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When the Hunter Becomes the Hunted: Impacts of Hunting on the Foraging Behavior of the Brown Bear (*Ursus arctos*) in Sweden

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Summary

Predation is a vital process in nature that has the potential to reduce prey populations, while also causing a wide range of risk effects such as changed prey behavior as a response to predation. Research has shown that animals may change their spatiotemporal use of a landscape as a response to human hunting, and such behavioral changes can occur also in apex predators. The brown bear (*Ursus arctos*) has previously been driven to near extinction in Scandinavia due to human persecution, and is still strongly limited by hunting. In Sweden, the hunting season overlaps with the bears' hyperphagia stage, when bears depend on a near constant intake of berries prior to hibernation. In this thesis, I have explored the spatiotemporal foraging patterns of brown bears in south-central Sweden, using resource selection functions to show how bears select for spatially predicted bilberry (*Vaccinium myrtillus*), and lingonberry (*Vaccinium vitis-idaea*) availability, as well as foraging in areas with high predicted risk of hunting mortality. All bears selected for areas of high availability of bilberry and avoided areas of high lingonberry availability. Bears that survived the hunting season generally avoided areas of high risk, while the bears that were killed foraged in high risk areas prior to the hunting season. Different foraging strategies in relation to risk did not affect the bears' selection for berry availability. In the 10 days before the start of the hunting season, none of the bears selected against areas of high risk, but during the 10 first days of hunting all bears shifted their foraging away from areas of high risk. There were individual differences between bears in relation to selection for bilberry and risk, but few differences in relation to selection for lingonberry and risk. I found no consistent differences in foraging behavior between different sexes and age classes of bears. I conclude that bilberries are important food resources for bears during hyperphagia, and that bears adapt their foraging behavior to the risk of being killed by human hunters. Changed behavior in apex predators as a result of human hunting may have implications for the entire ecosystem, and require increased research attention in the future.

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Introduction

Predation is one of the most important processes in nature and plays an important role in structuring ecosystems through direct and indirect effects on prey populations (Estes et al. 2011; Lima 1998; Prugh et al. 2009; Ripple et al. 2014; Ritchie et al. 2012). Predation can have direct effects on prey populations by reducing prey numbers, which can have cascading effects throughout the ecosystem (Estes et al. 2011; Prugh et al. 2009; Ripple & Beschta 2004). Predation can also cause a wide range of risk effects such as changes in prey behavior as a response to the risk of predation, which can have an even larger impact on prey populations dynamics (Brown et al. 1999a; Creel & Christianson 2008; Lima 1998). The theory on the 'fear ecology' was first developed to describe the behavioral effects that predators induce on their prey (Brown et al. 1999a; Brown 1999b; Brown et al. 2001). Predator presence and unequal distribution of food resources creates a 'landscape of fear', where access to resources must be balanced with the risk of predation in order to survive and reproduce (Brown et al. 2001; Laundré et al. 2001; Laundré et al. 2010). Predation can change foraging patterns of their prey, which may have population wide consequences for species distribution and utilization of ecosystems (Creel & Christianson 2008; Fortin et al. 2005; Lima 1998). Foraging makes animals vulnerable to predation, which they often attempt to mitigate by changing time allocation, increased vigilance, or selecting feeding sites with low perceived predation risk (Brown 1999b; Brown & Kotler 2004; Lima & Bednekoff 1999). In addition to behavioral adaptions to avoid predation, animals may also show distinct changes in spatiotemporal foraging patterns in regards to changes in quantity and quality of food resources (Bischof et al. 2012; Brown et al. 2001; Coogan et al. 2012; Nielsen et al. 2010). Prey often attempt to balance energy and security needs through behavioral responses, which increases the likelihood of recognizing and escaping predators, but can also reduce foraging efficiency (Brown 1999b; Brown et al. 2001; Brown & Kotler 2004; Lima 1998). Sustained psychological stress induced by the threat of predation can result in reduced food intake, physiological effects, and reduced reproduction, leading to stress induced population declines (Clinchy et al. 2013; Creel et al. 2007).

Such fear-mediated behavioral effects usually have been studied in relation to the effects of large carnivores on their prey, but it is increasingly recognized that fear ecology also may be applied to the effects of human disturbances (Frid & Dill 2002). Human hunting has become a dominant factor that impacts wildlife populations, change demography and causes behavioral changes related to avoidance of human hunters (Coltman et al. 2003; Darimont et al. 2009; Frid & Dill 2002; Milner et al. 2007). Not only have studies shown that human disturbances impacts the behavior of typical prey species, such as ungulates (Lone et al. 2015; McLoughlin et al. 2005), but also the behavior of large carnivores (Ordiz et al. 2011; Treves 2009; Wam et al. 2012). Large carnivores have been persecuted for centuries due to conflicts with human communities and negative human attitudes (Treves 2009; Woodroffe et al. 2005). Hunting has previously caused ecosystem-wide population declines and local extinctions of large carnivores (Swenson et al. 1995; Treves 2009; Woodroffe et al. 2005). During the last decades, research has indicated that large carnivores have a vital role in the ecosystem as apex predators, and contributes to conserve biodiversity through both direct and indirect effects of predation (Estes et al. 2011; McShea 2005; Ray 2005; Ripple et al. 2014; Ritchie et al. 2012). Human attitudes towards large carnivores have gradually changed and populations have started to recover in the highly modified and human-dominated landscapes of Europe (Chapron et al. 2014; Linnell et al. 2001). To mitigate conflicts between people and large carnivores, hunting has become a common strategy to maintain low populations, and thereby reduce conflicts with humans (Treves 2009). Thus, large carnivores have changed from being apex predators with few natural enemies to become strongly limited by human hunting, which may alter their evolutionary trajectory and role in the ecosystem (Frank & Woodroffe 2001; Milner et al. 2007; Treves 2009; Wallach et al. 2009; Zedrosser et al. 2011)

The brown bear (*Ursus arctos*) was driven to near extinction in Scandinavia by the beginning of the 20th century due to human hunting (Swenson et al. 1995). After being protected on state land in Sweden in 1913 (Swenson et al. 1995), the bear population gradually recovered and the population was estimated to be 2782 bears in 2013 (Kindberg & Swenson 2014). Legal hunting of bears in Sweden was reintroduced in 1943 (Swenson et al. 1995) and quotas have increased gradually (Swenson et al. 1994). The hunting quota was 11.0% of the estimated population in 2013 (Kindberg & Swenson 2014; Statens veterinärmedicinska anstalt 2015), with an estimated sustainable harvest rate of 11.2% (Bischof & Swenson 2009b). Legal hunting is the single most important source of mortality of bears in Sweden (Bischof et al. 2008; Swenson et al. 2010), and the population has been declining 3.2% every year from 2008-2013, due primarily to human hunting (Kindberg & Swenson 2014). In addition to the direct numerical effect of hunting, bears may also be indirectly affected through behavioral changes induced by the fear of being hunted (Ordiz et al. 2012; Stillfried et al. 2015). The risk of being killed by human hunters can vary across the landscape (Nielsen et al. 2004), and in south-central Sweden the highest hunting mortality for bears are close to areas of human activity, such as roads, buildings, agricultural areas, and villages (Steyaert et al. In press). Different sexes and age classes may respond differently to the risk of predation (Elfström et al. 2014b; Laundré et al. 2001; Lone et al. 2015; Nellemann et al. 2007; Ordiz et al. 2012; Rode et al. 2006b). In bears, sexual dimorphism, different energetic requirements, and social interactions such as infanticide, cause different sexes and age classes to balance foraging and avoidance of risk differently (Ben-David et al. 2004; Elfström et al. 2014b; Rode et al. 2001; Rode et al. 2006b). Especially females with cubs and subadults are prone to forage in more risky areas close to human settlements and in open areas to avoid encountering larger males (Elfström et al. 2014b; Steyaert et al. 2013a; Steyaert et al. 2013b).

The bear hunting season in Sweden starts 21 August and continues for up to two months, overlapping with the bears' 'hyperphagia' stage (Ordiz et al. 2012). During hyperphagia bears depend on a near continuous intake of food, predominantly berries in the boreal forest, to gain weight for the subsequent hibernation (Dahle et al. 1998; Welch et al. 1997). There is a strong correlation between the body size of female bears and the abundance of food resources such as berries, which again affects sexual maturity, reproduction, and survival during hibernation (Zedrosser et al. 2006). Studies of captive bears showed that bears are able to consume 30-55% of their own body mass in fruit daily during this period (Welch et al. 1997), and by having an unspecific digestive system bears are able to efficiently digest berries (Bunnell & Hamilton 1983). Berries are one of the most important components of the bears' autumn diet in Scandinavia, and previous studies have shown that berries comprises 44-46% of the digestible energy in the bears' diets, and are rich in carbohydrates that can be converted to fat prior to hibernation (Dahle et al. 1998). The most important berry species in the diet of Scandinavian brown bears are crowberry (*Empetrum* spp.), bilberry (*Vaccinium myrtillus*), and lingonberry (*Vaccinium vitis-idaea*) (Dahle et al. 1998; Elfström et al. 2014a; Persson et al. 2001). Scat analysis from Sweden show that berries are found in 92% of all bear scats and make up 74% of the total scat volume during hyperphagia (Dahle et al. 1998). Bears' intake of berries is dependent on bite rate and bite size, which again is related to the density and visibility of berries (Rode et al. 2001; Welch et al. 1997). Foraging efficiency is highly reduced at densities lower than 50 berries per m^3, and bears tend to move between berry clusters to locate areas of high berry density (Welch et al. 1997). Intake of berries is also related to the amount of time bears spend foraging, and they subsequently increase their foraging activity during hyperphagia (Rode et al. 2001; Stelmock & Dean 1986; Welch et al.

1997). Bears are very dependent on availability of food resources and they often switch to the food resource most abundant in the landscape (McLellan & Hovey 1995; Persson et al. 2001). Herbivores are known to prolong the grazing period by following a green wave of plant growth through the landscape as plants mature in different locations at different times (Bischof et al. 2012). Bears may also utilize such spatiotemporal waves of plant growth, which leads to different habitat selection across the growing season (Coogan et al. 2012; Nielsen et al. 2010).

Bilberry, crowberry and lingonberry are widely distributed throughout Swedish forests, but their abundance varies spatially and temporally in relation to different habitat types, attacks by insects, ungulate grazing, and weather conditions (Kardell 1979; Kardell & Eriksson 2011). In Southern Sweden, the bilberry season usually begins in mid-July (Eriksson & Ehrlén 1991), but abundance of bilberries in Scandinavia generally varies from year to year with peaks in production every 2-5 years (Selås 2000). Lingonberry usually starts producing berries in the first half of August and continues into September (Eriksson & Ehrlén 1991). Crowberries have a very long fruiting season, which overlaps with both bilberry and lingonberry, from July to September (Eriksson & Ehrlén 1991). There are two subspecies of crowberry, *Empetrum nigrum* spp. *nigrum* and ssp *hermaphroditum*, where *E. nigrum* is the most common in Southern Sweden (Tybirk et al. 2000). Crowberry plants are able to outcompete both bilberry and lingonberry plants by forming dense clones that dominate the forest floor and produces chemicals that inhibits other plants (Tybirk et al. 2000), but the species is not as common in Southern Sweden (Kardell & Eriksson 2011). Production of all the berry species varies across the landscape depending on sun exposure (Atlegrim & Sjöberg 1996; Parlane et al. 2006; Tybirk et al. 2000), and between different habitat types (Atlegrim & Sjöberg 1996; Kardell 1979; Kardell & Eriksson 2011; Nybakken et al. 2013). This implies that berries are not equally spatially and temporally available, and that berry abundance varies across the landscape, as well as over time. In Sweden, the bears' hyperphagia stage and the bear hunting season overlaps, and previous research has shown that bears change their movement patterns and diurnal activity during this period as a behavioral response to human hunting (Ordiz et al. 2012). However, little research has yet been conducted on how this affects bears' foraging on berries, and how different foraging strategies among bears affect hunting mortality.

In this thesis I explore how an apex predator, the brown bear in a boreal forest ecosystem in Sweden, is impacted by human hunting in terms of foraging behavior on berries during hyperphagia in the period between mid-July and late September. I will explore the spatiotemporal foraging behavior of bears in relation to the availability of three berry species; bilberry, crowberry and lingonberry. I hypothesize that bears will forage on the berries that are most abundant in the landscape during hyperphagia. Specifically, that they will select for areas with high bilberry availability at the beginning of the study period, before increasing their selection of areas of high lingonberry availability later in the season when lingonberries ripen, and that they will forage on crowberries throughout the study period (H1). I also hypothesize that bears will select against risky areas with high potential hunting mortality (H2), and that bears that survived the hunting season will display a stronger selection against areas of high risk compared to the bears that were killed during hunting (H3). Further, I expect that selection against areas of high risk will increase when the hunting season starts (H4). I also hypothesize that selection against areas of high risk may represent a tradeoff between selection for berry availability and risk (H5). Lastly, I hypothesize that selection for areas with high berry availability and risk will vary between different individuals, as well as between different sex and age classes (H6).

To test my hypotheses, I sampled berries in the field and obtained habitat data from GIS-derived maps to create predictive maps of berry availability across the landscape in six different periods during hyperphagia. I used a risk map showing the risk of hunting induced mortality across the study area (Steyaert et al. In press). Next, I applied resource selection functions (RSF), in which bear GPS positions consistent with foraging behavior represented ‘used’ positions and random positions generated within each bear’s home range represented ‘availability’, to explore the bears’ selection of berry availability and risk during hyperphagia.

Methods

Study area

Berry availability and bear foraging patterns were explored in a 2241 km^2 study area located in Dalarna and Gävleborg counties in south-central Sweden (Figure 1). The combined bear population of Dalarna and Gävleborg was estimated to be 793 bears in 2013, and the population has been declining in recent years (Kindberg & Swenson 2014). The landscape in the study area is gently rolling, with elevations varying from 175 m to 725 m above sea level (Martin et al. 2010). The area is mostly covered by productive forest, dominated by Scots pine (*Pinus sylvestris*), and Norway spruce (*Picea abies*), while heather (*Calluna vulgaris*), grasses, and berry shrubs dominates the understory (Elfström et al. 2008; Ordiz et al. 2012;

Sahlén et al. 2011). The area includes many lakes and bogs spread throughout the landscape (Elfström et al. 2008; Ordiz et al. 2012). The forests are managed and have rotations of 80-120 years, after which entire forest stands are harvested, and the clearcuts are later replanted (Kardell & Eriksson 2011; Ordiz et al. 2014). There is a dense network of gravel roads throughout the study area, which provides easy access to a wide range of recreational and commercial activities such as hiking, hunting, fishing, logging, and berry picking (Nellemann et al. 2007; Ordiz et al. 2014; Sahlén et al. 2011; Sténs & Sandström 2013). The area contains several small communities and the human density in 2011 was 5-7 habitants /km^2 (Ordiz et al. 2014).

Berry data

Berries were sampled at random locations within three different sampling areas in the study area in south-central Sweden (Figure 1), each named after the closest settlement (Noppikoski, Håven and Voxna). The different sampling areas were constructed in ArcMap 10.3 (ESRI 2014) to represent a variety of habitat types within the study area and to facilitate fieldwork by not being located too far from each other. Sampling locations were extracted chronologically from a list of random GPS coordinates every field day. Each sampling location was located using a handheld GPS, and from that initial location I randomly walked 0-9 meters depending on the last value in the Y coordinate in a northern, southern, eastern or western direction (depending on the last value in the X coordinate). A 1m^2 frame was placed directly in front of this new position, marking the berry plot, and the handheld GPS unit was used to register the approximate location of the plot. Within each berry plot I estimated the percentage cover and height of berry plants. All berries within the 1m^2 plot were collected and counted. Sampled berries were divided into species (bilberry, lingonberry and crowberry) and three categories of berry condition (unripe, ripe, and dehydrated/overripe). Berries were defined as ripe if they had an intact round shape, the overall color of the berry was red or blue, and fluids could be squeezed from the berry. Fieldwork was conducted from 11 July until 18 September, and sampling ended a few days before the first frost. I assigned every day during the study period a Julian day to represent the sampling days. I assigned the first day of field work, 11 July, Julian day 1, and so on until the last date of field work, 18 September, which I assigned Julian day 70.

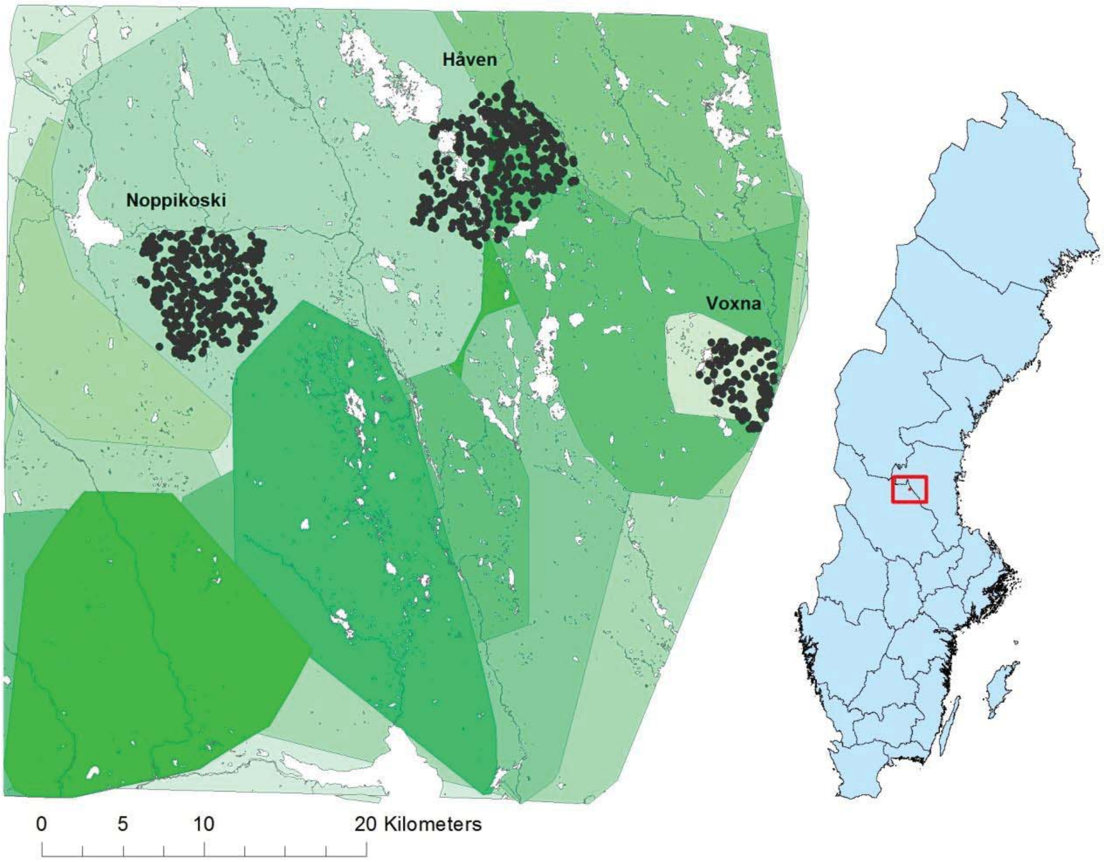

Figure 1: The study area located in south-central Sweden, with the three different sampling areas, and the berry plots where bilberries, lingonberries and crowberries were sampled. The 100% MCP home ranges of the GPS collared brown bears in the study area are displayed in green.

