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A human-induced landscape of fear influences foraging behavior of brown bears

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Abstract

Animals adapt their foraging behavior to variations in food availability and predation risk. In Sweden, brown bears (*Ursus arctos*) depend on a nearly continuous intake of berries, especially bilberries (*Vaccinium myrtillus*) during late summer and early autumn to fatten up prior to hibernation. This overlaps with the bear hunting season that starts on 21 August. Bilberry occurrence varies across space, as does human-induced mortality risk. Here, we hypothesize that brown bears select for areas with a high probability of bilberry occurrence across a boreal forest ecosystem in Sweden (H1), and that human-induced mortality risk reduces bear selection for bilberries (H2). In addition, we hypothesized that bears that survived the hunting season avoided bilberry areas associated with high risk, whereas bears that were later killed selected more strongly for berries and less against risk prior to the hunting season (H3). To evaluate our hypotheses, we used resource selection functions to contrast bear GPS relocation data (N = 35,

2012-2015) and random positions within the bears´ home range with generalized linear mixed effect models against two focal variables: a map predicting bilberry occurrence and a map predicting human-induced mortality risk. We found that bears selected for areas with a high probability of bilberry occurrence (supporting H1), but avoided these areas if they were associated with and high risk of hunting mortality (supporting H2). The killed and surviving bears did not differ in their selection for bilberries, but they did differ in their selection against risk (partially supporting H3). Surviving bears strongly avoided high risk areas, whereas killed bears responded less to risk and selected for high-risk areas with a low probability of bilberry occurrence. This suggests that killed bears selected for other food sources than berries in high risk areas, which exposed them to human hunters. We conclude that bears respond to a landscape of fear during the berry season and that different foraging strategies may have a direct impact on individual mortality during the hunting season.

Introduction

Animals may adapt spatial foraging patterns in response to changes in the quantity and quality of food resources (Hebblewhite et al. 2008). These responses to variation in temporal and spatial food availability may also expose the animals to different predators (McArthur et al. 2014). Predator presence can create a 'landscape of fear', which in combination with an uneven distribution of food resources, forces animals to balance access to food with the risk of predation in order to survive and reproduce (Brown et al. 2001; Laundré et al. 2010). Animals can, however, mitigate the risk of predation by adjusting their allocation of foraging time (Brown

1999; Lima & Bednekoff 1999), increasing vigilance (Brown 1999), or selecting foraging sites with low perceived predation risk (Brown & Kotler 2004). These behavioral responses often come at the cost of reduced food intake (McArthur et al. 2014). Gerbils (*Gerbillus allenbyi* and *G. pyramidum*), for example, select areas with denser cover, but with less resources, instead of open, resource-rich areas when predation risk is high (Kotler et al. 1991). In Yellowstone National Park, USA, the reintroduction of gray wolves (*Canis lupus*) altered movement patterns of elk (*Cervus canadensis*) and reduced their foraging on aspen (*Populus tremuloides*, Laundré et al. 2001; Ripple et al. 2001).

Behavioral changes in response to predation have usually been studied in relation to the effects of large carnivores on their prey. However, it is increasingly recognized that fear ecology may also apply to the effects of human disturbance on wildlife (Cromsigt et al. 2013; Frid & Dill 2002). Not only may human hunting impact the behavior of typical prey species, such as ungulates (Lone et al. 2015; Lone et al. 2016), it may also impact the behavior of apex predators (Brook et al. 2012; Ordiz et al. 2011). Historically, large carnivores were extirpated by human hunting and organized persecution throughout many ecosystems (Estes et al. 2011; Woodroffe 2000), and legal, regulated hunting is still a common tool for managing populations of large carnivores (Treves 2009). Legal hunting is currently the single most important source of mortality of Scandinavian brown bears (*Ursus arctos*) (Bischof et al. 2018; Gosselin et al. 2015) and causes bears to become more nocturnal at the onset of the hunting season (Hertel et al. 2016a; Ordiz et al. 2012). In Sweden, the hunting season overlaps with the period of hyperphagia, and this hunting activity has been shown to reduce bear foraging efficiency (Hertel et al. 2016a).

