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Risky Berry Business?
Brown Bear (*Ursus arctos*) Foraging Behaviour in a Landscape of Fear.

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Acknowledgements

"Kia kaha" – "Stand strong" (Maori saying)

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Summary

Mobile animals are expected to optimize their diet and foraging strategies, and balance the cost of resource gain with the perceived predation risk, and therefore trade-off risky areas for safer areas with fewer resources. Large carnivores have few natural enemies and their mortality, forage behaviour, and response to risk are mostly related to human induced disturbances. Scandinavian brown bears feed exclusively on berries during late summer and autumn to gain sufficient carbohydrates to survive hibernation. The purpose of this thesis was to predict spatiotemporal berry availability and whether berry availability created a temporal "blue/red wave" across the berry season. I analysed how bear selection for berries was influenced by various anthropogenic structures and whether bears treaded-off good berry areas for poor berry areas further away from anthropogenic structures. Both bilberries and lingonberries were included in the analysis.

Spatiotemporal berry availability was evaluated through a threefold process of modelling berry presence, berry availability and calculating the relative berry availability index. The berry season was divided into 6 periods and models were ranked using Akaike's information criteria (AIC), cut-off at $\Delta AIC_c < 2$. Berry presence and availability were multiplied and translated into berry index maps in ArcMap. Bear resource selection was assessed with Resource Selection Functions (RSF), with a 1:1 ratio between the number of bear foraging positions and random positions and RSF models were ranked by AIC. Interaction terms between anthropogenic variables and berry variables were included.

The results indicated a temporal "blue/red wave" of bilberry availability, and bears selected for bilberries, but not for lingonberries. While bears overall avoided areas close to large roads, buildings and open water, bears selected forest roads in the beginning of the berry season and avoided forest roads for the remainder. As bears selected bilberries at its peak abundance, bears therefore likely "chased the blue wave". Bears did not "chase the red wave". Bears generally selected for residential areas throughout the berry season and for forest roads in the beginning of the season, but avoided forest roads for the remainder. Bears possibly traded-off good bilberry areas close to forest roads for poor bilberry areas further away. Bears generally selected areas close to residential areas, but did not trade-off good berry areas for poor areas further away from residential areas.

Habitat type such as old and mature forests were important for bilberry availability, and bilberries are more likely to occur in environments associated with higher NDVI values.

Bilberries were also predicted to occur on clear-cuts, but this is most likely related to a delayed temporal response (i.e. time lag). Lingonberries occurred in areas with low NDVI, probably related to the need for dry and more sun exposed areas. Bear selection for forest roads in the beginning of the berry season could be related to highly available herbaceous feed, the lack of mature bilberries, or that bears used forest roads during the mating season. Human activity along forest roads increases during the hunting season, and bears avoided forest roads during that period to avoid people. Bears become more nocturnal during the hunting season and likely foraged along forest roads at night, and possibly traded-off highly bilberry and lingonberry rich areas for poor areas further away from forest roads. Bears overall selected residential areas, probably related to predictable human activity patterns. As bears did not trade-off good bilberry areas for poor areas further away from residential areas, also not during the hunting season, bears could have avoided humans by temporally adapting to human activity patterns and using bilberry rich areas close to residential areas at low-human activity hours.

As bears avoided most anthropogenic structures, these structures had an overall negative impact on bear foraging behaviour. This became clearer when the hunting season started, and a possible the trade-off mechanism was experienced in relation to forest roads. Berries are an important resource for bears, and any increase or decrease in berry availability could therefor influence bear foraging behaviour. Potential drivers of berry availability alterations could be climatic or forest structural changes, as well as commercial berry picking. Further research should focus on how forest structure alteration and berry picking might reduce the overall berry availability, and how anthropogenic influence such as the hunting season effect optimal bear foraging on berries.

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Introduction

The abundance and density of food for any given species varies in time and space. Individuals of mobile species have to choose where and when to forage to acquire sufficient energy to maintain their physical functions and to facilitate growth and reproduction (Krebs 2009). Although animals are expected to optimize their diet and foraging strategies, animals also balance the cost of resource gain in relation to the perceived predation risk (i.e. optimal foraging theory, OFT) (Charnov 1976; Smith & Smith 2001) or a "landscape of fear" (Laundré et al. 2001). Individuals therefore have to trade between the resources needed to maintain physical functions and keeping safe (Krebs 2009). Consequently, animals often trade-off more risky areas with greater resource benefits for safer foraging areas with less resource and energy gain (Brown & Kotler 2004). Eating efficiency, risk analysis, and forage quality and availability are therefore important elements of an animal`s foraging strategy. Examples of trade-offs between predation risk and foraging are plentiful throughout the animal kingdom, including insects such as Colorado potato beetles (*Leptinotarsa decemlineata*) that reduce their foraging activity in the presence of the predatory spined soldier bug (*Podisus maculiventris*) or the scent of the bug (Hermann & Thaler 2014). Gerbil owls` (*Gerbillus allenbyi* and *Gerbillus pyramidum*) foraging behaviour also changes in response to increased predation risk, as they select denser areas with less resources instead of open areas associated with more resources and higher predation risk (Kotler et al. 1991). The introduction of wolves (*Canis lupus*) in Yellowstone National Park have altered movement patterns of elk (*Cervus canadensis*), and increased predation risk by wolves has reduced elk foraging on aspen (*Populus tremuloides*) (Laundré et al. 2001), initiating trophic cascades throughout the ecosystem (Estes 1996; Ripple et al. 2001).

Large carnivores have few natural enemies, and their mortality, forage behaviour, and response to risk is mostly related to human disturbances (Elfström et al. 2014b; Klar et al. 2008; Nevin & Gilbert 2005; Nielsen et al. 2004). For example, European wildcats (*Felis silvestris*) select for habitat at least 200m away from both roads and single standing houses, and 900m away from towns, suggesting that anthropogenic structures influence wildcat spatial behaviour (Klar et al. 2008). Grey wolves in Canada spatially and temporally trade-off areas with great resource availability if human disturbance risk is high, for areas with less resources (Hebblewhite & Merrill 2008). While wolves generally avoid human presence (Hebblewhite & Merrill 2008), grizzly bears (*Ursus arctos ssp.*) sometimes select for human related areas such as roads, forest

edges, clear-cuts associated with high vegetative forage availability (Ciarniello et al. 2007; Frank et al. 2015; Roever et al. 2008a; Roever et al. 2008b), and settlements with food attractants (Elfström et al. 2014b; Swenson 1999). However, the sex and age structure of bears is important in terms of bear selection for habitat in proximity to anthropogenic structures, as adult grizzly males generally are less likely to forage in close proximity to humans than females with cubs (Nevin & Gilbert 2005; Steyaert et al. 2013). Anthropogenic structures can even have a positive fitness effect in female brown bears (*Ursus arctos*), as females with cubs of the year that select for areas close to humans and roads experience less infanticide than females avoiding human related structures (Steyaert et al. in revision-a). Although forest roads are essential for efficient forest harvesting (Gumus 2009), a high road density also facilitates both legal and illegal bear hunting and stimulates general human use of the forest (McLellan 1989). Human caused mortality facilitated by such roads is the leading grizzly bear mortality cause in Canada (Nielsen et al. 2004) and Scandinavia (Bischof et al. 2009; Steyaert et al. in revision-b).

Human population growth and natural resource exploitation in Europe have led to significant deforestation and habitat fragmentation (Kaplan et al. 2009). Consequently, species that used to occupy various ecosystems throughout most European countries, such as brown bears (Nilsen 2002; Zedrosser et al. 2001), are currently restricted to a fraction of their former range. Brown bears have low reproductive rates and therefore vulnerable to extensive harvesting (Steyaert et al. 2012; Zedrosser et al. 2001). State-financed and supported hunting operations during the 1800s reduced the brown bear population to near extinction in Scandinavia (Swenson et al. 2011). The brown bear was considered functionally extinct throughout most of Scandinavia during the early and mid-1900s (Swenson et al. 1995). Following hunting bans and conservation initiatives, the brown bear population gradually increased in both size and range (Swenson et al. 1995) in forested areas with low human influence (Martin 2009). The Scandinavian bear population was considered one of the World's most productive brown bear populations (Zedrosser et al. 2001), and currently contains approximately 3300 individuals (Kindberg et al. 2011). Bears are currently managed through harvesting quotas in Sweden and the quotas have drastically increased from 55 individuals in 1999, to 233 in 2008 (Kindberg et al. 2011), and to 306 in 2013 (www.sva.se), as a response to brown bear population growth and increased demand for bear hunting (Kindberg et al. 2011). The quota was however reduced to 225 individuals in 2015 (www.sva.se). As a consequence of bear hunting, Scandinavian bears have altered their

behaviour and are considered less aggressive and more wary about humans than grizzly bears (Swenson 1999).

Brown bears are omnivores and scat analyses suggest that the Scandinavian brown bear diet generally consists of ungulates (reindeer *Rangifer tarandus* and moose *Alces alces*), ants (*Formica* and *Camponotus)*, forbs (blue sow thistle *Cicerbita alpine*) and berries (bilberries *Vaccinium myrtillus*, lingonberries *V. vitis-idaea,* crowberries *Empetrum* spp. and raspberries *Rubus idaeus*) (Dahle et al. 1998; Elfström et al. 2014a). Ungulates and insects provide protein and lipids, and are important during spring to regain muscle mass after hibernation (Bojarska & Selva 2012), whereas the summer diet contains more forbs and insects. Berries dominate the autumn diet (Dahle et al. 1998; Persson et al. 2001). Bears loose little protein during hibernation compared to fat (Barboza et al. 1997), and the low-protein diet during summer and autumn is the most efficient way to gain sufficient carbohydrates (stored as fat) to survive the long hibernation (November-April) (Bojarska & Selva 2012; Felicetti et al. 2003). Bears increase their bodyweight by 30-35% during hyperphagia (excessive overeating prior to hibernation) (Hissa et al. 1998) and bears ability to forage excessively on berries during the berry season from mid-July to late October provides vital carbohydrates (Nilsen 2002; Swenson et al. 2000). Berries are the most important source of carbohydrates during hyperphagia and provide 44-46% of the annual bear energy intake (Dahle et al. 1998). The intake of berries increases rapidly with increased berry density (Welch et al. 1997), and bears are therefore expected to forage in areas with high berry abundance (Nilsen 2002).

As climate change is expected to alter berry distribution and availability (Gwynn-Jones et al. 1997; Phoenix et al. 2001), this might influence the phenology or "the timing of seasonal activities of animals and plants" (Walter et al. 2002, p. 389) and consequently influence brown bear foraging on berries. Little research has been conducted on bear-berry interactions. Management decisions, however, often rely on resource- and population estimates at a local scale (Nielsen et al. 2002). The objective of my thesis was to map berry availability in space and time, and to provide knowledge about how berry availability influences bear foraging behaviour in relation to anthropogenic structures.

The overall aim of this study was to 1) predict spatiotemporal availability of bilberries and lingonberries, 2) to analyse how bears select for these resources, and 3) evaluate how selection for berries is influenced by anthropogenic structures such as main roads, forest roads, residential

areas and buildings. Because berry phenology depends on site characteristics such as canopy cover, soil type, forest type, and elevation (Gustavsson 2001; Nybakken et al. 2013; Parlane et al. 2006), berry abundance varies not only in space, but also in time. Therefore, I hypothesize that H1) bilberries and lingonberries mature over time and create a temporal 'blue/red wave' of berry availability across the landscape and that H2) bears select for areas with high berry abundance: "chasing the blue/red wave". Additionally, I hypothesize that H3) anthropogenic structures such as main roads, forest roads, residential areas, buildings and areas in close proximity to open water have a negative impact on bear foraging. This could H4) force bears to trade-off good berry areas for areas further away from anthropogenic structures but with less berry availability. Overall, this thesis could increase our understanding of how bears adapt to a human dominated landscape and the potential impacts human presence have on bear habitat selection and foraging behaviour.

Materials and methods

Study area

The study was conducted in Dalarna and Gävleborg counties (61° N, 18° E) in south-central Sweden, within the southern boreal vegetation zone. The study area cover approximately 13000 km^2, with clear-cutting as the dominating forestry practice (Bischof et al. 2008; Steyaert et al. 2012). Rivers, small hills, lakes, bogs (Bellemain et al. 2005), and some agricultural fields are scattered throughout the study area (Bischof et al. 2008). The area is dominated by commercial Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) (Zedrosser et al. 2013). The elevation ranges from 200 masl in the south to 750 masl in the northwest (Bellemain et al. 2005). Permanent human resident density is low (Ordiz et al. 2012), but increases during the summer and hunting season (Nellemann et al. 2007). There are few high-traffic roads (0.14 km/km^2) within the study area, while low-traffic gravel roads (0.7 km/km^2) are very densely distributed (Martin et al. 2010; Ordiz et al. 2011). Cabins are found throughout the area, whereas permanent residents are associated with villages (> 200 inhabitants) north and south of the study area and several settlements (< 200 inhabitants) scattered throughout the area. The 2001 bear population was estimated to 286 (range: 251-337) and 264 (range: 232-311) individuals in Dalarna and Gävleborg counties, respectively (Zedrosser et al. 2013), with a general bear density of about 30 bears per 1000 km^2 (Bellemain et al. 2005; Solberg et al. 2006).
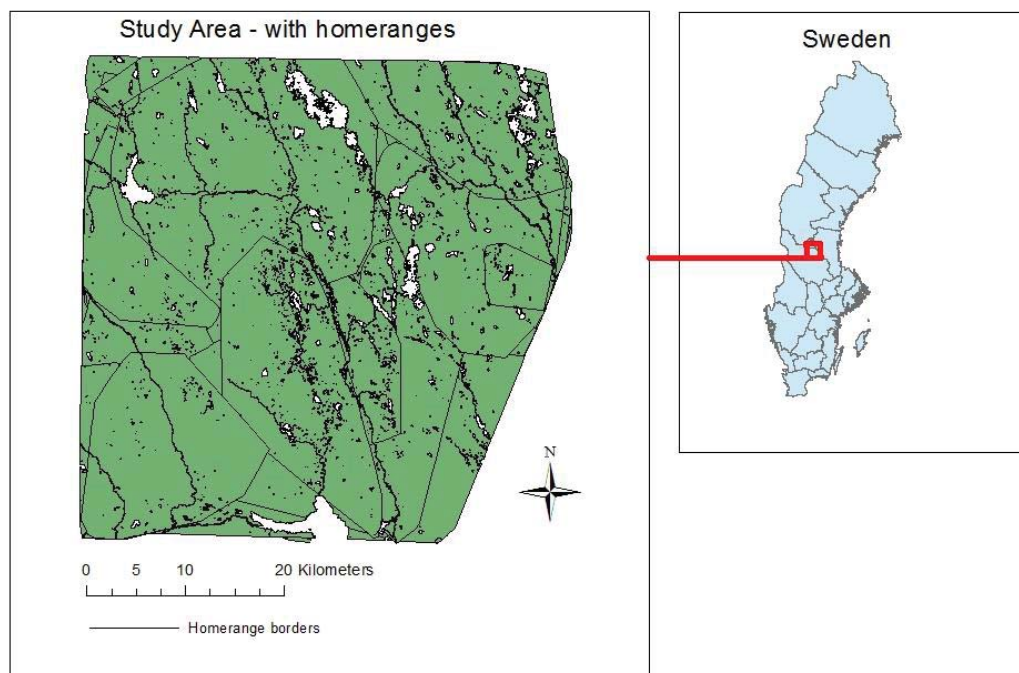
Figure 1: Map of study area in south-central Sweden. Homeranges (black lines) for bears used during the 2014 berry season (11 July – 18 September), and white areas represent open water.

Berry data

Data collection

To document berry availability in the study area, berries were sampled at random sites. Therefore, I defined three sub-study areas that were representative for the entire study area, and distributed 5000 random locations throughout these three areas. With a team of students and volunteers, I attempted to visit as many random plots as possible throughout the study period (11 July – 18 October 2014), and conducted berry inventories at these plots. The fieldwork consisted of collecting two different berries: bilberry and lingonberry. The berry season starts when bilberries first begin to ripe and become available, and the end of the berry season is defined as the first week of frost, as berries fall to the ground and become unavailable for bears. The random sites were located by the use of GPS with a 10m accuracy (Moe et al. 2007). To account for the randomness, 0-9 steps were taken in a random direction (N,S,E,W), depending on the last number of the Y- and X coordinates, respectively. At the berry plot, a 1m^2 square was placed and all bilberries and lingonberries within the square where collected and counted, as well as measuring the berry shrub height and cover.