Extraction of landscape variables

Land-cover maps (Swedish Land Cover database, SMD-data), satellite imagery (Resourcesat, IRSP-LISS3 Imagery, 25 * 25 m pixel size, images was obtained in July and August 2014), and a digital elevation model (DEM) (2 * 2 m pixel size) were obtained from National Land Survey Sweden (www.lantmateriet.se, i2014/764). Different habitat types in the land cover maps were merged into the habitat categories: clearcut, mid-aged forest, old forest, tree rich bog, bog, young forest, water, and other. Slope steepness and aspect were calculated from the DEM. From the satellite imagery, a Normalized Difference Vegetation Index (NDVI) map (20 * 20) was derived and used as a proxy for vegetation density. NDVI is a vegetation index constructed from reflectance of red and near-red electromagnetic light from different land cover types and provides data on vegetation distribution and vegetation biomass across a landscape (Pettorelli et al. 2005). The preprocessing of all the landscape maps was conducted by Sam Steyaert and Anne G. Hertel.

Berry models

Prior to the analysis, all sampling plots located in habitats defined as “other” were excluded, because they represented areas without forest vegetation such as roads, agricultural areas, urban areas, and rocky areas. I used 843 sample plots to model berry presence and berry density per m^2 of berry plant. I divided the number of ripe berries per plot by the percentage cover of berry plants, and multiplied it by 100 to obtain berry density per m^2 of berry plant. Crowberries were found in just a few plots each period, which I considered too few to be able to accurately predict crowberry presence and density in the different time periods. Only ripe bilberries and lingonberries were therefore used to model the presence and density of berries across the landscape. The berry data was highly overdispersed, implying that the variance in the data was larger than the mean, which could result in poor model fit (Zuur et al. 2009). The data also had a high proportion of zeros, and I therefore modeled berry presence and berry density separately with hurdle model design (Zeileis et al. 2007). Bilberry and lingonberry presence was modeled with generalized linear models (GLMs) and a binomial distribution appropriate for absence/presence data (Zuur et al. 2009). Bilberry and lingonberry density was modeled with berry density per m^2 of berry plant, in the plots where berries were present, assuming that in all locations with zero berries, the growing conditions were not suitable for berry production. To compensate for overdispersion of the residuals, I applied GLMs with negative binominal distribution to model bilberry and lingonberry density, as recommended by Zuur et al. (2009) and Zeileis et al. (2007). To test whether there was a temporal trend in the berry availability during the study period I ran two generalized additive models (GAMs) on the number of bilberries and the number of lingonberries collected in the study plots, one using Julian date as a spline, and a null model. Model selection was conducted using the model.sel function in the MuMIn package (Barton 2014), which compares models based on Akaike information criterion (AIC_c) corrected for small sample sizes (Arnold 2010; Manly et al. 2002; Zuur et al. 2009). Considering the temporal trend in the data (Figure A1, Appendix), bilberry and lingonberry presence and density were modeled in six time periods of 20 days length with 10 days overlap (Table 1). I chose to model berry occurrence and presence in periods of 20 days because I found that each period then contained adequate data to enable predictions with reasonable predictive accuracy, as well as capturing the temporal change in berry presence and density across the study period. I ensured that the periods overlapped each other by 10 days to avoid abrupt changes in predictive berry presence and density between the periods.

Table 1: The six 20-day periods with 10 days overlap in which berry density and presence and brown bear foraging behavior was modeled in south-central Sweden in the study period 11 July - 18 September with actual dates and Julian days representing the field days.

Period	**Dates**	**Julian days**	**No. of berry plots**
1	11 July - 1 August	1 - 22	244
2	22 July – 11 August	12-32	324
3	1 August – 21 August	22-42	332
4	11 August – 31 August	32-52	261
5	21 August – 10 September	42-62	214
6	31 August – 18 September	52-70	180

The density and presence of ripe lingonberries were only modeled in the last four periods after 1 August, as they were virtually absent in the study area during the first two periods. I tested all the numerical variables for collinearity using variance inflation factor (VIF) with a cut-off value of 3 (Zuur et al. 2009), and collinearity with the categorical variables using boxplots, but I found no collinearity between the variables. I constructed eight *a priori* candidate models to predict both berry presence and density, which included a full model containing all the explanatory variables (habitat type, NDVI, elevation, slope and aspect), and a null model (Table 2). In each time period, the candidate models were compared using AIC_c model selection, and models separated by $\Delta AIC_c < 2$ from the top ranked model ($AICc = 0$) were selected as having the most explanatory power. If several models were selected I used model averaging to obtain the most accurate estimates for spatial predictions in each period (Zuur et al. 2009). If the null model was selected as one of the models with the highest explanatory power, I did not include it in the model average, as I did not consider it useful to make spatial predictions. The model coefficients with shrinkage were extracted in each time period to make spatial predictions in ArcMap. I validated the models using the cv.binary function from the DAAG package (Maindonald & Braun 2010; Maindonald et al. 2014) to obtain a cross validation estimate of accuracy. When several models were selected as having the highest explanatory power, cross validation of accuracy as well as the dispersion parameter, was calculated for each of the models and then averaged to obtain one estimate for all the models included in the model average. I uploaded the model coefficients into ArcMap, and created predictive maps of berry density and presence for the different time periods. There were, however, some inherent weaknesses with the berry predictions that made it challenging to apply them to explore bear foraging. The berry presence predictions only predicted the presence or absence of berries across the landscape and not the abundance of berries. The density predictions may have overestimated berry density since they were modeled with data only from plots that contained berries. To mitigate these inherent weaknesses I multiplied the two prediction maps into a third prediction map that showed an index of berry availability. This map incorporated the differences in berry density across the landscape, but also displayed low berry availability in the locations with close to zero probability of berry presence. This berry availability index is referred to as the berry availability throughout this thesis, and was applied to explore bears' selection for berries.

Table 2: Candidate models with model terms to predict presence and density of lingonberry and bilberry in the study area in south-central Sweden in the 20-day periods with 10 days overlap during the study period 11 July – 18 September.

Model	**Model terms**				
	Habitat type	NDVI	Slope	Aspect	Elevation
Berry full	×	×	×	×	×
Berry 1	×	×		×	×
Berry 2	×	×		×	
Berry 3	×	×			
Berry 4	×			×	
Berry 5		×		×	
Berry 6		×			
Berry 0					

Bear position data

All bears were collared with GPS-GSM collars (Vectronic Aerospace GmBh, Berlin, Germany) as part of a long-term study project in the Scandinavian Brown Bear Research Project. Capture procedures were approved by the Swedish Ethical Committee (Uppsala Djurförsöksetiska Nämnd) following the protocol by Arnemo and Fahlman (2011). I excluded all positions with a dilution of precision (DOP) metric higher than 4 to increase spatial accuracy (Lewis et al. 2007). DOP represents a measure of how many satellites were used and the satellite constellation, which affects the accuracy of the position fix (Frair et al. 2010; Lewis et al. 2007). All GPS positions from 2014 were uploaded (including non-foraging positions) to construct home ranges for each individual bear using 100% minimum convex polygons (MCP) (Gillies et al. 2006; Moe et al. 2007). To explore bears' foraging on berries I used hourly positions from the study period between 11 July and 18 September from bears who's home range was located partly or entirely within the study area. During the study period some bears were occasionally approached by field technicians on foot or by hunting dogs as part of other research projects, and the positions of these bears were excluded on the day of the approach, as well as the two following days due to previously documented changes in behavior (Moen et al. 2012; Ordiz et al. 2013a). Positions from bears that were killed during hunting were excluded on the day the bear was killed, as the GPS collars still sent out positions after death. Positions from yearlings accompanied by their mother were also excluded to avoid spatial dependency between individuals. Bears' foraging on berries has been described as slow, continuous movement between patches of high berry density (Welch et al. 1997). To avoid confusing foraging with other behaviors, such as resting or long-distance travel, I used only hourly positions that were at least two fixes in a row and located more than 100 meters, but less than 800 meters apart. These foraging trajectories were prepared by Anne G. Hertel, who tested a similar trajectory with half-hour positions, three successive points, at distances of between 25-300 meters in the study area, and found field evidence of bear foraging on berries in 70% of these locations (Hertel et al. In press). The R package adehabitatLT was used to measure the Euclidean distance between successive GPS locations (Calenge 2006).

Habitat selection

Bear foraging was explored within each bears' home range with third-order resource selection functions (RSFs) (DeCesare et al. 2012; Manly et al. 2002; Northrup et al. 2013). RSFs are a common statistical approach to explore habitat selection of animals (Boyce et al. 2002; Gillies et al. 2006; Manly et al. 2002). I uploaded foraging positions to represent 'used' positions within the home ranges and created an equal number of random positions as foraging positions within each bear's home range to represent the 'available' foraging areas (Manly et al. 2002; Northrup et al. 2013). I also uploaded a map showing the predicted risk of being killed by human hunters across the study area, created by Steyaert et al. (In press). The risk map was constructed based on models including the locations where bears have been killed by human hunters in the period 1982-2012, in relation to distance to nearest village, roads, and buildings (Steyaert et al. In press). The availability of lingonberry and bilberry, as well as the level of risk for all the random and used positions, were extracted for further statistical analysis. To reduce the effects of variation between individual bears, and the unequal number of positions from each bear, I included 'bear id' as a random effect on the intercept of the RSFs (Gillies et al. 2006). I applied generalized linear mixed modeling (GLMM) from the lme4 package (Bates et al. 2014) to model the resource selection of all the bears (Gillies et al. 2006; Hebblewhite & Merrill 2008), with use/available as the binary response variable. I created eleven *a priori* candidate models, each based on a specific hypothesis about bear forging (Table 3). The candidate models included a full model with all variables and interactions, as well as a null model.

Table 3: The candidate models for the resource selection of brown bears in south-central Sweden in the 20-day periods with 10 days overlap (1-6) during the study period 11 July - 18 September, with a specific hypothesis underlying each model. The different model terms include predicted bilberry and lingonberry availability, risk of being killed by hunters, and the fate of the bears (whether they survived or were killed during hunting). Lingonberry availability was not included in any of the candidate models in period 1 and 2 because I did not have accurate lingonberry predictions this early in the season. The interaction with the fate of the bears was not included in period 6, because all the killed bears were already dead by that time.

Model	**Hypothesis**	**Difference between killed and surviving bears (fate)**	**Random term**	**Model structure**
RSF full	Bears select for bilberry and lingonberry in areas with low levels of risk / Bears select for areas with high risk if there is a high availability of berries	Killed bears select more strongly for bilberry and lingonberry, and weakly against risk.	Bear ID	Bilberry*fate + lingonberry*fate + risk*fate + bilberry*risk + lingonberry*risk
RSF1	Bears select for bilberry and lingonberry and against risk	Killed bears select more strongly for bilberry and lingonberry, and weakly against risk	Bear ID	Bilberry*fate + lingonberry*fate + risk*fate
RSF2	Bears select for bilberry and lingonberry and against risk	No difference between killed and surviving bears	Bear ID	Bilberry + lingonberry + risk
RSF3	Bears select for bilberry and lingonberry and against risk	Killed bears select more strongly for bilberry and lingonberry, but equally against risk	Bear ID	Bilberry*fate + lingonberry*fate + risk
RSF4	Bears select for bilberry and lingonberry and against risk	Killed bears select weakly against risk	Bear ID	Bilberry + lingonberry + risk*fate
RSF5	Bears select for bilberry and lingonberry	Killed bears select strongly for bilberry and lingonberry	Bear ID	Bilberry*fate + lingonberry*fate
RSF6	Bears select more strongly for bilberry and lingonberry in areas with low risk / Bears select for areas of high risk if there is a high availability of berries	No difference between killed and surviving bears	Bear ID	Bilberry*risk + lingonberry*risk
RSF7	Bears select against risk	Killed bears select weakly against risk	Bear ID	Risk*fate
RSF8	Bears select against risk	No difference between killed and surviving bears	Bear ID	Risk
RSF9	Bears select for bilberry and lingonberry	No difference between killed and surviving bears	Bear ID	Bilberry + lingonberry
RSF0	Bears do not select for bilberry and lingonberry and not against risk	No difference between killed and surviving bears		~ 1 (intercept only)

The candidate models included different combinations of the variables; bilberry availability, lingonberry availability, risk of being killed by human hunters, and the fate of the bears (whether the bear was killed or survived the hunting season). Interactions between berry availability and risk were included to explore whether risk of being killed affected the bears' selection for berry availability. I included the interaction between the fate of the bears and berry availability and risk to explore whether there were differences in foraging behavior between killed and surviving bears. The other habitat variables (habitat type, NDVI, aspect, slope and elevation), were not included in the RSFs, because the berry predictions were based on these variables and they were therefore inherently collinear. I chose to model bear foraging behavior separately in the six periods because the availability of the berries and level of risk changes during hyperphagia, and bears are known shift their selection for resources according to which are temporally most abundant, as well as to avoid risk that also varies temporally (McLellan & Hovey 1995; Nielsen et al. 2010; Ordiz et al. 2012; Stelmock & Dean 1986).

All the continuous variables were tested for collinearity in each period using a corvif test and pair plots, as recommended by Zuur et al. (2009), but this did not reveal any collinearity. In each period, I selected the models with most explanatory power using AIC_c model selection (Arnold 2010; Boyce et al. 2002), and if several candidate models were separated by $\Delta AIC_c < 2$, the most simple model was selected as the most parsimonious, to avoid pretending variables (Arnold 2010). Pretending variables can often occur during AIC model selection, as complex models can have $\Delta AIC_c < 2$, but still include variables with very little explanatory power (Arnold 2010). I also applied the full model on each of the six periods to compare the strength of selection in a visual manner.

Model validation

I tested model performance of the most parsimonious model in each time period with the cross validation procedure proposed by Boyce et al. (2002) and modified by Klar et al. (2008). As described by Klar et al. (2008), I spatially mapped the most parsimonious RSF model in each period, which resulted in six maps showing the probability of selection within the study area in each period. The most parsimonious models were slightly simplified by not including the interaction with fate, which meant that, within each time period, one probability of selection map was created for all the bears. I divided each probability map into ten equal area sized bins (1-10), representing areas with different probability of selection, where bin no. 1 represented the lowest probability of selection and bin 10 the highest probability of selection. I calculated the proportion of each probability bin in the study area and the proportion of used positions located within each of the probability bins. The proportion of used positions per bin was divided by the total proportion of each bin to obtain area-adjusted frequencies of bear occurrence. I correlated these area-adjusted frequencies of occurrence in each period with the probability bins using Spearmen rank correlation tests (r_s) (Boyce et al. 2002; Klar et al. 2008).

Effects of hunting season, individuals, sex and age

The same candidate models (Table 3) were applied to model bear selection 10 days prior to the start of the hunting season, and the first 10 days of the hunting season. The models with highest explanatory power were selected through AIC_c model selection and the simplest model of the ones separated by $\Delta AIC_c < 2$ was selected as the most parsimonious model. I also preformed an additional analysis of the foraging behavior of each individual bear to explore how much individual variation they displayed. Individual GLM models for resource selection were created for the bears with more than 40 foraging positions during the whole study period. These models were run on data from the entire study period and the berry availability index of each period was averaged to obtain one continuous index of berry availability. Selection for bilberry and lingonberry availability was modeled in two separate models for each bear to avoid too much model complexity, each with risk as an additive effect. Selection coefficients for berry availability and risk for each bear was tested for correlation using Spearmen rank correlation (r_s). In addition I constructed two additional models in each of the six periods, one with the age class of the bears and one with sex, each interacting with berry availability and risk. I conducted this additional analysis to explore whether different age classes and sexes displayed different habitat selection. The effect of interactions with sex and age were analyzed by looking at the significance of the interactions in each time period. I did not include these interactions in the candidate models, because they would become very complex and have small sample sizes in some of the combinations between sex, age, and the fate of the bears. I defined two age classes for the bears: adult > 4.0 years and subadults < 4.1 years of age, following the definition by Zedrosser et al. (2006) for female bears. A third age category for yearlings was not constructed, because all yearlings accompanied by their mother were excluded from the analysis and I defined unaccompanied yearlings (all > 1 year old) as subadults. All statistical analyses were done using R version 3.1.1 (R Core Team 2014), and all geographical mapping and spatial predictions was done in ArcMap 10.3 (ESRI 2014).

Results

Berry prediction models

Bilberries and lingonberries were found in 421 (50%) and 164 (20%) of the sampling plots respectively, while crowberries were found in 89 plots (10%). The average density of berries per m^2 of berry plant in the plots that contained berries was $31/m^2$ for bilberry, $57/m^2$ for lingonberry, and $34/m^2$ for crowberry. Modeling the number of berries per plot using Julian day as a spline compared to a null model, showed that the model with Julian date as spline was the most parsimonious for both bilberry and lingonberry, which indicated a temporal trend in the availability of berries (Figure A1, Appendix). The effective degrees of freedom (edf) of the GAMs, were 2.691 and 2.996 for bilberry and lingonberry, respectively, and indicated a nonlinear trend (Zuur et al. 2009). Bilberries ripened earlier in the season and continued to be abundant throughout most of the season, but declined towards the beginning of September (Figure A1, Appendix). Lingonberries ripened later and continued to abundant after bilberries declined, but started to decline in abundance towards the middle of September (Figure A1, Appendix). The predictive accuracy of the berry presence models across the periods varied between 60-71%, and 60-92% for bilberry and lingonberry presence, respectively. See tables A1 and A2 in the appendix for outputs of the most parsimonious models that were used to predict bilberry and lingonberry presence and density across the six periods, and which was combined to predict berry availability across the landscape (Figure 1 & Figure A2, Appendix).