Brown bears depend on a nearly continuous intake of food during hyperphagia to gain weight for the subsequent hibernation. In many areas in both North America and Europe, berries are one of the most important food resources (Dahle et al. 1998; Welch et al. 1997).

Lingonberries (*Vaccinium vitis-idaea*), crowberries (*Empetrum nigrum*), and particularly the highly preferred bilberries (*V. myrtillus*) are the most important food resources for bears during hyperphagia in southcentral Sweden (Hertel et al. 2016b; Stenset et al. 2016). Feeding trials on captive bears have shown that bear foraging efficiency is positively related to berry density (Welch et al. 1997). The body mass of female bears in autumn and yearlings in spring in Sweden increases linearly with the annual bilberry abundance, which has a positive effect on the reproductive success of females with relatively low body mass (Hertel et al. 2018). Bilberries are keystone species in the boreal forests throughout Fennoscandia and production peaks in early August (Eriksson & Ehrlén 1991; Nilsson & Wardle 2005). Bilberry production tends to vary spatially across the landscape in relation to forest structure, which influences the occurrence and density of berries (Atlegrim & Sjöberg 1996; Kardell & Eriksson 2011; Nybakken et al. 2013).

We explore how brown bears in a boreal ecosystem in southcentral Sweden select for bilberries, while avoiding areas with a high risk of being killed by human hunters, and the impact of individual foraging strategies on hunting survival. Specifically, we look at how the bears' selection for bilberry fruit occurrence under varying levels of human-induced mortality risk was related to whether they survived or were killed during the hunting season. We focused our study period on the berry season prior to the start of the hunting to observe how the bears' foraging behavior in this period affected their survival during the subsequent bear hunt. We hypothesized that bears selected foraging locations with a high probability of bilberry occurrence (H1) and that bears avoided foraging in areas associated with a high risk of hunting mortality (H2). In addition, we hypothesized that bear foraging behavior prior to the hunting season differed between bears that survived and were killed in the following hunt (H3). Specifically, we predicted that bears that were killed displayed stronger selection for bilberry

fruit occurrence and less selection against risk of hunting mortality, compared to surviving bears.

Material and methods

Study system

The study area encompassed 4,200 km^2 in Dalarna and Gävleborg counties (61° N, 15° E) in southcentral Sweden. Rivers, hills, lakes, bogs, and some agricultural fields are scattered throughout the landscape, which is dominated by commercial forests of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) (Hertel et al. 2016b; Zedrosser et al. 2006). The landscape in the study area is gently rolling, with elevations varying from 200 to 1000 m above sea level (Zedrosser et al. 2006). Although the area is sparsely populated, with a human density of 5-7 inhabitants/km^2 (Ordiz et al. 2014), human activity in the forest increases during the autumn for hunting and berry picking (Nellemann et al. 2007). There are few high-traffic roads (0.14 km/km^2) within the study area, but a high density of low-traffic gravel roads (0.7 km/km^2) (Ordiz et al. 2011). The bear hunting season starts on 21 August and lasts until the quotas have been filled, but no later than 15 October. In the two counties of Dalarna and Gävleborg, the total bear hunting quota varied between 92-100 animals each year during our study. Every hunter is required to report the location where bears were shot to the Swedish hunting authority.

Focal variables: bilberry fruit occurrence, mortality risk, and survival

Sampling bilberry fruit occurrence in the field
We documented bilberry fruit occurrence (0 or >0 berries) (hereafter bilberry occurrence) at 2087 plots, each 1 m x 1 m, during the summers of 2014 (N = 1152) and 2017 (N = 935). In 2014, we sampled bilberry occurrence at 816 random and 336 bear foraging locations from mid-July until the beginning of September. The plot locations were randomly generated in three different sampling areas within the larger study area. The bear foraging positions were selected

from GPS positions with a 30-min fix rate and successive positions located 25-300 m between them, which we defined as foraging trajectories: the second position in each of these trajectories was sampled for berry occurrence. In July and August 2017, we again sampled bilberry occurrence at 935 random locations on clearcuts aged 1-14 years. These were randomly generated within areas recorded as clearcuts using ArcGIS. We located all the sampling locations with a handheld global positioning system (GPS). To avoid field observer bias regarding the exact placement of the plot, after the GPS point was reached, the plot was shifted by 0-9 m in one of the cardinal directions following randomization rules. See Hertel et al. (2016b) for more details about the sampling procedure.