Spatiotemporal berry predictions

For each berry plot, I derived a set of spatial variables of potential importance for determining berry availability in a Geographic Information System (GIS) named ArcMap. The set of covariates was based on expert knowledge (Nybakken 2014, pers.comm.) as well as literature (Gustavsson 2001; Ihalainen et al. 2002; Ihalainen et al. 2003; Nybakken et al. 2013; Parlane et al. 2006; Raatikainen et al. 1984; Selås 2000). The spatial variables considered for the berry availability models were NDVI, habitat type, elevation, slope and aspect. NDVI (normalized difference vegetation index) is expected to be essential for berry availability, as lingonberry is associated with high sun exposure and bilberry with moderate sun exposure (Gustavsson 2001; Ihalainen et al. 2003; Parlane et al. 2006). Bilberries are shade tolerant and associated with mature conifer forests (Ihalainen et al. 2002), and I expect bilberry availability to be high in both mature and old forests. In contrast, lingonberries need more dry and open habitats (Gustavsson 2001), and lingonberry availability is therefore expected to be associated with clear-cuts. Plants mature at different elevational gradients in time, suggesting that the altitude might be important in terms of early or late ripening of berries (Cox et al. 1993), and elevation was therefore included as a predictive variable of lingonberry and bilberry availability. Southern facing slopes are often associated with more species diversity as such slopes are more exposed to sun and have a higher temperature (Kubin et al. 2007; Walker et al. 1991). I expect berries to mature across the study area, but argue that berries on southern facing slopes might be the first berries to ripen due to more sun exposure and expected higher temperature earlier in the season. Both aspect and slope steepness were therefore considered as predictive variables for lingonberry and bilberry availability.

NDVI is a measure of near-infrared radiation and visible radiation, equivalent to the density of plant growth/'greenness'(Carlson & Ripley 1997) and was calculated based on satellite imagery captured in July 2014 (www.lantmateriet.se, pixel size 20*20m). There are six different habitat types: bog, tree rich bog, clear-cut, young forest, midaged forest and old forest. The habitat types are a combination of digital topographical data maps (Swedish Land Cover database, SMD-data) and a supervised classification of 2014 Resourcesat satellite imagery (IRSP-LISS3 Imagery, images obtained in July and August 2014, resolution = 25*25). Aspect (Cardinal direction) (factor: north, south, east and west), elevation (m) and slope (%) are derived

from a 2*2 m digital elevation model (DEM) (www.lantmateriet.se). Sam Steyaert and Anne Hertel conducted the pre-processing of the habitat layers.

The berry data collected in the field was analysed in R (R core Team, 2014, R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/) and exported to ArcMap (ESRI 2011, ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute) for both extracting satellite-derived habitat information from each berry plot and for developing graphics. Random berry plots that were located in unsuitable berry habitat, such as habitat category 'other', 'agricultural fields', 'urban areas' and 'water' were excluded from further analyses.

I hypothesized that berries mature over time and create a nonlinear "blue/red wave" of berry availability across the berry season, and I verified this with a generalized additive model (GAM). I used "collection day" (calendar day from 11 July 2014 onwards) as smoothing spline and the berry count as response variable. The GAM with the spline and the null-model GAM were ranked using the corrected Akaike's information criterion (AIC_c) (see below 'Model selection framework'), and the result indicated a significant nonlinearity with the GAMs with a spline. Due to a clear nonlinear trend ($\beta \pm SE$; 9.63$\pm$0.68 and edf=2.69 for bilberry, and 8.73$\pm$1.44 and edf=3.87 for lingonberry), I chose to divide the study period into six overlapping sub-periods to incorporate the temporal trend using generalized linear models (GLMs). After testing different overlapping periods, I settled on 20-day periods with a 10-days overlap, or "moving window" to incorporate the temporal change in berry abundance. The time-periods with Julian days are as followed; P1: 1-22, P2: 12-32, P3:22-42, P4: 32-52, P5:42-62 and P6: 52-70. Although the first Julian Day Number normally is associated with 1 January, Julian day 1 in my thesis is henceforth defined as the first day of the study (11 July 2014).

I used GLMs to make spatial predictions of lingonberry and bilberry abundance for each time period. First, I tested for collinearity between the potential explanatory variables, i.e., different habitat types, slope, aspect, NDVI, elevation and berry availability. I used variance information factors (VIF) and collinearity matrixes from Zuur et al. (2009) to assess collinearity between numeric variables to identify which variables to exclude from the models. VIF values >3 and collinear matrix values >0.6 indicate collinearity (Zuur et al. 2009). Boxplots were used to test collinearity between the berry availability and the categorical variables. As no collinearity

was found between habitat variables and berry availability, all variables were included in the candidate models (see Table 1).

Since the berry data is count data, I first ran a set of models using a Poisson distribution. The models were highly overdispersed, which suggests that the variance was larger than the mean (Zuur et al. 2009). Therefore, a three step approach to model berry availability was implemented to account for the overdispertion and the relatively high number of zeros (i.e., no berries found in a monitored plot) in the data. The first step consisted of using logistic regression to estimate the probability of berry occurrence at each berry plot (from here on referred to as berry presence). In step two, negative binomial generalized linear models were used to estimate the number of berries on locations with positive occurrence of berries (from here on referred to as berry counts) (see Zuur et al. 2009 for negative binomial GLMs). After running both presence and count models, the parameter estimates of the explanatory variables that were retained in the most parsimonious model (see below 'Model selection framework') from each time period were plotted into ArcMap, and into a period specific occurrence and abundance map, separately for each berry species. In step three, the respective presence and count maps from the same period and berry species were multiplied to generate a relative spatiotemporal berry index layer. As the berry index considers both the presence of berries and the number of berries at a location with berries, the berry index is a representative measure of berry availability at any particular site and time across the berry season. Because lingonberries mature later than bilberries (Eriksson & Ehrlén 1991), lingonberries were only modelled for the last 4 periods.

Model selection framework

Akaike's information criterion (AIC) is widely used to identify the model that explains the most variation with the least variables, among a set of candidate models (Burnham & Anderson 2002). However, Hurvich and Tsai (1989) argue that AIC might cause overfitting problems with small sample sizes, and promote the use of the corrected AIC; AIC_c, as model selection with AIC_c had the best performance. All covariates and candidate models in my study follow ecological principles and literature, and ΔAIC_c was used as a tool to rank the candidate models. All models scoring $\Delta AIC_c < 2$ were considered informative (Arnold 2010). If more than one model turned out informative, model averaging was implemented. Model averaging is commonly used in studies that aim to make predictions, were uninformative covariates are minimized while the

precision of the most informative covariates is maintained (Arnold 2010; Burnham & Anderson 2002). If more than one model were informative and the null model was one of the models with $\Delta AIC_c < 2$, then all models excluding the null model were averaged. If only one model remained after excluding the null model, this model was considered the most informative for the respective period. I did not consider it useful to include the null model in any predictions. The candidate models are listed in Table 1, and were used for both berry species, as well as modelling both berry presence and count. Overdispersion was evaluated by dividing the residual deviance with the degrees of freedom and ratios close to 1 were considered non-overdispersed (Zuur et al. 2009). If >1 model were informative in a period, dispersion parameters for each model was calculated and the sum of the dispersion parameters averaged. Model validation of the spatiotemporal berry predictions was conducted using the *cv.binary* function (DAAG package) to assess the predictive accuracy of the models, where models with an estimate of accuracy >0.8 were considered good, whereas models were considered bad if the predictive accuracy was < 0.5 (Maindonald & Braun 2010). The dispersion parameters were used as a measure of model fit for the berry count models (Steyaert 2015, pers.comm.).

Table 1: List of candidate models for both lingonberry and bilberry presence and count used for each in each 20-day period with 10 days overlap (1-6), within the study area in south-central Sweden, for the 2014 berry season (11 July – 18 September).

Candidate models	Variables
Full 1	Habitat + NDVI + slope + aspect + elevation
2	Habitat + NDVI + aspect + elevation
3	Habitat + NDVI + aspect
4	Habitat + NDVI
5	Habitat + aspect
6	NDVI + aspect
7	NDVI
8 (null)	~ 1

Bear telemetry data and foraging positions

The Scandinavian Brown Bear Research Project (SBBRP) has been monitoring brown bears since 2003 with global positioning systems GPS-GSM collars (Vectronic Aerospace GmBh, Berlin, Germany), which deliver detailed information about bear movement (i.e.1 position/1/30/60 minutes). Bear captures are conducted during early spring and with the use of a helicopter and on the ground handled by the SBBRP veterinary team. Both the capture and the

handling was approved by the Ethical Committee on Animal Experiments, Uppsala, Sweden and the Swedish Environmental Protection Agency. See Arnemo and Fahlman (2011) for details on bear capturing methods. The dataset was reduced after excluding positions with a dilution of precision (DOP) quality > 4 to increase the positional accuracy (D'eon & Delparte 2005). As most GPSs are programmed to only send signals every hour, all positions except hourly positions were removed. I excluded juveniles that travel with their mother to account for data dependencies (Boyce 2006). Positions from the days a specific bear was killed and days when human and dog approaches were carried out for other studies were also excluded, as such positions affect bear behaviour (Sahlén et al. 2015). The following two days after a bear has been approached were excluded, as bears spend up to two days to regain normal foraging behaviour after being approached (Ordiz et al. 2012). As human presence in the study area increases from the middle and towards the end of the study period due to berry pickers and hunters, bears are more likely to be approached by people during this period and their foraging behaviour might be altered. However, accidental approaches are difficult to predict, only organized approaches carried out by the SBBRP were excluded from the data.

Brown bear behaviour changes throughout the day and season (Elfström et al. 2014a; Moe et al. 2007; Ordiz et al. 2011; Ordiz et al. 2012). According to Moe et al. (2007), Scandinavian brown bears rest both during the day (09.00-17.29) and night (00.00-03.29) during the berry season (11 July – 18 September), and are foraging berries both in the morning (03.30-08.59) and in the evening (17.30-23.59). However, brown bear foraging behaviour changes rapidly following the start of the hunting season (21 August) and bears become more nocturnal and usually forage between 20.00-06.00 and rest during the day (Ordiz et al. 2012). Bears feed almost exclusively on berries during hyperphagia (Dahle et al. 1998). To encompass foraging behaviour both before and during the hunting season, all bear positions throughout the study period were subsetted according to a movement criterion (Hertel et al. in revision). This criterion implies a bear movement distance of more than 100m but less than 800m per hour, and with at least two positions after another. Observational studies from Glacier National Park suggest that grizzly bears move slowly and constantly while foraging on berries (Welch et al. 1997), suggesting that the distance travelled is moderate and fits with the projected 100-800m movement criterion per hour (Hertel et al. in revision).

Brown bear resource selection functions (RSFs)

RSFs were used to model brown bear resource selection, and to investigate bear foraging on berries in relation to anthropogenic structures. The same six overlapping periods used for the spatiotemporal berry predictions were used for the bear RSFs. An RSF is a tool often used to study animal movement and habitat selection, in relation to the distribution of available resources (Boyce & McDonald 1999; Hebblewhite et al. 2005; Manly et al. 2002). As the bear distribution in my study area is known from GPS data, RSFs can be used to estimate the probability of bears using a particular habitat or resource, as well as making predictions about bear movement and resource selection in a similar ecosystem outside my study area. In my case, RSFs were used to study brown bear optimal foraging in relation to large roads, forest roads, residential areas, buildings and open water. The response variable in my RSF was the probability of "use", and availability was assessed by using the same number of used:available positions within each bear-homerange. Both RSFs and a 1:1 ratio of used and available positions are commonly used within the SBBRP (i.e. Steyaert et al. (2014)).

Open water was removed in ArcMap to avoid making predictions for open water and to avoid random positions being distributed in water, as water is an unsuitable berry habitat. I used the raw dataset with 265 881 GPS bear positions of 2014 to generate 100% Minimum Convex Polygon (MCP) homeranges for each bear. I used the MCPs to estimate homeranges, as this method is commonly used in RSF modelling (Bastille-Rousseau et al. 2011). MCP includes the outermost positions, and the entire variation of resources available for each bear was therefore encompassed (Burgman & Fox 2003). Although the use of MCP is recommended by the IUCN (Syfert et al. 2014), homeranges can also be slightly overestimated by the use of MCP (Burgman & Fox 2003). Both the MCP and kernel density estimator (KDE) can be used to estimate homeranges. However, as the sample size of the total number of used bear positions is large and the data has a wide variation of homerange sizes, either estimates are sufficient (Nilsen et al. 2008). Additionally, MCP is also commonly used within the SBBRP (i.e. Steyaert et al. (2014) and Dahle et al. (2006)).

Used/available positions were identified as either used (1) or available (0). Spatiotemporal information about berry and anthropogenic variables were extracted in ArcMap from all random and used positions. I used the same periods for the RSF data as I used in the spatiotemporal berry predictions, and applied the same collinearity tests. Based on the same thresholds for collinearity

as for the berry predictions, no collinearity was discovered between the berry indexes or any anthropogenic variable.

Explanatory variables

The explanatory variables in my RSFs consist of the berry availability index and anthropogenic variables. As bears forage heavily on berries during the berry season (Dahle et al. 1998; Welch et al. 1997), I expect that the lingonberry and bilberry availability index are important explanatory variables for modelling bear foraging behaviour in most periods (lingonberry maps were only available from period 1 to 4). Brown bear foraging behaviour is greatly affected by human presence (Ciarniello et al. 2007; Nevin & Gilbert 2005; Roever et al. 2008a; Swenson 1999) and bears rapidly become more nocturnal during the hunting season when human activity increases significantly (Ordiz et al. 2012). Research also reveals that bears generally avoid areas < 10km to resorts, settlement and towns, and that juvenile bears (specifically males) more often occupy areas close to human settlement compared to older bears (Elfström et al. 2014a; Elfström et al. 2014b; Nellemann et al. 2007; Nevin & Gilbert 2005). This suggests that the distance to settlements and villages could influence bear foraging behaviour and justify the importance of including settlements, villages, and buildings as explanatory variables. Additionally, there are a few high volume traffic roads intersecting the study area (Martin et al. 2010) and the web of forest roads is dense following decades of intense commercial forestry (Linder & Östlund 1998). I expect bears to generally avoid roads and forest roads as these structures are consistently and periodically, respectively, associated with humans, and bear foraging behaviour could therefore be explained by proximity to roads and forest roads. Although the human density within the study area is the lowest in bear related areas in Western Europe (Ordiz et al. 2012), the hunting season attracts numerous hunters and I expect that this will alter bear foraging behaviour rapidly (i.e. within the scope of days). As no explanatory variable accounts for the hunting season alone, I expect that bears foraging behaviour in relation to most anthropogenic structures will alter when the hunting season starts. Open water is in theory not an anthropogenic structure, but previous research reveals that bears avoid areas close to open water and argue that this avoidance could be related to an association of water and humans (Elfström et al. 2008; Steyaert 2015, pers.comm.). Water is therefore included as one of the anthropogenic explanatory variables.

The same habitat variables used to explain the bilberry and lingonberry index in the spatiotemporal berry predictions could be incorporated in the bear RSFs as habitat variables also

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could influence bear selection for berries. However, as the main purpose of the RSFs is to investigate how bear selection of berries is influenced by the proximity to anthropogenic structures (H3 and H4), further analysis of habitat variables such as habitat type, NDVI, slope, aspect and elevation are therefore inessential for the purpose of this study. Additionally, as these habitat variables already are included in the bilberry and lingonberry indexes, one could argue that including the habitat variables in RSF models were the indexes would be used, could cause problems with collinearity.

The anthropogenic variables are derived from a digital topographic map (freely available at www.lantmateriet.se) and is the calculated Euclidean distance from each pixel (in km) in the study to the nearest road, forest road, settlement, village, building and open water. As large pixel values indicate distances far away, positive parameter estimates for the 'distance to' variables should from hereafter be interpreted as "avoidance", while negative estimates indicate selection for areas close to a specific structure.

Bear behaviour response to villages and settlements is similar as all are associated with permanent and predictable residents (Nellemann et al. 2007), and a new variable, all_residents, was generated to reduce the number of explanatory variables and the complexity of the candidate models. As village and settlement are combined, the shortest distance from any used/available position to the respected structure is considered. Buildings are single standing without permanent residents, and as I expect bears to behave differently around cabins and resorts than around permanent residential areas (Nellemann et al. 2007), d_building therefore remains as an explanatory variable. All variables used in the RSF models are listed in Table 2.

Statistical Analysis
In the RSF models, used and available positions represented the response variable, while the anthropogenic variables and both the bilberry and lingonberry index were predictive variables. The RSF models therefore indicates were bears forage on bilberries and lingonberries in relation to anthropogenic structures. Generalized linear mixed models (GLMMs) were used to predict bear resource selection across the study area, as GLMMs incorporate both fixed and random effects (Pinheiro & Bates 2006; Zuur et al. 2009). Fixed effects represent the explanatory variables explained, while the random effect is "Bear ID". The random effect is included in

Table 2: List of both response and explanatory variables used in the RSF models in each 20-day period with 10 days overlap (1-6), within the study area in south-central Sweden, for the 2014 berry season (11 July – 18 September).

