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Original article

Resource selection by sympatric free-ranging dairy cattle and brown bears *Ursus arctos*

Sam M.J.G. Steyaert, Ole-Gunnar Støen, Marcus Elfström, Jens Karlsson, Ron Van Lammeren, Jan Bokdam, Andreas Zedrosser, Sven Brunberg & Jon E. Swenson

Livestock depredation is an important factor that contributes to low public acceptance of large carnivores, and it is often used as an incentive to reduce large carnivore populations. In central Sweden, brown bears *Ursus arctos* coexist with a traditional cattle husbandry system that allows daytime free-ranging of dairy cattle. Despite a growing brown bear population, depredation on cattle remained stable during the last decade and is among the lowest rates reported worldwide. Nevertheless, major stakeholders argue for a substantial reduction in brown bear numbers, among other reasons, to safeguard the traditional husbandry system. Based on satellite tracking data, we assessed and correlated the resource selection of nine brown bears that were sympatric with six daytime free-ranging cattle herds during the free-ranging season (i.e. June-August) in 2008. We found a significant and negative relationship between resource selection of brown bears and free-ranging cattle during the study period, mainly because of inverse relationships between the species towards vegetation density and human-related infrastructure, such as forest roads, buildings and settlements. We predict that the probability of an encounter between these species, given that there is no directed predation, is highest in dense vegetation patches close to the human habitation-related variables. Because of the low reported depredation rates and the apparent habitat segregation between the species, our results provide no support for the argument to reduce brown bear numbers to safeguard the traditional cattle herding system.

Key words: brown bear, cattle, coexistence, depredation, human-wildlife conflict, resource selection, Ursus arctos

Please note that supplementary information including Appendices SI - SIV mentioned in this article is available in the online version of this article, which can be viewed at www.wildlifebiology.com

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Minimising conflicts between wildlife and humans is essential for the conservation of wildlife and biodiversity in general (Berger 2006, Rondinini & Boitani 2007, Zabel & Holm-Muller 2008). Human-wildlife coexistence is becoming increasingly challenging on a global scale because of human encroachment on wildlife habitat, which may lead to an increase of conflicts (Rajpurohit 1999, Woodroffe et al. 2005, Nellemann et al. 2007). These conflicts may lead to legal and illegal persecution, often specifically targeting large carnivores, to prevent them from killing livestock, other wildlife or people (Boitani 2000, Swenson et al. 2000, Woodroffe et al. 2005). For example, populations of wolves *Canis lupus* and brown bears *Ursus arctos* are often under severe human pressure, despite the current more enlightened management practices that have lead to an increase in the species in several areas (Boitani 2000, Swenson et al. 2000).

The brown bear is a carnivore with a mainly omnivorous diet (Pasitschniak-Arts 1993); however, it commonly preys upon livestock throughout its distribution range (Servheen et al. 1999, Swenson et al. 2000), e.g. in Scandinavia (Zimmermann et al. 2003, Swenson & Andrén 2005), Spain (Kaczensky 1999), USA (Murie 1948, Knight & Judd 1983), Canada (Horstman & Gunson 1982), Russia (Vaisefeld & Chestin 1993), Turkey (Can & Togan 2004) and the Indian Himalaya (Chauhan 2003). Knight & Judd (1983) and Linnel et al. (1999) suggested that brown bears generally do not actively prey upon livestock, but may do so given the opportunity. For example, brown bears cause severe damage to free-ranging unattended sheep *Ovis* spp. in Norway, although such damage is considerably less severe in neighbouring Sweden, despite a larger bear population, because sheep are kept in enclosures close to farms and damage compensation is connected to prevention measures (Swenson & Andrén 2005).

Human persecution led to the functional extinction of brown bears in Sweden in the 1930s (Swenson et al. 1995). However, the population has recovered since then and consisted of an estimated 3,298 (2,968-3,667) individuals in 2008 (Kindberg et al. 2011). Despite the growing brown bear population (Kindberg et al. 2011), depredation numbers have remained stable during the last decade (Karlsson et al. 2006, Viltskadecenter 2010), and thus, they do not reflect the general bear population trend. However, livestock may also be affected indirectly by an increased carnivore presence. Indirect effects may be related to increased stress levels and may lead to e.g. decreased milk production, decreased mass gain, difficulties to handle livestock (Murie 1948, Zimmermann et al. 2003) as well as shifting grazing routines and habitat use (Brown et al. 1999, Ripple & Beschta 2004, Kluever et al. 2009).

Summer pasture farming was common in Sweden in the past. Farmers moved their livestock to grazing grounds in forested areas outside the villages during spring and summer, because the pastures near villages were used to grow hay to feed livestock during winter (Larsson 2009). Young family members usually accompanied the livestock to the summer feeding grounds to move them to suitable grazing areas as well as to protect them from depredation (Larsson 2009). Typically, livestock were moved to pens or barns during the night (Larsson 2009). Nowadays, only ca 200 summer farms remain in use in Sweden (Anon. 2007); most of them in the the distribution range of brown bears. Of these summer farms, 80% have dairy cattle (Elfström 2005), which commonly range free and unattended during daytime. Because dairy cattle are milked every day, they are penned overnight for this purpose. Also cattle used for beef production are often penned overnight, among other reasons because Swedish animal welfare laws stipulate that animals must have daily supervision (Anon. 2010). In Dalarna in south-central Sweden, bear-related cattle mortality accounts for $< 0.0007\%$ of the free-ranging cattle population (calculated from data in Lidberg 2009). However, $> 30\%$ of the summer-pasture farmers claimed that they had experienced disturbances, which might have been caused only by the presence of large carnivores (Elfström 2005, Lidberg 2009).

Livestock depredations and potential stress in livestock caused by bear presence may lead to income loss. These arguments, among others, are often used by major stakeholders to reduce bear numbers (Ericsson et al. 2010), partly to preserve the tradition of summer pasture farming in Sweden (Wanström & Dahlin 2008, Sjölander-Lindqvist 2009, Weberyd & von Essen 2009, Sjölander-Lindqvist et al. 2010).