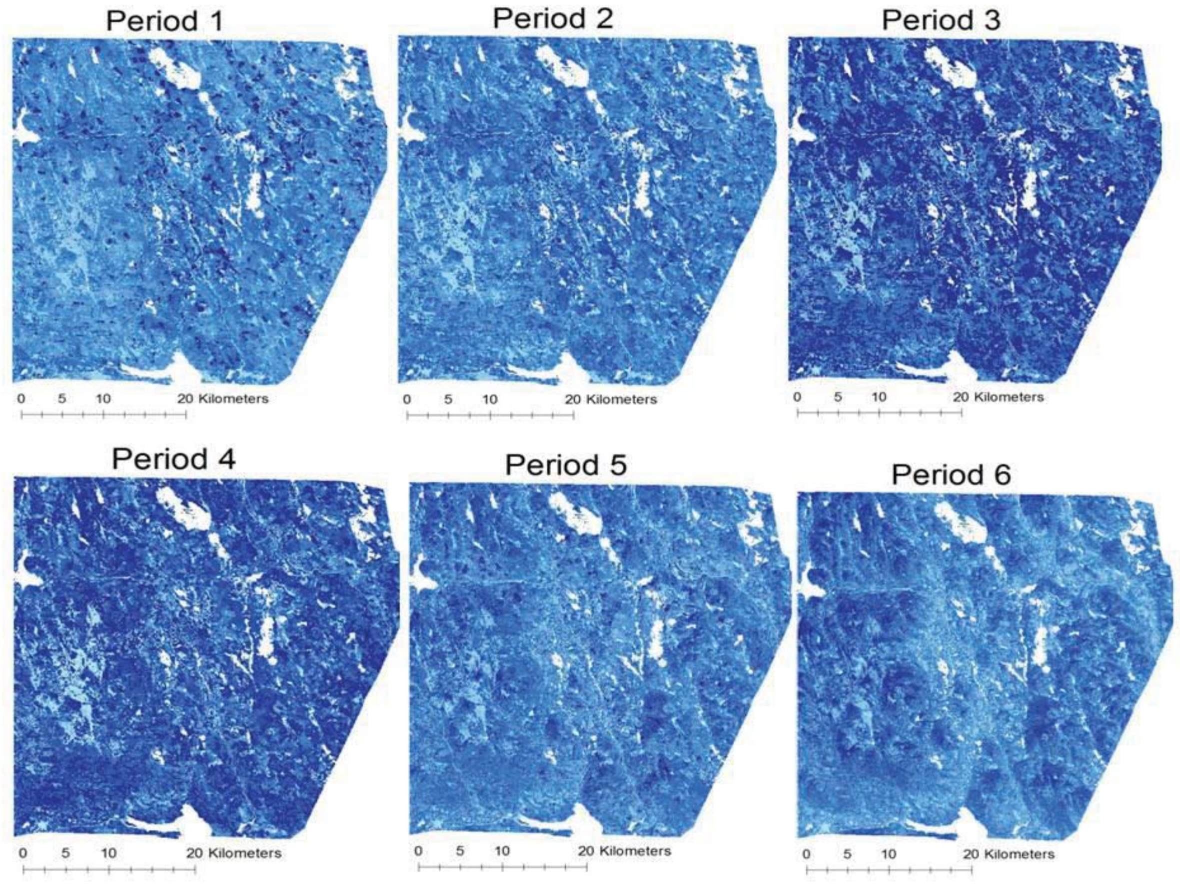

Figure 1: Spatial predictions of bilberry availability in the study area in south-central Sweden across the 20-day periods with 10 days overlap (1-6) during the study period from 11 July - 18 September. Darker color represents higher predicted bilberry availability.

Habitat selection by bears

In total, 4747 GPS positions from 29 bears whose 100% MCP home range fully or partly overlapped the study area during 2014 were included in the study. These included 10 males and 19 females, consisting of 8 subadults (<4.1 years) and 21 adults (>4.0 years). The age of the bears varied between 1-21 years, with a mean age of 8 years. Five of the study bears were killed by hunters, including one female and four males. A total of 24 bears had sufficient number of positions that I could model their foraging behavior with individual models.

In period 1, RSF1 was selected as the most parsimonious model, which contained bilberry availability and risk interacting with the fate of the bears. The second best model in period 1 was the full model (ΔAIC_c= 0.64). In period 2, RSF7 was the most parsimonious model containing only risk interacting with fate, and RSF4 was the second best (ΔAIC_c= 1.88). RSF4 was the most parsimonious model in period 3, which included bilberry availability, lingonberry availability, and risk interacting with fate, followed by RSF1 (ΔAIC$_c$= 3.25). In period 4, 5, and 6, the most parsimonious model was RSF2, which included bilberry availability, lingonberry availability, and risk without any interactions, followed by RSF4 in period 4 (ΔAIC$_c$= 2.56), RSF6 in period 5 (ΔAIC$_c$= 3.47), and RSF6 in period 6 (ΔAIC$_c$= 3.78) (Table A3, Appendix). The RSFs showed that bears generally selected for areas with high availability of bilberries and selected against areas with high availability of lingonberries, as well as against areas of high risk, but there were differences in foraging behavior between killed and surviving bears in periods 1-3 (Table A4, Appendix). Cross validation of the RSF models showed that the area-adjusted frequency of occurrence was highly correlated with the probability bins in period 1-3, whereas the correlation test in periods 4-6 showed that the relationship was insignificant (Table A5, Appendix). These periods had 7-14 foraging positions each in the lowest probability bin, and removing the lowest bin caused a significant correlation between the area-adjusted frequency of occurrence and the probability bins, indicating that predictive abilities of the models were generally good, but underestimated bear occurrence in the poorest habitat class (Table A5, Appendix).

Selection for berries

Bears selected for areas with high bilberry availability across the entire season, except for in period 2, when selection for berries was not included in the most parsimonious model (Table A4, Appendix & Figure 2). In period 1, the surviving bears displayed a significantly weaker selection for bilberries (-0.042±0.018, test statistics=2.38, p=0.02), compared to the bears that were killed during the hunting season (0.031±0.017, test statistics=1.85, p=0.06) (Table A4, Appendix). In the remaining periods (3-6), all bears selected for areas of high availability of bilberries with p values <0.001 across all these periods (Table A4, Appendix). Selection for bilberry among all bears generally increased later in the study period (Figure A3, Appendix). Lingonberry availability was included in the candidate models only in period 3-6 and was generally avoided by all bears throughout those periods (Table A4 & Figure A4, Appendix & Figure 2).

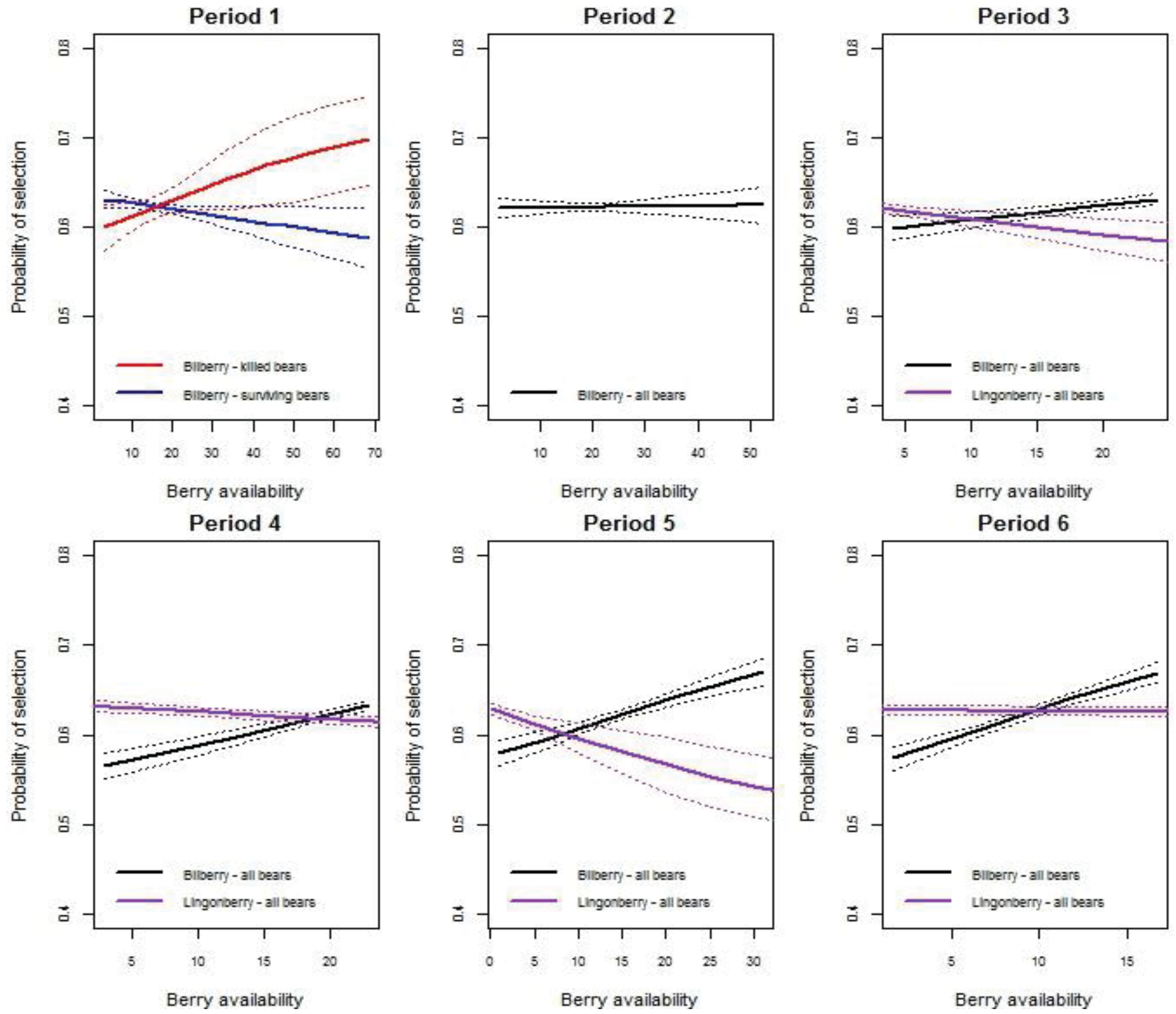

Figure 2: Predicted effect of bilberry availability and lingonberry availability on the probability of selection of brown bears in south-central Sweden, based on the most parsimonious candidate model across the 20-day periods with 10 days overlap during the study period (11 July - 18 September). In period 2, the predicted effect is based on the second most parsimonious model $\Delta AIC_c < 2$, to be able to visually display selection for bilberry also in this period. Selection for lingonberry is only displayed in period 3-6, because lingonberry availability was not predicted earlier in the season. In period 1, the most parsimonious model included an interaction with fate, and selection for bilberry is therefore presented separately for killed and surviving bears. Probabilities have been converted back from the logit scale and represent actual probabilities of selection. The 95% confidence intervals are marked by the dashed line.

Selection against risk

The most parsimonious candidate models in the three first periods of the study showed that killed and surviving bears behaved differently in relation to risk prior to the hunting season (Table A4, Appendix & Figure 3). In the first three periods prior to hunting, 11 July - 21 August, the most parsimonious model always included risk interacting with the fate of the bears (Table A4, Appendix). The most parsimonious models showed that killed bears selected for areas of high risk intensity in periods 1-3 (Period 1: 0.182±1.187, test statistic=0.15, p=0.88, Period 2: 3.40±1.220, test statistic=2.79, p<0.01, Period 3: 3.644±1.245, test statistic=2.93, p<0.01), although insignificant in period 1. Whereas surviving bears avoided high-risk areas during those periods (Period 1: -3.659±1.259, test statistic=-2.91, p<0.01, Period 2: -7.351±1.310, test statistic=-5.61, p<0.001, Period 3: -5.754±1.342, test statistic=4.29, p<0.001) (Table A4, Appendix & Figure 3). In the remaining three periods (4-6) after the start of the hunting season, all bears selected against areas of high risk and there was little difference between killed and surviving bears (Table A4, Appendix & Figure 4).

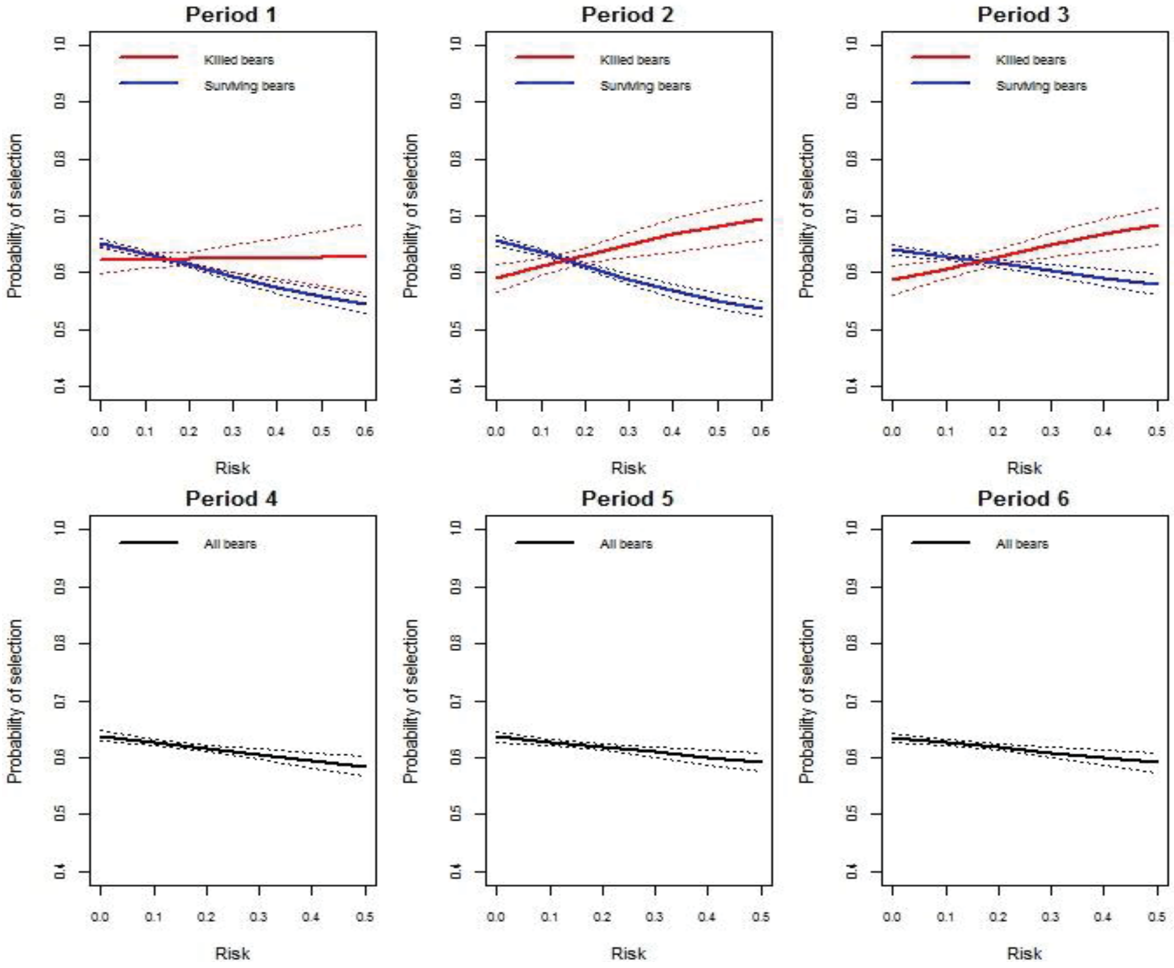

Figure 3: Predicted effect of risk on brown bears' probability of selection in the study area in south-central Sweden, based on the most parsimonious candidate model across the 20-day periods with 10 days overlap (1-6), during the study period 11 July - 18 September. The 95% confidence intervals are marked by the dashed lines. In period 1-3, the most parsimonious model included an interaction with fate, and selection in relation to risk is therefore presented separately for killed and surviving bears. Probabilities have been converted back from the logit scale and represent actual probabilities of selection.

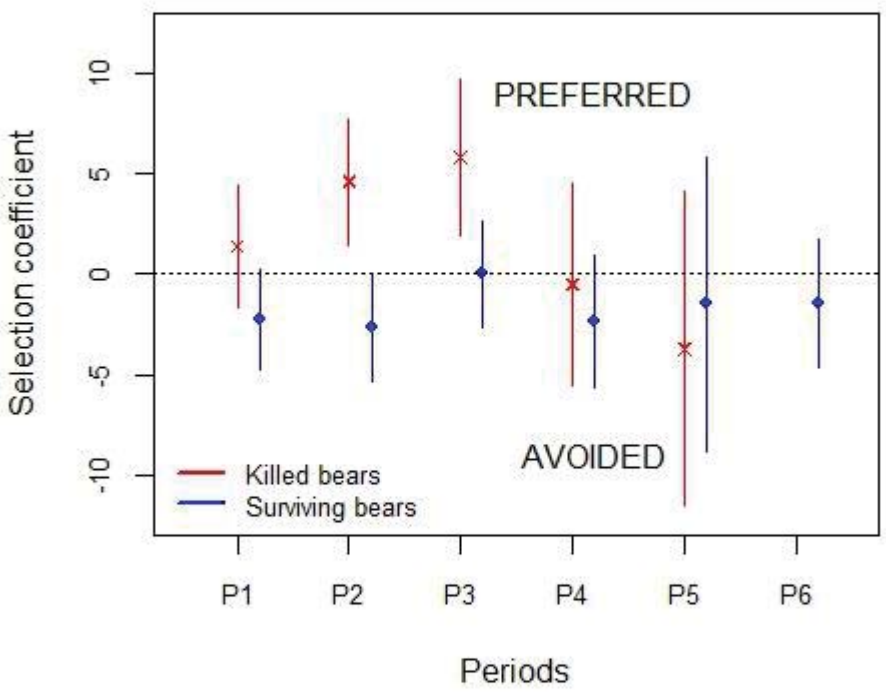

Figure 4: Selection coefficients (logit scale) based on the full model for killed and surviving brown bears in relation to risk in the study area in south-central Sweden, across all the 20-day time periods with 10 days overlap (1-6), during the study period from 11 July - 18 September. The selection coefficients are based on the full model to allow for comparisons across the time periods. In period 6, selection in relation to risk was modeled for all bears, because no killed bears were still alive in period 6. The error bars indicate standard errors around each estimate.