Variable name	Variable type	Explanation
d_settlement	Explanatory	Distance to settlement (km)
d_village	Explanatory	Distance to village (km)
d_building	Explanatory	Distance to building (km)
d_road	Explanatory	Distance to road (km)
d_forest_road	Explanatory	Distance to forest road (km)
d_water	Explanatory	Distance to water (km)
all_residents	Explanatory	Distance residential areas (km), d_settlement and d_village merged and the distance accounts for the shortest distance from either d_settlement or d_village.
bcomp	Explanatory	Bilberry index
lcomp	Explanatory	Lingonberry index
Used.Available	Response	All used and available positions, dummy coded (used=1, available=0)

all RSF candidate models to account for individual variation in bear habitat selection, as the data is both nested and has a hierarchal structure. The *glmer* function from the lme4 package was used with a binomial structure to model the GLMMs. Additionally to both fixed and random effects, I considered interactions between berry availability indexes and anthropogenic predictive variables, as such interactions could identify trade-offs between berry availability and anthropogenic structures (H4). I suggest that bear resource selection depends on more than just berry availability or anthropogenic variables, and that it could depend on the distance from an anthropogenic structure. I created 11 candidate models to evaluate which anthropogenic variable(s) affect bear resource selection. Excluding interactions, the RSFs took the general form:

$$W = exp(\mu + \beta_{Road} X_{Road} + \beta_{Forest\,Road} X_{Forest\,Road} + \beta_{Water} X_{Water} + \beta_{Residents} X_{Residents} + \beta_{Building} X_{Building} + \beta_{Bilberry} X_{Bilberry} + \beta_{Lingonberry} X_{Lingonberry})$$

Where W represents the predicted RSF scores, μ the intercept, and β the parameter estimate for any explanatory variable X. The RSF candidate models (Table 3) are associated with H3 and H4. GAM, GLM and GLMM were fitted using the *gam* and *lme4* packages.

RSF model selection framework

I used the same model selection framework for the RSF models as for the spatiotemporal berry predictions (see "Model selection framework" above), and the candidate models are listed in Table 3.

Candidate models

Full model

I hypothesize that bears trade good berry areas close to any anthropogenic structure for less berry rich areas further away from any structure.

Candidate 1

I hypothesize that bears trade good berry areas close to both forest roads and residential areas, for less berry rich areas further away from forest roads and residential areas. Bears avoid all main roads and buildings in general.

Candidate 2

I hypothesize that bears trade good berry areas close to roads and forest roads, for areas less berry rich further away from all roads. Bears generally avoid residential areas, buildings and water.

Candidate 3

I hypothesize that bears trade good berry areas close to forest roads and buildings for poor berry areas further away from such structures.

Candidate 4

Bears generally avoid roads, forest roads, and areas close to water, and I hypothesize that bears trade good berry areas close to both residential areas and buildings, for poor berry areas further away.

Candidate 5

Bears generally avoid roads, forest roads, residential areas and buildings and I hypothesize that bears trade good berry areas close to water, for less berry rich areas further away from water.

Candidate 6

Bears generally avoid main roads, forest roads, water, buildings and residential areas. Bears also select for areas with high lingonberry or bilberry availability. No trade-off occurring.

<u>Candidate 7</u>

Bears generally avoid main roads, buildings and areas close to water, while I hypothesize that bears trade good berry areas in close proximity to residential areas for poor berry rich areas further away from residential areas.

<u>Candidate 8</u>

Bears generally avoid roads, residential areas and areas close to water. I hypothesize that bears trade good berry areas for less berry rich areas further away from forest roads.

<u>Candidate 9</u>

Bears generally avoid main roads, forest roads and areas close to water, and I hypothesize that bears trade good berry areas close to buildings for less berry rich areas further away from buildings.

<u>Null Model</u>
Foraging locations of bears do not differ from a random distribution over the landscape.

Model validation

The RSFs model accuracy was tested using the cross validation method as suggested by Boyce et al. (2002) and further clarified by Klar et al. (2008). First, the most parsimonious RSF model for all six periods were plotted in ArcMap, providing all pixels in the maps with a value representing the probability of a bear selecting that pixel. Secondly, the prediction maps were divided into eight equally sized bins, were the probability of bear selection ranged from low (bin 1) to high (bin 8). Third, the areal proportion of all eight bins (A) and the proportion of the number of bear GPS positions within each bin (B) were calculated. Fourth, proportions of bear GPS positions within each bin were divided by the proportion of resources available in the respective bins (B/A), creating an adjusted frequency of bear occurrence within the study area. Last, the Spearman-rank correlation was used to evaluate the predictive accuracy of the RSF models, and high correlation scores suggest that areas that are predicted to be selected by bears generally are more used in relation to available resources. This means that the higher the Spearman correlation ranking, the better the RSF model accuracy is.

Table 3: List of explanatory variables/fixed effects (road, forest road, residents, building and water) and the random effect (Bear ID) in the RSF models, used to study bear selection on berries in each 20-day period with 10 days overlap (1-6), within the study area in south-central Sweden, for the 2014 berry season (11 July – 18 September). BindexX and LindexX represent the bilberry and lingonberry index, respectively, and the X represent the period (1-6) during the berry season. The same set of RSF models were used in all six periods.

Candidate models	Variables and interactions
Full	road * BindexX + forest road * BindexX + residents * BindexX + building * BindexX + water * BindexX + road * LindexX + forest road * LindexX + residents * LindexX + building * LindexX + water * LindexX + Bear ID
1	road + forest road * BindexX + residents * BindexX + forest road * LindexX + residents * LindexX + building + Bear ID
2	road * BindexX + forest road * BindexX + road * LindexX + forest road * LindexX + residents + building + water + Bear ID
3	forest road * BindexX + building * BindexX + forest road * LindexX + building * LindexX + Bear ID
4	road + forest road + residents * BindexX + building * BindexX + residents * LindexX + building * LindexX + water + Bear ID
5	road + forest road + residents + building + water * BindexX + water * LindexX + Bear ID
6	road + forest road + residents + building + water + BindexX + LindexX + Bear ID
7	road + residents * BindexX + residents * LindexX + building + water + Bear ID
8	road + forest road * BindexX + forest road * LindexX + residents + water + Bear ID
9	road + building * BindexX + building * LindexX + forest road + water + Bear ID
Null	1 + Bear ID

Additional statistical analysis

Bear selection for berries

One of the main hypotheses is to investigate whether bears "chase the blue/red wave" of bilberry and/or lingonberry availability (H2). This can be achieved by comparing the temporal availability of berries and spatiotemporal bear selection for berries. To visualize bear selection for bilberries and lingonberries throughout the berry season, a new GLMM (glmer) model was constructed for the relevant periods. In order to compare the model output across the berry season, the most informative model has to be the same in all periods (Steyaert 2015, pers.comm.). Although the results from this GLMM did not represent the real RSF results of bear resource selection, the use of the same GLMM model in all periods enabled me to compare bear selection for bilberries and lingonberries across the season, and to compare these trends with the temporal berry availability trend. Similar bear selection and temporal berry availability trends could suggest that bears indeed "chase the blue/red wave". I emphasize that this GLMM model differs from the RSF

models, and henceforth refer to the new GLMM as <u>the new prediction</u> for bear selection for berries.

Do bears trade-off good berry sites for safety?

As one of my main research goals was to investigate whether bears trade-off good berry available sites with poor berry sites further away from anthropogenic structures (H4), all significant interactions occurring in at least one period were analysed further to test Hypothesis 4. To test Hypothesis 4 to for any bear trade-offs, a GLM model was constructed with main effects, interaction terms between all relevant "distances to anthropogenic structures" variables that were significant in the RSF models. The distance levels were made based on the longest distance from the particular anthropogenic structure to a point, with equal distance intervals. As this new test uses a different model than any of the most informative RSF models, these prediction results should be considered as general bear selection trends, and are henceforth referred to as <u>the new predictions</u> for bear selection in relation forest roads and residential areas.

Results

Berry Spatiotemporal Predictions

A total of 913 random berry plots were visited during the berry season 2014, and bilberries and lingonberries were present at 420 and 164 plots, respectively. This data is the basis for the spatiotemporal berry predictions, and Table 4 highlights the most informative candidate models for bilberry and lingonberry availability. The model validation in Table 4 suggests that all informative models for both bilberry and lingonberry presence had reasonably good predictive accuracy (> 0.6). The dispersion parameter for most berry presence and occurrence models were close to 1, indicating no overdispersion.

Table 4a,b: List of the most informative candidate models for a) bilberry and b) lingonberry presence and count in each relevant 20-day period with 10 days overlap (1-6), within the study area in south-central Sweden, for the 2014 berry season (11 July – 18 September). Informative models marked in bold, and model averaging used when >1 model was informative. Dispersion parameter for the most informative models included (close to 1 = no overdispersion). Model validation of all informative berry presence models included (> 0.6 good model accuracy).

a) Bilberry

Period	Model Selection – ΔAIC$_c$								Model Validation	Dispersion parameter
	Full 1	2	3	4	5	6	7	Null 8		
P1 presence	2.83	4.45	3.92	**0.00**	5.54	13.82	9.05	19.28	0.60	1.29
P1 count	6.98	6.53	8.00	8.25	9.42	**1.83**	**0.00**	8.11	NA	1.18
P2 presence	5.88	4.45	2.83	**0.00**	12.62	29.99	27.64	55.73	0.68	1.20
P2 count	5.75	4.64	2.34	5.54	3.99	**0.00**	**0.63**	11.79	NA	1.14
P3 present	7.66	5.91	3.79	**0.00**	18.14	23.76	19.10	57.18	0.71	1.19
P3 count	10.77	8.45	6.17	**1.48**	5.54	3.41	**0.00**	8.84	NA	1.14
P4 present	8.60	7.25	5.42	**0.00**	20.55	12.15	6.77	33.07	0.65	1.24
P4 count	17.48	16.05	13.74	8.62	14.47	3.71	**0.00**	**1.25***	NA	1.14
P5 present	**0.00**	**0.24**	**0.33**	3.79	13.96	**0.10**	4.14	28.57	0.66	1.23
P5 count	15.43	13.93	11.39	4.91	13.67	4.90	**0.00**	**0.13***	NA	1.17
P6 present	3.13	0.84	5.17	5.17	3.96	12.44	**0.00**	11.62	0.63	1.29
P6 count	13.52	10.82	9.98	8.25	7.47	**1.72**	**1.01**	**0.00***	NA	1.17

*Null model not included in model averaging when other models were significant

b) Lingonberry

Period	Model Selection – ΔAIC$_c$								Model Validation	Dispersion parameter
	Full 1	2	3	4	5	6	7	Null 8		
P3 presence	2.15	**0.00**	4.18	**1.42**	2.96	5.63	2.48	2.78	0.92	0.52
P3 count	43.07	35.85	26.90	12.70	27.08	4.95	**0.00**	9.30	NA	1.24
P4 presence	6.00	6.47	5.87	**1.72**	3.73	6.20	**1.88**	**0.00***	0.71	1.21
P4 count	6.24	3.34	3.83	10.07	17.27	**0.00**	5.28	25.74	NA	1.20
P5 presence	3.33	3.42	2.05	3.19	**0.00**	5.79	7.03	6.08	0.63	1.33
P5 count	5.13	2.98	**1.24**	**0.00**	10.55	3.12	**0.12**	21.77	NA	1.27
P6 presence	**0.00**	2.10	2.58	2.66	**1.21**	8.43	10.85	8.96	0.60	1.30
P6 count	3.03	2.77	**0.04**	4.62	9.14	**0.00**	6.08	20.28	NA	1.28

*Null model not included in model averaging when other models were significant

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Bilberries and the "blue wave"

I hypothesized (H1) that bilberry counts show a temporal trend ("blue wave") and this was supported by an initial GAM in Figure 2a, displaying a non-linear trend of bilberry numbers ($\beta\pm$SE; 9.63$\pm$0.68 and edf=2.69). The GAM predicted bilberry counts to peak between Julian date 25 and 45 (4-24 August 2014) (Figure1a). The peak of both lingonberry and bilberry counts is the period of maximum berry availability. During the peak period, bilberries were on average occurring at 56-58% (Figure 3a) of any site within the study area. As bilberry presence only considered plots where bilberries occurred, the combination of the probability of presence and the mean number of predicted bilberries per m^2 provides a relative abundance of bilberries per m^2 of habitat (bilberry index, Figure 3b). Figure 3b illustrates the temporal change in the mean bilberry index during the berry season, indicating that the relative abundance of bilberries peaked between 7-14 August (Julian date 28-35). During the peak bilberry period, good bilberry sites were predicted to contain at least 19 bilberries/m^2 (Figure 2b). Model validation of the presence of bilberries was conducted and as all bilberry presence models had a model validation value > 0.60, and models were considered to have reasonable predictive accuracy (Table 4a).
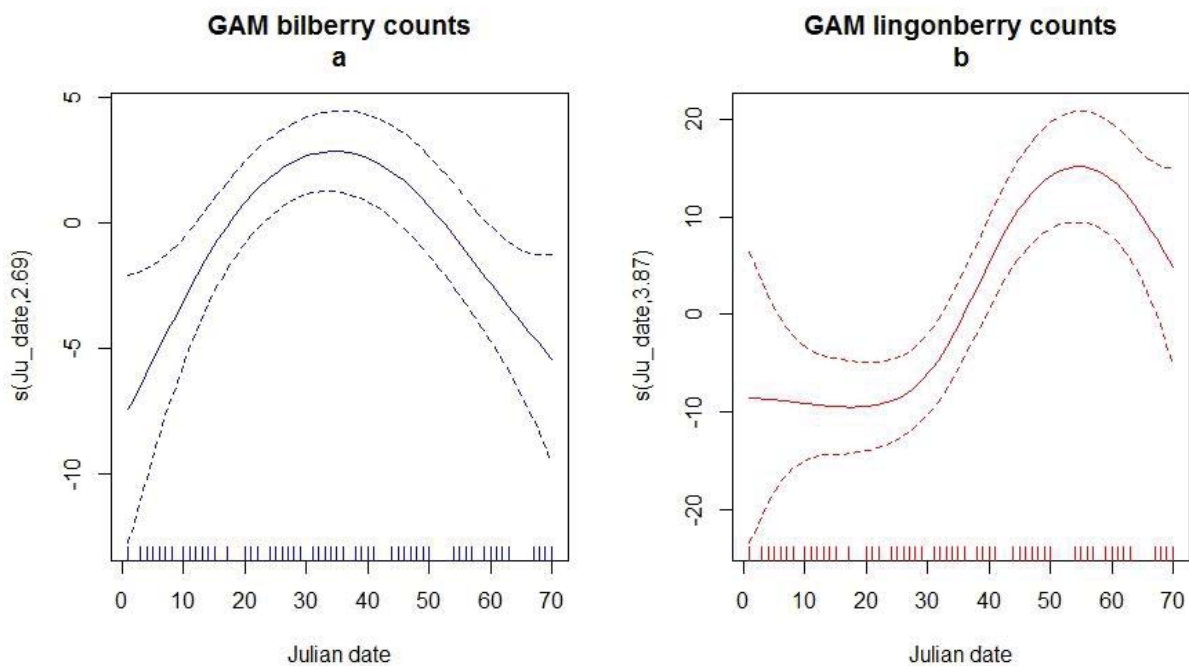
Figure 2: Estimated smoothing curves for temporal a) bilberry and b) lingonberry counts using GAM, throughout the study period (11 July – 18 September,) within the study area in south-central Sweden. indicating a temporal trend. The solid lines are the smoothers and the dotted lines are indicate the 95% confidence bands.
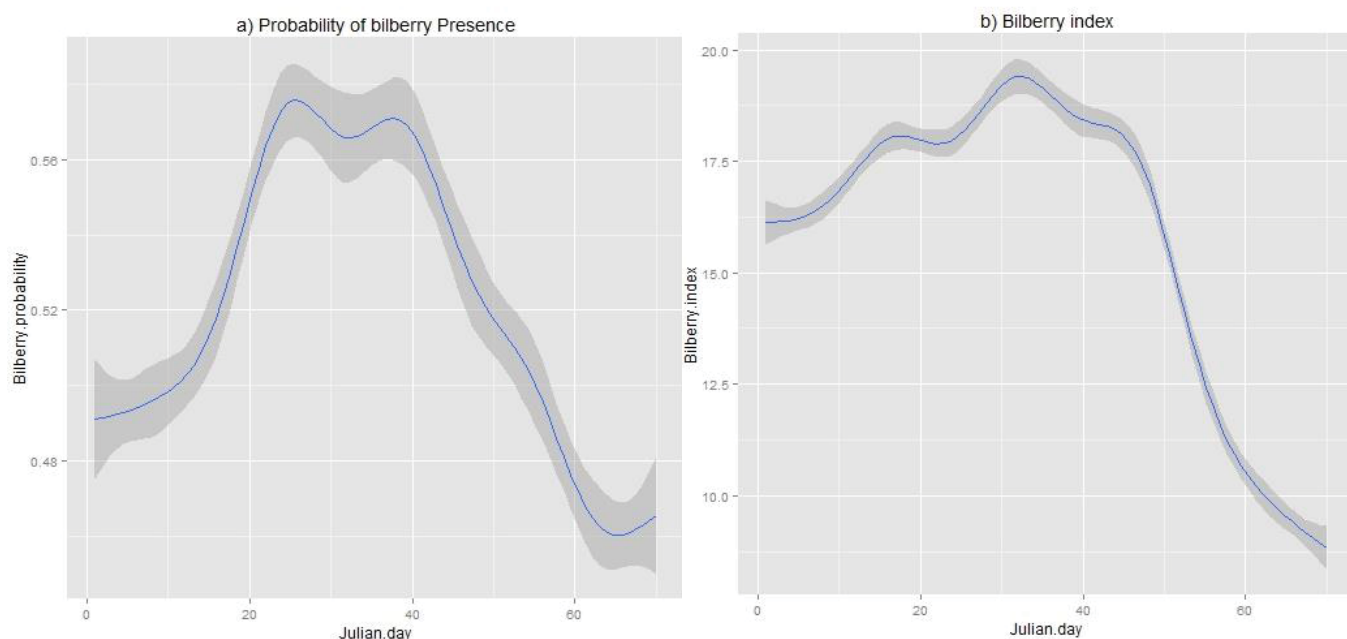
Figure 3: "The Blue Wave" or the a) mean relative probability of bilberry presence and b) relative mean bilberry index of bilberry availability, during the study period (11 July – 18 September) and within the study area in south-central Sweden.