In our study, we attempt to evaluate the potential

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effect of bear presence and bear habitat use on grazing habitat selection of dairy cattle by comparing and assessing the relationship between the resource selection of sympatric brown bears and semi free-ranging dairy cattle. In addition, we assess the importance of several environmental variables that may determine the relative probability of an encounter between the species.

Material and methods

Study area

Our study was conducted in the county of Dalarna, south-central Sweden (61°N, 15°E). More than 80% of the area consists of intensively managed boreal forest, with Norway spruce *Picea abies*, Scots pine *Pinus sylvestris*, lodgepole pine *P. contorta* and the birch species silver birch *Betula pendula* and downy birch *B. pubescens* as dominating tree species (Friebe et al. 2001, Moe et al. 2007). The turnover rate of the managed forest is 90-100 years, and $< 60\%$ of the forest is older than 35 years (Swenson et al. 1999). The prevailing logging system resulted in a patchy forest landscape of relatively small stands of different age-cohorts (median patch size $\sim$ 22,500 m^2; Moe et al. 2007). The remaining 20% of the area is mainly covered by bogs or lakes. The forest floor is dominated by lichens, heather *Calluna vulgaris* and the berry-bearing species bilberry *Vaccinium myrtillis,* cowberry *V. vitis-idaea* and crowberry *Empetrum hermaphroditum*. Elevations in the gently undulating terrain range from 200 to 700 m a.s.l. (Moe et al. 2007). Daily average temperature range from a minimum of -7°C in January to a maximum of 15°C in July, and snow cover lasts from late October to early May. The area is sparsely populated and contains a few scattered small settlements, but has a dense network of gravel roads (0.3 km/km^2; Nellemann et al. 2007). The population density of brown bear was estimated to be around 30 individuals/1,000 km^2 (Bellemain et al. 2005). In spring, moose *Alces alces* carrion and moose calves form an important source of protein for brown bears in our study area (Dahle et al. 1998, Swenson et al. 2007). The summer brown bear diet consists mainly of ants *Formica* spp. and *Camponotus herculeanus*, forbs and moose, and the autumn diet consists primarily of bilberry, cowberry and crowberry (Dahle & Swenson 2003). In the county of Dalarna, about 1,500 free-ranging cattle are distributed over 74 summer pasture farms, which corresponds to ca 20 cattle/farm (Lidberg 2009).

Study design

We studied resource selection of free-ranging cattle on six of the seven active summer farms in our study area. These farms kept their cattle inside pens during the night. No disturbance or depredation had been reported on three of the studied farms, whereas three farms claimed to have experienced disturbance caused by large carnivores. None of the farms had lost cattle to carnivore depredation; however, one cow was injured by a bear on one farm in 2006. Our own field observations, as well as personal communications with the cattle farmers, assured us that the herds travelled as one and almost never split up. We therefore equipped one cow in the herd of each farm with a Global Positioning System -Global System for Mobile communication (GPS-GSM) collar to represent herd movements (Televilt Tellus™ GPS collars). We replaced five of these collars with Vectronic Aerospace GPS-plus collars because of their performance (the average fix rate was 38.2%, ranging between 4.6 and 78.5%) at the onset of the study. Herd sizes per farm were four, five, 12, 20, 23 and 28 and comprised adult cows. The GPS collars were programmed to transmit one location every 30 minutes. Vectronic GPS-plus collars had an average fix rate of 95.7%. The fix rate per diurnal interval varied between 93.1 and 97.4%, and did not show a diurnal trend. We monitored the cattle herds from 14 June to 22 August 2008, i.e. the period when the cattle were ranging free and unattended between 05:00 and 20:30. The radio-locations were downloaded via GSM and imported into a Geographical Information System (GIS) for further analysis (ArcGIS 9.3 and the ET Geowizards 9.9 extension).We discarded all cattle locations before 05:00 and after 20:30 hours and all locations within a 25-m range around each summer farm, to avoid including locations from when the cattle were either not free-ranging or on the farm. Using the remaining locations ($N = 2{,}518$), we estimated a 95% contour kernel density home range for each herd, defined as the 'cattle range'. We sampled resource use and availability within each cattle range. Cattle locations were assigned as 'use', and an equal number of randomly drawn locations were used to represent availability.

We captured and equipped 39 brown bears with GPS-GSM collars (Vectronic Aerospace GPS-plus)

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in 2008, using aerial darting with an immobilisation drug from a helicopter (for a detailed description, see Arnemo & Fahlman 2007). The collars were programmed to obtain one position/30 minutes. The cattle range was frequented by nine GPS-marked brown bears during the study period and were therefore selected for our study. Five of the bears were males (four, six, 10 and 17 years old, and one of unknown age, but obviously > 3 years old based on its weight at the capture in spring). The remaining four females, of which the oldest had three yearlings, were three, five, nine and 14 years of age. We used all data from these bears that were obtained during 1 June - 31 August, except for the period 15 - 31 July. Resource use and availability were sampled within the 95% kernel density estimate home range of each individual bear. Bear GPS locations represented 'use', and an equal number of randomly drawn points represented resource availability. Sample size of used locations per bear varied between 3,698 and 5,072 data points.

There is a pronounced seasonal shift in bear diet in our study area. Ungulates, forbs and insects contribute 98% to the estimated dietary energy content (EDEC) during June and July. Berries only contribute with 1-2% to the EDEC during that period (Dahle et al. 1998). However, during August-October, berries contribute up to 81% to the EDEC (Dahle et al. 1998). Because this pronounced seasonal dietary shift affects brown bear behaviour and habitat selection (Dahle & Swenson 2003), we divided the location data for both bears and cattle into two seasons, based on berry availability (i.e. pre-berry season: before 1 July; berry season: after 16 July; Dahle & Swenson 2003).