Prehunting vs. hunting season

In the prehunting period RSF9 was the most parsimonious model, which included only bilberry availability and lingonberry availability, followed by RSF2 (ΔAIC_c= 1.25) which was the second best model. In the hunting period, the most parsimonious model was RSF2, which included bilberry, lingonberry, and risk, followed by RSF6 (ΔAIC_c= 3.09) (Table A3, Appendix). Bears selected for areas of high bilberry availability both before and during the hunting season and avoided areas of high lingonberry availability in both periods (Figure A5, Figure A6 & Table A6, Appendix). The bears' foraging behavior in relation to the intensity of risk differed between the two periods. The most parsimonious model in the prehunting period did not include risk, but when the hunting season started, all the bears strongly selected against areas of high risk (-2.931±0.674, test statistics= -4.35, $p < 0.001$) (Figure 5 & Table A6, Appendix).

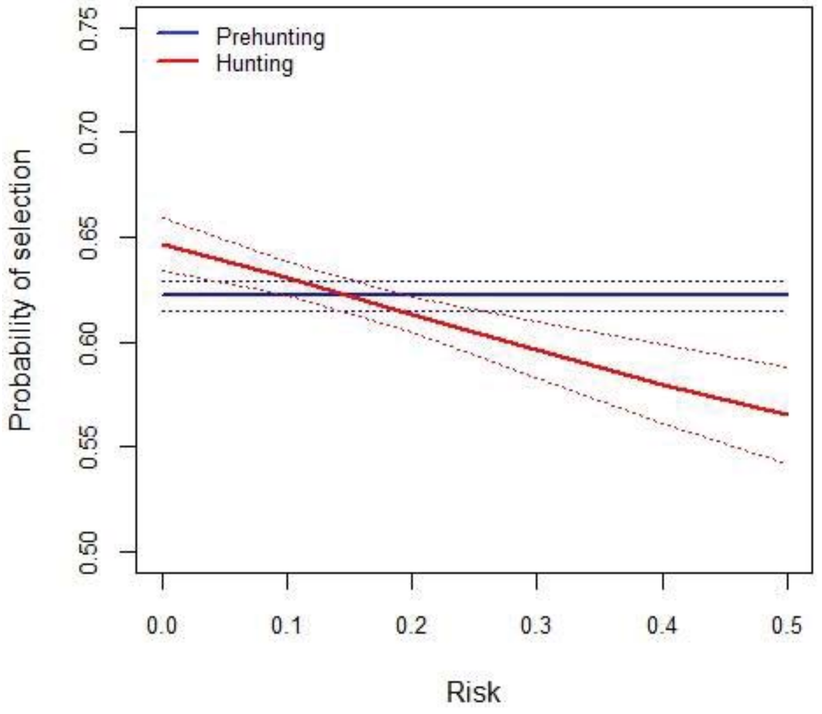

Figure 5: The predicted effect of risk on brown bear's probability of selection in the study area in south-central Sweden 10 days before and the first 10 days of the hunting season which started 21 August. All probabilities have been log link converted and represent actual probabilities of selection. The 95% confidence intervals are marked by the dashed lines.

Sex, age, and individual differences

I found minimal differences in habitat selection between the two sexes and the two age classes (Table A7 & Table A8, Appendix). The only significant difference between the two sexes was in period 6, when males selected more strongly for areas of high risk (2.238±0.912, test statistic= 2.45, p=0.01) than females (-2.268±0.518, test statistic=-4.37, p <0.001) (Table A7, Appendix). Subadults selected stronger against areas of high lingonberry availability in period 4 (-0.019±0.008, test statistic=-2.41, p=0.02), than adult bears (-0.010±0.003, test statistic= -2.97, p <0.01) and more strongly for areas of high risk in period 5 (2.052±0.944, test statistic=2.17, p=0.03), compared to adult bears (-2.160±0.50, test statistic=-4.32, p<0.001) (Table A8, Appendix).

The individual models applied to explore individual foraging behavior showed that bears selected differently for bilberry and lingonberry availability and risk (Table A9 & A10, Appendix). Some of the bears selected for areas of high bilberry availability in combination with high risk, others selected against both bilberry availability and risk, and a few selected for areas of high availability of bilberry in combination with low risk (Figure 6). There was a trend towards a positive correlation between selection for risk and selection for bilberries, but this trend was not significant ($r_s = 0.31$, $p = 0.14$) (Figure 6). The bears that were killed during hunting also selected differently from each other in relation to both bilberry and risk, with two selecting for areas of high bilberry availability and risk, and the two others avoiding both. Most bears seemed to avoid areas of high lingonberry availability and there was no correlation between bears' selection for lingonberry and risk ($r_s = -0.08$, $p = 0.73$) (Figure A7, Appendix).

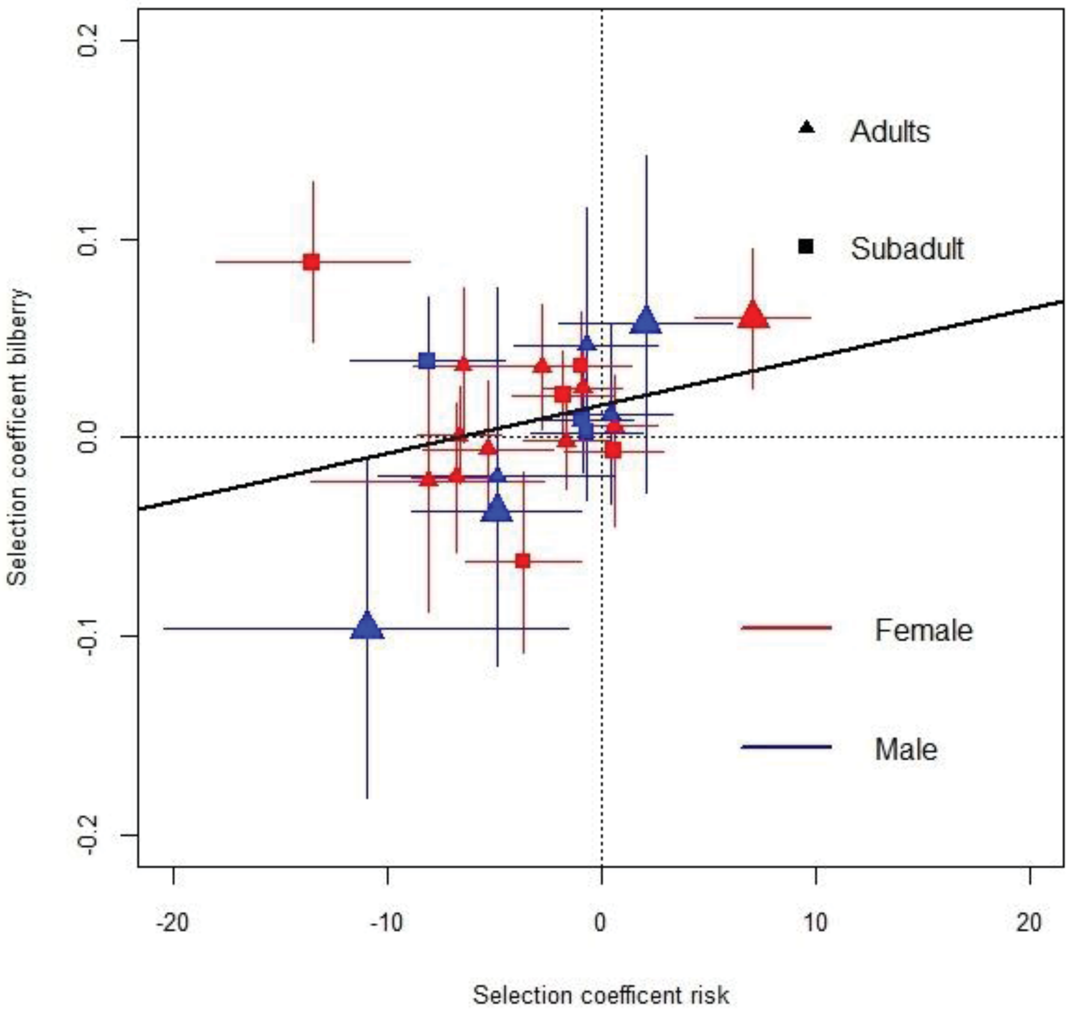

Figure 6: Selection coefficients of individual brown bears for risk and bilberry availability within the study area in south-central Sweden across the whole study period 11 July - 18 September. Selection coefficient is on the logit scale. The horizontal bars represent standard error around each risk estimate and the vertical bars for the standard error around each bilberry estimate. The larger triangles represent the bears that were killed during the hunting season. The black line represents a linear regression trend line between selection for bilberry availability and risk which showed a weak correlative trend ($r_s = 0.31$, $p = 0.14$).

Discussion

Spatial and temporal scales constitute one of the major challenges for studies of animal habitat selection (Boyce 2006; DeCesare et al. 2012), as it also did in this study. Firstly, predicting bilberry and lingonberry availability on a fine spatial scale using large-scale GIS-derived habitat data was challenging. Finer-scale spatial data could probably have resulted in more accurate berry models, which in turn would have increased the predictive accuracy of the RSFs when exploring third order habitat selection. Model validation of the RSFs indicated that they had a better predictive accuracy in the first three periods compared to the last three periods. The weak correlative trend between the area adjusted frequency of occurrence and the probability bins in the last three periods were due to a few unexpected bear positions in poor bear habitat, and excluding these led to highly improved model validation. The cross validation indicated that across the whole study period, the models overall predicted bear foraging well. I incorporated temporal changes of both berry availability and bear behavior by modeling both in overlapping time periods. This made it more difficult to compare the predicted berry availability and bear behavior across the periods, but it also made the spatial predictions more accurate on a spatial scale within each period. The hourly foraging positions used in this study may also give a too broad view of fine scale foraging behavior of bears on berries and overlook short-term foraging activity. Including positions from more bears across several years could have improved the models by enabling analysis of more demographic variables interacting with habitat selection. These challenges could be met in future studies by applying more temporally clustered bear positions, including bear foraging positions over several years, and by conducting inventories of berry availability on the actual foraging locations of the bears.

I have shown that bears selected for areas with a high availability of bilberry throughout hyperphagia, with the exception of period 2, which partly confirmed H1 in terms of selection for areas of high bilberry availability. Previous dietary studies have indicated that bilberries are an important part of bears' diet in Scandinavia (Dahle et al. 1998; Elfström et al. 2014a; Persson et al. 2001). Bilberries were found in 50% of the study plots and were the most common sampled berry species in this study. Bilberries are usually more than double the weight of crowberries and lingonberries, and have much higher carbohydrate content (Eriksson & Ehrlén 1991). The density and size of berries can have direct implications for intake and foraging efficiency of bears (Welch et al. 1997). The common occurrence of bilberries could partly explain why bears selected so strongly for areas of high bilberry availability, but lingonberries are found in higher densities. The bears generally increased their selection for bilberries later in the berry season, which partly contradicts H1 in terms of the expectation that bears should switch to increased selection of lingonberries, as bilberries declined later in the season.

Bears are known for switching between food resources according to availability, required handling time, and quality of the food resource (McLellan & Hovey 1995; Nielsen et al. 2010; Stelmock & Dean 1986). Lingonberries were increasingly more abundant during the latter periods of the study, but bears did not switch to select more strongly for areas with high lingonberry availability, as expected according to H1. The bears rather selected against areas of high lingonberry availability. Several studies in other parts of Scandinavia have shown that lingonberries do occur in diets of bears, but are not a very important food source (Dahle et al. 1998; Elfström et al. 2014a; Persson et al. 2001). This does not, however, explain why bears significantly selected against areas of high lingonberry availability. Lingonberries are often most abundant in open areas (Kardell 1980; Kardell & Eriksson 2011), which could mean that bears selected against these areas due to high perceived disturbance or mortality risk. Clearcuts with high lingonberry availability may represent areas of high risk for bears, because they are both open and located near roads, giving easy access for people. Bears could simply be unable to locate areas of high lingonberry availability in combination with low risk, which could explain their selection against areas with high lingonberry availability. Another explanation for the lack of selection for lingonberries could be that they are often found in very high densities (Kardell & Eriksson 2011), which could increase the bears' foraging efficiency, and enable them to forage considerable amounts of lingonberries in a very short time. Because this study used hourly bear positions with foraging trajectories of at least two successive locations with movements between 100-800 meters, such short term foraging behavior may have been overlooked.

The study by Dahle et al. (1998) showed that crowberries were the most important berry species for foraging bears in Jämtland, Sweden. In my study area however, the presence of crowberry was so low that I could not accurately predict its availability on a landscape scale over time. Availability of different berry species tends to vary from year to year (Selås 2000), as well as between different parts of Sweden (Kardell & Eriksson 2011). Bears may have switched to increased foraging on bilberries in response to the low abundance of crowberries, which similar response has been observed elsewhere (Stelmock & Dean 1986). Due to the low occurrence of crowberries, however, we cannot determine to which degree bears forage on crowberries in the study area. Studying bears' selection for crowberries in years or areas with very low occurrence may require different study techniques other than spatial modeling of berry availability.

Surviving bears selected against areas of high risk of being killed by human hunters throughout the study period, which supports H2. Bears' selection against areas of high risk as a response to predation can be described as a type of risk effect. Similar risk effects have been found in other species, such as elk (*Cervus canadensis*), avoiding areas with high risk of encountering gray wolves (*Canis lupus*) (Creel et al. 2005; Fortin et al. 2005), and in mesopredators, such as red foxes (*Vulpes vulpes*) and African wild dogs (*Lycaon pictus*), becoming more conspicuous and avoiding areas with increased risk of being predated by larger carnivores (Creel & Creel 1996; Glen & Dickman 2005; Letnic et al. 2012). Similar effects have also been observed in large carnivores, such as avoidance of habitats with high human density by Eurasian lynx (*Lynx lynx*) (Basille et al. 2009; Bunnefeld et al. 2006), wolves shifting to more concealed resting sites after being approached by humans (Wam et al. 2012), and avoidance of areas used by human pastoralists by spotted hyenas (*Crocuta crocuta*) (Boydston et al. 2003). Previous research has shown that bears also change their behavior and spatiotemporal use of the landscape in response to a wide variety of human disturbances, such as changed circadian activity patterns during hunting season (Ordiz et al. 2012), spatial avoidance of human settlements, and increased use of rugged terrain (Martin et al. 2010; Nellemann et al. 2007), and selection of dens, day beds, and home ranges away from human settlements and roads (Elfström et al. 2014b; Martin et al. 2010; Nellemann et al. 2007; Ordiz et al. 2011; Sahlén et al. 2011; Steyaert et al. 2013a).

Not all the study bears displayed a similar avoidance of areas with high risk. In the first three periods, there were distinct differences in foraging behavior between the bears that were killed and those that survived the hunting season. This gives support to H3, which predicted a difference in foraging behavior between bears of different fate. The bears that were killed during the hunting season had a higher probability of selection of high risk areas in periods 1-3 compared to the surviving bears. The difference in foraging behavior between the killed and surviving bears indicated that hunting mortality may not have been completely random, and that bears with a particular type of foraging behavior may have been more exposed to human hunters. Such selective effects of hunting could have unknown impacts on the population by removing individuals with certain foraging behaviors. The difference in habitat selection between killed and surviving bears disappeared in period 4, when the hunting season started. The lack of difference in those periods could be due to the bears that were killed changing their behavior as a response to the hunting season, but more likely due to lack of data on their behavior in this period as most of them were killed during the first days of hunting.

Comparing foraging behavior of bears 10 days before and the first 10 days during the hunting season indicated that bears changed their foraging behavior at the onset of the hunting season, confirming H4, that the hunting season impacts the foraging behavior of bears. All bears selected for areas of high bilberry availability and avoided areas of high lingonberry availability during both the 10 days periods prior and during hunting. In the prehunting period, risk of being killed by human hunters had little influence on the bears' foraging behavior, but during hunting the bears started to strongly avoid high risk areas. This indicates that the bears recognized the start of the hunting season and shifted foraging away from risky areas. They were still able to select for areas of high bilberry availability, while they continued to avoid areas of high lingonberry availability. Several studies have indicated that animals are indeed able to recognize the start of the hunting season and shift their behavior accordingly (Lone et al. 2015; Ruth et al. 2003). Such a temporal change in behavior has also been found in bears in Sweden that increased nighttime activity by 21%, while they substantially reduced daytime activity during the hunting season (Ordiz et al. 2012). Also American black bears (*Ursus americanus*) have been found to shift their spatial use away from unpaved roads as a response to the start of hunting (Stillfried et al. 2015). This illustrates how animals have a well developed ability to assess the risk of predation in both space and time and respond quickly by adapting their behavior in shorter periods of high predation risk (Lima & Bednekoff 1999).

Selection against areas of high risk may represent a tradeoff between avoiding risk and foraging in areas of high food quality and abundance food (Brown 1999b; Brown & Kotler 2004; Frid & Dill 2002; McArthur et al. 2014; McLoughlin et al. 2005). Avoidance of risk may force animals to forage in poorer habitat, increase vigilance, and thereby decrease the time spent foraging, and reduce foraging efficiency (Boydston et al. 2003; Brown & Kotler 2004; Bunnefeld et al. 2006; Lone et al. 2015; White Jr et al. 1999). I did not confirm that the bears' selection for areas of high berry availability was reduced by avoidance of areas of high risk. Consequently, I found no support for H5, which predicted that the bears would experience a tradeoff between selection for areas of high berry availability and selection against areas of high risk. The bears that were killed during hunting selected for areas of high risk during the first three time periods, but they did not display stronger selection for bilberries compared to the surviving bears in the same periods. The surviving bears selected against areas of high risk throughout the berry season, but were still able to select for areas of high bilberry availability. This indicates that avoidance of areas of high risk does not necessarily lead to a tradeoff with foraging on bilberries, possibly because they are so abundant across the study area. I have, however, only explored spatial selection for berry availability, and not the bears' circadian foraging patterns or foraging efficiency. Changes in foraging behavior can affect individual fitness and population viability depending on both how it affects an animal's spatial access to food and time spent foraging (McArthur et al. 2014; Welch et al. 1997). This may be especially true in the case of bears foraging on berries in the critical period of hyperphagia, when the time they spend foraging may have implications for daily intake of berries (Welch et al. 1997). Some studies suggest that bears depend on visibility to locate sites with high berry abundance and distinguish between berries and plant material (Bacon & Burghardt 1976; Welch et al. 1997). As human hunting causes bears to change their circadian foraging patterns by foraging more at night (Ordiz et al. 2012), it could potentially reduce their foraging efficiency due to reduced visibility. Reduced energy intake by bears as a consequence of human disturbances has been found in several previous studies (Olson et al. 1997; Rode et al. 2006a; White Jr et al. 1999). Further research is required to determine whether bears experience reduced foraging efficiency on berries due to shifts in circadian foraging patterns.