Figure 4: "The Red Wave" or the a) relative lingonberry probability of occurrence and b) relative mean lingonberry index of lingonberry availability, during the study period (11 July – 18 September) and within the study area in south-central Sweden.

Lingonberries and the "red wave"

The GAM results of lingonberry counts showed a temporal non-linear trend (8.73±1.44 and edf=3.87), indicating lingonberry counts to peak between Julian day 45 and 65 (24 August – 13 September) (Figure 2b). The probability of mean lingonberry presence gradually increas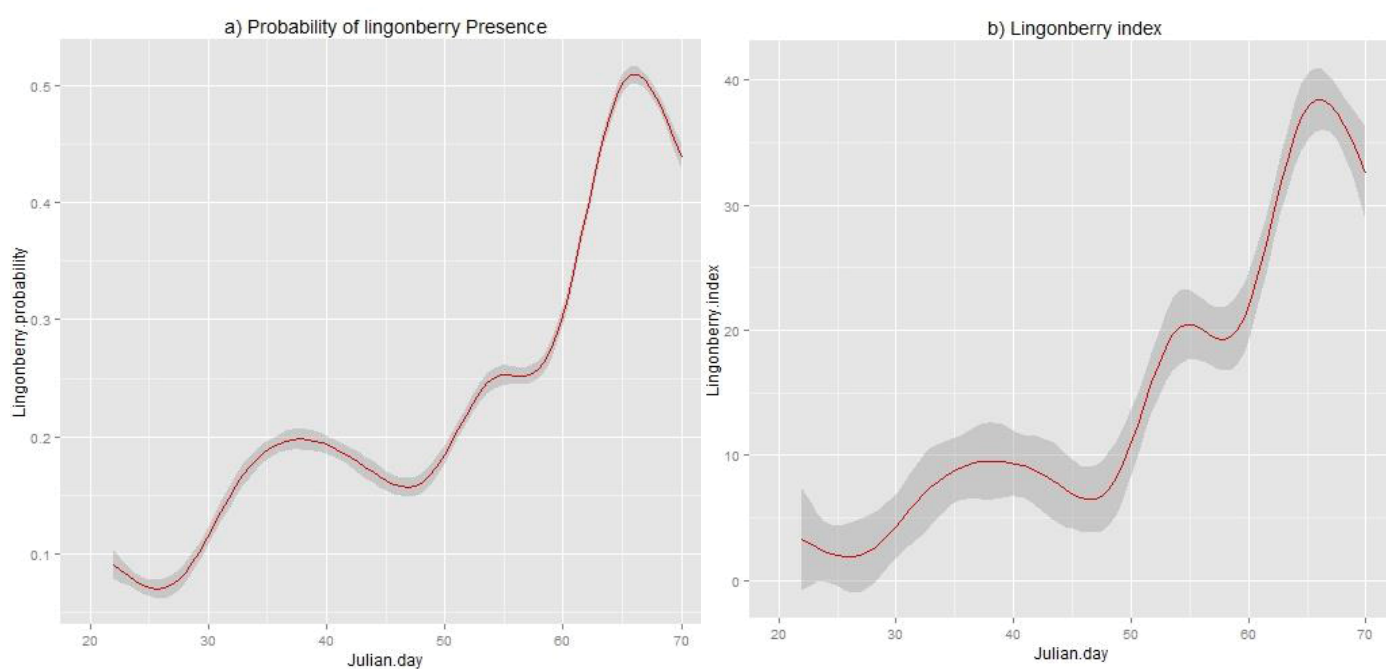ed until the peak around 8 September (Julian date 60, Figure 3a). Lingonberry presence dropped rapidly after the peak, and the continuation of the drop occurred after the study ended (Julian date 70 or 18 September). More than 50% of all random berry sites were likely to contain mature lingonberries during the peak (Figure 4a). Good lingonberry sites were predicted to contain approximately 40 lingonberries/m^2 on average during the peak (Figure 4b). My models suggest that during both the bilberry and lingonberry peak period, lingonberries were expected to have a higher mean density of berries/m^2. As the model validation indicated > 0.60, the predictive accuracy of the lingonberry presence models were considerd reasonable (Table 4b).

Spatiotemporal berry predictions

Bilberry presence

Model 4 was the most parsimonious model to predict berry presence in period 1-4 ($\Delta AIC_c = 0.00$) (Table 4a), and consisted of habitat type, NDVI and the responses per period. As model 1, 2, 3 and 6 all had a $\Delta AIC_c < 2$ ($\Delta AIC_c = 0.00$, 0.24, 0.33, and 0.10, respectively) (Table 4a) in period 5 for bilberry presence, a model average was made and all predictive variables included. Only model 7 had a $\Delta AIC_c < 2$ ($\Delta AIC_c = 0.00$) in period 6, which suggested that NDVI was the only variable to predict bilberry presence at the end of the berry season. All bilberry presence models were cross-validated, and as all values were > 0.6, all models were considered reasonable.

Bilberry availability

All periods had at least two informative models with $\Delta AIC_c < 2$ (Table 4a). Model average of model 6 and 7 was conducted for period 1 ($\Delta AIC_c = 1.3$ and 0.00, respectively). Model 6 consisted of NDVI and aspect and model 7 of NDVI, and both aspect and NDVI were included in the model average. Both model 6 and 7 were the most informative models in period 2 ($\Delta AIC_c = 0.00$ and 0.63, respectively), and both NDVI and aspect were included in the model average for bilberry availability in period 2 (Table 4a). Model 4 and 7 had an $\Delta AIC_c < 2$ in period 3 ($\Delta AIC_c = 1.48$ and 0.00, respectively) (Table 4a), and model averaging was conducted. As model 4

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consisted of both habitat type and NDVI and model 7 of NDVI, both habitat type and NDVI were included in the model average. After the null model exclusion, model 7 was the most informative model for both period 4 and 5 ($\Delta AIC_c = 0.00$ in both periods), suggesting that NDVI was an important predictor variable for predicting bilberry availability in these periods. Model averaging was conducted in period 6, of model 6 and 7 ($\Delta AIC_c = 1.72$ and 1.01, respectively) (Table 4a) which consisted of NDVI and aspect.

Bilberry index

The results from the bilberry presence and availability were multiplied to create a relative bilberry availability index, and translated into maps in ArcMap. A random section of the study area is illustrated in Figure 5, displaying the same area for habitat type (Figure 5a), ndvi (Figure 5b) and bilberry index (Figure 5c-h). Separate maps of the bilberry index is illustrated in Figure 5 c-h. where c = period 1, and h = period 6. Although few results can be generated, the maps visualize the general trends from the bilberry presence and availability results well.

Lingonberry presence

During period 3, both model 2 and 4 had $\Delta AIC_c < 2$ ($\Delta AIC_c = 0.00$ and 1.42, respectively) (Table 4b). Model 2 consisted of habitat type, NDVI, aspect and elevation, and model 4 of habitat type and the NDVI. Model averaging was conducted, and all variables in model 2 and 4 included. Both model 4 and 7 were informative in period 4 ($\Delta AIC_c = 1.72$ and 1.88, respectively) (Table 4b), and after model averaging, both habitat type and NDVI were considered important. In period 5, model 5 (habitat type and aspect) was the most informative ($\Delta AIC_c = 0.00$) (Table 4b). Both model 1 and 5 were informative in period 6 ($\Delta AIC_c = 0.00$ and 1.21, respectively) (Table 4b), and habitat type, NDVI, slope, elevation and aspect were all included in the model average. All lingonberry presence models were validated and considered reasonable (> 0.60) (Table 4b).
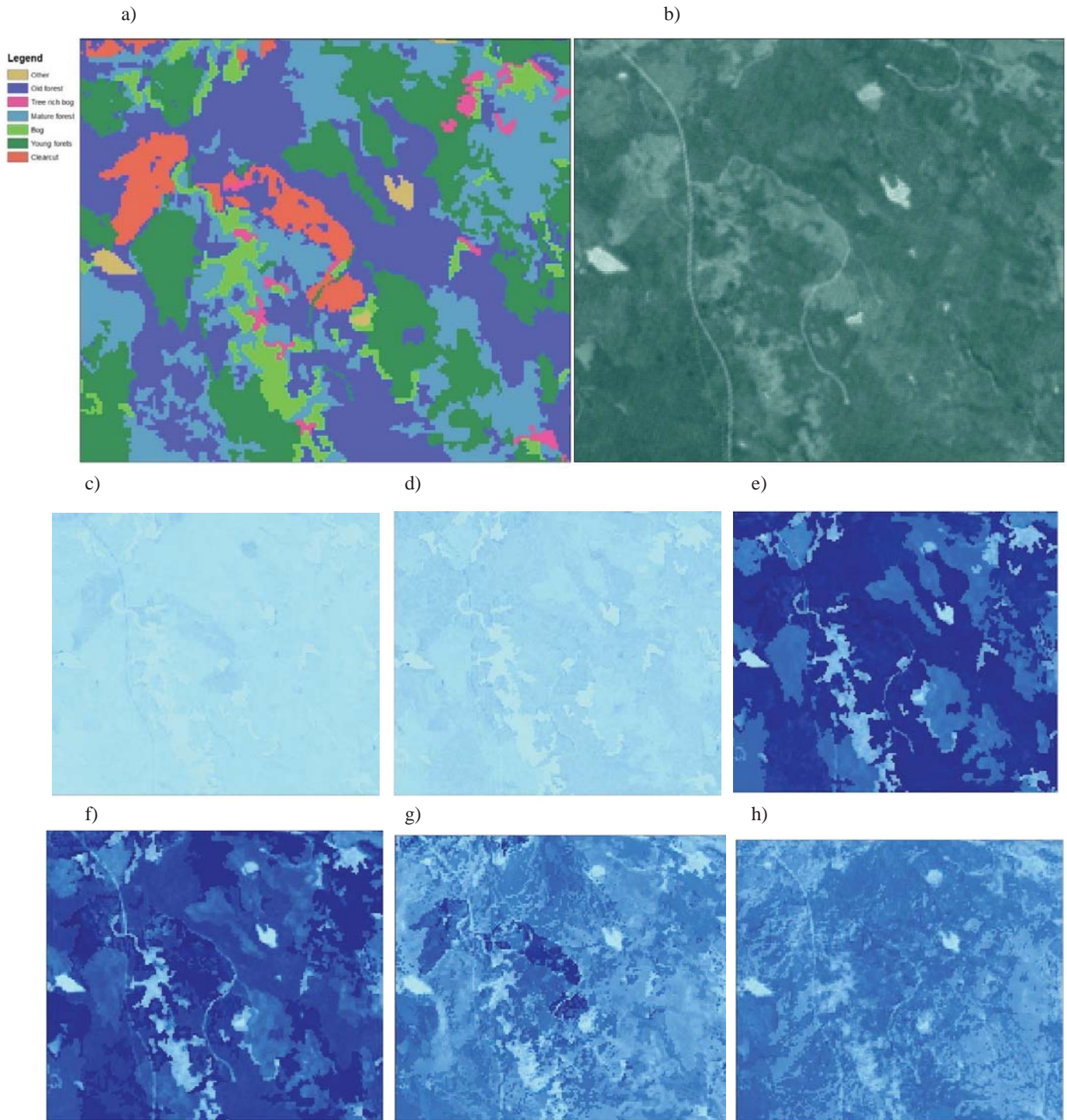
Figure 3: Displaying a section of the a) habitat type map and b) NDVI from ArcMap, as well as a section from the bilberry prediction maps for all six 20-day period with 10 days overlap (c-h). All maps display the same area within the study area in south-central Sweden during the study period (11 July – 18 September). In the bilberry prediction maps: the darker the blue colour, the higher predicted bilberry availability index. In the NDVI map: the darker the green colour, the higher predicted NDVI value.
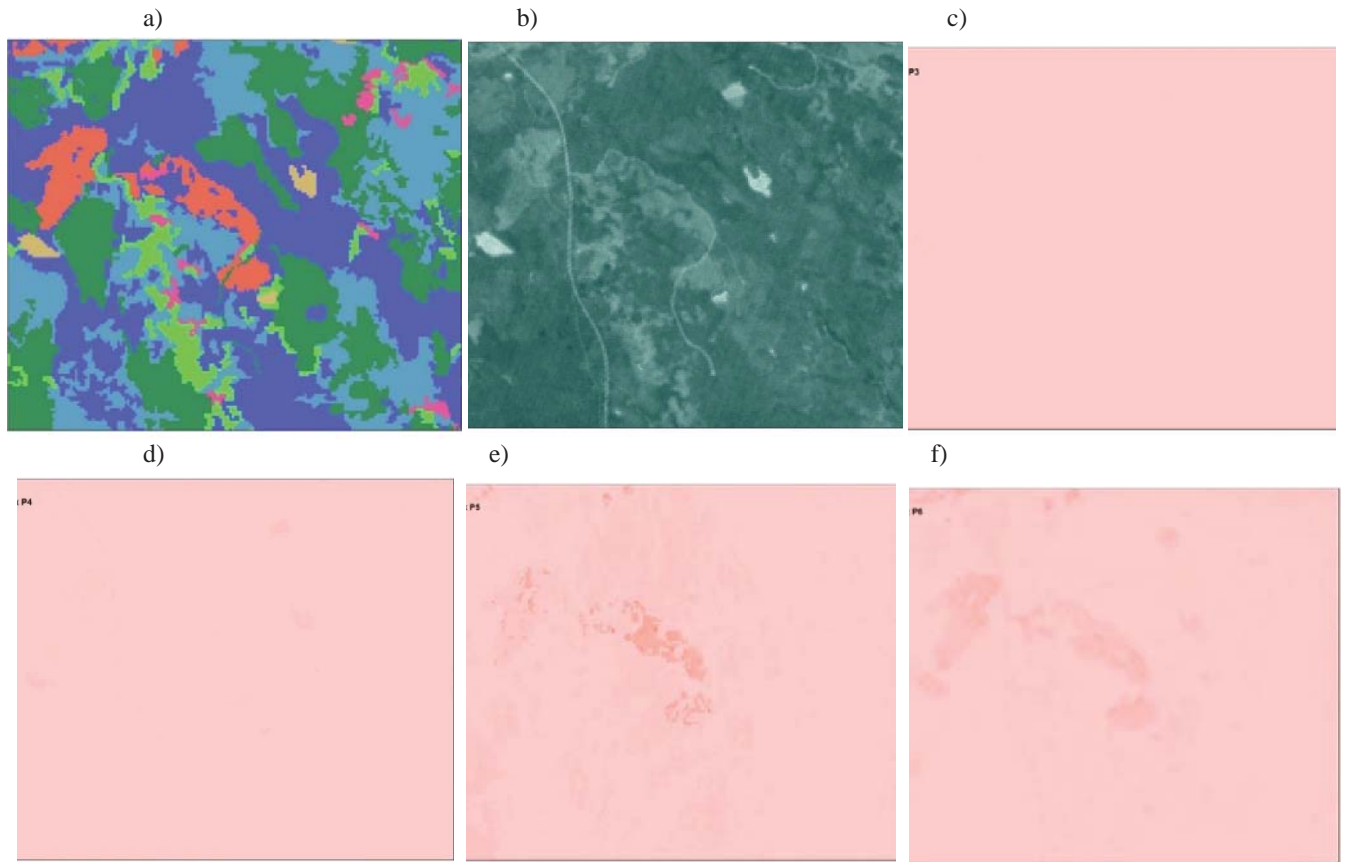
Figure 4: Displaying a section of the a) habitat type map (habitat legend see Figure 5a) and b) NDVI from ArcMap, as well as a section from the lingonberry predictions maps for all four 20-day period with 10 days overlap (c-d). All maps display the same area within the study area in south-central Sweden during the study period (11 July – 18 September). In the lingonberry prediction maps: the darker the red colour, the higher predicted lingonberry availability index. In the NDVI map: the darker the green colour, the higher predicted NDVI value.