We distinguished diurnal intervals pragmatically, based on Rees & Hutson (1983), who reported that free-ranging cattle foraged mainly during mornings and evenings and rested and ruminated at midday. Moe et al. (2007) reported that the main activity period of bears was during early mornings and late evenings. Thus, we divided the diurnal period into five intervals; early morning (00:00-04:59), morning (05:00-09:59), midday (10:00-14:59), evening (15:00-20:59) and late evening (21:00-23:59).

Model variables

We selected variables to model resource selection by brown bears and free-ranging cattle based on a literature review and field experience. The variables were derived from three source layers, i.e. a digital elevation model (DEM, National Land Survey of Sweden, available at: www.lantmateriet.se), topographical maps (National Land Survey of Sweden, available at: www.lantmateriet.se) and IRSP6-LISS3 satellite imagery (images captured on 2 and 7 June 2007). We processed the satellite images with Erdas Imagine 9.1 (Leica Geosystems) software or derived data from the DEM and topographical maps using ArcGIS 9.2 (ESRI 2007).

We used the DEM to obtain data on slope steepness and terrain ruggedness. We calculated the terrain ruggedness index (TRI) for each 50 × 50 m raster cell based on the index developed by Riley et al. (1999), as a function of the variation in altitude (σ) for each cell relative to its eight neighbouring cells, the maximum observed altitude in the study area (σ_x) and the relative variety in classes of slope aspect (A, 45° classes (1-8)), steepness (S, 5° classes (1-9)) and curvature (C, from maximum upward concave to maximum upward convex (1-6); Equation 1). We standardised the resulting TRI values between 0 and 1 by dividing each pixel value by the maximum observed TRI value (TRI_x) and binned values in quartiles. We created a second ruggedness variable (TRI1000) to assess the importance of terrain ruggedness on resource selection by cattle and brown bears on a larger spatial scale, by calculating the average TRI value for each 50 × 50 m cell, based on all its neighbouring cells within a 1,000-m radius with a moving window approach.

$$\mathrm{TRI} = \frac{\sqrt{(\sigma/\sigma x)} \cdot [(S \cdot C \cdot A)/(S + C + A)]}{\mathrm{TRIx}} \quad (1).$$

Because an up-to-date land cover classification covering the study area was not available, we classified IRSP6-LISS3 satellite imagery with a supervised maximum likelihood classifier after image referencing and atmospherical correction. The spatial resolution of IRSP6-LISS3 imagery is 23.5 m (ISRO 2008). We collected ground-truth to train the classification during fieldwork in spring and summer 2008 (N = 395). Ground-truth of non dynamic land use classes, such as water bodies and habitation was derived from topographical maps (N = 75). We distinguished the following land-cover classes: bog, young dense forest, young open forest, older forest, water and other open land. The overall user's accuracy of the classified images was 87%. We validated the classification from 498 ground control points obtained in 2007, of which 77% were identified correctly.

The NDVI is a spectral vegetation index that indicates net primary above-ground production and

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Table 1. Description of model variables that we used to model resource selection by brown bears and free-ranging cattle during the free-ranging season of 2008 in our study area in central Sweden.

Category	Variable	Scale	Remarks
Terrain ruggedness	TRI	Four ordinal classes	TRI for a central 50 × 50 m cell, based on terrain characteristics of its eight neighbours.
	TRI1000	Four ordinal classes	Average TRI for each cell in a 1,000-m radius circle.
Slope steepness	Slope	Nine ordinal classes of 5 degrees of steepness each	-
Land-cover	Bog	Nominal land-cover classes	Bogs and tree rich bogs.
	Young dense forest		Average tree height in a 30-m radius circle < 7 m with a density of > 10,000 stems/ha.
	Young open forest		Average tree height in a 30-m radius circle < 7 m with a density of < 10,000 stems/ha.
	Older forest		Average tree height in a 30-m radius > 7 m high.
	Other open		Mainly forest pastures.
Vegetation density	NDVI	Ratio scale, between -1 and 1	Negative values indicate vegetation absence.
Distance to:	Water	Continuous variables, in m.	Lakes, ponds and rivers.
	Creek		Small streams.
	Trail		< 1-m wide hiking tracks.
	Forest road		Mainly plowed gravel roads.
	Building		E.g. single standing buildings, holiday houses and hunting cabins.
	Settlement		Settlements with < 200 inhabitants.

is used as a proxy for vegetation density (Osborne et al. 2001, Pettorelli et al. 2005). The index is based on contrasting reflectance by vegetation of red and near infrared electromagnetic energy (Gamon et al. 1995) and was derived from the IRSP6-LISS3 satellite imagery. Each pixel returns a value between -1 and 1. Negative values indicate vegetation absence, and high pixel values correspond to dense vegetation cover (Chen & Brutsaert 1998).

We derived raster data (25×25 m) on the distance (in m) to settlements, buildings, forest roads (gravel roads), trails, creeks and open water from the topographical maps. None of the variables were correlated (Pearson correlation coefficient > 0.6), and therefore, all were included for statistical modelling. A summary of the model variables is presented in Table 1.