Modeling individual habitat selection partly confirmed H6 in terms of variability in the foraging behavior of individual bears in relation to bilberry and risk, but there were limited differences between individuals in regards to selection for lingonberry. The individual models indicated that several of the bears foraged in risky areas with a high availability of bilberries, but others seemed to avoid areas of both high bilberry availability and risk. The correlation coefficients between selection for risk and bilberry showed a slight positive relationship, but this was not significant. Two of the bears that got killed during hunting displayed a strong selection against both bilberry and risk, but two others selected for areas with higher availability of bilberry and higher levels of risk. Some of the individual models seem to contradict the most parsimonious candidate models, which showed that there were no interactions between selection for risk and berry availability, and that the bears that got killed all selected for areas of high risk. However, the individual models explored foraging behavior throughout the whole study period and may therefore miss changes in behavior between different time periods. The models of individual selection are also impeded by small sample sizes of foraging positions, and therefore have varying predictive accuracy. The candidate models in the different periods, however, analyzes the behavior of all the bears combined and may therefore be unable to include the foraging behavior of bears that differ in behavior from the majority. The individual foraging models did not generalize bear behavior in different groups of bears, and are therefore able to capture more individual subtleties in the bears' habitat selection.

There were no consistent differences between the sexes and age classes in relation to habitat selection, as was also expected in H6, which is surprising as behavioral effects of human disturbances in bears have been documented to differ between different sexes and age groups (Elfström et al. 2014a; Nellemann et al. 2007; Ordiz et al. 2012; Stillfried et al. 2015). Bear hunting in Sweden is not especially selective towards certain sexes or age groups (Bischof et al. 2009a; Steyaert et al. In press), with the exception of family groups that are protected from hunting (Bischof et al. 2008). The lack of differences in foraging behavior between the different age classes and sexes in relation to risk of being killed could offer one explanation to why hunting is not especially selective in relation to sex and age classes in south-central Sweden.

Conclusion

Bilberries are an abundant and important food source for bears during hyperphagia in south-central Sweden. Bears strongly avoided areas of high lingonberry availability, which could be due to these areas being associated with high risk, or that bears were simply very effective at foraging on lingonberries in short time periods. The occurrence of crowberries was too low to be able to spatially predict their availability, and I did therefore not explore bears' foraging on crowberries. I have shown that bears respond to a landscape of fear when foraging during hyperphagia. Surviving bears strongly selected against areas of high risk, and all bears responded quickly to the onset of the hunting season by shifting their foraging even further away from areas of high risk. I have also shown that bears that were killed during the hunting season were more likely to select for areas of high risk. No evidence was found implying that selection against risk negatively affected the bears' ability to select for areas of high bilberry availability. Hunting has a strong numerical impact on the Swedish bear population (Bischof et al. 2009a; Bischof & Swenson 2009b; Kindberg & Swenson 2014), and this thesis shows that there are also behavioral impacts of hunting, reinforcing previous studies (Ordiz et al. 2012). Bears are apex predators that may induce behavioral changes in their prey, and which have the potential to cause major top-down structuring of ecosystems (Estes et al. 2011; Ordiz et al. 2013b; Ripple et al. 2014). In Sweden, human hunting strongly impacts the behavior and foraging patterns of bears, which may also have consequences for their role in the ecosystem (Ordiz et al. 2013b). Such complex behavioral effects of human hunting on a spatiotemporal scale may be of vital importance for both the conservation of apex predators and ecosystems in the future.

References

Arnemo, J. M. & Fahlman, Å. (2011). Biomedical protocols for free-ranging brown bears, gray wolves, wolverines and lynx. Evenstad, Norway: Hedmark University College.

Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management*, 74: 1175-1178.

Atlegrim, O. & Sjöberg, K. (1996). Response of bilberry (*Vaccinium myrtillus*) to clear-cutting and single-tree selection harvests in uneven-aged boreal *Picea abies* forests. *Forest Ecology and Management*, 86: 39-50.

Bacon, E. S. & Burghardt, G. M. (1976). *Learning and color discrimination in the American black bear*. Proceedings of the International Conference on Bear Research and Management 3, pp. 27-36.

Barton, K. (2014). MuMIn: Multi-Model Inference. R package version 1.12.1.

Basille, M., Herfindal, I., Santin-Janin, H., Linnell, J. D., Odden, J., Andersen, R., Høgda, K. A. & Gaillard, J. M. (2009). What shapes Eurasian lynx distribution in human dominated landscapes: selecting prey or avoiding people? *Ecography*, 32: 683-691.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014). *lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7.*

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: 465-474.

Bischof, R., Fujita, R., Zedrosser, A., Söderberg, A. & Swenson, J. E. (2008). Hunting patterns, ban on baiting, and harvest demographics of brown bears in Sweden. *Journal of Wildlife Management*, 72: 79-88.

Bischof, R., Swenson, J. E., Yoccoz, N. G., Mysterud, A. & Gimenez, O. (2009a). The magnitude and selectivity of natural and multiple anthropogenic mortality causes in hunted brown bears. *Journal of Animal Ecology*, 78: 656-665.

Bischof, R. & Swenson, J. (2009b). Preliminary predictions of the effect of increasing hunting quotas on brown bear population growth in Sweden. *Scandinavian Brown Bear Research Project Report 2009-3*.

Bischof, R., Loe, L. E., Meisingset, E. L., Zimmermann, B., Van Moorter, B. & Mysterud, A. (2012). A migratory northern ungulate in the pursuit of spring: Jumping or surfing the green wave? *The American Naturalist*, 180: 407-424.

Boyce, M. S., Vernier, P. R., Nielsen, S. E. & Schmiegelow, F. K. (2002). Evaluating resource selection functions. *Ecological Modelling*, 157: 281-300.

Boyce, M. S. (2006). Scale for resource selection functions. *Diversity and Distributions*, 12: 269-276.

Boydston, E. E., Kapheim, K. M., Watts, H. E., Szykman, M. & Holekamp, K. E. (2003). Altered behaviour in spotted hyenas associated with increased human activity. *Animal Conservation*, 6: 207-219.

Brown, J. S., Laundré, J. W. & Gurung, M. (1999a). The ecology of fear: optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy*: 385-399.

Brown, J. S. (1999b). Vigilance, patch use and habitat selection: foraging under predation risk. *Evolutionary Ecology Research*, 1: 49-71.

Brown, J. S., Kotler, B. & Bouskila, A. (2001). Ecology of fear: foraging games between predators and prey with pulsed resources. *Annales Zoologici Fennici*, 38: 71-87.

Brown, J. S. & Kotler, B. P. (2004). Hazardous duty pay and the foraging cost of predation. *Ecology Letters*, 7: 999-1014.

Bunnefeld, N., Linnell, J. D., Odden, J., Van Duijn, M. & Andersen, R. (2006). Risk taking by Eurasian lynx (*Lynx lynx*) in a human-dominated landscape: effects of sex and reproductive status. *Journal of Zoology*, 270: 31-39.

Bunnell, F. L. & Hamilton, T. (1983). *Forage digestibility and fitness in grizzly bears*. Proceedings of the International Conference on Bear Research and Management 6. 179-185 pp.

Calenge, C. (2006). The package “adehabitat” for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling*, 197: 516-519.

Chapron, G., Kaczensky, P., Linnell, J. D. C., von Arx, M., Huber, D., Andrén, H., López-Bao, J. V., Adamec, M., Álvares, F., Anders, O., et al. (2014). Recovery of large carnivores in Europe’s modern human-dominated landscapes. *Science*, 346: 1517-1519.

Clinchy, M., Sheriff, M. J. & Zanette, L. Y. (2013). Predator-induced stress and the ecology of fear. *Functional Ecology*, 27: 56-65.

Coltman, D. W., O'Donoghue, P., Jorgenson, J. T., Hogg, J. T., Strobeck, C. & Festa-Bianchet, M. (2003). Undesirable evolutionary consequences of trophy hunting. *Nature*, 426: 655-658.

Coogan, S. C., Nielsen, S. E. & Stenhouse, G. B. (2012). Spatial and temporal heterogeneity creates a “brown tide” in root phenology and nutrition. *ISRN Ecology*, 2012: 1-10.

Creel, S. & Creel, N. M. (1996). Limitation of African wild dogs by competition with larger carnivores. *Conservation Biology*, 10: 526-538.

Creel, S., Winnie Jr, J., Maxwell, B., Hamlin, K. & Creel, M. (2005). Elk alter habitat selection as an antipredator response to wolves. *Ecology*, 86: 3387-3397.

Creel, S., Christianson, D., Liley, S. & Winnie, J. A. (2007). Predation risk affects reproductive physiology and demography of elk. *Science*, 315: 960-960.

Creel, S. & Christianson, D. (2008). Relationships between direct predation and risk effects. *Trends in Ecology & Evolution*, 23: 194-201.

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 *Ovis aries*. *Wildlife Biology*, 4: 147-158.

Darimont, C. T., Carlson, S. M., Kinnison, M. T., Paquet, P. C., Reimchen, T. E. & Wilmers, C. C. (2009). Human predators outpace other agents of trait change in the wild. *Proceedings of the National Academy of Sciences*, 106: 952-954.

DeCesare, N. J., Hebblewhite, M., Schmiegelow, F., Hervieux, D., McDermid, G. J., Neufeld, L., Bradley, M., Whittington, J., Smith, K. G., Morgantini, L. E., et al. (2012). Transcending scale dependence in identifying habitat with resource selection functions. *Ecological Applications*, 22: 1068-1083.

Elfström, M., Swenson, J. E. & Ball, J. P. (2008). Selection of denning habitats by Scandinavian brown bears *Ursus arctos*. *Wildlife Biology*, 14: 176-187.

Elfström, M., Davey, M. L., Zedrosser, A., Müller, M., De Barba, M., Støen, O.-G., Miquel, C., Taberlet, P., Hackländer, K. & Swenson, J. E. (2014a). Do Scandinavian brown bears approach settlements to obtain high-quality food? *Biological Conservation*, 178: 128-135.

Elfström, M., Zedrosser, A., Støen, O. G. & Swenson, J. E. (2014b). Ultimate and proximate mechanisms underlying the occurrence of bears close to human settlements: review and management implications. *Mammal Review*, 44: 5-18.

Eriksson, O. & Ehrlén, J. (1991). Phenological variation in fruit characteristics in vertebrate-dispersed plants. *Oecologia*, 86: 463-470.

ESRI. (2014). *ArcMap 10.3*: ESRI (Environmental Systems Resource Institute).

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., Jackson, J. B. C., et al. (2011). Trophic downgrading of planet earth. *Science*, 333: 301-306.

Fortin, D., Beyer, H. L., Boyce, M. S., Smith, D. W., Duchesne, T. & Mao, J. S. (2005). Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*, 86: 1320-1330.

Frair, J. L., Fieberg, J., Hebblewhite, M., Cagnacci, F., DeCesare, N. J. & Pedrotti, L. (2010). Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 365: 2187-2200.

Frank, L. G. & Woodroffe, R. (2001). Behaviour of carnivores in exploited and controlled populations. In Gittleman, J. L., Funk, S. M., Macdonald, D. & Wayne, R. K. (eds) *Carnivore Conservation*. Cambridge: Cambridge University Press.

Frid, A. & Dill, L. M. (2002). Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, 6: 11.

Gillies, C. S., Hebblewhite, M., Nielsen, S. E., Krawchuk, M. A., Aldridge, C. L., Frair, J. L., Saher, D. J., Stevens, C. E. & Jerde, C. L. (2006). Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology*, 75: 887-898.

Glen, A. S. & Dickman, C. R. (2005). Complex interactions among mammalian carnivores in Australia, and their implications for wildlife management. *Biological Reviews*, 80: 387-401.

Hebblewhite, M. & Merrill, E. (2008). Modelling wildlife–human relationships for social species with mixed-effects resource selection models. *Journal of Applied Ecology*, 45: 834-844.

Hertel, A. G., Steyaert, S., Zedrosser, A., Mysterud, A., Lodberg-Holm, H. K., Gelink, H. W., Kindberg, J. & Swenson, J. E. (In press). Bears and berries: selective foraging on a patchily distributed food resource.

Kardell, L. (1979). Occurrence and production of bilberry, lingonberry and raspberry in Sweden's forests. *Forest Ecology and Management*, 2: 285-298.

Kardell, L. (1980). Forest Berries and Mushrooms: An Endangered Resource? *Ambio*: 241-247.

Kardell, L. & Eriksson, L. (2011). Blåbärs-och lingonrisets återhämtning 30 år efter kalavverkning och markberedning 1977-2010. *Rapport / Sveriges lantbruksuniversitet, Institutionen för skoglig landskapsvård*, 1101-0525. Uppsala: Institutionen för skoglig landskapsvård, Sveriges lantbruksuniversitet.

Kindberg, J. & Swenson, J. (2014). Björnstammens storlek i Sverige 2013–länsvisa skattningar och trender. *Skandinaviske bjørneprosjektet Rapport Nr. 2013-4*.

Klar, N., Fernández, N., Kramer-Schadt, S., Herrmann, M., Trinzen, M., Büttner, I. & Niemitz, C. (2008). Habitat selection models for European wildcat conservation. *Biological Conservation*, 141: 308-319.

Laundré, J. W., Hernández, L. & Altendorf, K. B. (2001). Wolves, elk, and bison: reestablishing the" landscape of fear" in Yellowstone National Park, USA. *Canadian Journal of Zoology*, 79: 1401-1409.

Laundré, J. W., Hernández, L. & Ripple, W. J. (2010). The landscape of fear: ecological implications of being afraid. *Open Ecology Journal*, 3: 1-7.

Letnic, M., Ritchie, E. G. & Dickman, C. R. (2012). Top predators as biodiversity regulators: the dingo *Canis lupus dingo* as a case study. *Biological Reviews*, 87: 390-413.

Lewis, J. S., Rachlow, J. L., Garton, E. O. & Vierling, L. A. (2007). Effects of habitat on GPS collar performance: using data screening to reduce location error. *Journal of Applied Ecology*, 44: 663-671.

Lima, S. L. (1998). Nonlethal effects in the ecology of predator-prey interactions. *Bioscience*, 48: 25-34.

Lima, S. L. & Bednekoff, P. A. (1999). Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *American Naturalist*, 153: 649-659.

Linnell, J. D., Swenson, J. E. & Anderson, R. (2001). Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. *Animal Conservation*, 4: 345-349.

Lone, K., Loe, L. E., Meisingset, E. L., Stamnes, I. & Mysterud, A. (2015). An adaptive behavioural response to hunting: surviving male red deer shift habitat at the onset of the hunting season. *Animal Behaviour*, 102: 127-138.

Maindonald, J. & Braun, W. J. (2010). *Data Analysis and Graphics Using R - an Example-Based Approach*. Cambridge: Cambridge University Press.

Maindonald, J. H., Braun, W. J. & (2014). *DAAG: Data Analysis And Graphics data and functions. R package version 1.20.*

Manly, B. F., MacDonald, L. L., Thomas, D. L., McDonald, T. L. & Erickson, W. P. (2002). *Resource selection by animals: Statistical Design and Analysis for Field Studies*: Kluwer Academic Publishers.

Martin, J., Basille, M., Van Moorter, B., Kindberg, J., Allaine, D. & Swenson, J. E. (2010). Coping with human disturbance: spatial and temporal tactics of the brown bear (*Ursus arctos*). *Canadian Journal of Zoology*, 88: 875-883.

McArthur, C., Banks, P. B., Boonstra, R. & Forbey, J. S. (2014). The dilemma of foraging herbivores: dealing with food and fear. *Oecologia*: 1-13.

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: 704-712.

McLoughlin, P. D., Dunford, J. S. & Boutin, S. (2005). Relating predation mortality to broad-scale habitat selection. *Journal of Animal Ecology*, 74: 701-707.

McShea, W. J. (2005). Forest ecosystems without carnivores: when ungulates rule the world. In Ray, J. C., Redford, K. H., Steneck, R. S. & Berger, J. (eds) *Large Carnivores and the Conservation of Biodiversity*, pp. 138-152. Washington DC: Island Press.

Milner, J. M., Nilsen, E. B. & Andreassen, H. P. (2007). Demographic side effects of selective hunting in ungulates and carnivores. *Conservation Biology*, 21: 36-47.

Moe, T., Kindberg, J., Jansson, I. & Swenson, J. (2007). Importance of diel behaviour when studying habitat selection: examples from female Scandinavian brown bears (*Ursus arctos*). *Canadian Journal of Zoology*, 85: 518-525.

Moen, G. K., Støen, O.-G., Sahlén, V. & Swenson, J. E. (2012). Behaviour of solitary adult Scandinavian brown bears (*Ursus arctos*) when approached by humans on foot. *PLoS ONE*, 7: e31699.

Nellemann, C., Støen, O.-G., Kindberg, J., Swenson, J. E., Vistnes, I., Ericsson, G., Katajisto, J., Kaltenborn, B. P., Martin, J. & Ordiz, A. (2007). Terrain use by an expanding brown bear population in relation to age, recreational resorts and human settlements. *Biological Conservation*, 138: 157-165.

Nielsen, S. E., Herrero, S., Boyce, M. S., Mace, R. D., Benn, B., Gibeau, M. L. & Jevons, S. (2004). Modelling the spatial distribution of human-caused grizzly bear mortalities in the Central Rockies ecosystem of Canada. *Biological Conservation*, 120: 101-113.

Nielsen, S. E., McDermid, G., Stenhouse, G. B. & Boyce, M. S. (2010). Dynamic wildlife habitat models: seasonal foods and mortality risk predict occupancy-abundance and habitat selection in grizzly bears. *Biological Conservation*, 143: 1623-1634.

Northrup, J. M., Hooten, M. B., Anderson Jr, C. R. & Wittemyer, G. (2013). Practical guidance on characterizing availability in resource selection functions under a use-availability design. *Ecology*, 94: 1456-1463.

Nybakken, L., Selås, V. & Ohlson, M. (2013). Increased growth and phenolic compounds in bilberry (*Vaccinium myrtillus* L.) following forest clear-cutting. *Scandinavian Journal of Forest Research*, 28: 319-330.

Olson, T. L., Gilbert, B. K. & Squibb, R. C. (1997). The effects of increasing human activity on brown bear use of an Alaskan river. *Biological Conservation*, 82 (1): 95-99.