Lingonberry availability

Model 7 was the most informative in period 3 ($\Delta AIC_c = 0.00$), which indicated that NDVI was the most important variable for predicting lingonberry availability in period 3 (Table 4b). In period 4, model 6 was the most informative model ($\Delta AIC_c = 0.00$), and consisted of both NDVI and aspect. Model 3, 4 and 7 were averaged, as they all were considered informative in period 5 with $\Delta AIC_c < 2$ ($\Delta AIC_c = 1.24$, 0.00 and 0.12, respectively) (Table 4b). Model 3 consisted of habitat, NDVI and aspect, model 4 of habitat and NDVI, and model 7 of NDVI. In period 6, model 3 and 6 were averaged, as they both had $\Delta AIC_c < 2$ ($\Delta AIC_c = 0.04$ and 0.00, respectively) (Table 4b). Habitat type, NDVI and aspect were the predictor variable for model 3, while model 6 consisted of NDVI and aspect, and all variables were included in the model average.

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Lingonberry index

The same map of the study area used to display the spatiotemporal bilberry index was used to display the spatiotemporal lingonberry index (Figure 6). The habitat type (Figure 6a) and NDVI (Figure 6b) are identical to Figure 5a and b, while figure 6c-f display the changes in lingonberry availability for period 3-6, where c = period 3, and f = period 6. Although few results can be generated based on these maps, the maps visualize the general trends from the lingonberry presence and abundance results well.

Bear Resource Selection – RSF models

The RSF data consisted of 4747 foraging positions (from here on referred to as used positions) and with a 1:1 ratio of random and used positions per bear. The total number of positions came to 9494. Although the SBBRP in 2014 had GPS positions for 54 bears, only the 29 bears (19 females and 10 males) with homeranges within my study area were included in my study. The model selection procedure suggested that the bear resource selection can be explained by one informative model for each period, except for period 2 were a total of three models had $\Delta AIC_c <$ 2. Table 5 lists the RSF candidate models for each period. All parameter estimates for the RSF models, in all periods are listed in Appendix 1.

Table 5: List of List of ΔAICc scores for RSF models for all 20-day period with 10 days overlap (1-6, within the study area in south-central Sweden during the study period (11 July – 18 September).The most informative model(s) are marked in bold. Model validation of best model(s) included.

Period	Model Selection – ΔAIC_c										
	Full	1	2	3	4	5	6	7	8	9	Null
P1	7.98	75.48	3.41	70.86	10.85	10.46	8.53	8.69	**0.00**	8.85	132.86
P2	4.89	134.17	**0.00**	34.80	3.69	**1.30**	**0.29***	6.83	3.20	3.01	170.74
P3	12.75	75.28	5.72	34.37	4.77	3.99	**0.00**	11.54	4.64	16.00	125.99
P4	13.28	47.07	5.64	36.12	4.92	3.63	**0.00**	6.87	6.23	4.09	157.50
P5	4.15	45.57	**0.00**	76.47	7.41	6.28	4.89	5.61	2.08	8.50	113.09
P6	10.36	32.55	9.86	70.70	4.46	7.22	5.79	**0.00**	17.64	14.21	160.40

*Simplest model

Model validation

As the predicted resource use and available resources overall correlated well, the RSF models are indeed good at predicting bear resource selection across the study area. The Spearman-ranking reveals that the predicted use and available habitat from period 2 to 6 correlates more than 60%

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(Table 6), suggesting that the RSF models generally are good predictive models for bear resource selection in period 2 to 6 (Zuur et al. 2009). The Spearman-rank correlation for period 1 however, only suggests a 25% (Table 6) correlation, indicating that the RSF model for period 1 poorly predict bear resource selection.

Table 6: Spearman rank coefficients (r_s) and significance values (p) of correlation between area adjusted frequencies of brown bear positions in the study area in Sweden and the bear selection probability bins in each 20-day period with 10 days overlap (1-6), within the 2014 berry season (11 July – 18 September). Correlation between area-adjusted frequency and selection probability bins have also been calculated for the entire berry season.

Model validation		
Period	r_s	*p*
1	0.250	0.595
2	1.000	< 0.001
3	0.786	0.028
4	0.619	0.115
5	0.600	0.242
6	0.595	0.132
Entire berry season	0.952	< 0.001

Bear selection and avoidance during the berry season

Period 1
Model 8 was the most informative for bear selection in period 1 ($\Delta AIC_c = 0.00$) (Table 5), and included interactions between forest roads and the bilberry index. The model results indicated that bears generally avoided areas close to roads and open water (0.11±0.02 and 0.68±0.08, respectively) (Figure 7a). Bears selected areas close to forest roads in period 1 (-0.57±0.24, note that negative estimates for all anthropogenic 'distance to' variables indicate selection) (Appendix 1 and Figure 7a). Also, the interaction term between distance to forest roads and the bilberry index suggested that bears selected for areas with high bilberry availability in close proximity to forest roads (0.04±0.01) (Appendix 1and Figure 7a). Additionally, bears generally did not select for bilberries (-0.03±0.01) in period 1 (Appendix 1).

Period 2
The RSF model results suggested that three models were equally informative in period 2: model 2, 5 and 6 ($\Delta AIC_c = 0.00$, 1.30 and 0.29, respectively) (Table 5). Interaction terms between the bilberry index and roads, forest roads and water were included in the model averaging, but none

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of the interaction terms were significant (Appendix 1). However, the results of the model average revealed that bears also avoided areas close to large roads (0.09 ± 0.02) and open water (0.92 ± 0.16) in period 2 (Appendix 1 and Figure 7b). Bears also avoided areas close to buildings (0.12 ± 0.05) (Appendix 1 and Figure 7b). There was no significant selection for or against bilberries in period 2 (Appendix 1).

Period 3
Model 6 was the most informative model for bear resource selection in period 3 ($\Delta AIC_c = 0.00$) (Table 5), and model 6 did not include any interaction terms. Bears also avoided large roads, water and forest roads ($0.0.7\pm0.01$, 0.73 ± 0.1, and 0.28 ± 0.1, respectively) (Appendix 1 and Figure 7c) in period 2. However, bears selected for areas close to permanent residential areas (-0.03 ± 0.02) (Appendix 1 and Figure 7c). Period 3 was the first time bears selected for areas with high bilberry availability (0.03 ± 0.01) (Appendix 1 and Figure 7c). Bears selected against areas with high lingonberry availability (-0.03 ± 0.01) (Appendix 1 and Figure 7c).

Period 4
Model 6 was the most informative for bear resource selection in period 4 ($\Delta AIC_c = 0.00$) (Table 5), and did not include any interaction terms. A general avoidance of large roads, water and forest roads was also obvious in period 4 (0.08 ± 0.01, 0.64 ± 0.1 and 0.24 ± 0.11, respectively) (Appendix 1 and Figure 7d). Bears selected for areas close to permanent residential areas in period 4 (-0.05 ± 0.02) (Appendix 1 and Figure 7d). However, bears avoided buildings (0.12 ± 0.05) in period 4 (Appendix 1 and Figure 7d). Bears selected for bilberries (0.06 ± 0.01), and avoided lingonberries (-0.01 ± 0.00) in period 4 (Appendix 1 and Figure 7d).

Period 5
Model 2 was the most informative for bear resource selection in period 5 ($\Delta AIC_c = 0.00$) (Table 5), and included interaction terms between roads and both berry indexes, and between forest roads and both berry indexes. Bears neither selected nor avoided areas close to large roads in period 5 (Figure 7e). However, bears avoided forest roads, open water and buildings (1.15 ± 0.31, 0.69 ± 0.1 and 0.10 ± 0.04, respectively) (Appendix 1 and Figure 7e). Residential areas were not significant, but bears selected for bilberries (0.08 ± 0.02) (Appendix 1 and Figure 7e). Bears selected against lingonberries (-0.11 ± 0.04) (Appendix 1 and Figure 7e). Both bilberry and

Figure 7: Bear resource selection for each 20-day period with 10 days overlap (1-6), within the 2014 berry season (11 July – 18 September), in the study area in south-central Sweden. Displaying parameter estimates for all predictive variables. Location of anthropogenic variables in relation to the dotted horizontal line indicate bear selection or avoidance of areas in proximity to anthropogenic structures. Points below the horizontal line indicate selection, and points above indicate avoidance. In contrast, berry indexes above the horizontal line indicate selection, while indexes below indicate avoidance. Variables on the horizontal line are considered non-significant. The interpretation of the interaction terms depend on whether berries are selected for or against.

lingonberry interactions with forest roads were significant, suggesting that bears selected for highly bilberry and lingonberry rich areas further away from forest roads (-0.08±0.02 and 0.11±0.05 for bilberries and lingonberries, respectively) (Appendix 1 and Figure 7e) in period 5.

Period 6
Model 7 was the most informative for bear resource selection in period 6 (ΔAIC_c = 0.00) (Table 5), and included interaction terms between residential areas and both the bilberry and lingonberry index. Bears avoided areas close to large roads, open water and buildings in period 6 (0.09±0.01, 0.53±0.10 and 0.15±0.04, respectively) (Appendix 1 and Figure 7f). There was no significant selection for bilberries in the last period, but bears selected against lingonberries (0.004±0.002) (Appendix 1 and Figure 7f). Bears also selected for areas close to residential areas in period 6 (-0.30±0.08) (Appendix 1 and Figure 7f). The interaction between residential areas and the bilberry index suggested that bears selected for areas with high bilberry availability close to residential areas (0.02±0.01) (Appendix 1 and Figure 7f).

Bear selection for berries
Bears selected for bilberries in most periods (p3-p6), and against lingonberries (Figure 8). As the bear selection for bilberries and the "blue wave" coincide well, bears indeed "chase the blue wave" (H2). Although Figure 4 suggested a "red wave" for lingonberry availability, bears did not select for lingonberries, and did not "chase the red wave" of lingonberry availability (contrast to H2).

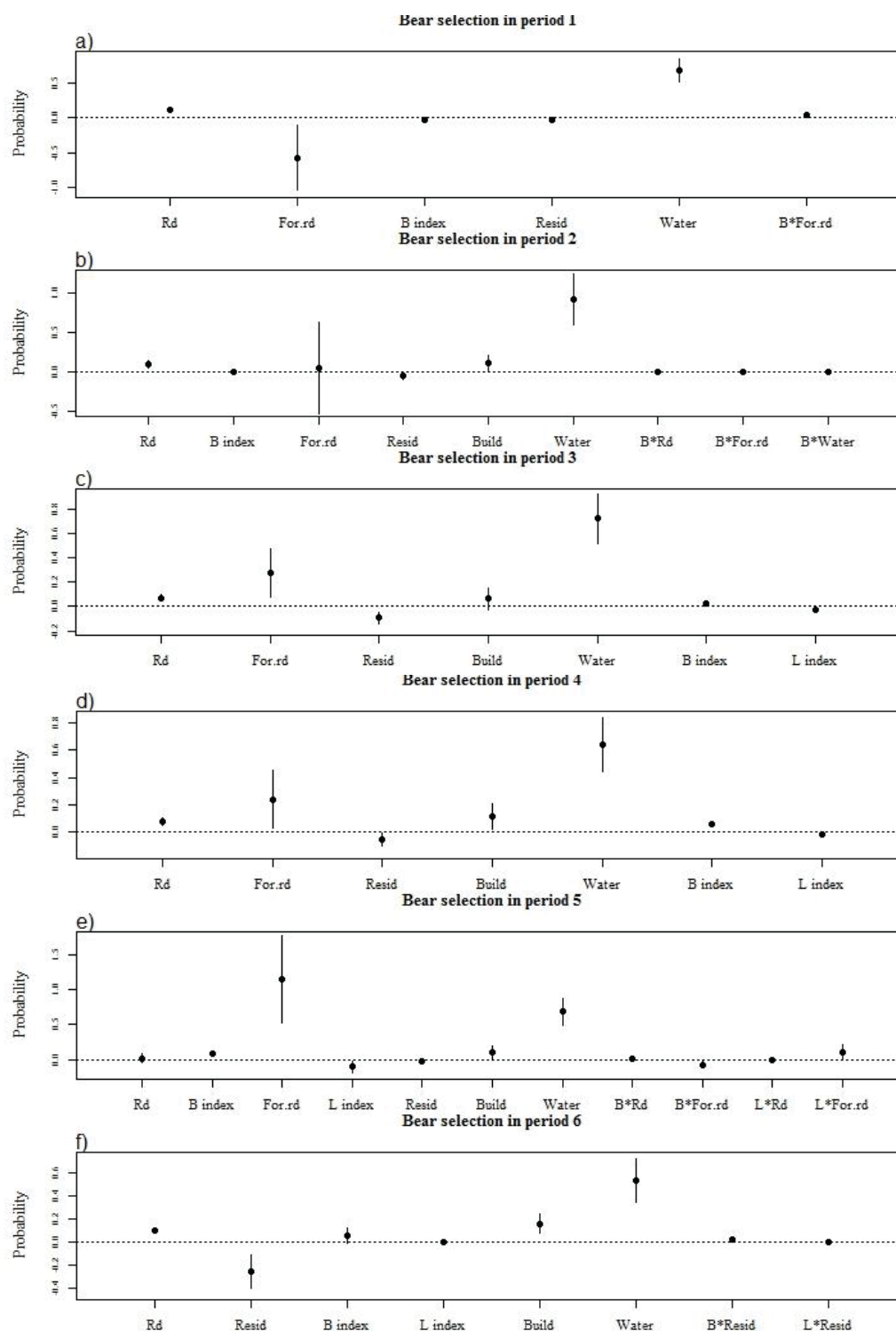*Figure 8: Displaying the parameter estimates for bear selection for lingonberry and bilberry index in each relevant 20-day period with 10 days overlap (1-6), within the 2014 berry season (11 July – 18 September), in the study area in south-central Sweden. The dotted line represent the selection line, were points above indicate selection by bears, and points below indicate avoidance. No sign of lingonberry selection, but selection of bilberries in period 3-6 (P2-P6)*
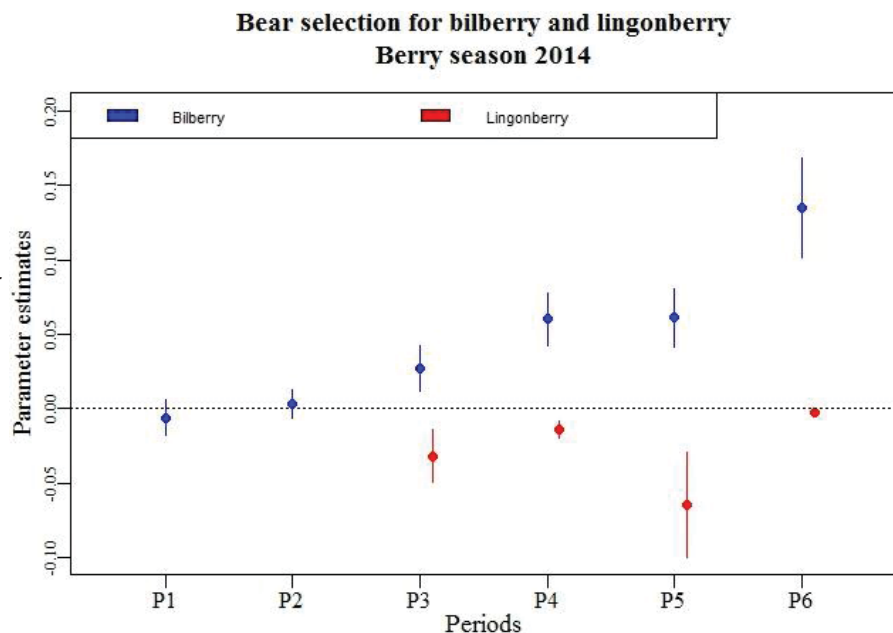
Do bears trade-off good berry sites for poor sites?

The interaction between forest roads and the bilberry index in the RSF models was highly significant in period 1 and 5 (Appendix 1). Additionally, the interaction term between permanent residential areas and the bilberry index in the RSF models, was significant in period 6 (Appendix 1). Although Figure 8 suggested that bears selected against lingonberries in all periods, the RSF modelling result from period 5 indicated that the interaction between forest roads and the lingonberry index was significant (Appendix 1 and Figure 7e). Based on the RSF modelling results, new predictions were made to analyse the interaction terms further, which are illustrated in Figure 9, 10 and 11.