Statistical models

We modelled resource selection by brown bears and cattle herds with generalised linear mixed models (GLMMs) of the binomial family with the Laplace approximation using the statistical programming language and environment R 2.10.1 (R Development Core Team 2009) and the 'lme4' package (Bates & Maechler 2010). We followed Manly's design type III (Manly et al. 2002), in which each individual study unit (i.e. individual GPS - marked cows and bears) remains identifiable. We used logistic regression with the binomial use and availability data as the response variable, and a set of model variables (e.g. NDVI, land cover, terrain ruggedness; see Table 1) as explanatory variables. We included individual bear or farm as random effects in our models to account for structured errors caused by repeated measurements (Pinheiro & Bates 2000, McCulloch & Searle 2001). We modelled resource selection for each defined diurnal interval and season. We randomly assigned each record into a training or a validation data set with an equal probability. We fitted the brown bear and cattle training data for each diurnal interval and season with four *a priori* defined candidate models (Table 2), following the information theory approach (Burnham & Anderson 2002). We used Akaike's Information Criteria (AIC), Akaike's difference (ΔAIC) and Akaike's weights (AIC_w) to assess model parsimony for each candidate model (Akaike 1973, Anderson 2008). To ensure comparability, we modelled the validation data sets according to the most parsimonious candidate model obtained by their corresponding training data set. We created resource selection maps (25 × 25 m cell size) for each selected training and

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Table 2. *A priori* defined candidate models with binary response variables (UA) that we used to model resource selection by brown bears and free-ranging cattle during the free-ranging season of 2008 in our study area in central Sweden.

Model type	Abbreviations	Model formulation
All inclusive	ALL	UA Individual ID + Bog + Young open + Young dense + Older + Other open + NDVI + Creek + Water + Building + Settlement + Trail + Forest road + TRI + TRI1000 + Slope
Land cover	LC	UA Individual ID + Bog + Young open + Young dense + Older + Other open
Human infrastructure	HI	UA Individual ID + Building + Settlement + Trail + Forest road
Expert	EX	UA Individual ID + Bog + Young open + Young dense + Older + Other open + NDVI + Water + Settlement + Trail + Forest road + TRI

validation data set by plotting parameter estimates of fixed effect variables in a GIS, yielding pixel values representing the relative probability that the pixel will be used by a cattle herd and bear during the same time interval. We standardised resource selection values between 0 and 1 and classified pixel values into 256 bins (the maximum number of bins possible in ArcGIS 9.2). We extracted binned pixel values for all training and validation data sets from 5,504 randomly drawn points (2 points/ha) in the cattle range, after masking water bodies, the cattle summer farms, and immediately adjacent grasslands. We then assessed model validation using a Spearman Rho correlation test for each training data set and its corresponding validation data set.

Spatial autocorrelation is a general property of ecological variables (Legendre 1993), and it may inflate Type I errors in statistical tests. We used a Bonferroni correction to adjust the 95% confidence intervals for each parameter estimate in each model, to remain conservative in our conclusions. We considered the responses of cattle and bears to a given variable as significant when its Bonferroni corrected confidence interval did not contain 0.

We assessed the relationship between the resource selection of brown bears and cattle using Pearson correlation tests, after accounting for spatial autocorrelation in the bear and cattle resource selection maps (Legendre 1993). We determined the level of spatial autocorrelation in each resource selection map using exponentially fit semivariograms and used the semivariogram range as the threshold distance to reach spatial independency between map locations. We used the 'automap' package in R to assess spatial autocorrelation (Hiemstra et al. 2009, R Development Core Team 2009). The semivariogram range of the strongest autocorrelated resource selection map was 1,345.4 m (Appendix SI). We used this distance as the minimum distance between points (N = 165) that were randomly drawn within the 95% kernel home range of all bear positions. For each point, we then extracted cattle and bear resource selection values and applied a Pearson correlation test between cattle and brown bear resource selection values for each diurnal interval and season.

We assessed the relative encounter risk between brown bears and cattle by multiplying the resource selection maps of both species for each appropriate diurnal interval per season. We standardised the pixel values of the resulting relative encounter risk probability maps and classified them in 256 bins. We drew 5,504 random points (2 points/ha) over the cattle range, and extracted the relative encounter risk values for each point. We fitted generalised linear models (GLMs) of the Poisson family for each diurnal interval per season, with relative encounter risk values as the response variable. Initially, we included all model variables in Table 1 in the model structure as explanatory variables. We determined the most parsimonious models with a stepwise AIC procedure. We assessed model validation with a leave-one-out cross validation procedure, yielding an estimate for the prediction error for each selected model. We calculated this as the mean squared error between the predicted and the observed values of all iterations in the validation process, using the 'stats' package in R (R Development Core Team 2009).

Results

Resource selection

Model selection

The all-inclusive candidate model during all diurnal intervals per season was selected as the most parsimonious for both brown bear and cattle (Table 3). The lowest Akaike's weight (0.701) was for cattle during mornings in the berry season (see Table 3).

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Table 3. The most parsimonious model for each season (S; PB = pre-berry, B = berry) and each diurnal interval (DI; EM = 00:00-4:59, M = 5:00-9:59, A = 10:00-14:59, E = 15:00-20:59, LE = 21:00-23:59) for both cattle and brown bear studied in central Sweden in 2008. Model shows candidate model (ALL = All inclusive model), N shows sample size, AIC_w the Akaike's model weight, $\sigma 2_{(r\ eff)}$ the variance of the random component in the GLMM, $p_{(t\text{-}v)}$ the Spearman Rho correlation coefficient between the training and validation data, and $p_{(p)}$ the P-value for the Spearman Rho correlation test.

Species	S	DI	Model	N	AIC_w	$\sigma^2_{(r\ eff)}$	$p_{(t\text{-}v)}$	$p_{(p)}$
Cattle	PB	M	ALL	953	0.997	0.011	0.932	< 0.001
		A	ALL	917	0.998	0.012	0.754	< 0.001
		E	ALL	846	0.886	0.013	0.660	< 0.001
	B	M	ALL	1079	0.701	1.180	0.872	< 0.001
		A	ALL	1114	1.000	5.606	0.847	< 0.001
		E	ALL	871	0.931	1.072	0.683	< 0.001
Brown bear	PB	EM	ALL	10843	1.000	0.002	0.852	< 0.001
		M	ALL	10923	1.000	0.002	0.949	< 0.001
		A	ALL	10879	1.000	0.002	0.986	< 0.001
		E	ALL	11038	1.000	0.002	0.930	< 0.001
		LE	ALL	10604	0.982	0.002	0.838	< 0.001
	B	EM	ALL	11654	1.000	0.002	0.928	< 0.001
		M	ALL	11736	1.000	0.002	0.980	< 0.001
		A	ALL	11712	0.953	0.002	0.991	< 0.001
		E	ALL	12057	1.000	0.002	0.988	< 0.001
		LE	ALL	11085	1.000	0.002	0.793	< 0.001

The variance component of the random factors in the selected GLMM model fits was generally small, except for cattle during the berry season (see Table 3). This indicates a considerable variation in resource selection during the berry season among the six cattle herds. The Spearman Rho correlation coefficients (p) used to validate the models were always significant (P-value < 0.001) and were generally higher for brown bear resource selection models ($0.793 < P < 0.991$) than for cattle models ($0.660 < P < 0.932$; see Table 3). Model selection diagnostics for all candidate models per diurnal interval and season for both free-ranging cattle and brown bear are presented in Appendix SII.