Ordiz, A., Støen, O.-G., Delibes, M. & Swenson, J. E. (2011). Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. *Oecologia*, 166: 59-67.

Ordiz, A., Støen, O.-G., Sæbø, S., Kindberg, J., Delibes, M. & Swenson, J. E. (2012). Do bears know they are being hunted? *Biological Conservation*, 152: 21-28.

Ordiz, A., Støen, O. -G., Sæbø, S., Sahlén, V., Pedersen, B. E., Kindberg, J. & Swenson, J. E. (2013a). Lasting behavioural responses of brown bears to experimental encounters with humans. *Journal of Applied Ecology*, 50: 306-314.

Ordiz, A., Bischof, R. & Swenson, J. E. (2013b). Saving large carnivores, but losing the apex predator? *Biological Conservation*, 168: 128-133.

Ordiz, A., Kindberg, J., Sæbø, S., Swenson, J. E. & Støen, O.-G. (2014). Brown bear circadian behavior reveals human environmental encroachment. *Biological Conservation*, 173: 1-9.

Parlane, S., Summers, R., Cowie, N. & Van Gardingen, P. (2006). Management proposals for bilberry in Scots pine woodland. *Forest Ecology and Management*, 222: 272-278.

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.

Pettorelli, N., Vik, J. O., Mysterud, A., Gaillard, J.-M., Tucker, C. J. & Stenseth, N. C. (2005). Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology & Evolution*, 20: 503-510.

Prugh, L. R., Stoner, C. J., Epps, C. W., Bean, W. T., Ripple, W. J., Laliberte, A. S. & Brashares, J. S. (2009). The rise of the mesopredator. *Bioscience*, 59: 779-791.

R Core Team. (2014). *R: A language and environment for statistical computing*. Computing, R Foundation for Statistical Computing. Vienna, Austria.

Ray, J. C. (2005). Large carnivorous animals as tools for conserving biodiversity: assumptions and uncertainties. In Ray, J. C., Redford, K. H., Steneck, R. S. & Berger, J. (eds) *Large Carnivores and the Conservation of Biodiversity*, pp. 34-56. Washington DC: Island Press.

Ripple, W. J. & Beschta, R. L. (2004). Wolves and the ecology of fear: can predation risk structure ecosystems? *BioScience*, 54: 755-766.

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M. P., et al. (2014). Status and Ecological Effects of the World's Largest Carnivores. *Science*, 343: 1241484.

Ritchie, E. G., Elmhagen, B., Glen, A. S., Letnic, M., Ludwig, G. & McDonald, R. A. (2012). Ecosystem restoration with teeth: what role for predators? *Trends in Ecology & Evolution*, 27: 265-271.

Rode, K. D., Robbins, C. T. & Shipley, L. A. (2001). Constraints on herbivory by grizzly bears. *Oecologia*, 128: 62-71.

Rode, K. D., Farley, S. D. & Robbins, C. T. (2006a). Behavioral responses of brown bears mediate nutritional effects of experimentally introduced tourism. *Biological Conservation*, 133: 70-80.

Rode, K. D., Farley, S. D. & Robbins, C. T. (2006b). Sexual dimorphism, reproductive strategy, and human activities determine resource use by brown bears. *Ecology*, 87: 2636-2646.

Ruth, T. K., Smith, D. W., Haroldson, M. A., Buotte, P. C., Schwartz, C. C., Quigley, H. B., Cherry, S., Murphy, K. M., Tyers, D. & Frey, K. (2003). Large-carnivore response to recreational big-game hunting along the Yellowstone National Park and Absaroka-Beartooth Wilderness boundary. *Wildlife Society Bulletin*: 1150-1161.

Sahlén, E., Støen, O.-G. & Swenson, J. E. (2011). Brown bear den site concealment in relation to human activity in Sweden. *Ursus*, 22: 152-158.

Selås, V. (2000). Seed production of a masting dwarf shrub, *Vaccinium myrtillus*, in relation to previous reproduction and weather. *Canadian Journal of Botany*, 78: 423-429.

Statens veterinärmedicinska anstalt. (2015). *Licensjakt på björn 2013*. Available at: http://www.sva.se/djurhalsa/vilda-djur/stora-rovdjur/licensjakt_pa_bjorn/licensjakt-pa-bjorn-2013 (accessed: 24.11.15).

Stelmock, J. J. & Dean, F. C. (1986). *Brown bear activity and habitat use, Denali National Park: 1980*. Proceedings of the International Conference on Bear Research and Management 6, pp. 155-167.

Sténs, A. & Sandström, C. (2013). Divergent interests and ideas around property rights: The case of berry harvesting in Sweden. *Forest Policy and Economics*, 33: 56-62.

Steyaert, S., Zedrosser, A., Elfström, M., Ordiz, A., Leclerc, M., Frank, S. C., Kindberg, J., Støen, O.-G., Brunberg, S. & Swenson, J. E. (In press). Ecological implications from spatial patterns in human-caused brown bear mortality.

Steyaert, S. M., Kindberg, J., Swenson, J. E. & Zedrosser, A. (2013a). Male reproductive strategy explains spatiotemporal segregation in brown bears. *Journal of Animal Ecology*, 82: 836-845.

Steyaert, S. M., Reusch, C., Brunberg, S., Swenson, J., Hackländer, K. & Zedrosser, A. (2013b). Infanticide as a male reproductive strategy has a nutritive risk effect in brown bears. *Biology Letters*, 9: 20130624.

Stillfried, M., Belant, J. L., Svoboda, N. J., Beyer, D. E. & Kramer-Schadt, S. (2015). When top predators become prey: Black bears alter movement behaviour in response to hunting pressure. *Behavioural Processes*, 120: 30-39.

Swenson, J. E., Sandegren, F., Bjärvall, A., Söderberg, A., Wabakken, P. & Franzén, R. (1994). Size, trend, distribution and conservation of the brown bear (*Ursus arctos*) population in Sweden. *Biological Conservation*, 70: 9-17.

Swenson, J. E., Wabakken, P., Sandegren, F., Bjärvall, A., Franzén, R. & Söderberg, A. (1995). The near extinction and recovery of brown bears in Scandinavia in relation to the bear management policies of Norway and Sweden. *Wildlife Biology*, 1: 11-25.

Swenson, J. E., Støen, O.-G., Zedrosser, A., Kindberg, J., Brunberg, S., Arnemo, J. & Sahlén, V. (2010). Bjørnens status og økologi i Skandinavia. *Skandinaviske bjørneprosjektet Rapport Nr. 2008-3*.

Treves, A. (2009). Hunting for large carnivore conservation. *Journal of Applied Ecology*, 46: 1350-1356.

Tybirk, K., Nilsson, M.-C., Michelsen, A., Kristensen, H. L., Shevtsova, A., Tune Strandberg, M., Johansson, M., Nielsen, K. E., Riis-Nielsen, T. & Strandberg, B. (2000). Nordic *Empetrum* dominated ecosystems: function and susceptibility to environmental changes. *AMBIO*, 29: 90-97.

Wallach, A. D., Ritchie, E. G., Read, J. & O'Neill, A. J. (2009). More than mere numbers: the impact of lethal control on the social stability of a top-order predator. *PLoS One*, 4: e6861.

Wam, H., Eldegard, K. & Hjeljord, O. (2012). From overlooking to concealed: predator avoidance in an apex carnivore. *European Journal of Wildlife Research*, 58: 1001-1003.

Welch, C. A., Keay, J., Kendall, K. C. & Robbins, C. T. (1997). Constraints on frugivory by bears. *Ecology*, 78: 1105-1119.

White Jr, D., Kendall, K. C. & Picton, H. D. (1999). Potential energetic effects of mountain climbers on foraging grizzly bears. *Wildlife Society Bulletin*, 27: 146-151.

Woodroffe, R., Thirgood, S. & Rabinowitz, A. (2005). The impact of human–wildlife conflict on natural systems. In Woodroffe, R., Thirgood, S. & Rabinowitz, A. (eds). Conservation Biology (No. 9) *People and Wildlife: Conflict or Coexistence?*, pp. 13–26. Cambridge: Cambridge University Press.

Zedrosser, A., Dahle, B. & Swenson, J. E. (2006). Population density and food conditions determine adult female body size in brown bears. *Journal of Mammalogy*, 87: 510-518.

Zedrosser, A., Steyaert, S. M., Gossow, H. & Swenson, J. E. (2011). Brown bear conservation and the ghost of persecution past. *Biological Conservation*, 144: 2163-2170.

Zeileis, A., Kleiber, C. & Jackman, S. (2007). Regression models for count data in R.

Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A. & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. New York: Springer.

Appendix

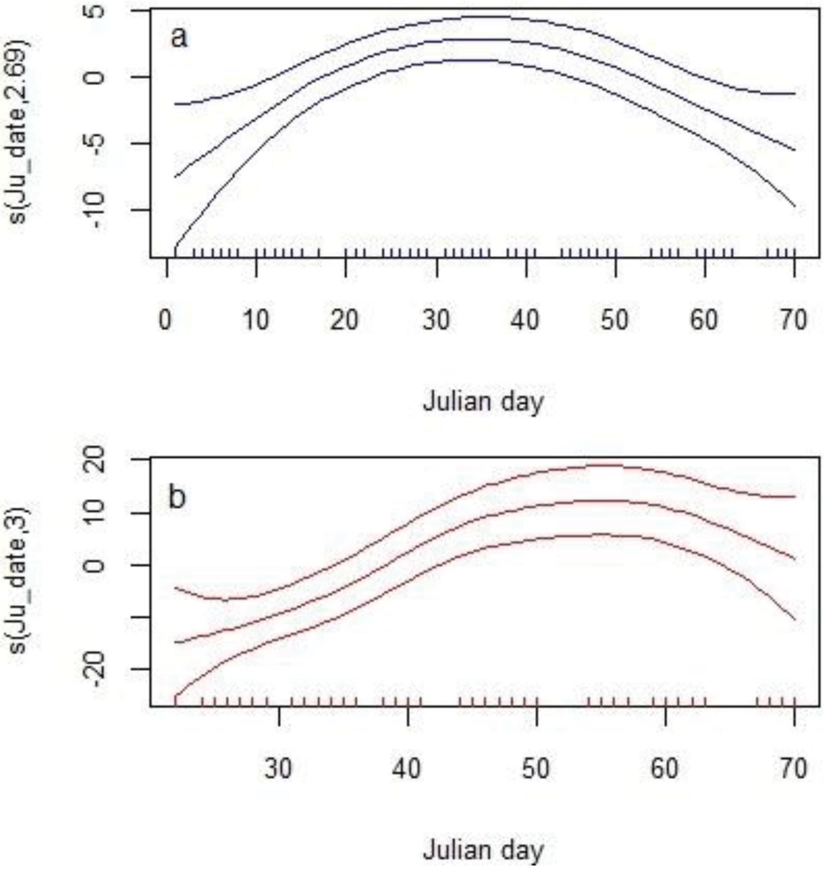

Figure A1: Bilberry and lingonberry abundance (number of berries sampled in the plots) within the study area in south-central Sweden modeled with GAMs using Julian day as spline. Panel a displays the estimated smoothing curve of bilberry abundance across the study period (11 July - 18 September), and panel b shows the estimated smoothing curve of lingonberry abundance across the part of the study period when lingonberries were ripe (1 August - 18 September).

Table A1: The most parsimonious candidate models for predicting bilberry density and presence in the study area in south-central Sweden with $\Delta AIC_c < 2$ in the 20-day periods with 10 days overlap (1-6), during the study period 11 July - 18 September. When several models have been selected as having the most explanatory power, they have been model averaged, not including the null model, and used to spatially predict bilberry presence and density. Dispersion parameter show model fit for the most parsimonious models, and values close to 1 indicate good model fit. The cross validation estimate of accuracy assesses the predictive power of the berry presence models, higher values indicate increased predictive accuracy. When several models have been selected, the dispersion parameters and cross validation estimates of accuracy have been averaged.

Period	Model Selection – ΔAIC_c								Cross validation	Dispersion parameter
	Full	1	2	3	4	5	6	Null		
P1 presence	2.83	4.45	3.92	**0**	5.54	13.82	9.05	19.28	0.60	1.29
P1 density	6.98	6.53	8	8.25	9.42	**1.83**	**0**	8.11	NA	1.18
P2 presence	5.88	4.45	2.83	**0**	12.62	29.99	27.64	55.73	0.68	1.2
P2 density	5.75	4.64	2.34	5.54	3.99	**0**	**0.63**	11.79	NA	1.14
P3 present	7.66	5.91	3.79	**0**	18.14	23.76	19.1	57.18	0.71	1.19
P3 density	10.77	8.45	6.17	**1.48**	5.54	3.41	**0**	8.84	NA	1.14
P4 presence	8.6	7.25	5.42	**0**	20.55	12.15	6.77	33.07	0.65	1.24
P4 density	17.48	16.05	13.74	8.62	14.47	3.71	**0**	**1.25**	NA	1.14
P5 presence	**0**	**0.24**	**0.33**	3.79	13.96	**0.1**	4.14	28.57	0.66	1.23
P5 density	15.43	13.93	11.39	4.91	13.67	4.9	**0**	**0.13**	NA	1.17
P6 presence	3.13	**0.84**	5.17	5.17	3.96	12.44	**0**	11.62	0.63	1.29
P6 density	13.52	10.82	9.98	8.25	7.47	**1.72**	**1.01**	**0**	NA	1.17

Table A2: The most parsimonious candidate models for predicting lingonberry density and presence in south-central Sweden with an $\Delta AIC_c < 2$ in the four last 20-day periods with 10 days overlap (3-6) during the study period when lingonberries are ripe 1 August - 18 September. When several models have been selected as having the most explanatory power, they have been averaged, not including the null model, and used to spatially predict lingonberry presence and density. Dispersion parameter show model fit for the most parsimonious models, and values close to 1 indicate good model fit. The cross validation estimate of accuracy assesses the predictive power of the berry presence models, higher values indicate increased predictive accuracy. When several models have been selected, the dispersion parameters and cross validation estimates of accuracy have been averaged.

Period	Model Selection – ΔAIC_c								Cross validation	Dispersion parameter
	Full	1	2	3	4	5	6	Null		
P3 presence	2.15	**0**	4.18	**1.42**	2.96	5.63	2.48	2.78	0.916	0.522
P3 density	43.07	35.85	26.9	12.7	27.08	4.95	**0**	9.3	NA	1.243
P4 presence	6	6.47	5.87	**1.72**	3.73	6.2	**1.88**	0.00	0.705	1.213
P4 density	6.24	3.34	3.83	10.07	17.27	**0**	5.28	25.74	NA	1.204
P5 presence	3.33	3.42	2.05	3.19	**0**	5.79	7.03	6.08	0.626	1.326
P5 density	5.13	2.98	**1.24**	**0**	10.55	3.12	**0.12**	21.77	NA	1.267
P6 presence	**0**	2.1	2.58	2.66	**1.21**	8.43	10.85	8.96	0.6	1.297
P6 density	3.03	2.77	**0.04**	4.62	9.14	**0**	6.08	20.28	NA	1.28

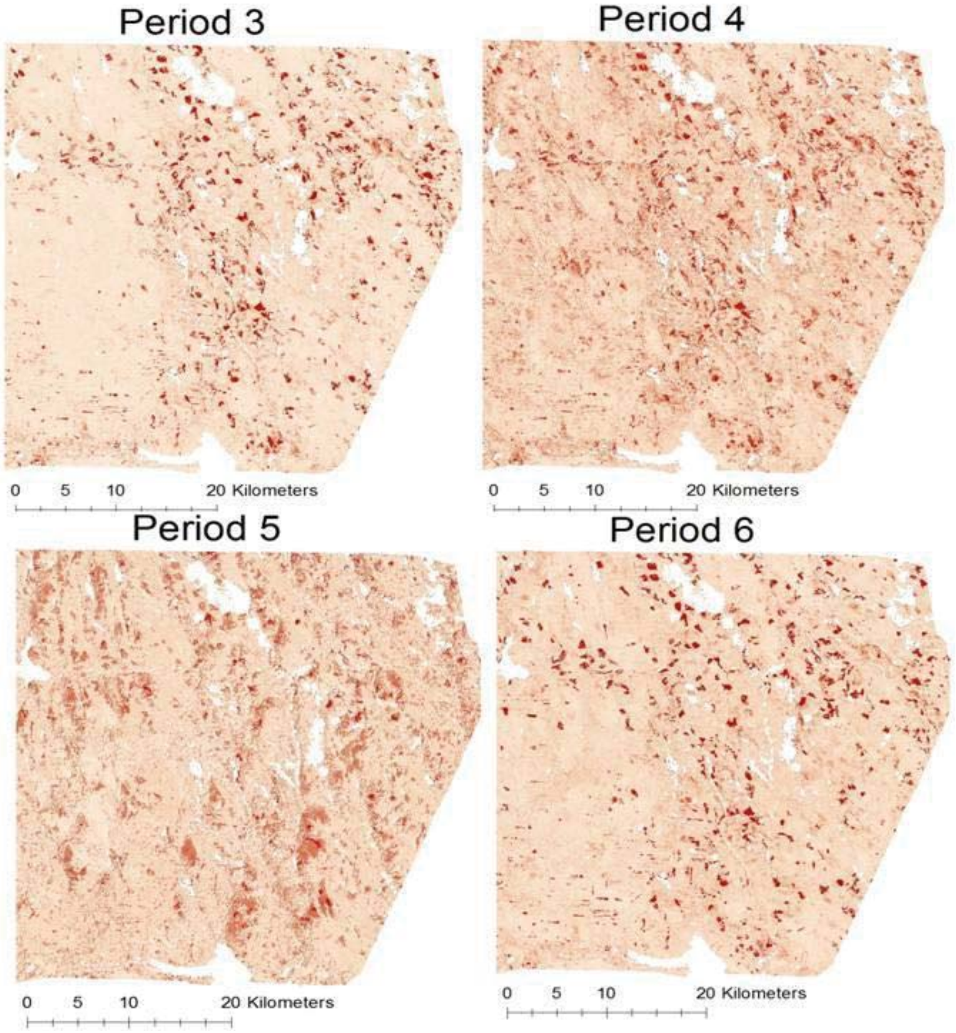

Figure A2: Spatial predictions of lingonberry availability in the study area in south-central Sweden across the last four 20-day periods with 10 days overlap (3-6) during the study period when lingonberries were ripe 1 August - 18 September. Darker color represents higher predicted lingonberry availability.

