Norwegian University
of Life Sciences

Master's Thesis 2016 60 credits

Norwegian University of Life Sciences
Faculty of Environmental Science and Technology
Department of Ecology and Natural Resource Management

Denning ecology of Scandinavian brown bears (*Ursus Arctos*) in a dynamic landscape

Alja H. I. Mannaart
Master in Biology

Photo: Danny Green photography.

Ås, 13 May 2016

Alja H. I. Mannaart

Table of contents

Summary

Human encroachment, habitat fragmentation, resource exploitation, and hunting can affect the presence, habitat use, behavior, life history, and population dynamics of wildlife species. Wide-ranging large mammals with low reproductive rates are especially susceptible to negative fragmentation effects at the population level. In Scandinavia, brown bears (*Ursus arctos*) were persecuted for centuries, almost leading to extinction. However, they recovered after being protected in the early 20th century. As an adaptation to survive the winter in environments with strong seasonality and when food is scarce, the brown bear hibernates. Therefore, they spend about 5-7 months in a den every winter. Den disturbance by humans leads to arousal from hibernation and den abandonment, which is extremely costly in terms of energy loss and offspring survival. This makes the choice of den site and den type important, and is a reason why the brown bear avoids human activity. Especially pregnant females are more selective in choice of den type as they give birth to multiple altricial young in their winter den. Because reproduction is costly in terms of energy use, pregnant females may show a preference for anthill dens, as these seem to result in the best reproductive success. However, there is an indication of a decline in the use of anthill dens by brown bears in our study area, which might indicate a decline in the availability of suitable, i.e., large, inactive, anthills. This could partially be because anthills probably take a long time to reach dimensions suitable for denning and therefor are most likely found in old forest. Also, clearcuts are probably destroying anthills directly, and therefore potential dens. Intensive forestry could therefore be a cause to the decline in anthill use for denning. To sum up, good quality denning sites are probably far away from anthropogenic activity and in older growth forests containing big anthills. I hypothesize (H1) that there has, in fact, been a decrease in the probability of female bears denning in an anthill den in the study area over the years 1986-2014. Secondly, I hypothesize (H2) that the probability of denning in an anthill den is positively related to (H2a) old growth forests and to (H2b) areas far from human disturbance (e.g., settlements and roads). I also predict (H2c) that anthill dens occur less frequently in clearcuts than random. Thirdly, I hypothesize (H3) that habitat loss and fragmentation has negatively affected the availability of good-quality denning sites during the study period (1986-2014). I used a logistic mixed effect regression model to predict the probability for a bear (all bears) to use an excavated anthill as a den. I also did this separately for adult pregnant females (< 3 years) and adult females (< 3 years) that entered the den with cubs (1 year and older). Results showed a temporal decline (1986-2014), and a positive correlation with age of the bear. I used the resource selection function (RSF) modeling approach to evaluate spatial patterns in den site selection by comparing resource ‘use’ with resource ‘availability’ with a logistic regression model. Results showed avoidance of anthropogenic structures, and clearcuts and bogs. I also mapped the model output of the most parsimonious model of the RSF models to assess den site selection for all dens, and for anthill dens alone (used by females of all age classes). With this I visualized general denning and anthill den habitat suitability in the study area (2000-2014). The results showed a degradation in quality of habitat over the study period.

Sammendrag

Menneskelige inngrep, fragmentering av habitat, ressursutnyttelse, og jakt kan påvirke tilstedeværelse, habitatbruk, adferd, livshistorie og populasjonsdynamikk av dyrearter. Store pattedyr som beveger seg over store områder og har lav reproduksjon, er spesielt utsatt for negative effekter av fragmentering på populasjonsnivå. I Skandinavia ble brunbjørnen (*Ursus arctos*) intensivt jaktet på i århundrer, noe som nesten førte til utryddelse. Populasjonen tok seg derimot opp igjen etter å ha blitt beskyttet i begynnelsen av det 20. århundre.