Cattle resource selection

Free-ranging dairy cattle did not select or avoid bogs and young open forests (Table 4). Cattle generally avoided young dense and older forest types. Terrain characteristics (TRI, TRI1000 and slope steepness) and NDVI appeared to have no strong influence on cattle resource selection, except that cattle selected steeper slopes during evening in the pre-berry season (see Table 4). Also distances to open water and creeks appeared to have no significant effect on resource selection by free-ranging cattle (see Table 4). However, cattle did select areas closer to human habitation-related variables (buildings, settlements, trails or forest roads) than random (see Table 4). The responses to model variables were relatively consistent during the berry and the pre-berry season. The parameter estimates of fixed variables of the cattle resource selection models per season and diurnal interval are included in Appendix SIII.

Brown bear resource selection

During our study period, brown bears did not show preference or avoidance for the habitat type 'other open', and they also did not select or avoid older forest types during the berry season (see Table 4). Brown bears selected for young open forest during the diurnal intervals early morning, evening and late evening in the pre-berry season and during early morning and late evening in the berry season (see Table 4). They significantly avoided young open forest during midday in the berry season and showed a general preference for young dense forest, except during the early morning and late evening in the berry season. During both seasons, brown bears selected areas characterised by a high NDVI value, i.e. dense vegetation, during daytime (morning, midday and evening diurnal intervals; see Table 4). They selected habitats closer to creeks than random during the pre-berry season, but showed an inverse response during the berry season. Open water was

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Table 4. Bonferroni-corrected responses by free-ranging cattle and brown bears to the model variables of the most parsimonious model for the pre-berry and the berry season of 2008, in central Sweden during the diurnal intervals (EM = 00:00-4:59, M = 5:00-9:59, A = 10:00-14:59, E = 15:00-20:59, LE = 21:00-23:59). '-' indicates a negative significant effect, '+' indicates a positive significant effect, and 0's indicate no significant effect. We changed the sign of the responses to the variables 'Creek', 'Water', 'Building', 'Settlement', 'Track' and 'Forest road' for interpretation purposes. They can now be interpreted as attractant (+) and avoidant (-).

	Cattle						Brown bear									
	Pre-berry			Berry			Pre-berry					Berry				
Variable	M	A	E	M	A	E	EM	M	A	E	LE	EM	M	A	E	LE
Bog	0	0	0	0	0	0	0	-	-	-	0	0	-	-	-	0
Young open	0	0	0	0	0	0	+	0	0	+	+	+	0	-	0	+
Young dense	-	0	0	-	-	0	+	+	+	+	+	0	+	+	+	0
Older	-	-	0	-	-	-	-	0	-	-	0	0	0	0	0	0
Other open	0	+	+	+	+	0	0	0	0	0	0	0	0	0	0	0
NDVI	0	0	0	0	0	0	0	+	+	+	0	0	+	+	+	0
Creek	0	0	0	0	0	0	+	+	+	+	0	-	-	0	-	-
Water	0	0	0	0	0	0	0	-	0	0	0	-	-	0	-	-
Building	+	+	0	0	+	0	0	0	0	0	0	0	-	-	-	0
Settlement	+	+	+	+	0	0	0	0	-	-	0	0	0	-	0	0
Trail	+	0	0	+	+	+	0	0	0	0	0	-	-	-	-	0
Forest road	0	+	0	+	0	+	0	0	0	0	0	0	-	-	-	0
TRI	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0
TRI1000	0	0	0	0	0	0	+	0	0	+	0	+	0	0	0	+
Slope	0	0	+	0	0	0	+	+	+	+	0	+	+	0	+	0

avoided during the morning in the pre-berry season and all diurnal intervals except midday during the berry season. Of the human habitation-related variables, brown bears tended to avoid settlements during midday and evening in the pre-berry season. During the berry season, however, human habitation-related variables were avoided generally, mainly during daytime (morning, midday and evening; see Table 4). Brown bears only selected for less rugged terrain in the berry season during midday. On a larger scale, more rugged terrain was selected (TRI1000) during early morning, evening and late evening during both the pre-berry and berry season (see Table 4). Brown bears generally selected steeper slopes during both seasons and their responses during both seasons were less consistent than in cattle resource selection. Human habitation appeared to be more determinative in brown bear resource selection during the berry season. The parameter estimates of fixed variables of the brown bear resource selection models per season and diurnal interval are given in Appendix SIII.

Relationship between brown bear-cattle resource selection

The Pearson correlation tests revealed significant and negative relationships between cattle and brown bear resource selection. During the pre-berry season, the correlation coefficients (C) were lower ($N = 165$, morning: $C = -0.390$, $t = -5.413$, $P < 0.001$; afternoon: $C = -0.314$, $t = -4.223$, $P < 0.001$ and evening: $C = -0.335$, $t = -4.541$, $P < 0.001$), than during the berry season ($N = 165$, morning: $C = -0.462$, $t = -6.659$, $P < 0.001$; afternoon: $C = -0.562$, $t = -8.694$, $P < 0.001$ and evening: $C = -0.435$, $t = -6.174$, $P < 0.001$).