Modeling and spatial prediction of bilberry occurrence

Bilberry occurrence was modeled and predicted separately for forested habitat, bogs, and clearcuts. This was necessary, because different drivers affect bilberry occurrence in different habitat types, i.e., in forested habitats tree height is an influential covariate, but tree height is by default neither available nor an influential covariate on clearcuts or bogs. To explain and predict spatial patterns of bilberry occurrence, we extracted a set of habitat and landscape covariates for each data subset (Table 1). The data were split into two datasets; one for training the models (75% of data points) and one for testing them (25% of data points). We used a random forest model with 2000 iterations using the R package 'randomForest' (Liaw & Wiener 2002) to explain drivers of bilberry occurrence within the three habitat categories. We used the variable importance measure for a backward elimination, removing the least important variable one at a time until the out-of-bag error rate increased to select the final model (Barber et al. 2016). We predicted the probability of bilberry occurrence for the testing dataset (25% of data points not used to build the model) to evaluate model performance. This model-predicted probability of bilberry occurrence was compared to the true presence/absence at each sampling

point. Predictive performance was then validated using the area under the Receiver Operating Characteristic (ROC) curve (Fawcett 2006). ROC values of 0.5 represent a performance at random, values >0.7 and <0.9 represent good model accuracy, and >0.9 represents high model accuracy (Fawcett 2006). Probability of bilberry occurrence was predicted spatially using those input habitat layers that proved to be influential in the model selection procedure. For spatial predictions, all habitat layers were cropped to the extent of the study area, projected into SWEREF 99 TM, and resampled to a resolution of 12.5 x 12.5 m. Predictions were updated annually to account for aging of clearcuts and emergence of new clearcuts over the time of the study (2012-2015).

Hunting mortality risk - The risk of human-induced mortality was extracted from a risk map (25×25 m) based on locations of shot bears during the 1982-2012 hunting seasons and modeled in a Resource Selection Functions (RSF) framework (Steyaert et al. 2016). Human-induced mortality risk was found to be highest close to human infrastructure, such as roads, villages, and agricultural fields. Because hunting causes 84% of the mortality of research bears in the study area (Gosselin et al. 2015), we used this map as a proxy for bear mortality risk.

Survival data – The Scandinavian Brown Bear Research Project recorded the fate of instrumented bears during each year of the study. This monitoring data was used to distinguish bears that were killed and those that survived the hunting season (2012-2015). We monitored the survival of each instrumented bear during the hunting season and defined bears that had been killed in the hunting season the same year as a killed bear. Surviving bears were defined as those that survived the hunting season the same year.

Bear position data - Bears were captured and fitted with GPS collars with Global System for Mobile Communication (GSM, Vectronic Aerospace GmBh, Berlin, Germany). See Arnemo and Fahlman (2011) for details on bear capturing and handling. All capture and handling of

bears were approved by the Ethical Committee on Animal Experiments, Uppsala, Sweden, and the Swedish Environmental Protection Agency. All bear positions were collected into the Wireless Remote Animal Monitoring (Dettki et al. 2013) database system for data validation and management. We used the bears' hourly GPS positions from 11 July to 20 August (prior to the hunting season) during 2012-2015, excluding positions with a dilution of precision (DOP) metric higher than 4, to increase the spatial accuracy of relocations (Lewis et al. 2007). To reduce data dependencies, we excluded all subadults (< 3 years) as they might have accompanied their mother. We discarded positions from the days with known disturbance (e.g. captures, experimental approaches). From the resulting GPS relocations, we extracted all 'foraging positions', i.e., GPS locations where bears had moved 100-800 m between hourly consecutive GPS relocations, similar to the approach used by Hertel et al. (2016b). We used all bear positions during the berry season to construct home ranges for each bear in each year using minimum convex polygons (MCP). Within the bears' home ranges, we created an equal number of random positions and removed all random and foraging positions within habitats that are unsuitable for berry plants, such as water and agricultural fields. We sampled the risk of hunting mortality and bilberry occurrence at each foraging location (1) and random location (0) in a 1:1 ratio. From the predictive bilberry occurrence maps, we extracted the probability of bilberry occurrence for each position (foraging and random positions).