Forest roads and bilberries

Figure 9 demonstrates the temporal probability of bears using an area in relation to the distance to forest roads and the abundance of bilberries. The density of forest roads ranged from 0-2.4km, and the four coloured lines illustrated the probability of bear selection at different distances away from forest roads (red=0km, orange=0.8km, yellow=1.6km and green=2.4km) (Figure 9). The
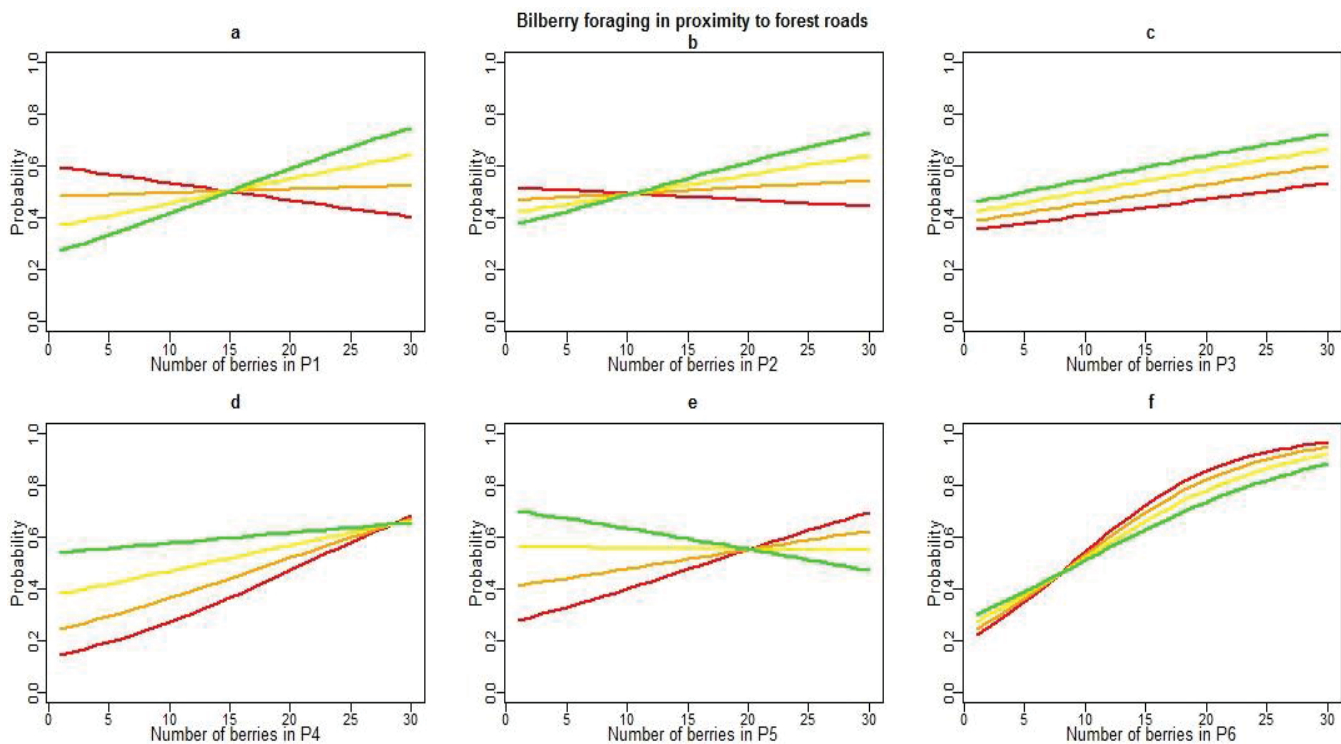
Figure 9: New predictions: Bear probability of selecting areas for bilberry foraging in relation to forest roads in each 20-day period with 10 days overlap (1-6), within the 2014 berry season (11 July – 18 September), in the study area in south-central Sweden. A-f representing the six periods and illustrating the temporal change of selection. Lines represent different distances to forest roads: red=0km, orange=0.8km, yellow=1.6km and green=2.4km. The interaction term was significant in period 1 and 5 in the RSF models.

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curve of the lines predicted bear selection in response to the berry index, ranging from 1-30 bilberries/m^2.

The interaction term "distance to forest roads * bilberry availability index" was significant in period 1 and 5 (0.040±0.014 and -0.079±0.024, respectively) (Appendix 1) in the RSF models. The new predictions suggested that at the onset of the study (period 1 and 2), bears selected areas close to roads (red line), even if these areas contained low numbers of bilberries (Figure 9a and b). During these periods, bears also selected for areas far away from forest roads (green line) with high availability of bilberries. As the season progressed (period 3 and 4) bears generally selected areas further from roads and with relatively high numbers of bilberries (Figure 9c and d). However, in period 4 bears also selected for areas with few bilberries further away from forest roads. During period 5 (Figure 9e), bears avoided areas close to forest roads with low numbers of bilberries, but selected for these areas when bilberry availability was relatively high. Then, areas further from roads were generally selected for, even if the bilberry availability was low. Towards the end of the study (period 6), bears selected for sites with high bilberry abundance, irrespective of distance to forest roads (Figure 9f).

Residential areas and bilberries

Figure 10 illustrates the new predictions of bears selecting an area in relation to the distance to residential areas and bilberry index. The density of residential areas within the study area was less than forest roads, with distance to residential areas ranging between 0.13-11.2km. The four coloured lines represented different distances away from residential areas (red=0km, orange=3.6km, yellow=7.2km and green=10.8km) (Figure 10). The curve of the lines predicted bear selection in relation to the bilberry index, ranging from 1-30bilberries/m^2. The interaction term "distance to residential areas * bilberry availability index" was significant in period 6 (0.020±0.007) (Appendix 1) in the RSF models.

The new predictions indicated that bears were indifferent to the distance away from residential areas in period 1 and 2 (figure 10a and b). During the middle of the berry season (period 3 and 4) bears selected for highly available bilberry sites closer to residential areas (red line, figure 11c and d). Although bears were more likely to select areas close to residential areas in period 3 and 4, bears also selected for highly bilberry rich sites further away from residential areas (green line, figure 10c and d). This suggests that bears generally selected for sites with high

availability of bilberries in period 3 and 4. In period 5 and 6, bears selected highly berry rich sites further away from residential areas (figure 10e and f). However, bears still used bilberry poor areas close to residential areas. In short, bears selected for highly berry rich sites close to residential areas in period 3 and 4, and for highly rich bilberry sites further away from residential areas period 5 and 6.
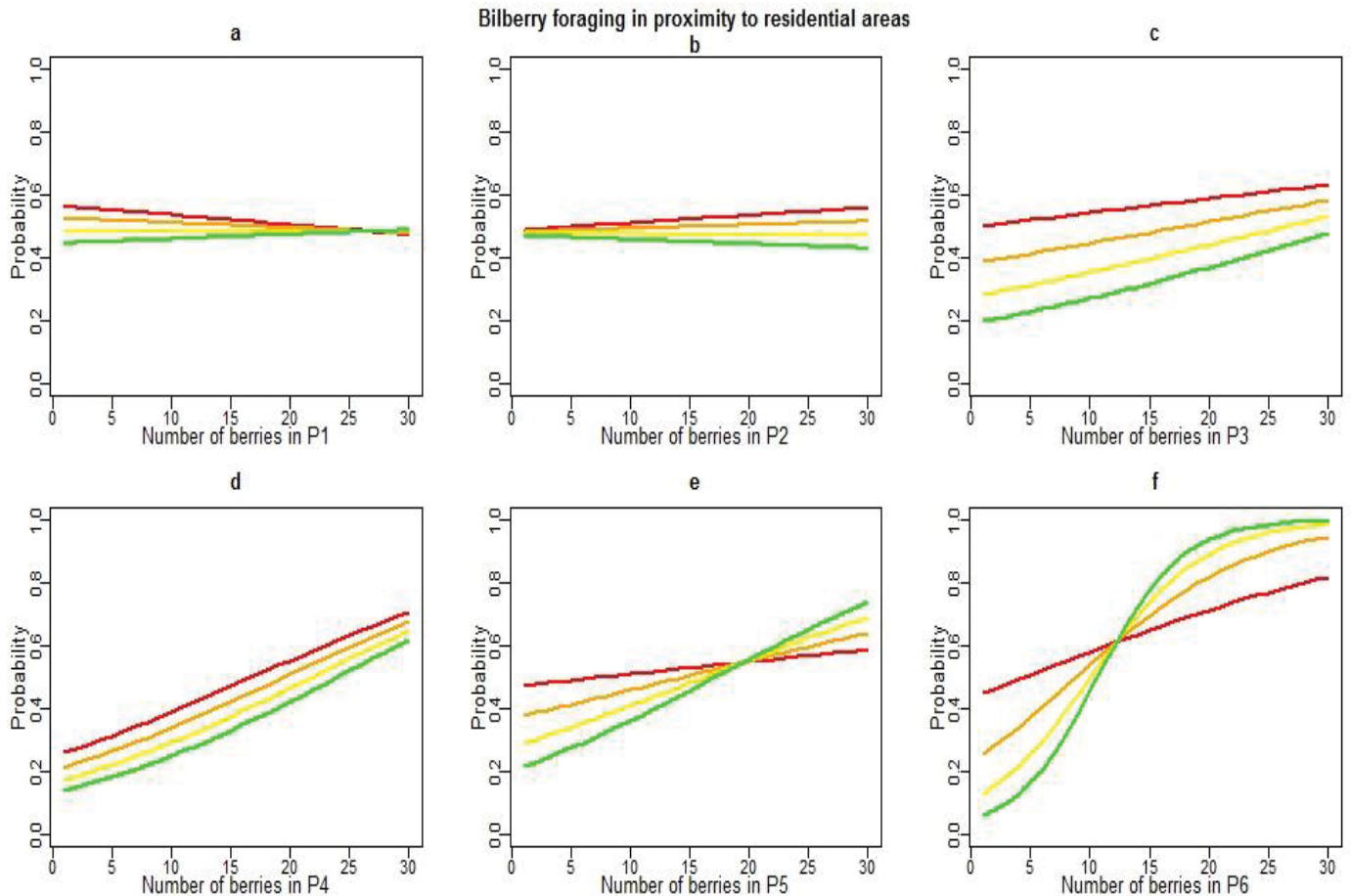
Figure 10: New predictions: Bear probability of selecting areas for bilberry foraging in relation to residential areas in each 20-day period with 10 days overlap (1-6), within the 2014 berry season (11 July – 18 September), in the study area in south-central Sweden. A-f representing the six periods and illustrating the temporal change of selection. Lines represents different distances: red=0km, orange=3.6km, yellow=7.2km and green=10.8km. The interaction term was significant in period 6 (f) in the RSF models.

Forest roads and lingonberries

Bears did not select for lingonberries in any period (Figure 8), but the interaction term between the "distance to forest roads * lingonberry index" was significant in period 5 (0.020±0.007) (Appendix 1) in the RSF models.

In the new predictions, bears generally selected against areas with high lingonberry availability in period 3, 4 and 6 (Figure 11a, b and d), regardless of distance to forest roads. However, in period 5 bears selected areas with high lingonberry availability further away from forest roads (Figure 11c). The probability of such an occurrence was close to 100% (Figure 11c), suggesting that forest roads had a negative impact on bear resource selection in period 5.
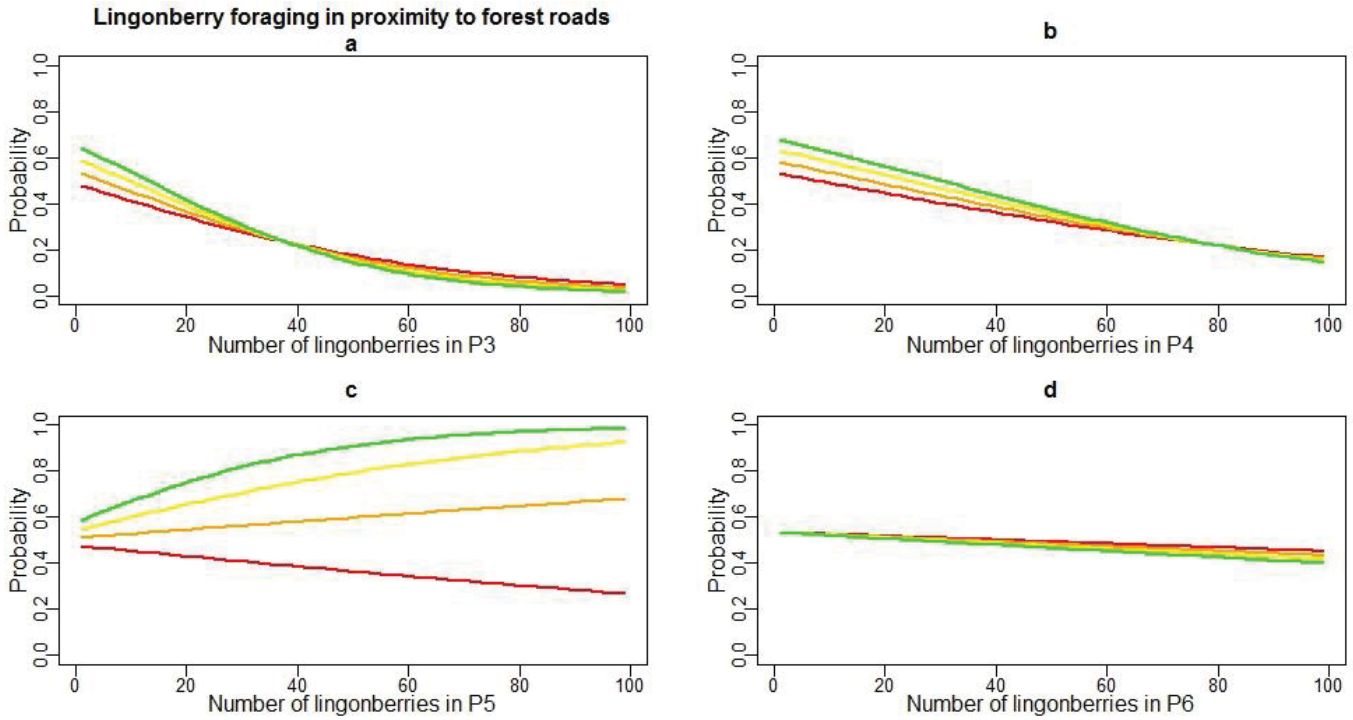
Figure 11: New predictions: Prediction of bear proximity to forest roads in relation to lingonberries, in the last four 20-day periods with 10 days overlap (3-6), within the 2014 berry season (11 July – 18 September), in the study area in south-central Sweden. *Lines representing different distances:* red=0km, orange=0.8km, yellow=1.6km and green=2.4km. *The interaction term was significant in period 5 (d) in the RSF models.*

Discussion

My study produced four key findings. First, I showed that a temporal "blue and red wave" indeed occurs in my study area (H1). Second, I showed that bears indeed selected for sites with high bilberry abundance in most periods and suggesting that bears could have "chased the blue wave" (H2). Bears did not select for lingonberries and did not chase the "red wave" (in contrast to H2). Third, I found that bears avoided areas close to main roads, forest roads, open water and buildings (H3). Fourth, I discovered that bears might be trading-off highly abundant bilberry and

lingonberry sites for areas further away from forest roads in period 5 (H4). Although bears did not trade-off good berry sites for poor sites further away from residential areas, bears did indeed feed on bilberries further away from residential areas during some periods.

Spatiotemporal predictions

Bilberry predictions

Bilberries are keystone species in boreal forests and mast at 3-4 year intervals and dominate the forest floor of boreal forests in Fennoscandia (Nybakken et al. 2013; Selås 2000). The bilberry shrub is associated with moderate tree density due to its shade-tolerance, but also grows in more open habitats if there is less competition with other shrubs (Parlane et al. 2006). The GAM results correlated well with the GLM results, which predicted the mean bilberry presence to peak between 1-21 August (Julian date 22-42) (Figure 3a), creating a temporal "blue wave" of bilberry availability (Figure 3). This means that bilberries indeed temporally matured across the berry season, supporting my main hypothesis (H1). As expected, my berry models also predicted high abundance of bilberries in habitats with high NDVI values, which corresponds with other studies suggesting bilberries to be abundant in old and mature forests associated with moderate sun penetration (Ihalainen & Pukkala 2001; Ihalainen et al. 2002; Ihalainen et al. 2003; Raatikainen et al. 1984). The most ideal bilberry habitat is mature coniferous forests with 10-50% sun penetration (Raatikainen et al. 1984). Spruce forests are denser and have less sun penetration, and bilberry production is therefore higher in pine- or mixed conifer forests (Ihalainen & Pukkala 2001). Although the maps of spatiotemporal bilberry availability only suggest a general trend and no clear results, the maps did suggest higher bilberry availability in mature and old forests, as well as clear-cuts (Figure 5). Although unexpected, bilberries could seem abundant on clear-cuts due to a delayed temporal response of the forest floor to logging (i.e. time lag) (Bergstedt & Milberg 2001). Bergstedt and Milberg (2001) discovered that bilberry production on clear-cuts decreases with time due to increased competition and that bilberry production was drastically reduced by the time the clear-cut turned into a young forest.