Brown bear-free-ranging cattle encounter risk

Model selection

The stepwise AIC selection procedure of GLMs predicting encounter risk varied in the selection of variables included in the most parsimonious model. The habitat types 'bog', 'young dense forest', 'older forest' and 'other open' were always included, as were the NDVI, distance to creek and distance to open water variables (Table 5). Distances to trails, settlements and forest roads, and slope steepness were included for all diurnal intervals in the pre-berry season, but not in the berry season (see Table 5). The 'young open forest' habitat type, terrain ruggedness and distance to buildings were included as model variables in all diurnal intervals during the berry season, but not in the pre-berry season (see

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Table 5. Model formulation of the most parsimonious brown bear-free-ranging cattle encounter risk models after a stepwise AIC selection procedure during the pre-berry and the berry season of 2008 in central Sweden. The models were made for each diurnal interval (DI; M = 5:00-9:59, A = 10:00-14:59 and E = 15:00-20:59). Δ indicates the leave-one-out cross validation estimates of the predictor errors.

	DI	Δ	Model formulation
Pre-berry	M	0.113	Risk ~ Bog + Young dense + Young open + Older + Other open + NDVI + Creek + Water + Building + Settlement + Trail + Forest road
	A	0.122	Risk ~ Bog + Young dense + Older + Other open + NDVI + Creek + Water + Building + Settlement + Trail + Forest road + Slope + TRI + TRI1000
	E	0.117	Risk ~ Bog + Young dense + Young open + Older + Other open + NDVI + Creek + Water + Settlement + Trail + Forest road + Slope + TRI + TRI1000
Berry	M	0.209	Risk ~ Bog + Young dense + Young open + Older + Other open + NDVI + Creek + Water + Building + Settlement + Slope + TRI + TRI1000
	A	0.171	Risk ~ Bog + Young dense + Young open + Older + Other open + NDVI + Creek + Water + Building + Trail + TRI
	E	0.192	Risk ~ Bog + Young dense + Young open + Older + Other open + NDVI + Creek + Water + Building + Settlement + Trail + Slope + TRI + TRI1000

Table 5). Parameter estimates with their confidence intervals for each encounter risk model are presented in Appendix SIV. We considered the estimates of the prediction errors of the leave-one-out cross validation to be small (0.113-0.209), especially when considering the measurement scale (0-255; see Table 5).

Relative encounter risk models

We multiplied resource selection maps of brown bears and cattle, as a measure of resource selection similarity of relative encounter risk (Figs. 1 and 2). The risk for a brown bear-free-ranging cattle encounter was significantly and negatively affected by the habitat types 'bog', 'older forest' and 'other open landscapes', and significantly and positively affected by 'young dense forest' during all diurnal intervals in both seasons (Table 6). NDVI did not appear to affect encounter risk during morning in the pre-berry season, but during all other diurnal intervals in both seasons, we found a positive effect of NDVI on encounter risk (see Table 6). During the pre-berry season, encounter risk increased with a decreasing distance to creeks. During the berry season, this relationship was inverse during morning and evening, and encounter risk increased with an increasing distance from creeks (see Table 6). Except for the morning during the pre-berry season, encounter risk increased with an increasing distance from open water such as lakes and rivers. The general tendency was that encounter risk increased with decreased distances to human habitation (buildings, settlements, trails and forest roads). Forest roads, however, were not included in the most parsimonious models during the berry season, indicating that they had no profound effect on encounter risk during that season. We observed no clear trends for the effects of terrain ruggedness, on local or larger scales (TRI1000). Slope steepness, however, positively affected encounter risk during midday and evening in the pre-berry season, and during morning and evening in the berry season (see Table 6).

Discussion

Cattle resource selection

Cattle responses towards the model variables were relatively consistent during our study period. In general, cattle resource selection was higher in proximity to human habitation-related variables (settlements, buildings, forest roads and trails) and in the habitat type 'other open', which comprised mostly forest pastures. Cattle avoided older forest and young dense forest. Young open forest and bogs did not contribute significantly to resource selection by cattle, probably because these habitat types do not provide sufficient suitable food for cattle. Cattle are preferential grazers (Putman 1986), preferring green lush vegetation (Guevara et al. 1996). This explains the selection for the habitat class 'other open', as well as their preferred proximity to forest roads and trails. Pratt et al. (1986) and Putman (1986) showed that roadside verges were the most preferred habitat type for cattle in New Forest, United Kingdom. Roadside verges are considered important grazing grounds