Modeling habitat selection of killed and surviving bears

Most of the study bears that were killed in the hunting season were killed during the first days of hunting (Statens veterinärmedicinska anstalt 2015), leading to censored individual GPS series for killed bears with few foraging positions after the start of the hunting season. We therefore explored foraging behavior only prior to the hunting season to determine whether foraging behavior differed between subsequently killed and surviving bears. We applied RSFs with generalized linear mixed effects models (GLMM) to model differences between bear

foraging positions (used) and random positions (availability) following the approach by Manly et al. (2002). We constructed eight different candidate models with different interactions between probability of bilberry occurrence, risk of hunting mortality, and the fate of the bears (see Appendix A: Table 1). We included bear ID has a random intercept to account for selection preferences of individual bears (Leclerc et al. 2016). Additionally, we created a null model that contained only the random intercept. We selected the most parsimonious model using AIC_c model selection (Burnham & Anderson 2003) and selected the simplest model within $AIC_c<2$ to avoid pretending variables. Pretending variables are variables that are included in the most supported model, but explain very little of the variation in the response variable, which is indicated by a small AIC_c value separating it from a simpler model without the variable (Arnold 2010). All statistical modeling and spatial predictions were conducted in the software R (R Development Core Team 2013).

Results

Bilberry occurrence

Forest – Of 980 sampling locations, 656 (67%) contained bilberries. Tree height and percent of pine, based on total tree volume, were the most influential covariates explaining bilberry occurrence (see Appendix A: Fig. 1 & 2). Bilberry occurrence was more likely in forest stands of higher tree height and with an increasing proportion of pine volume. Predictive performance for bilberry occurrence, measured using the Receiver Operating Characteristic (ROC) curve, was 0.78, indicating good predictive performance (see also Appendix A: Fig. 3). *Clearcut* – Of 935 sampling locations on clearcuts, 504 (54%) contained bilberries. The most influential spatial covariates explaining bilberry occurrence on clearcuts were terrain ruggedness, elevation, slope, and clearcut age (see Appendix A: Fig. 4 & 5). Predictive performance for bilberry occurrence, measured using the ROC curve, was 0.73, indicating good predictive performance (see also Appendix A: Fig. 6). *Bog* - Of 177 sampling locations in bogs, only 26

contained bilberries. Bogs were thus a relatively unsuitable habitat for bilberry. Soil variables and terrain ruggedness were the only explanatory variables of importance in predicting bilberry occurrence (see Appendix A: Fig. 7 & 8). The predictive accuracy was 0.73 (see also Appendix A: Fig. 9). Merging spatial predictions for bilberry occurrence in forests, clearcuts, and bogs revealed strong heterogeneity in the probability of bilberry occurrence across the study area (Fig. 1).

Bear selection for forage and risk

We used 18,984 foraging positions from 35 bears during 2012-2015 and matched these with a n equal number of random positions. This included 10 males and 25 females, ranging from 3 to 22 years of age. Of those, 11 were killed by hunters during the study period (2012: 1 bear, 2013: 5 bears, 2014: 2 bears, 2015: 3 bears).

We selected the most parsimonious model (model 3), which included an interaction between berry occurrence and risk, as well as an interaction between risk and fate of the bear (Table 2). The model output indicated that bears selected for areas with a high probability of bilberry occurrence, but they avoided these areas when combined with a high risk of hunting mortality (Fig. 2 & Table 2). The most supported model did not contain an interaction between the fate of the bears and berry selection. However, there was a difference between killed and surviving bears regarding their selection against areas with high risk of hunting mortality. Killed bears responded less to increasing risk compared to surviving bears (Fig. 3), and seemed to select for areas with both a low probability of bilberries and high risk of hunting mortality (Fig. 2). In contrast, bears that survived selected against areas with a high risk of hunting mortality both in areas with high and low probabilities of bilberry occurrence.

