & Abraham, K.F. (1995) Performance of a GPS animal location system under boreal forest canopy. *Journal of Wildlife Management*, 59, 543-51.

Rodgers, A.R., Rempel, R.S. & Abraham, K.F. (1996) A GPS-based telemetry system. *Wildlife Society Bulletin*, 24, 559-66.

Sagør, J.T., Swenson, J.E. & Røskaft, E. (1997) Compatibility of brown bear Ursus arctos and free-ranging sheep in Norway. *Biological Conservation*, 81, 91-95.

Sand, H., Zimmermann, B., Wabakken, P., Andren, H. & Pedersen, H.C. (2005) Using GPS technology and GIS cluster analyses to estimate kill rates in wolf-ungulate ecosystems. *Wildlife Society Bulletin*, 33, 914-25.

Sato, Y., Mano, T. & Takatsuki, S. (2005) Stomach contents of brown bears *Ursus arctos* in Hokkaido, Japan. *Wildlife Biology*, 11, 133-44.

Singer, F.J., Harting, A., Symonds, K.K. & Coughenour, M.B. (1997) Density dependence, compensation, and environmental effects on elk calf mortality in Yellowstone National Park. *Journal of Wildlife Management*, 61, 12-25.

Solberg, K.H., Bellemain, E., Drageset, O.M., Taberlet, P. & Swenson, J.E. (2006) An evaluation of field and non-invasive genetic methods to estimate brown bear (*Ursus arctos*) population size. *Biological Conservation*, 128, 158-68.

Swedish Environmental Protection Agency. (2005.). Beslut om skyddsjakt på bjørn 2005. - Descisions on bear hunting of 2005 (In Swedish).

Swenson, J.E. & Andrén, H. (2005). A tale of two countries: large carnivore depredation and compensation schemes in Sweden and Norway. In *People and Wildlife: Conflict or coexistence?* (eds R. Woodroffe, S. Thirgood & A. Rabinowitz), Vol. 9, pp. 323-39. Cambridge University Press, New York.

Swenson, J.E., Arnemo, J.M., Bellemain, E., Brunberg, S., Dahle, B., Drageset, O.M., Hustad, H., Katajisto, J., Kindberg, J., Nerheim, E., Solberg, K.H., Segerström, P., Støen, O.G., Söderberg, A. & Zedrosser, A. (2005). Rovvilt og Samfunn (RoSa) - Det skandinaviske bjørneprosjektet. Oversikt over gjennomførte aktiviteter; Sluttrapport til Norges Forskningsråd. -Large carnivores and society (RoSa). Overview of completed activities; Final report to the Research Council of Norway. (In Norwegian, abstract in English). In *NINA Rapport*, p 24. Norwegian Institute for Nature Research, Trondheim, Norway.

Swenson, J.E., Dahle, B., Busk, H., Opseth, O., Johansen, T., Wallin, K. & Cederlund, G. (Unpublished data) Predation on moose by European brown bears.

Swenson, J.E., Sandegren, F., Brunberg, S. & Segerström, P. (2001) Factors associated with loss of brown bear cubs in Sweden. *Ursus*, 12, 69-80.

Swenson, J.E., Wallin, K., Ericsson, G., Cederlund, G. & Sandegren, F. (1999) Effects of ear-tagging with radiotransmitters on survival of moose calves. *Journal of Wildlife Management*, 63, 354-58.

Wabakken, P. & Aronson, Å. (2006). Ulv i skandinavia pr 15. april 2006. -Grey wolf in Scandinavia per 15 April 2006 (In Norwegian). In. Hedmark University College, Faculty of Forestry and Wildlife Management, Evenstad, Norway.

Young, D.D. & McCabe, T.R. (1997) Grizzly bear predation rates on caribou calves in northeastern Alaska. *Journal of Wildlife Management*, 61, 1056-66.