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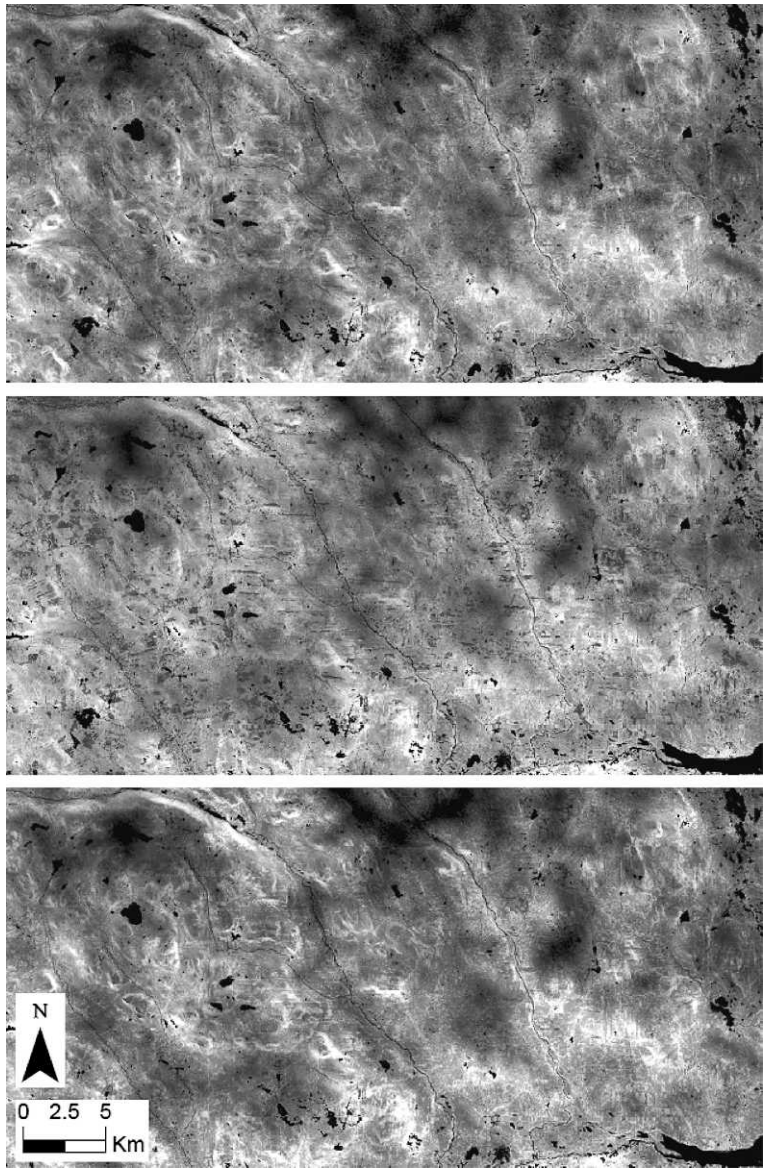


Figure 1. Multiplied standardised resource selection maps of brown bears and free ranging cattle for the morning (05:00-09:59; upper panel), afternoon (10:00-14:59; middle panel) and evening (15:00-20:59; lower panel) diurnal intervals during the pre-berry season in central Sweden during 2008. Water bodies are masked black. The grayscale indicates relative probabilities for an encounter between cattle and bears, with dark pixels indicating low relative probabilities, and light pixels indicating a high relative probability.

also in forested parts of Scandinavia, because few other habitats with high quality foods are available and the area of forest meadows and pastures have declined (Anon. 2009). Roath & Krueger (1982) report on the intensive use of logging roads and trails by free-ranging cattle in Oregon, USA. They ascribed this to the use of roads for travel to their preferred grazing grounds, as well as, but of minor importance, a grazing habitat itself. Cattle showed avoidance of young dense forest, a habitat type that is generally selected by brown bears. In large predator-free areas, such as the New Forest, United Kingdom, and the Wolfhezerheide, the Netherlands, woodlands are selected by cattle as resting habitats (Pratt et al. 1986, Bokdam et al. 2003).

Brown bear resource selection

Many studies report on the avoidance of human-related infrastructure by brown bears. Nelleman et al. (2007) showed that brown bears in our study area avoid tourist resorts and villages, and select for areas that are more rugged, remote and presumably less disturbed. Also during the critical winter denning period, brown bears in this area select den sites in steeper terrain and farther from roads with higher disturbance potential (Elfström et al. 2008).

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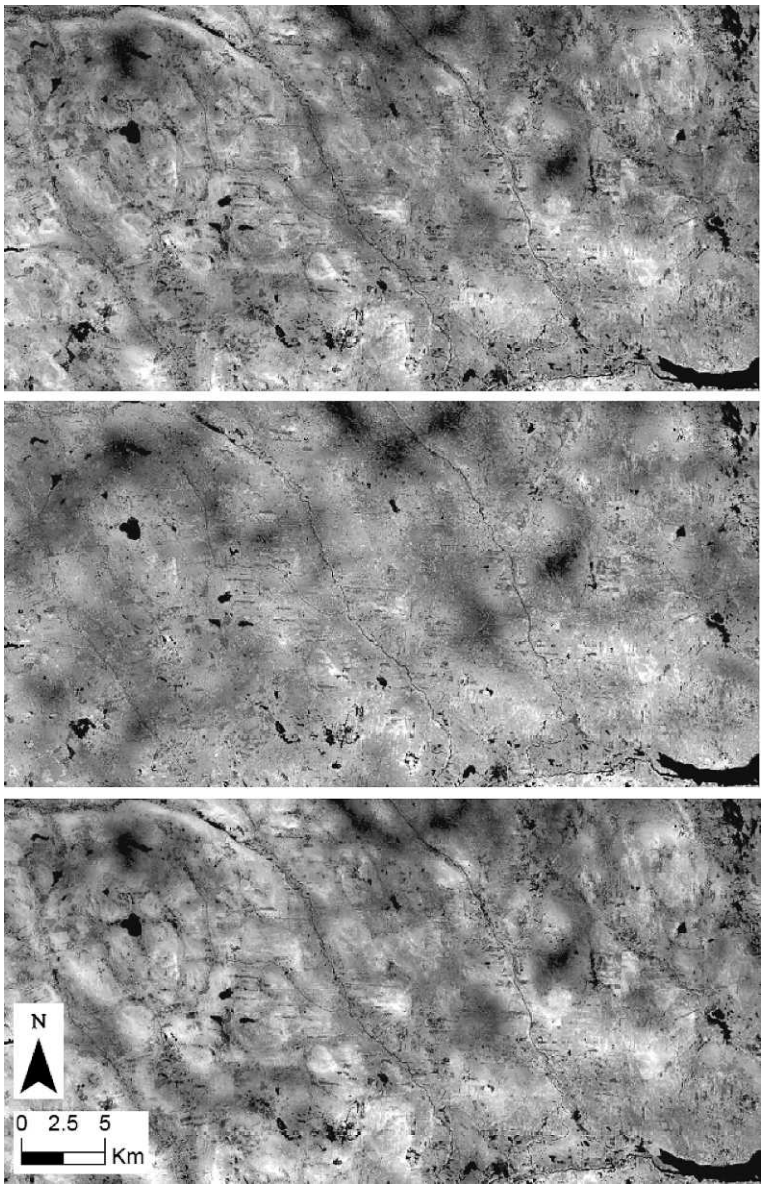


Figure 2. Multiplied standardised resource selection maps of brown bears and free ranging cattle for the morning (05:00-09:59; upper panel), afternoon (10:00-14:59; middle panel) and evening (15:00-20:59; lower panel) diurnal intervals during the berry season in central Sweden during 2008. Water bodies are masked black. The grayscale indicates relative probabilities for an encounter between cattle and bears, with dark pixels indicating low relative probabilities, and light pixels indicating a high relative probability.