Discussion

Brown bears selected for areas with a high probability of bilberry occurrence in areas with low

risk of hunting mortality, giving partial support to hypothesis 1. Spatial selection for areas with a high probability of bilberry occurrence reversed under high risk of hunting mortality, which supports hypothesis 2. While surviving bears only selected for bilberries at very low levels of risk and a high probability of bilberry occurrence, killed bears` had a slightly stronger selection for bilberries overall, and their selection for areas with a high probability of bilberry occurrence increased at lower levels of risk. Surprisingly, killed bears also selected for areas with high risk and a low probability of bilberry occurrence. Killed and surviving bears selected differently in response to risk, but did not vary in their selection of areas with a high probability of bilberries, thus we found only partial support for hypothesis 3.

Recent research from our study area suggests that bilberries are the most important food resource for bears during hyperphagia (Hertel et al. 2016b; Stenset et al. 2016). Bears usually forage in areas with high bilberry abundance, which is vital for their foraging efficiency and to obtain sufficient intake of berries (Welch et al. 1997). We were not able to predict bilberry abundance spatially with sufficient accuracy, due to a lack of high-resolution forest structure maps. However, we found that bears efficiently located areas with a high probability of bilberry occurrence, while also avoiding areas with a high risk of human-induced mortality, even before the start of the hunting season.

In general, both surviving and killed bears were less likely to forage in areas with both high probability of bilberry occurrence and high risk of hunting mortality, which supported hypothesis 2. This showed that despite their dependence on berries to gain weight during hyperphagia, bears are generally not willing to trade-off security to obtain bilberries. Surprisingly, killed bears showed a higher selection for high risk areas with low berry occurrence than high risk areas with high berry occurrence. One potential explanation for this risk taking behavior is that younger bears and females with cubs are displaced from berry areas and seek out high risk areas closer to human settlements to avoid larger male bears (Elfström

et al. 2014a & 2014b). Such displacement is most common during the mating season in spring when females with cubs are exposed to sexually selected infanticide, but differences in movement patterns tends to disappear later in summer when the berry season starts (Steyaert et al. 2013). Additionally, bilberries are evenly distributed across the boreal forests of Sweden and it seems unlikely that bears could be displaced from all areas with a high probability of bilberry occurrence. This risk taking behavior in poor berry habitats could alternatively be explained by bears foraging for other food resources than berries in high-risk areas. They may, for example, forage on road kills, slaughter remains close to settlements, or around oat (*Avena sativa*) fields, which are all high-risk areas with a low probability of berries. As this study focused on bear foraging on bilberries, we did not investigate foraging on other food sources. However, hunting mortality data show that a disproportionate number of bears are killed by hunters in or around oat fields, which represent a potential ecological trap for this bear population (Steyaert et al. 2016). The oat growing season overlaps with the berry season, and oats were found in 48.1% of bear scats collected in the same area (Elfström et al. 2014a). Judging from the common occurrence of oats in bear scats and the high number of bears killed in oat fields, it seems likely that this high-risk food source attracts some bears, while also exposing them to human hunters. We suggest more future research on how such anthropogenic food sources affect bear foraging behavior and hunting mortality.

Humans represent the greatest mortality risk for bears in Scandinavia (Bischof & Swenson 2009; Gosselin et al. 2015), and we have shown that bears adjusted their foraging tactics in relation to the risk of hunting mortality prior to the hunting season. Areas of increased hunting mortality for bears included areas close to villages, buildings, and roads, as well as agricultural areas. These areas are easily accessible for human hunters, thus increasing the mortality risk for bears that are using these areas (Steyaert et al. 2016). Hunting pressure in the study area has increased in intensity since 2006 (Gosselin et al. 2015), but hunters show little