Lingonberry predictions

Lingonberries are widely distributed in Scandinavia (Gustavsson 2001) and the GAM results correlated well with the GLM results, predicting the mean lingonberry presence to peak between 24 August – 13 September (Julian date 45-65) (Figure 3b). The model results created a temporal

"red wave" of lingonberry availability (Figure 4), supporting H1. The "red wave" suggests that lingonberries matured at the end of the berry season, which was visualized in Figure 6. Overall, NDVI was the most important variable to predict lingonberry presence and availability, suggesting that highly dense lingonberry areas are associated with forest gaps or other open areas with much sun exposure (low NDVI values). Lingonberries do not grow in moist and dense spruce forests (Ihalainen & Pukkala 2001), supporting the model results about the importance of low NDVI values. During some periods, habitat type was also an important predictive variable for lingonberry availability and the most important habitat type was probably clear-cuts (Figure 6). Large open clear-cuts with high sun exposure are associated with low NDVI and could be expected to dry up the forest floor and promote favorable dry lingonberry conditions (Gustavsson 2001).

RSF models

Main effects
Overall trends from the RSF models suggest that bears selected for bilberries in period 3-5, and selected against lingonberries. Bears consistently avoided areas close to larger roads and water in all periods. While buildings were not included in the RSF model for period 1, bears consistently avoided buildings for the remaining periods. In contrast, bears selected residential areas in all periods, except period 1 when residential area was not considered an informative predictor. Less consistent was the response to forest roads, as bears selected forest roads in period one, but avoided forest roads in the other periods.

Bear selection for berries
The RSF model results suggested that bears did not select for bilberries in the two first periods and in the last period (Figure 9). According to the "blue wave", bilberry availability was predicted to peak from the middle of period 3 until the end of the study period (Figure 3). In the new predictions, bears selected for bilberries in all periods except period 1 and 2 (Figure 8). The abundance of mature bilberries was generally low in period 1 and 2, suggesting that bears selected for other resources than bilberries (Dahle et al. 1998). However, the peak of bilberry availability occurred at the same time when bears started to select for bilberries (Figure 8), supporting my hypothesis about bears "chasing the blue wave" (H2). Welch et al. (1997) report that bears often select for bilberries when they are visually abundant, and as the bears in my study

selected for bilberries during the bilberry peak-period, the visual abundance of bilberries likely facilitated bear selection for bilberries. Lingonberries also formed a "red wave" of availability (Figure 4) and the literature shows that lingonberries are highly abundant in Sweden (Gustavsson 2001; Ihalainen & Pukkala 2001). However, bears did not select for lingonberries (Figure 8) and therefore did not "chase the red wave" (in contrast to H2). Lingonberries could be available *at libitum* (bears self-regulate intake of lingonberries according to biological needs), which suggests that bears would not have to select for lingonberries in order to meet their requirements (Hertel et al. in revision).

Main roads

One of the larger roads in my study area is the longest national road (E45) in Sweden leading tourists and industry from the south all the way to the north and traffic volume can be high, especially during the tourist season. Northrup et al. (2012) revealed that bears show strong avoidance of medium- and highly traffic volume roads. This is supported by Gibeau et al. (2002) who found that large paved roads in Canada functioned as barriers for most bears, and especially for females. The high traffic volume during the berry season and predictable road activity on major roads in the study area probably explain why bears avoided larger roads, as bears might fear such roads due to high risk of human encounters or predation (Charnov 1976; Laundré et al. 2001). Humans are the greatest mortality risk for bears (Bischof & Swenson 2009), and bears are expected to optimize their foraging tactics in relation to the perceived predation risk by humans or the "landscape of fear" and avoidance of roads could therefore be expected.

Forest roads

According to the modelling results, bears selected forest roads in period 1. This could be unexpected as exposure to human encounters along forest roads is higher the in the forest and assuming that the fear of humans influence bears optimal foraging strategies (Laundré et al. 2001). During the early berry season, forest roads verges might trigger an earlier ripening of bilberries due to more sun and heat exposure, and bears might be attracted to these edges to forage on bilberries (Roever et al. 2008b). However, bears did not select for berries in period 1 and 2, and the selection for areas close to forest roads could be explained by the abundance of herbaceous plants growing close to roads during early berry season (Roever et al. 2008a). Bear summer diet is dominated by forbs and insects (Dahle et al. 1998), which could be highly

abundant along sun exposed forest roads. Alternatively, brown bear mating behaviour could explain the selection for forest roads (Steyaert in prep.). The mating season lasts from early May to mid-July (Dahle & Swenson 2003; Steyaert et al. 2012). Steyaert (in prep.) argues that adult males and lone adult females used forest roads to facilitate the search for a suitable mate. Forest roads are easier to travel along compared to the more rough terrain in the surrounding forests, which makes it energetically more efficient to follow forest roads. In addition, these roads could act as social-spatial networks for bears to meet. Additionally, the traffic volume on forest roads is generally low and less predictable than main roads (Roever et al. 2008b), which could be a complementary explanation to why bears use forest roads in period 1. By the end of July, the mating season is over and the new predictions suggested that bears avoided forest roads for the remainder of the season (Figure 9).

Residential areas

A study by Nellemann et al. (2007) suggests that the traffic pattern related to settlements and villages with permanent residents was very different to traffic patterns of resorts. The recreational zone surrounding resorts was 0-10 km, while activity in residential areas was more restricted to roads. Cabins are popular in my study area, and one could argue that cabins could attract the same recreational users as resorts, and a similar recreational zone as Nellemann et al. (2007) propose could be applied to cabins in my study area. This means that the bear I studied could have been more likely to encounter humans in close proximity to resorts and cabins, compared to residential areas. As the probability of human encounters was lower close to residential areas, highly abundant bilberry areas close to human settlements could have attracted bears. Although one of my main hypotheses (H3) postulated that anthropogenic structures such as residential areas has a negative impact on bear foraging behaviour, the results suggested that bears selected for residential areas closer than I expected. This could be related to my sampling method, where sampling across the study area rather than within the homeranges, could have been more appropriate as there are few residential areas within the study area. The few actual residential areas could be skewing the results in favour of residential areas, as some homeranges or bears could be overrepresented.

Additionally, as the traffic volume and human behavioural patterns associated with residential areas could be predictable (Nellemann et al. 2007), bears could be temporally avoiding the time periods of the day when human activity related to residential areas is high. Brown bear behaviour

in response to both long-term mine reclamation and road construction in the Cook City basin in the US revealed that bears foraging on white bark pine were not negatively impacted by the residential area or the landscape changes, as long as some natural areas with favourable resources remained intact (Tyers 2015, pers.comm.). The bears avoided the reclamation sites and construction work temporally by using the surrounding vegetation to access white bark pines at different times of the day when human activity was low (Tyers 2015, pers.comm.). The bears in my study could show a similar temporal movement pattern as the bears in Cook City, and utilize good bilberry sites close to residential areas at different times of the day when human activity is low.

Do bears trade-offs poor berry sites for good sites?

Bears should consume at least > 50 berries/m^3 in order to gain sufficient weight for hibernation (Welch et al. 1997), and bears in my study area selects for areas with an average of 55 berries/m^3 (Hertel et al. in revision). Although the average bear in my study foraged in areas with sufficient amount of berries, the RSF results suggests that some anthropogenic structures had a negative impact on bear resource selection in some periods during the berry season (H3).

The new models were used to test hypothesis 4 and potential trade-offs, as bears might trade highly abundant berry areas for areas further away from forest roads and residential areas in some periods. Although, trading-off highly resource rich areas for poor areas could have a negative impact on bears fitness (Brown & Kotler 2004), bears most likely avoided foraging close to forest roads and residential areas due to the predation risk associated with such anthropogenic structures (Laundré et al. 2001; Nevin et al. 2005).

Forest roads - Bilberries

The new predictions suggested that bears selected for abundant bilberry areas, regardless of the distance to forest roads in the beginning of the berry season. Bear selection for bilberries was therefore not negatively impacted by forest roads in period 1 (in contrast to H3) and bears did not trade good bilberry sites for poor sites further away from forest roads (in contrast to H4) in the beginning of the berry season. In contrast, bears overall selected areas with high bilberry availability further away from forest roads in the middle of the berry season, suggesting that forest roads indeed impacted bear resource selection negatively, supporting H3.

Legal bear hunting in Sweden starts 21 August, and is likely to increase the human use of forest roads (Ordiz et al. 2012). Bears are expected to alter their active foraging behaviour rapidly when the hunting season starts (Ordiz et al. 2012), probably related to balancing their foraging strategy in relation to the increased risk of predation (Charnov 1976; Laundré et al. 2001; Smith & Smith 2001). The new predictions suggested that bears avoided good bilberry rich areas close to forest roads and were more likely to select poor bilberry areas further away from forest roads in period 5 (Figure 9g). This might indicate that bears traded-off good bilberry areas for safer areas with less berries, supporting H4. The interaction term between forest roads and the bilberry index in period 5 were considered significant in the real RSF models, supporting the probability of the trend. However, bears also selected for bilberry rich areas close to forest roads during period 5 if these areas contained large amounts of bilberries, suggesting that bears also were willing to take large risks to access bilberries in period 5.

Bears showed tendencies of both foraging in poor bilberry areas further from forest roads and foraging in highly abundant bilberry areas close to forest roads in period 5, and this could reflect bears temporal adaptation to the hunting season by becoming more nocturnal feeders (Ordiz et al. 2012). Additionally, brown bears in Canada almost exclusively used forest roads at night, presumably because of the lower traffic volume during night time (Moe et al. 2007; Northrup et al. 2012). As the pattern in period 5 was only found in this period, which correlated well with start of the hunting season, bears in my study might select for highly bilberry rich sites along forest roads at night, and spend their daytime further away from forest roads in areas with less bilberries, to avoid humans. The time of day was not included in my RSF models, and the results could therefore be more nuanced than was presented (Moe et al. 2007). Further research should include "the time of the day" as a predictive variable for bear resource selection in relation to anthropogenic structures. By the end of the berry season, most legal bear harvesting quotas were filled and the overall hunting pressure reduced (SVA 2014, www.sva.se). Bears selected for highly bilberry abundant areas at the end of the berry season (Figure 9h), regardless of the distance to forest roads.

Forest roads - Lingonberries
Although bears did not select for lingonberries, bears were predicted to select for good lingonberry areas further away from forest roads in period 5 (Figure 11c). This suggests that forest roads might have a negative impact on bear resource selection in relation to lingonberries

in period 5, possibly supporting H3. The probability of bears selecting lingonberries further away from forest roads in period 5 ranges from 60% (less good lingonberry availability) to 100% (good lingonberry availability) (Figure 11c). As bears possibly were trading-off good lingonberry areas for poor areas further away from forest roads in the beginning of the hunting season, bears might show a similar trade-off pattern described for bilberries, possibly supporting Hypothesis 4. The increased human activity along forest roads during the start of the hunting season could explain why bears alter their behaviour in relation to lingonberries in period 5 (Ordiz et al. 2012). The interaction term between forest roads and lingonberry index for period 5 was significant in the original RSF models, suggesting that the possible trade-off trend discovered in period 5 in the new predictions could indeed have occurred.

Residential areas - bilberries

According to the new predictions, bears foraged close to residential areas in period 1-4, suggesting that residential areas did not have a negative impact on bear resource selection in those periods (in contrast to H3). At the end of the berry season, bears selected for good bilberry areas further away from residential areas. The new predictions did not indicate that bears traded-off good berry areas close to residential areas for poor berry areas further away (Figure 10) (in contrast to H4). Changes in resource selection could be triggered by rapidly increased human activity related to cabins, resorts and towns caused by the hunting season, ultimately altering bear resource selection behaviour (Ordiz et al. 2012). Human behavioural patterns and traffic volume related to residential areas as described by Nellemann et al. (2007) could become less predictable during the hunting season, which could explain why bears selected for highly bilberry rich areas further away from residential areas. Residential areas did indeed have a negative impact on bear foraging behaviour at the end of the berry season, supporting H3, as bears selected abundant bilberry areas further away from residential areas. The interaction term between residential areas and bilberries in period 6 was significant in the original RSF models, supporting the new prediction of bears also selecting good bilberry areas further away from residential areas. The trend in period 6 could be explained by bears ability to temporally adapt to certain human activities and avoid time periods with high human activity to access vital resources (Tyers 2015, pers.comm.). The bears could have selected good bilberry areas close to residential areas at night, as bears are known for becoming more nocturnal during increased human activity levels (Ordiz et al. 2012; Roever et al. 2008b).

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Alternatively, individual bears might perceive fear of residential areas differently, as some bears might be young and inexperienced, and generally expose themselves to higher risks (Nellemann et al. 2007) than adults (Gibeau et al. 2002). Younger bears are more likely to occupy areas in close proximity (<10km) to settlements and towns in Sweden (Elfström et al. 2014b; Nellemann et al. 2007), while adult (>7 years) males were 92% more likely to occupy areas more than 10 km from resorts and settlements (Nellemann et al. 2007). Bears that selected areas close to residential areas in my study could be young and less experienced, and further research should therefore include age as a predictor variable to investigate whether different age classes respond differently to bilberry foraging in proximity to residential areas. Additionally, bears temporal response to residential areas could vary throughout the year as bears select densely vegetated resting sites further away from residential areas during the berry season than the spring (Ordiz et al. 2011). Further analysis of temporal activity patterns of bears is therefore needed to comprehend the complexity of bear spatiotemporal selection for bilberries in relation to residential areas.

Scandinavian bears do not visit residential areas to forage on human foods (Elfström et al. 2014a), and the overall trend of bears selecting areas in relative close proximity to residential areas could be explain by drivers such as social organization (Steyaert et al. in revision-a) or bear selection for natural resources surrounding residential areas. Nature close to residential areas could be mature and old forest associated with high bilberry availability (Ihalainen et al. 2002; Raatikainen et al. 1984), and therefore explain bears immediate attraction to surrounding residential areas. The range of used positions in relation to residential areas was 0.103-11.457 km, suggesting that my bears stayed at the minimum 100 meters away from any residential area. The relationship between distance to residential areas and bear habitat use was non-linear throughout the berry season (Appendix 2), suggesting that a different method might have been more appropriate to capture this non-linear response. I suggest that the distance to residential areas (continuous variable) could be broken up into a categorical factor. Either by using "Jenks natural breaks classification method", which minimizes the variance within each group while maximizing the variance between the groups (Jiang 2013), or by using a regression spline in the models, similar to the method used for the spatiotemporal berry predictions. This could provide more details about which distance group away from residential areas bears actually select or avoid.

Critique of method

The scale used in the RSF models should reflect the purpose of the project (Boyce et al. 2003; Boyce 2006) and as this project aimed to analyse bear selection for berries, I chose to focus on the berry season, as this is when berries are available. Additionally, scale could also influence the distribution of available positions as these were randomly distributed within each bear homerange, and the minimum distance from the used bear positions to residential areas therefore restricts the minimum distance of available positions to residential areas. The results could have been very different if random available positions were distributed across the entire study area, as available positions might have fallen closer to residential areas. However, few residential areas were included in the homeranges, and this could explain why the density curve of used and available positions in relation to residential areas are close to identical, in terms of close proximity to residential areas (Appendix 2).

My interpretation of "chasing the blue/red wave" was based on visual comparisons of the peak-period of berries in the two figures: bear selection for berries (Figure 8) and temporal bilberry/lingonberry availability (Figure 3 and 4, respectively). Without sufficient quantitative results, the "chasing of the blue/red wave" remains a visual trend and cannot be scientifically proved at this stage. Such a trend could however indicate that there is a relationship and more research is needed to investigate this further. Additionally, the new bear selection predictions for both bear selection for berries and the bear selection for berries in relation to anthropogenic structures, were not based on the most parsimonious RSF models, but on new models created to visualize selected trends. This means that any new prediction based on either the results from the bear selection for berries, or the bear selection for berries in relation to anthropogenic structures models are not significantly predicted to occur. However, if the new predictions correlates with the results from the original RSF models, the new predictions could be considered more likely to occur.

Although most findings have been discussed, the arguments used to analyse my results originated from the selected literature used. Other aspect of bear foraging behaviour not presented in my thesis could however be applicable.

Model validation

Although the role of model validation is debated, model validation could be important in terms of model result credibility (Rykiel 1996), and all models produced for this thesis were therefore validated. The models for berry presence were validated by the commonly used *cv.binary* function, were the model predictive accuracy is considered better the higher the value (Maindonald & Braun 2010; Zuur et al. 2009). As all models for both lingonberry and bilberry presence had values > 0.6, they all were considered reasonable. Dispersion parameters were used as a measure of model validity, and as all bilberry and most lingonberry availability models had dispersion parameter values close to 1, all were considered good. The exception was the lingonberry availability model in period 3, which had a value of 0.52. This suggests that the model is underdispersed (exhibit less variation than the mean or expected), but the model could still be considered positive. All RSF models were cross validated and ranked according to the Spearman correlation, suggesting good predictive accuracy for the RSF model in period 2 and 3 (1.00 and 0.79) (Boyce et al. 2002; Klar et al. 2008). The RSF models from period 4, 5 and 6 could be considered reasonably good (0.62, 0.60 and 0.60, respectively) (Westerling et al. 2006). The Spearman rank correlation was only 0.25 for the RSF model in period 1, suggesting weak predictive accuracy of the RSF model in this period. However, the relation is positive, suggesting that there could be a relationship between two or more predictive variables (Weir 2015; Zuur et al. 2009).