Table A3: Model selection of nine candidate models predicting resource selection of brown bears within the study area in south-central Sweden during study period 11 July - 18 September. The ΔAIC_c are presented for each candidate models in each in the 20-day periods with 10 days overlap (1-6) as well as for the 10 days before hunting season starts on 21 August (prehunting) and the first 10 days after 21 August (hunting season). The models with highest explanatory power with $\Delta AIC_c < 2$ are marked in bold and the simplest was selected as the most parsimonious.

Model	**Period 1** ΔAIC_c	**Period 2** ΔAIC_c	**Period 3** ΔAIC_c	**Period 4** ΔAIC_c	**Period 5** ΔAIC_c	**Period 6** ΔAIC_c	**Pre-hunting** ΔAIC_c	**Hunting season** ΔAIC_c
RSF full	**0.64**	4.06	4.34	9.66	10.73	NA	11.75	10.62
RSF1	**0.00**	3.17	3.25	6.39	7.20	NA	8.36	7.54
RSF2	8.18	31.08	15.57	**0.00**	**0.00**	**0.00**	**1.25**	**0.00**
RSF3	6.38	39.94	21.14	5.63	5.59	NA	7.20	5.71
RSF4	3.76	**1.88**	**0.00**	2.56	3.71	NA	4.33	3.74
RSF5	68.44	80.77	26.88	19.78	17.18	NA	5.97	23.59
RSF6	8.68	29.81	16.12	3.13	3.47	3.78	4.60	3.09
RSF7	3.18	**0.00**	21.60	91.69	31.87	NA	32.60	54.47
RSF8	7.49	29.13	39.19	90.08	27.99	76.49	30.20	50.45
RSF9	69.65	77.03	21.30	14.03	11.56	10.83	**0.00**	17.72
RSF0	68.41	75.25	46.14	104.46	41.13	89.14	29.20	68.20

Table A4: The most parsimonious models explaining brown bear habitat selection within the study area in south-central Sweden, in the 20-day periods with 10 days overlap (1-6), during the study period 11 July - 18 September. Model terms included in the most parsimonious model are displayed, with estimates on logit scale, standard error (SE), test statistics, and significance levels (P) for each model term. S symbolizes bears that survived the hunting season. Killed bears (K) are included in the intercept as reference level. All significant model terms (p < 0.05) are marked in bold.

Period	**Foraging positions**	**Model**	**Model terms**	**Estimate**	**SE**	**Test statistics**	**P**
1	1769	RSF1	Variance explained by random term (Bear ID)	<0.001	<0.001	NA	NA
			Intercept	-0.515	0.334	-1.54	0.12
			Bilberry (K)	0.031	0.017	1.85	0.06
			Risk (K)	0.182	1.187	0.15	0.88
			Bilberry*fate (S)	-0.042	0.018	-2.38	**0.02**
			Risk*fate (S)	-3.659	1.259	-2.91	**<0.01**
2	1439	RSF7	Variance explained by random term (Bear ID)	<0.001	<0.001	NA	NA
			Intercept	-0.538	0.218	-2.47	**0.01**
			Risk (K)	3.400	1.220	2.79	**<0.01**
			Risk*fate (S)	-7.351	1.310	-5.61	**<0.001**
3	1224	RSF4	Variance explained by random term (Bear ID)	<0.001	<0.001	NA	NA
			Intercept	-1.016	0.273	-3.73	**<0.001**
			Bilberry (K)	0.026	0.008	3.29	**<0.001**
			Lingonberry (K)	-0.029	0.009	-3.36	**<0.001**
			Risk (K)	3.644	1.245	2.93	**<0.01**
			Risk*fate (S)	-5.754	1.342	-4.29	**<0.001**
4	1164	RSF2	Variance explained by random term (Bear ID)	<0.001	<0.001	NA	NA
			Intercept	-0.707	0.209	-3.38	**<0.001**
			Bilberry	0.060	0.009	6.67	**<0.001**
			Lingonberry	-0.014	0.003	-4.61	**<0.001**
			Risk	-1.842	0.464	-3.97	**<0.001**
5	1259	RSF2	Variance explained by random term (Bear ID)	<0.001	<0.001	NA	NA
			Intercept	-0.457	0.148	-3.08	**<0.01**
			Bilberry	0.054	0.010	5.59	**<0.001**
			Lingonberry	-0.056	0.018	-3.14	**<0.01**
			Risk	-1.524	0.417	-3.66	**<0.001**
6	1319	RSF2	Variance explained by random term (Bear ID)	<0.001	<0.001	NA	NA
			Intercept	-0.715	0.175	-4.08	**<0.001**
			Bilberry	0.116	0.017	6.92	**<0.001**
			Lingonberry	-0.003	0.001	-4.12	**<0.001**
			Risk	-1.506	0.423	-3.56	**<0.001**

Table A5: Spearman rank coefficients (r_s) and significance values of correlation between area adjusted frequencies of brown bear occurrence in the study area in south-central Sweden and probability of selection bins in the 20-day periods with 10 days overlap (1-6) within the study period 11 July - 18 September. Correlation between area-adjusted frequency and probability bins have also been calculated for the entire study period. The correlation results are also presented when the lowest probability bin has been excluded from the analysis, which lead to improved model validation due to a few unexpected bear positions in the lowest probability class.

With 10 probability bins			**Excluding probability bin 1**	
Period	r_s	P	r_s	P
1	0.806	< 0.01	0.733	0.03
2	0.875	< 0.001	0.833	< 0.01
3	0.954	< 0.001	0.950	< 0.001
4	0.539	0.11	0.983	< 0.001
5	0.248	0.49	0.717	0.04
6	0.430	0.22	0.967	< 0.001
Entire study period	0.944	< 0.001	0.945	< 0.001

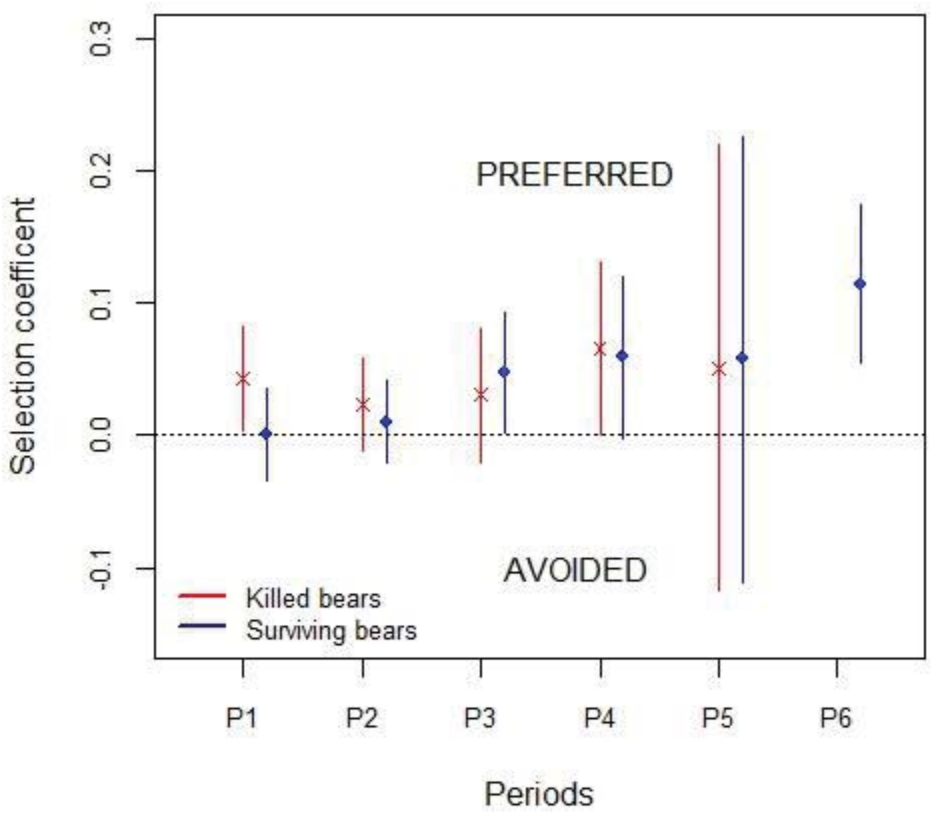

Figure A3: The selection coefficients for bilberry on a logit scale for killed and surviving brown bears in the 20-day periods with 10 days overlap (1-6) during the study period 11 July - 18 September. This is based on the full model representing the hypothesis that the bears' selection of berries varies between bears of different fate (whether the bears were killed or survived the hunting season). In period 6 bilberry selection is modeled for all bears, because no killed bears were still alive in period 6. The error bars indicate standard errors around each estimate.

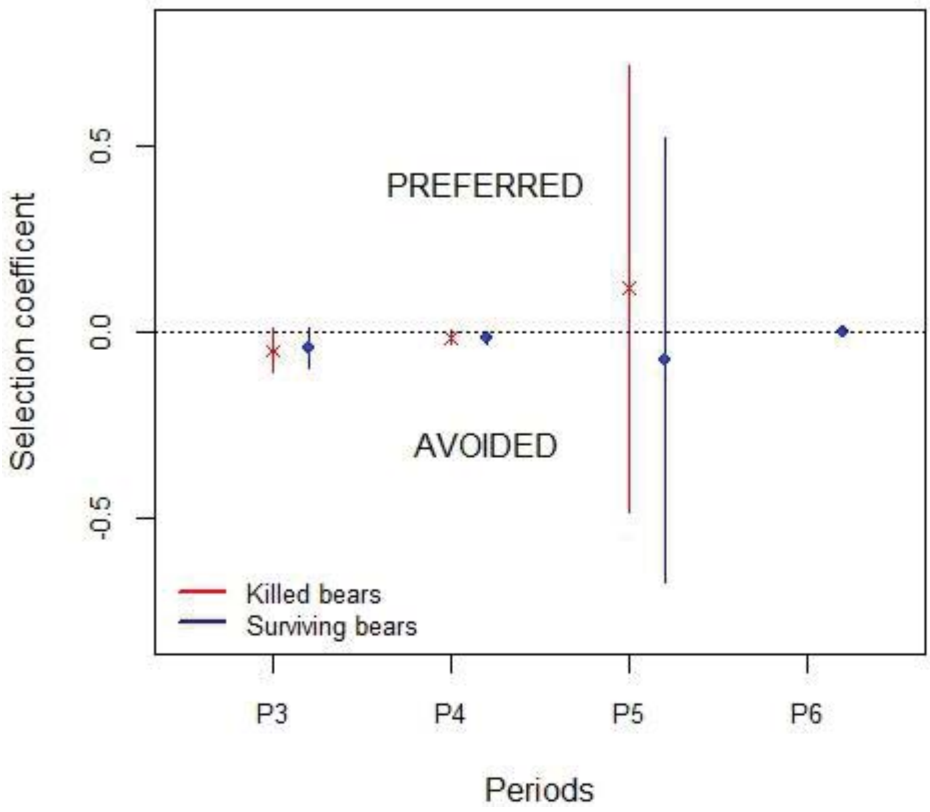

Figure A4: Selection coefficient on a logit scale for killed and surviving brown bears in relation to lingonberry availability in south-central Sweden across the last four 20-day periods with 10 days overlap (3-6) in the period when lingonberry are ripe during the study period 1 August - 18 September. This is based on the full model representing the hypothesis that the bears' selection of berries varies between bears of different fate (whether the bears were killed or survived the hunting season). The error bars indicate standard errors around each estimate.

Table A6: The most parsimonious model explaining brown bear habitat selection within the study area in south-central Sweden in the 10 days prior to the hunting season on 21 August (prehunting) and 10 first day of hunting (hunting season) after 21 August. Model terms included in each model are displayed, with estimates on logit scale, standard error (SE), test statistics, and significance levels (P), for each model. All significant model terms ($p < 0.05$) are marked in bold.

Period	**Foraging positions**	**Model**	**Model terms**	**Estimate**	**SE**	**Test statistic**	**P**
Pre-hunting	540	RSF9	Variance explained by random term (Bear ID)	0.000	0.000	NA	NA
			Intercept	-0.887	0.284	-3.12	**< 0.01**
			Bilberry	0.053	0.013	4.08	**< 0.001**
			Lingonberry	-0.010	0.004	-2.53	**0.01**
Hunting season	564	RSF2	Variance explained by random term (Bear ID)	0.000	0.000	NA	NA
			Intercept	-0.604	0.306	-1.97	**0.05**
			Bilberry	0.066	0.013	4.98	**< 0.001**
			Lingonberry	-0.019	0.005	-3.83	**< 0.001**
			Risk	-2.931	0.674	-4.35	**< 0.001**

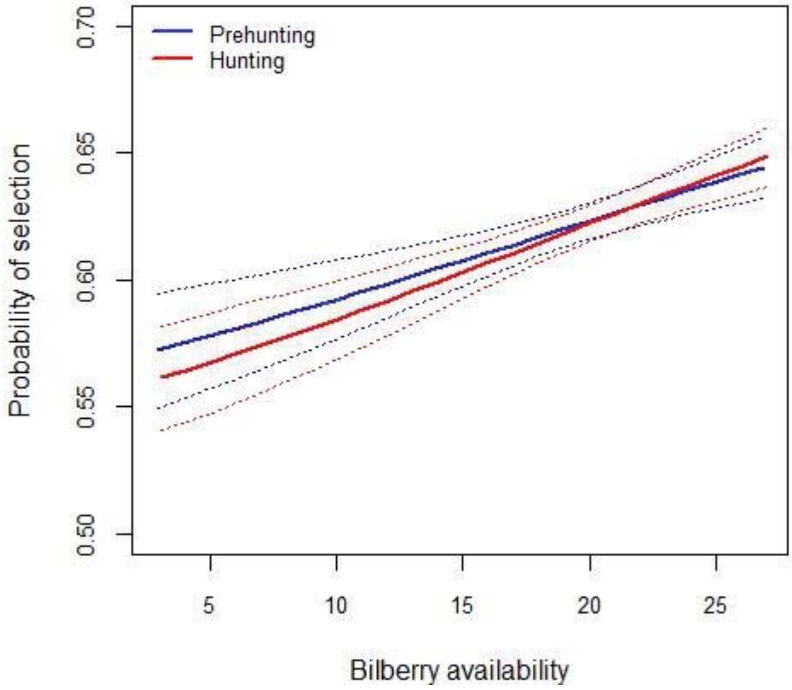

Figure A5: Effect of bilberry availability on brown bears' probability of selection in south-central Sweden 10 days before and 10 days during the hunting season that starts on 21 August. Probabilities have been converted from the logit scale and represent actual probabilities of selection. The dashed lines represent the 95% confidence intervals.

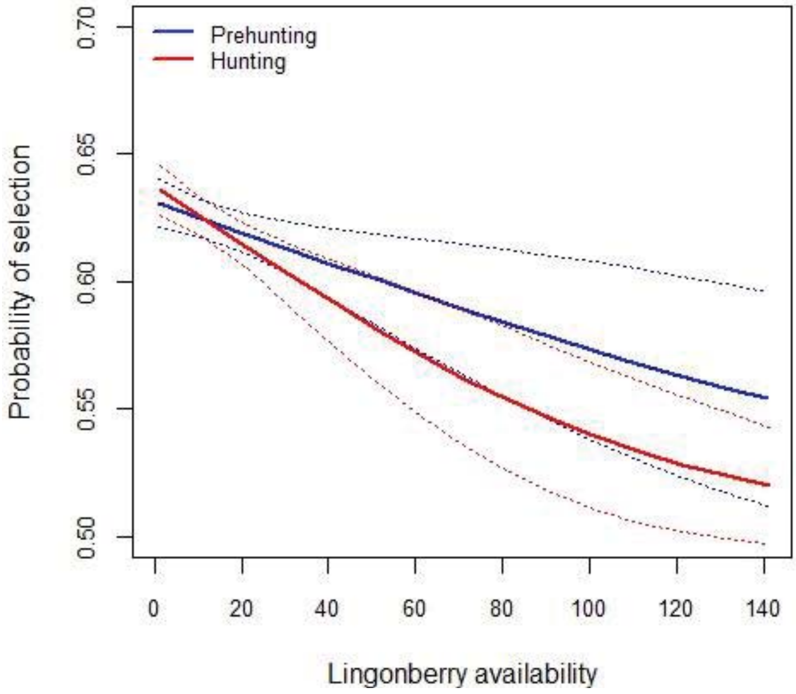

Figure A6: Effect of lingonberry availability on the probability of selection of brown bears in south-central Sweden 10 days before and 10 days during the hunting season that starts on 21 August. Probabilities have been converted from the logit scale and represent actual probabilities of selection. The dashed lines represent the 95% confidence intervals.

Table A7: Output of the most parsimonious models explaining brown bear habitat selection for males and females in the study area in south-central Sweden 11 July - 18 September, in the 20-day periods with 10 days overlap (1-6) during the study period 11 July – 18 September. Model terms with estimates on logit scale, standard error (SE), test statistics, and significance level (P). All significant model terms ($p < 0.05$) are marked in bold. M symbolizes males. Females (F) are included in the intercept as reference level.