selectivity towards age groups or sex (Bischof et al. 2009). The local bear hunting technique often involves driving on gravel roads, looking for bear signs before releasing hunting dogs to track the bears (personal observation). The bears' behavior prior to the start of the hunting season may therefore expose the bears to hunters days later, when the hunting season starts. Previous studies have found antipredator behaviors as a response to hunting. For example, red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) appear to avoid areas associated with a high risk of encountering hunters when the hunting season is ongoing (Ciuti et al. 2012; Lone et al. 2015; Lone et al. 2016). American black bears (*Ursus americanus*) avoid unpaved roads frequently used by human hunters (Stillfried et al. 2015), and coyotes (*Canis latrans*) and brown bears shift their daily activity patterns in response to hunting (Hertel et al. 2016a; Kitchen et al. 2000; Ordiz et al. 2012). We have shown, however, that brown bears in Sweden avoid high-risk areas even prior to the hunting season, which means that bears are impacted by human disturbance during a longer period than the hunting season itself.

Selection against areas of high mortality risk can represent a trade-off, if risky areas coincide with areas of high food abundance. Such trade-offs may force animals to increase vigilance or to forage in areas of poor food availability, which could reduce foraging efficiency and time spent foraging (Brown et al. 2001; McArthur et al. 2014). Such systematic antipredation behavior associated with a nutritive cost of reduced foraging efficiency over a prolonged period of time may affect the individual fitness of animals (Brown 1999; McArthur et al. 2014). Several studies suggest that human disturbance might disrupt or even restrict bears from utilizing important food sources (Hertel et al. 2016a; Olson et al. 1997; Robbins et al. 2007; White et al. 1999). Studies from North America indicate that bears require a high density of berries to enable them to take effective bites, and restricted access to dense berry areas may therefore reduce foraging efficiency (Welch et al. 1997). As bilberries are densely distributed throughout the boreal forest in Sweden, our study cannot conclude whether restricting bears

from certain high-density berry areas impacts individual fitness. We recommend that potential fitness effects of changed foraging behavior be explored in future studies within a boreal forest ecosystem. Additionally, commercial berry picking is common within the study area and future studies should address how the presence of berry pickers and the resulting removal of berries impact the bears.

Hunting has a strong limiting effect on the Swedish bear population (Bischof et al. 2018; Gosselin et al. 2015; Van de Walle et al. 2018) and we suggest that foraging strategies and habitat selection prior to the hunting season also influence the survival of individual bears. The foraging behavior of surviving and killed bears differed in our study; surviving bears avoided risky areas more than bears that were later killed. However, we only observed a slightly stronger selection for berries among the killed bears, indicating that surviving bears were still able to locate good foraging areas, while simultaneously avoiding risk. As the killed bears seemed to select for areas with high risk and low probability of berries, they were probably selecting for something other than berries, which later exposed them to hunters. We were unable to model the foraging behavior of subsequently killed bears during the hunting season itself, as most bears were killed within the first days of the season, resulting in an insufficient number of foraging positions to analyze. Although we do not have insight into the foraging behavior of the killed bears while the hunt was ongoing, their behavior prior to the hunting season suggests they may have been more exposed to humans than surviving bears. A study on personality types of common pheasants (*Phasianus colchicus*) in relation to hunting survival showed that shy birds that moved more slowly as juveniles were less likely to be killed during the hunting season, compared to bolder and fast-moving birds (Madden et al. 2014). We observed a similar behavioral difference in the bears in our study area, with hunter selection for the bears that foraged in risky areas. Whether this behavioral difference is due to different bear personalities would require a long-term study to assess the persistence of such behavioral traits over time.

However, the difference in foraging behavior between the killed and surviving bears may indicate a selective effect of human hunting, which could impact the persistence of bear personality types.

In today's highly anthropogenically modified landscapes, apex predators are strongly limited by human hunting, which affects both population density and behavior, as well as their potential effects on ecosystems (Kuijper et al. 2016; Ordiz et al. 2013; Ripple et al. 2014). We have shown that bears trade off foraging in areas with a high probability of bilberry occurrence when these are associated with a high risk of hunting mortality. Different foraging behavior during the hunting season may also have a direct impact on individual mortality. We conclude that bears select for areas with a high probability of bilberry occurrence, while also responding to a landscape of fear by avoiding areas with high risk of human-induced mortality.

Acknowledgement

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at XXXXX.