Management implications

It is obvious from both the RSF results and the new predictions that bears selected for bilberries in some periods, and that bear behaviour during the berry season could have revolved around balancing the risk of human encounters and gaining sufficient amounts of berries. The availability of berries could therefore be highly important for bears overall fitness, and any factors affecting either the access to highly bilberry available areas or the availability of berries directly, could be regarded as potential threats to bear fitness. Bear foraging behaviour changed rapidly when the hunting season started. Further analysis of this trend and its management implications would be highly informative in relation to anthropogenic influence on bear foraging behaviour. However, among several factors that could alter berry availability or access, I chose to focus on some factors that can reduce berry availability, such as climate change and forestry, commercial berry picking and structural forest change.

Climate Change and forestry

Climate change is expected to increase climatic variation, precipitation at northern latitudes and ultraviolet beta UV-B radiation, as well as the occurrence of winter warm spells (Bokhorst et al. 2008; Schultz 2000). Such winter warm spells are extremely harmful for the berry crop; i.e., repeated mid-winter thaw-frost events can reduce bilberry production by up to 80% (Bokhorst et al. 2008). Increased UV-B radiation reduced bilberry stem growth and increased bilberry herbivory (Phoenix et al. 2001), while increased UV-B radiation reduced herbivory on bog bilberries (*V. uliginosum)* and ultimately promoted bog bilberry growth at the expense of bilberries (Gwynn-Jones et al. 1997). Consequently, many northern species that rely on bilberries are expected to exhibit food stress due to climate change in the coming decennia. One possible way to buffer such events would be to achieve longer rotation rates in both pine- and spruce forests, as well as more thinning of the spruce forests to increase sun penetration and thus promote berry production (Miina et al. 2010). However, Nybakken et al. (2013) argue that although clear-cutting does not have a negative impact on bilberry availability, the quality of bilberries on clear-cuts might be reduced as the phenolic concentration is higher on clear-cuts, which could affect bilberry availability and consequently reduce herbivores` access to berries. Additionally, Selås (2000) reports that the local berry reproduction trend and weather conditions could influence bilberry floral development, pollination, and seed ripening, which means that clear-cutting (Nybakken et al. 2013), climate change (Atlegrim & Sjöberg 1996; Parlane et al. 2006), and previous reproduction and weather conditions (Selås 2000) combined could affect berry availability negatively. As bears clearly selected for bilberries (Figure 8) and depend on berries to gain sufficient carbohydrates for hibernation (Felicetti et al. 2003; Welch et al. 1997), altered berry availability could reduce bear foraging efficiency and ultimately reduce bears overall fitness. Further research on bears selection for berries in relation to forestry is needed to comprehend the negative impacts of clear-cutting on bilberries (Ihalainen & Pukkala 2001) to compensate for climatic induced bilberry reduction (Bokhorst et al. 2008).

Berry picking

Berry picking as a recreational, as well as a commercial activity is embedded in Fennoscandian culture. In Finland, 92-312 million kg of bilberries and 129-386 million kg of lingonberries were picked annually, which in 1997-1999 was equivalent to 5-6% and 8-10% of Finland's annual bilberry and lingonberry yield, respectively (Turtiainen et al. 2011). The 15.4 million kg

commercial berries picked in 1997 was valued EUR 115 million (Saastamoinen et al. 2000). Although most people picked for personal consumption prior to 1997 (Saastamoinen et al. 2000), todays commercial berry pickers outnumber recreational pickers (Turtiainen et al. 2011). Commercial berry agencies log the annual amount of berries picked, but I was not granted access to the local database in Sweden to analyse the amount of berries commercially picked during the 2014-berry season within my study area. Nevertheless, personal observations from the field suggests that foreign berry pickers efficiently clear large areas of bilberries and lingonberries. Although I mostly observed pickers close to forest roads (< 200m), I also met commercial berry pickers several kilometres from the nearest road. I would expect that the amount of berries picked in 2014 was larger than the 1997-estimates, as the commercial berry industry has increased (Saastamoinen et al. 2000). Commercial berry picking could influence bears resource selection for berries, as berry pickers could alter both bears foraging behaviour (Sahlén et al. 2015) and potentially the local berry availability.

Structural forest changes
The forest structure have changed dramatically following centuries of commercial logging, rotation time of 120 years and large clear-cuts (Linder & Östlund 1998). Linder and Östlund (1998) further argue that such intense harvesting methods have resulted in a forest dominated by younger, denser stands and that less than 1% old trees remain (more than 50cm). This has transformed the forest structure and altered the species composition. Bilberries are associated with half-shady conditions and sensitive to changing light and temperature (Atlegrim & Sjöberg 1996; Bokhorst et al. 2008). Bilberries are one of the most important forest resources for the Swedish fauna and one could expect changes in bilberry availability to influence the species relying on this resource, such as bears. Structural forest changes can alter foraging behaviour and a study by Maurer and Whitmore (1981) suggest that the foraging behaviour of American Redstarts (*Setophaga ruticilla*) changed in response to more mature forest complexity. The Redstarts showed a narrower foraging niche in younger and denser forests, while the bird became more opportunistic as the niche increased significantly in response to improved resource availability in mature forests. The structure of mature forests is overall more complex and Maurer and Whitmore (1981) argue that the observed foraging alterations relates to the change in forest complexity, and stress the need to study foraging behaviour in relation to the distribution of resources and plant community structure. I therefore argue that intense logging and rapid rotation

rates in Sweden could have increased the proportion of both young forest and open areas such as forest roads and large clear-cuts, and consequently promoted ideal lingonberry habitats in the expense of bilberry yield. Such changes in berry species proportions could influence bear resource selection, behaviour, and population structure. Further research is needed to investigate the relationship between changing plant community structures and bear resource selection, to comprehend how structural forest changes in Sweden influence resource availability and bear selection.

Conclusion

As animals constantly balance their optimal diet and foraging strategies in relation to the perceived predation risk, brown bear foraging behaviour in relation to anthropogenic variables were expected to illustrate this. Brown bears are apex animals and were, and still are in some places heavily hunted by humans. Human caused mortality is currently the main cause of brown bear mortality in several countries, and although most brown bears avoid humans, studies also reveal that some cohorts, age groups or individual bears might seek out human dominated areas for various reasons such as protection, due to lack of experience or due to human waste. Bears are omnivores and their diet varies depending on the season, where berries are the most important sources of carbohydrates for hibernation.

The spatiotemporal berry predictions suggested that both bilberry and lingonberry availability formed a temporal non-linear trend across the berry season, supporting the occurrence of a "blue/red wave" of berry availability (H1). Bears overall avoided large roads, open water and buildings throughout the berry season, but selected for bilberries in several periods (H2), but never selected for lingonberries (in contrast to H2). The overall results suggest that bears avoided any resources in close proximity to these anthropogenic structures and as bears could associate any activity along roads, open water and buildings with humans and the fear of either encountering or being killed by humans. Bears avoided forest roads in most periods and showed a weak trend of trading-off good bilberry sites close to forest roads for poor bilberry sites further away from forest roads in period 5. This could support H4. The trade-off mechanism could be related to the hunting season, as the increasing risk of getting shot or encounter humans near forest roads might have forced bears to use less resource rich areas associated with less predation

risk. However, bears also selected for the most bilberry rich areas close to forest roads in period 5, possibly weakening the suggestion of a trade-off mechanism occurring.

Bears pursuit for bilberries was not influenced by any proximity to residential areas during period 1 to 4, presumably due to predictable human activity patterns, suggesting that the perceived predation risk could be less in areas where human activity follow a regular pattern. However, bear selection for bilberries changed toward the end of the berry season as bears selected for highly bilberry rich areas further away from residential areas. The increased human activity associated with the start of the hunting season correlated with this behavioural change of avoiding residential areas. However, human activity patterns could be less predictable during the hunting season, as the overall human density within the study area increases, especially related to residential areas. Bears might avoid such human crowded areas as the risk of human encounters or the fear of being killed is increased. However, no trade-off occurred as bears were able to utilize good bilberry areas further away from residential areas. This means that bears might be able to utilize good bilberry areas closer to residential areas during night through temporal avoidance, also during the hunting season. Although bears were able to feed sufficiently in relation to residential areas during the hunting season, bears seemed to be more negatively impacted by the hunting season in relation to forest roads. The availability of berries correlated well with predicted bear selection for berries, as well as with the start of the hunting season, which means that bears access to berries along forest roads could be restricted by hunting.

My study clearly shows that bears selected bilberries during three periods, that bears most likely chased the "blue wave" and that bears pursuit of bilberries was indeed restricted by the dense network of large roads, buildings, open water, forest roads and residential areas, especially during the hunting season. With low human density within the study area, bears seemed to be able to access good berry sites through temporal adaptation to human activity patterns, also during the hunting season. Bear foraging behaviour was however more negatively impacted by the combination of forest roads and the hunting season, as this might have forced bears to use berry poor areas further away from forest roads. These findings correlates well with the general theory of both optimal foraging and how animals are expected to select resources in "a landscape of fear". Further research on bear resource selection in relation to anthropogenic structures is needed to fully comprehend the complexity of foraging behaviour.

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Appendix 1

Parameter estimates, standard error SE, test statistic/z and p values from all RSF models, in each 20-day period with 10-day overlap during the 2014 berry season (11 July – 18 September), within the study area in south-central Sweden (Table continue on the next page).
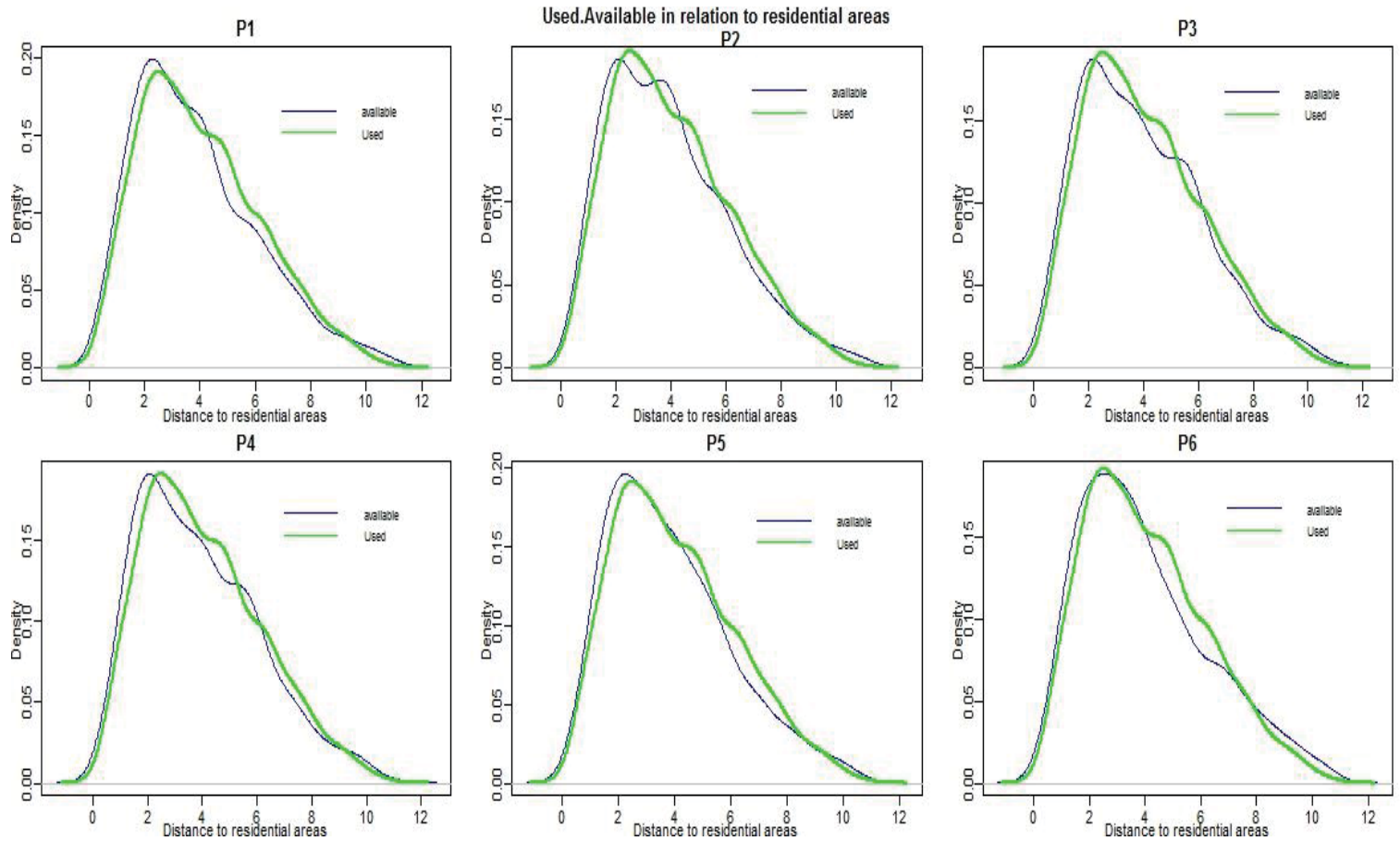
Period	Model	Model terms	Estimate	SE	Test statistic	*P*
1	8	Intercept	-0.541	0.200	-2.706	0.007
		Road	0.108	0.017	6.525	0.000
		Forest road	-0.570	0.239	-2.382	0.017
		Bilberry index p1	-0.027	0.009	-2.931	0.003
		Residential areas	-0.026	0.021	-1.253	0.210
		Water	0.682	0.081	8.391	< 2e-16
		Forest road * Bilberry index p1	0.040	0.014	2.901	0.004
2	2, 6 and 5#	Intercept	-1.259	0.241	5.719	< 2e-07
		Road	0.094	0.025	3.766	0.000
		Bilberry index p2	-0.001	0.010	0.113	0.910
		Forest road	0.055	0.294	0.188	0.851
		Residential areas	-0.041	0.024	1.739	0.082
		Buildings	0.123	0.049	2.550	0.011
		Water	0.923	0.163	5.643	< 2e-16
		Road * Bilberry index p2	-0.0005	0.001	0.466	0.641
		Forest Road * Bilberry index p2	0.010	0.014	0.694	0.488
		Water * Bilberry index p2	0.003	0.007	0.351	0.726
3	6	Intercept	-1.171	0.218	-5.370	0.000
		Road	0.072	0.015	4.894	0.000
		Forest road	0.277	0.102	2.711	0.007
		Residential areas	-0.093	0.025	-3.771	0.000
		Water	0.726	0.104	6.966	0.000
		Buildings	0.063	0.047	1.343	0.179
		Bilberry index p3	0.027	0.008	3.331	0.001
		Lingonberry index p3	-0.032	0.009	-3.523	0.000
4	6	Intercept	-1.912	0.258	-7.421	0.000
		Road	0.078	0.013	5.982	0.000
		Forest road	0.240	0.106	2.256	0.024
		Residential areas	-0.053	0.024	-2.247	0.025
		Water	0.643	0.100	6.407	0.000
		Buildings	0.117	0.046	2.532	0.011
		Bilberry index p4	0.060	0.009	6.580	0.000
		Lingonberry index p4	-0.014	0.003	-4.568	0.000
5	2	Intercept	-1.962	0.685	-6.463	0.000

		Road	0.017	0.034	0.516	0.606
		Bilberry index p5:Forest road	0.080	0.021	3.884	0.000
		Forest road	1.145	0.314	3.644	0.000
		Lingonberry index p5	-0.106	0.042	-2.514	0.012
		Residential areas	-0.024	0.022	-1.101	0.271
		Buildings	0.099	0.044	2.241	0.025
		Water	0.685	0.098	7.002	0.000
		Road * Bilberry index p5	0.004	0.002	1.775	0.076
		Bilberry index p5 * Forest road	-0.079	0.024	-3.285	0.001
		Road * Lingonberry index p5	-0.003	0.004	-0.648	0.517
		Forest road * Lingonberry index p5	0.106	0.051	2.094	0.036
6	7	Intercept	-1.172	0.345	-3.399	0.001
		Road	0.094	0.012	8.068	0.000
		Residential areas	-0.259	0.075	-3.447	0.001
		Bilberry index p6	0.052	0.034	1.527	0.127
		Lingonberry index p6	-0.004	0.002	-2.347	0.019
		Buildings	0.153	0.043	3.525	0.000
		Water	0.526	0.098	5.395	0.000
		Residential areas * Bilberry index p6	0.020	0.007	2.768	0.006
		Residential areas * Lingonberry index p6	0.000	0.000	0.605	0.545

Model average made of all informative models

Appendix 2

Line graph with both used and available bear positions in relation to the distance from permanent residential areas to used/available position, in each 20-day period with 10-day overlap during the 2014 berry season (11 July – 18 September), within the study area in south-central Sweden. The blue lines represent available positions and the green are used.

Used.Available in relation to residential areas