Ciarniello et al. (2007) reported that proximity to roads and highways, and the probability for human-induced mortality negatively affected resource selection by brown bears in North America. Kaczensky et al. (2003) documented that brown bear movement patterns are affected by highways.

Our results are consistent with these findings; brown bears generally avoided human related infrastructure, such as forest roads, trails, settlements and buildings. The responses were more pronounced during the berry season, however, when the forest is also more intensively used by humans, i.e. for hunting, fishing, berry and mushroom picking (Nellemann et al. 2007). Moe et al. (2007) showed that brown bears in the same study area show strong diurnal behavioural differences, with resting periods typically during daytime, as well as a short period of rest around midnight. Brown bear day beds are typically located under dense vegetation in woodlands (Moe et al. 2007, Ordiz et al. 2011). This was also reflected in our results; areas with high NDVI values, as well as the habitat type 'young dense forest' were selected more during daytime (morning, midday and evening) than during nighttime (early morning and late evening).

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Table 6. Effects of model variables on the encounter risk between brown bears and free-ranging cattle in the pre-berry and the berry season of 2008 in central Sweden, during diurnal intervals of daytime free-ranging of cattle (M = 5:00-9:59, A = 10:00-14:59, E = 15:00-20:59). '+', '-' and 0 indicate Bonferroni corrected significant positive, negative and no significant effects, respectively. Signs of the parameter estimates of the variables 'Creek', 'Water', 'Building', 'Settlement', 'Trail' and 'Forest road' were changed for interpretation purposes. 'NI' indicates variables that were not included in the most parsimonious model.

	Pre-berry season			Berry season		
Variable	M	A	E	M	A	E
Bog	-	-	-	-	-	-
Young open	-	NI	+	-	-	0
Young dense	+	+	+	+	+	+
Older	-	-	-	-	-	-
Other open	-	-	-	-	-	-
NDVI	0	+	+	+	+	+
Creek	+	+	+	-	0	-
Water	0	-	-	-	-	-
Building	+	+	NI	0	+	-
Settlement	+	+	+	+	NI	+
Trail	+	0	+	NI	+	+
Forest road	+	+	+	NI	NI	NI
TRI	NI	0	0	0	-	+
TRI1000	NI	0	+	0	NI	+
Slope	0	+	+	+	NI	+

Relationship between cattle and bear resource selection

Our results show a significant negative relationship between resource selection by brown bears and semi free-ranging cattle. This implies that brown bears avoid areas that are intensively used by cattle and *vice versa*. The inverse responses to human habitation-related infrastructure and dense vegetation most likely explain this difference. However, we could not determine whether this negative relationship was caused by different foraging requirements or predator avoidance of the dairy cattle.

We documented a low relative risk of encounters between brown bears and semi free-ranging cattle in the study area. This does not necessarily imply that predation does not occur. For example, Bastille-Rousseau et al. (2010) document that American black bears *Ursus americanus* in Canada apply an opportunistic predation strategy. Black bears did not select for areas with a high probability to encounter the calves of caribou *Rangifer tarandus* and moose *Alces alces*, which are both important food items for black bears. They did, however, have a relatively high probability of encountering calves through frequent movements between preferred habitat patches (Bastille-Rousseau et al. 2010). In our study area, bear-induced cattle mortality was low (< 0.0007% of the semi free-ranging cattle population during 2000-2006), and cattle is insignificant in the brown bear diet in our study area. This suggests that bears in our study area do not actively prey upon cattle during day-time, and that the relative probability for an encounter is a reflection of the resource selection of both bears and free-ranging cattle.

Pratt et al. (1986) and Putman (1986) reported that cattle are less active at night, and select denser vegetated patches to rest and ruminate. Brown bears are more active at night (Moe et al. 2007). Kaczensky (1999) mentioned higher rates of livestock depredation by large carnivores at night. This suggests that potential opportunistic predation by brown bears may be more pronounced at night. Since free-ranging cattle in Sweden are penned overnight, potential opportunistic nighttime predation on cattle by brown bears is largely prevented.

Management implications

Brown bears in our study area are mainly active during crepuscular and nighttime hours and rest during most of the day (Moe et al. 2007). Because the cattle husbandry system allows only daytime free-ranging of cattle, there is a mismatch between the two species' activity patterns, which likely reduces the relative probability of an encounter between the two species.

The ultimate causes (e.g. predator avoidance, activity budgets and intrinsic behaviour) of the observed differences in resource selection between the two species remain unknown. Thus, we cannot rule out that cattle avoid bears, and therefore trade-off between safety and optimal resource selection, which may reduce the cattle's fitness. Additional research on this topic is therefore required.

Various authors (e.g. Horstman & Gunson 1982, Linnell et al. 1999, Goldstein et al. 2006) report that depredation by bears occurs incidentally; and when repeated, likely involves the same individual. Our results suggest that, with the current dairy cattle husbandry system, direct interactions between bears and dairy cattle are low, which is also reflected in the low depredation rate. Our results do not support the claim that a reduction of the bear population would help support the summer farming

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system. However, with our approach, we cannot evaluate indirect effects in dairy cattle by bears. Therefore, research on secondary effects such as e.g. stress-induced reduction of the milk-yield and occurrence of mastitis would be required.

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