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Table 1. Spatial layers used to predict bilberry occurrence in the boreal forest of southcentral Sweden (2012-2015). Year of publication, resolution, and coordinate system of the original layers are given. All layers were projected into SWEREF 99 TM and resampled to a resolution of 12.5 x 12.5 m for spatial prediction.

Spatial layer	Year	Res (m)	Source	Coordinate system	Forested habitat	Clearcuts	Bogs
Biomass	2014	12.5	Skogstyrelse	SWEREF 99 TM	X		
Treeheight	2014	12.5	Skogstyrelse	SWEREF 99 TM	X		
DEM	2014	2	Lantmäteriet	SWEREF 99 TM	X	X	X
Slope		2	DEM derived	SWEREF 99 TM	X	X	X
Aspect		2	DEM derived	SWEREF 99 TM	X	X	X
Terrain ruggedness		2	DEM derived	SWEREF 99 TM	X	X	X
Percent Pine Volume*	2010	25	SLU Forest Map	RT90 2.5 gon V	X		
Percent Spruce Volume*	2010	25	SLU Forest Map	RT90 2.5 gon V	X		
Perscent Birch Volume*	2010	25	SLU Forest Map	RT90 2.5 gon V	X		
Silt	2016	500	European Soil Data Centre	LAEA	X	X	X
Clay	2016	500	European Soil Data Centre	LAEA	X	X	X
Water holding capacity	2016	500	European Soil Data Centre	LAEA	X	X	X
Bulk density	2016	500	European Soil Data Centre	LAEA	X	X	X
Coarse fragments	2016	500	European Soil Data Centre	LAEA	X	X	X
Sand	2016	500	European Soil Data Centre	LAEA	X	X	X
Clearcut age	2017	polygon	Skogsstyrelse	SWEREF 99 TM		X	
Distance to clearcut edge	2017			SWEREF 99 TM		X	