Period	**Foraging positions**	**Model**	**Model terms**	**Est.**	**SE**	**Test st.**	**P**
1	1769	Bilberry*sex + risk*sex	Intercept	0.526	0.128	4.12	**< 0.001**
			Bilberry (F)	-0.004	0.006	-0.69	0.49
			Risk (F)	-2.888	0.428	-6.75	**< 0.001**
			Bilberry*sex (M)	-0.011	0.014	-0.79	0.43
			Risk*sex (M)	-1.196	1.084	-1.10	0.27
2	1439	Bilberry*sex + risk*sex	Intercept	0.434	0.141	3.08	**< 0.01**
			Bilberry (F)	0.004	0.006	0.66	0.51
			Risk (F)	-3.267	0.487	-6.71	**< 0.001**
			Bilberry*sex (M)	-0.011	0.013	-0.85	0.40
			Risk*sex (M)	1.524	1.079	1.41	0.16
3	1224	Bilberry*sex + lingonberry*sex + risk*sex	Intercept	-0.404	0.190	-2.13	**0.03**
			Bilberry (F)	0.035	0.009	3.96	**< 0.001**
			Lingonberry (F)	-0.029	0.010	-2.95	**< 0.01**
			Risk (F)	-1.099	0.514	-2.14	**0.03**
			Bilberry*sex (M)	-0.039	0.020	-1.97	**0.05**
			Lingonberry*sex (M)	-0.009	0.022	-0.42	0.68
			Risk*sex (M)	-0.690	1.097	-0.63	0.53
4	1164	Bilberry*sex + lingonberry*sex + risk*sex	Intercept	-0.842	0.232	-3.64	**< 0.001**
			Bilberry (F)	0.062	0.010	6.23	**< 0.001**
			Lingonberry (F)	-0.012	0.004	-3.48	0.00
			Risk (F)	-1.479	0.529	-2.80	**< 0.01**
			Bilberry*sex (M)	-0.011	0.024	-0.46	0.64
			Lingonberry*sex (M)	-0.009	0.008	-1.17	0.24
			Risk*sex (M)	-1.763	1.128	-1.56	0.12
5	1259	Bilberry*sex + lingonberry*sex + risk*sex	Intercept	-0.354	0.168	-2.10	**0.04**
			Bilberry (F)	0.049	0.011	4.54	**< 0.001**
			Lingonberry (F)	-0.045	0.020	-2.31	**0.02**
			Risk (F)	-1.984	0.493	-4.02	**< 0.001**
			Bilberry*sex (M)	0.032	0.025	1.26	0.21
			Lingonberry*sex (M)	-0.066	0.049	-1.33	0.18
			Risk*sex (M)	1.484	0.951	1.56	0.12
6	1319	Bilberry*sex + lingonberry*sex + risk*sex	Intercept	-0.556	0.206	-2.70	**< 0.01**
			Bilberry (F)	0.109	0.019	5.66	**< 0.001**
			Lingonberry (F)	-0.003	0.001	-3.87	**< 0.001**
			Risk (F)	-2.268	0.518	-4.37	**< 0.001**

			Bilberry*sex (M)	0.031	0.040	0.79	0.43
			Lingonberry*sex (M)	0.001	0.002	0.61	0.54
			Risk*sex (M)	2.238	0.912	2.45	**0.01**

Table A8: Output of the most parsimonious models exploring brown bear habitat selection for adults and subadults in the study area in south-central Sweden, in the 20-day periods with 10 days overlap (1-6), during the study period 11 July - 18 September. Model terms with estimates on logit scale, standard error (SE), test statistics, and significance level (P) are displayed. All significant model terms ($p < 0.05$) are marked in bold. S represents subadults. Adults (A) are included in the intercept estimate as the reference level.

Period	**Foraging positions**	**Model**	**Model terms**	**Est.**	**SE**	**Test st.**	**P**
1	1769	Bilberry*age class + risk*age class	Intercept (A)	0.575	0.146	3.94	< **0.001**
			Bilberry	-0.003	0.007	-0.38	0.70
			Risk	-3.399	0.481	-7.06	< **0.001**
			Bilberry*age class (S)	-0.011	0.012	-0.91	0.36
			Risk*age class (S)	1.024	0.836	1.23	0.22
2	1439	Bilberry*age class + risk*age class	Intercept (A)	0.475	0.160	2.97	< **0.01**
			Bilberry	0.001	0.007	0.19	0.85
			Risk	-3.251	0.535	-6.08	< **0.001**
			Bilberry*age class (S)	0.000	0.011	-0.01	0.99
			Risk*age class (S)	0.898	0.916	0.98	0.33
3	1224	Bilberry*age class + lingonberry *age class + risk*age class	Intercept (A)	-0.171	0.207	-0.83	0.41
			Bilberry	0.021	0.010	2.21	**0.03**
			Lingonberry	-0.024	0.009	-2.67	< **0.01**
			Risk	-0.907	0.533	-1.70	0.09
			Bilberry*age class (S)	0.019	0.017	1.12	0.26
			Lingonberry*age class (S)	-0.046	0.027	-1.70	0.09
			Risk*age class (S)	-1.412	1.036	-1.36	0.17
4	1164	Bilberry*age class + lingonberry *age class + risk*age class	Intercept (A)	-0.610	0.253	-2.41	**0.02**
			Bilberry	0.054	0.011	4.85	< **0.001**
			Lingonberry	-0.010	0.003	-2.97	< **0.01**
			Risk	-1.756	0.551	-3.18	< **0.01**
			Bilberry*age class (S)	0.020	0.020	1.04	0.30
			Lingonberry* age class (S)	-0.019	0.008	-2.41	**0.02**
			Risk*age class (S)	-0.630	1.053	-0.60	0.55
5	1259	Bilberry*age class + lingonberry *age class + risk*age class	Intercept (A)	-0.147	0.186	-0.79	0.43
			Bilberry	0.041	0.012	3.31	< **0.001**
			Lingonberry	-0.042	0.021	-1.98	0.05
			Risk	-2.160	0.500	-4.32	< **0.001**

			Bilberry*Age class (S)	0.040	0.020	1.94	0.05
			Lingonberry*Age class (S)	-0.050	0.041	-1.23	0.22
			Risk*Age class (S)	2.052	0.944	2.17	**0.03**
6	1319	Bilberry*age class + lingonberry *age class + risk*age class	Intercept (A)	-0.717	0.233	-3.07	**< 0.01**
			Bilberry	0.130	0.023	5.67	**< 0.001**
			Lingonberry	-0.003	0.001	-3.25	**< 0.01**
			Risk	-2.039	0.518	-3.94	**< 0.001**
			Bilberry*Age class (S)	-0.027	0.034	-0.79	0.43
			Lingonberry*Age class (S)	-0.001	0.002	-0.39	0.70
			Risk*Age class (S)	1.459	0.933	1.56	0.12

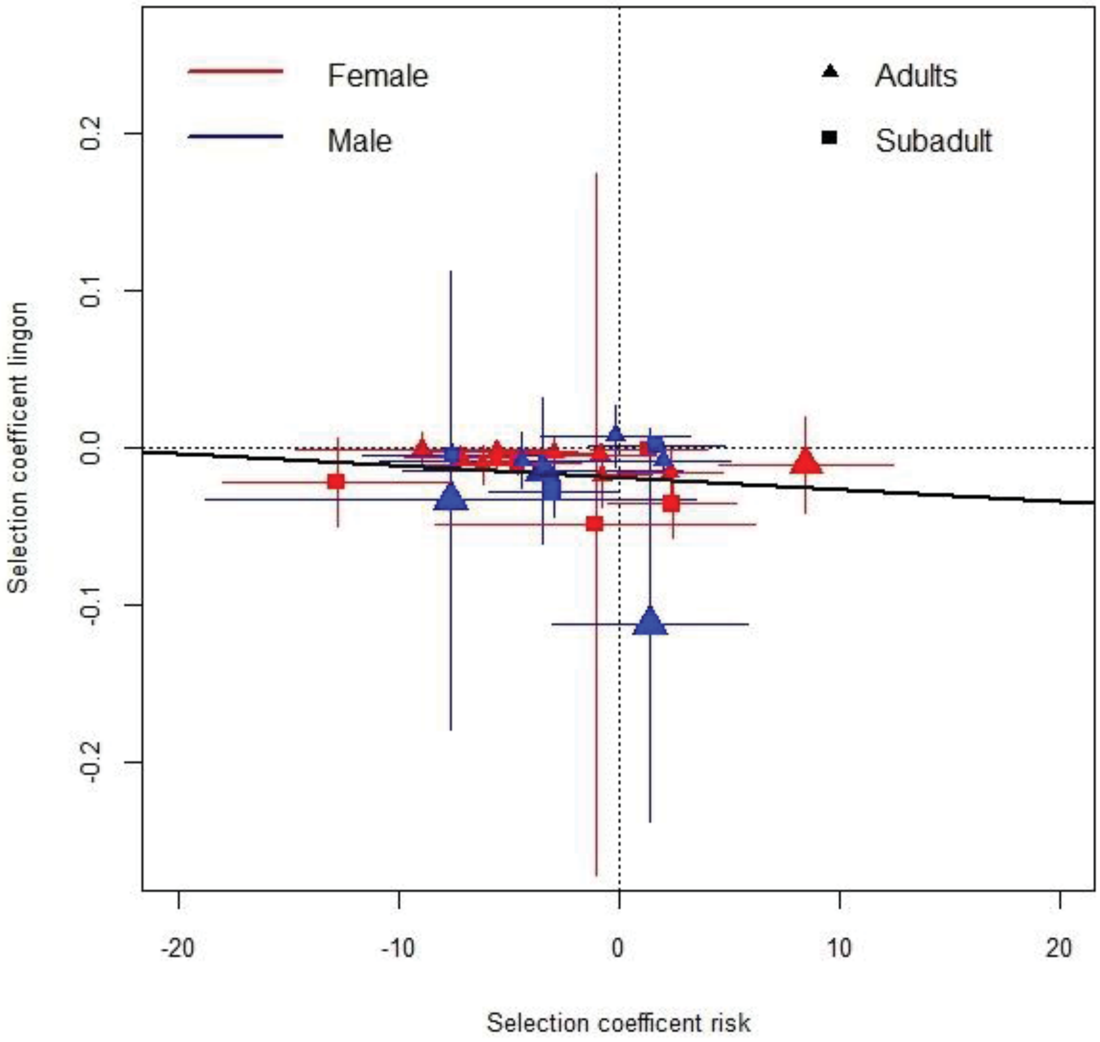

Figure A7: Selection coefficients of individual brown bears for risk and lingonberry availability in south-central Sweden across the study period, 11 July - 18 September. Selection coefficient is on the logit scale and the horizontal bars represent standard error around risk estimates and the vertical bars the standard error around the lingonberry estimates. The larger rectangles represent the bears that were killed during the hunting season. The black line represents a linear regression trend line for the relationship between selection for lingonberry availability and selection for risk, $r_s = -0.08$, $p = 0.73$ among the individual bears.

Table A9: Most parsimonious model for individual brown bears' selection for bilberry and risk across the study period 11 July - 18 September in south-central Sweden. Model terms, estimates on logit scale, standard error (SE), test statistics, and significance level (P) are displayed. All significant model terms ($p < 0.05$) are marked in bold.

Bear ID	Positions	Fate	Age class	Sex	Intercept	SE	Test st.	P	Bilberry	SD	Test st.	P	Risk	SE	Test st.	P
W0806	426	Killed	Adult	F	-2.208	0.390	-5.66	**< 0.001**	0.06	0.02	3.37	**< 0.001**	7.09	1.38	5.13	**< 0.001**
W1312	92	Killed	Adult	M	2.691	0.986	2.73	**< 0.01**	-0.10	0.04	-2.20	**0.03**	-10.93	4.81	-2.27	**0.02**
W0625	92	Killed	Adult	M	-1.425	0.863	-1.65	0.10	0.06	0.04	1.33	0.18	2.09	2.06	1.02	0.31
W0719	148	Killed	Adult	M	1.440	0.645	2.23	**0.03**	-0.04	0.03	-1.33	0.18	-4.88	2.01	-2.42	**0.02**
W1304	826	Alive	Sub	F	-0.145	0.238	-0.61	0.54	0.02	0.01	1.85	0.06	-1.76	1.23	-1.43	0.15
W1305	608	Alive	Sub	F	-0.373	0.282	-1.32	0.19	0.04	0.01	2.54	**0.01**	-0.94	1.21	-0.78	0.44
W0825	334	Alive	Adult	F	0.848	0.379	2.24	**0.03**	-0.01	0.02	-0.35	0.73	-5.28	1.55	-3.40	**< 0.001**
W9403	712	Alive	Adult	F	-0.195	0.261	-0.75	0.45	0.01	0.01	0.49	0.63	0.66	1.02	0.65	0.52
W1209	288	Alive	Sub	F	-0.026	0.402	-0.06	0.95	-0.01	0.02	-0.35	0.73	0.59	1.19	0.50	0.62
W0425	642	Alive	Adult	F	0.251	0.255	0.98	0.33	0.00	0.01	-0.15	0.89	-1.61	1.01	-1.60	0.11
W1416	58	Alive	Adult	M	1.053	0.888	1.19	0.24	-0.02	0.05	-0.40	0.69	-4.85	2.81	-1.73	0.08
W1408	286	Alive	Sub	F	1.822	0.506	3.60	**< 0.001**	-0.06	0.02	-2.70	**< 0.01**	-3.63	1.36	-2.67	**< 0.01**
W1105	402	Alive	Sub	F	-0.018	0.363	-0.05	0.96	0.09	0.02	4.27	**< 0.001**	-13.47	2.30	-5.85	0.00
W0720	734	Alive	Adult	F	0.960	0.253	3.79	**< 0.001**	0.00	0.01	0.08	0.94	-6.61	1.00	-6.61	**< 0.001**
W1314	96	Alive	Adult	M	-0.454	0.582	-0.78	0.44	0.05	0.04	1.33	0.18	-0.69	1.71	-0.41	0.68
W0610	684	Alive	Adult	F	-0.300	0.224	-1.34	0.18	0.02	0.01	2.33	**0.02**	-0.84	0.95	-0.89	0.38
W0605	404	Alive	Adult	F	0.591	0.368	1.61	0.11	0.04	0.02	1.83	0.07	-6.44	1.16	-5.55	**< 0.001**
W1317	316	Alive	Sub	M	0.044	0.319	0.14	0.89	0.00	0.02	0.15	0.88	-0.67	1.31	-0.51	0.61
W1319	148	Alive	Adult	F	1.143	0.582	1.97	**0.05**	-0.02	0.03	-0.65	0.51	-8.08	2.78	-2.91	**< 0.01**
W0716	370	Alive	Adult	F	1.321	0.385	3.43	**< 0.001**	-0.02	0.02	-1.06	0.29	-6.77	1.06	-6.37	**< 0.001**
W1211	222	Alive	Adult	M	-0.307	0.574	-0.54	0.59	0.01	0.02	0.51	0.61	0.49	1.43	0.34	0.73
W1316	348	Alive	Sub	M	0.362	0.324	1.12	0.26	0.04	0.02	2.34	**0.02**	-8.09	1.84	-4.40	**< 0.001**
W1307	576	Alive	Sub	M	0.004	0.288	0.01	0.99	0.01	0.01	0.67	0.51	-0.89	1.22	-0.73	0.47
W0620	586	Alive	Adult	F	0.318	0.292	1.09	0.28	0.04	0.02	-1.64	0.10	-2.75	0.89	-0.65	0.51

Table A10: Most parsimonious model for individual brown bears' selection for lingonberry and risk across the study period from 11 July 18 September in south-central Sweden. Model terms, estimates on logit scale, standard error (SE), test statistics, and significance level (P) values. All significant model terms ($p < 0.05$) are marked in bold.

Bear ID	Positions	Fate	Age class	Sex	Intercept	SE	Test st.	P	Lingon	SD	Test st.	P	Risk	SE	Test st.	P
W0806	426	Killed	Adult	F	-1.421	0.384	-3.70	**< 0.001**	-0.01	0.02	-0.65	0.52	8.49	2.01	4.22	0.00
W1312	92	Killed	Adult	M	0.926	0.736	1.26	0.21	-0.03	0.07	-0.44	0.66	-7.64	5.68	-1.35	0.18
W0625	92	Killed	Adult	M	0.251	0.556	0.45	0.65	-0.11	0.06	-1.76	0.08	1.41	2.26	0.63	0.53
W0719	148	Killed	Adult	M	0.651	0.600	1.08	0.28	-0.01	0.02	-0.61	0.54	-3.47	3.23	-1.07	0.28
W1304	826	Alive	Sub	F	0.614	0.187	3.29	**< 0.01**	-0.01	0.00	-2.10	**0.04**	-4.58	1.48	-3.09	**< 0.01**
W1305	608	Alive	Sub	F	-0.045	0.268	-0.17	0.87	-0.04	0.01	-3.28	**< 0.01**	2.43	1.49	1.63	0.10
W0825	334	Alive	Adult	F	0.864	0.309	2.79	**< 0.01**	0.00	0.00	-0.73	0.47	-5.54	1.86	-2.98	**< 0.01**
W9403	712	Alive	Adult	F	-0.205	0.232	-0.88	0.38	-0.02	0.01	-2.14	**0.03**	2.34	1.22	1.92	0.06
W1209	288	Alive	Sub	F	-0.298	0.358	-0.83	0.41	0.00	0.00	-0.33	0.74	1.38	1.37	1.01	0.32
W0425	642	Alive	Adult	F	0.825	0.215	3.85	**< 0.001**	-0.01	0.00	-2.17	**0.03**	-5.57	1.49	-3.73	**< 0.001**
W1416	58	Alive	Adult	M	0.892	0.708	1.26	0.21	-0.01	0.01	-0.81	0.42	-4.37	3.30	-1.33	0.19
W1408	286	Alive	Sub	F	0.335	0.969	0.35	0.73	-0.05	0.11	-0.43	0.67	-1.06	3.70	-0.29	0.78
W1105	402	Alive	Sub	F	1.464	0.321	4.57	**< 0.001**	-0.02	0.01	-1.50	0.13	-12.77	2.64	-4.84	**< 0.001**
W0720	734	Alive	Adult	F	1.127	0.207	5.45	**< 0.001**	-0.01	0.00	-2.25	**0.02**	-7.18	1.29	-5.57	**< 0.001**
W1314	96	Alive	Adult	M	-0.130	0.473	-0.28	0.78	0.01	0.01	0.78	0.43	-0.16	1.74	-0.09	0.93
W0610	684	Alive	Adult	F	0.177	0.181	0.98	0.33	0.00	0.00	-1.60	0.11	-0.83	1.20	-0.70	0.49
W0605	404	Alive	Adult	F	1.213	0.267	4.54	**< 0.001**	-0.01	0.01	-1.65	0.10	-6.19	1.32	-4.68	**< 0.001**
W1317	316	Alive	Sub	M	-0.254	0.264	-0.96	0.34	0.00	0.00	0.48	0.63	1.69	1.57	1.07	0.28
W1319	148	Alive	Adult	F	0.957	0.364	2.63	**< 0.01**	0.00	0.01	-0.09	0.93	-8.94	2.94	-3.04	**< 0.01**
W0716	370	Alive	Adult	F	0.582	0.274	2.12	**0.03**	0.00	0.01	-0.55	0.58	-2.90	1.20	-2.42	**0.02**
W1211	222	Alive	Adult	M	-0.430	0.477	-0.90	0.37	-0.01	0.01	-1.34	0.18	2.00	1.58	1.27	0.20
W1316	348	Alive	Sub	M	0.969	0.283	3.43	**< 0.001**	0.00	0.00	-1.20	0.23	-7.52	2.08	-3.61	**< 0.001**
W1307	576	Alive	Sub	M	0.804	0.270	2.98	**< 0.01**	-0.03	0.01	-3.23	**< 0.01**	-2.97	1.49	-1.99	**0.05**
W0620	586	Alive	Adult	F	0.318	0.292	1.09	0.28	-0.02	0.01	-1.64	0.10	-0.75	1.14	-0.65	0.51

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