* Calculated as species specific volume / total volume

Fig. 1. Satellite image of a part of the study area in southcentral Sweden (A), predicted probability of bilberry occurrence (B), and probability of hunting mortality (C).
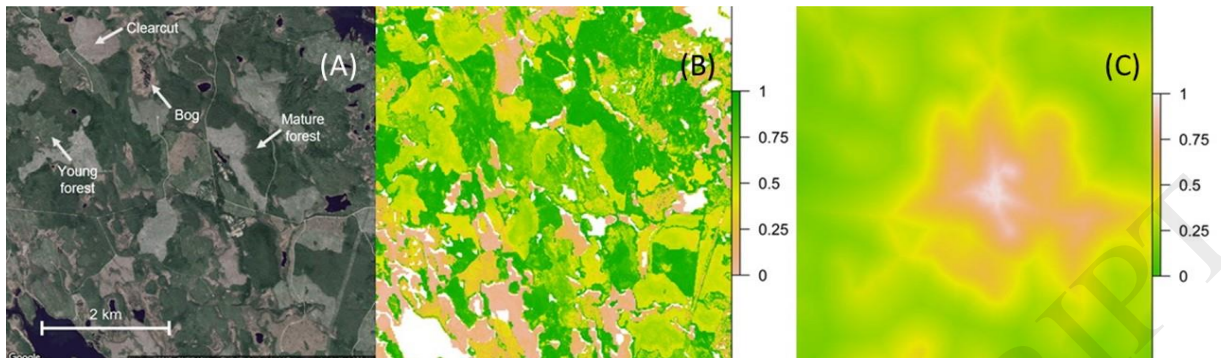
Fig. 2. Predicted selection for areas with varying probability of bilberry occurrence in southcentral Sweden in relation to different levels of risk of hunting mortality for surviving brown bears. Probabilities have been converted back from the logit scale and represent actual probabilities of selection. The dashed lines show the 95% confidence intervals.
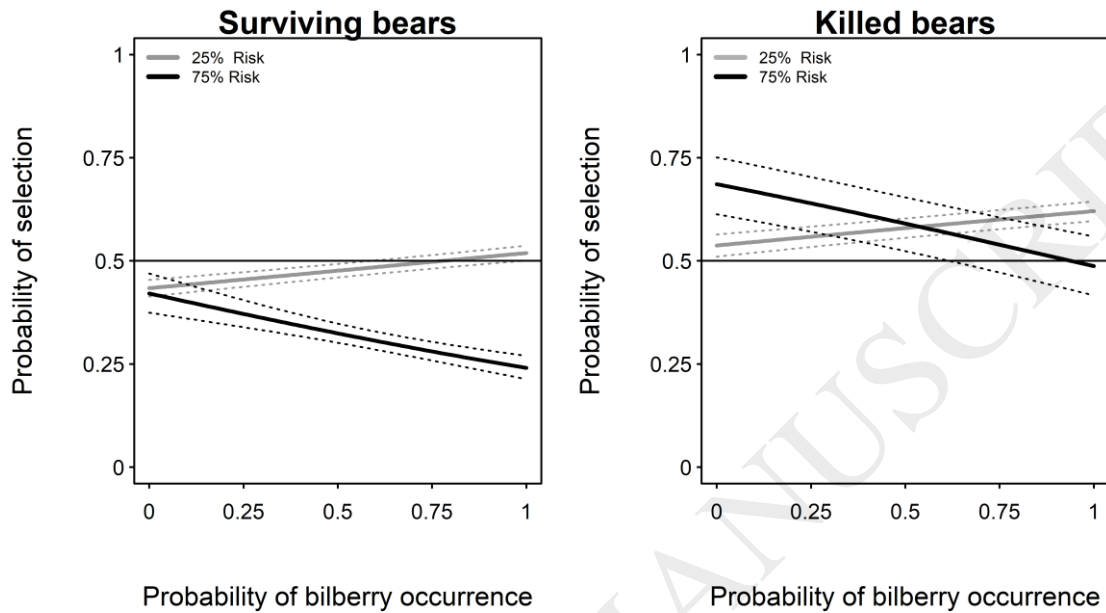
Fig. 3. Predicted selection of areas with varying risk of hunting mortality for killed and surviving brown bears at a 50% probability level of bilberry occurrence in southcentral Sweden. Probabilities have been converted back from the logit scale and represent actual probabilities of selection. The dashed line mark the 95% confidence intervals.
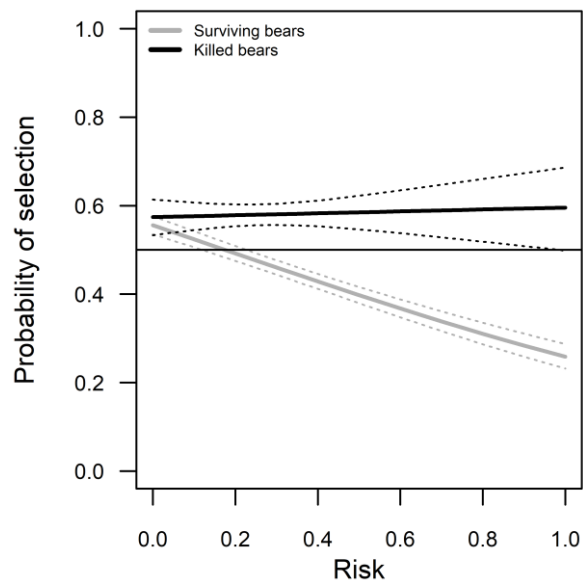
Table 2. Model covariates with estimates, standard error, tests statistics, and significance level for the most supported model to predict brown bear selection for berries and hunting mortality risk prior to the hunting season in the study area in southcentral Sweden (2012-2015). The most supported model included bilberry occurrence, risk of hunting mortality, bear fate and an interaction between bilberry occurrence and risk, as well an interaction between risk and the fate of the bears.

Model	Model parameters	Estimate	SE	Z	p-value
RSF3	Intercept	-0.154	0.099	-1.158	0.119
	Bilberry occurrence	0.924	0.082	11.263	< 0.001
	Risk	1.227	0.316	3.880	< 0.001
	Fate (Surviving)	-0.087	0.086	-1.001	0.317
	Bilberry occurrence $\times$ Risk	-2.347	0.279	-8.425	< 0.001
	Risk $\times$ Fate (Surviving)	-1.319	0.277	-4.770	< 0.001