Som en tilpasning til å overleve vinteren i miljøer med sterke sesongvariasjoner, og tider med lite mat, går brunbjørnen i dvale. Den tilbringer derfor ca. 5-7 måneder i et hi hver vinter. Forstyrrelse av mennesker kan føre til oppvåkning fra dvale og forlating av hiet, noe som er svært kostbart i form av energitap og overlevelsen av eventuelt avkom. Dette gjør valget av hi område og type hi viktig, og er en grunn til at bjørnen unngår områder med menneskelig aktivitet. Spesielt gravide hunner er mer selektive i valg av type hi, siden de føder flere hiboende unger i vinter hiet. Siden reproduksjon er kostbart i forhold til energibruk, kan gravide hunner vise en preferanse for maurtue hi, da disse ser ut til å resultere i best reproduktiv suksess. Men det er en indikasjon på at det er en nedgang i bruken av maurtue hi av brunbjørn i vårt studieområde, noe som kan tyde på en nedgang i selve tilgjengeligheten av egnede, dvs. store, inaktive, maurtuer. Dette kan delvis være fordi det trolig tar lang tid for maurtuer å bli av størrelser som er egnet for et hi, noe som gjør det mest sannsynlig å finne dem i gammel skog. Dessuten ødelegger flatehogst sannsynligvis maurtuer direkte, og derfor potensielle hi. Intensiv skogbruk kan derfor være en årsak til nedgangen i bruken av maurtuer som hi.

For å oppsummere, prefererte hi områder er trolig langt borte fra menneskelig aktivitet og har eldre skog som inneholder store maurtuer. Min første hypotese (H1) er at det faktisk har vært en nedgang i sannsynligheten for at binner lager hi i en maurtue i studieområdet i løpet av årene 1986-2014. Min andre hypotese (H2) er at sannsynligheten for at en bjørn lager hi i en maurtue er positivt relatert (H2A) til gammel skog og (H2b) til områder langt fra menneskelige forstyrrelser (for eksempel bosetninger og veier). Jeg forutsier også (H2c) at maurtue hi finnes sjeldnere i hogstflater enn tilfeldig. Min tredje hypotese er at (H3) tap av habitat og fragmentering negativt har påvirket tilgjengeligheten av gode kvalitets hi områder i løpet av studieperioden (1986-2014). Jeg brukte en logistisk blandet effekt regresjonsmodell for å forutsi sannsynligheten for at en bjørn (alle bjørner) bruker en utgravet maurtue som et hi. Jeg gjorde også dette separat for voksne gravide binner (<3 år) og voksne binner (<3 år) som gikk inn i hi med unger (1 år og eldre). Resultatene viste en tidsmessig nedgang (1986-2014), og en

positiv sammenheng med alderen på bjørnen. Jeg brukte ressurs valgfunksjonens (RSF) modellerings metode, for å evaluere romlige mønstre i valg av hi område ved å sammenligne ressurs 'bruk' med ressurs "tilgjengelighet", med en logistisk regresjonsmodell. Resultatene viste unngåelse av menneskeskapte strukturer, og hogstflater og myrer. Jeg har også kartlagt modellens ‘output’ av den beste og mest enkle RSF modellen for å vurdere valg av hi område for alle typer hi, og for typen maurtue hi alene (brukt av binner i alle aldersklasser). Med dette visualiserte jeg generell bruk av hi og habitat egnet til maurtue hi i studieområdet (2000-2014). Resultatene viste en degradering i kvalitet av habitat i løpet av studieperioden.

Introduction

Human population growth has accelerated dramatically over the last 300 years and has had an enormous impact on the environment (Cohen 1995). Human encroachment, habitat fragmentation, resource exploitation, and hunting can affect the presence (Fahrig 1997), habitat use (Sahlén et al. 2011), behavior (Swenson et al. 1999), and life history and population dynamics of wildlife (Cartwright et al. 2014; Rytwinski 2012). For example, gray wolves (*Canis lupus*) were formerly distributed throughout the USA south of Canada, but government-supported eradication programs extirpated wolves from 8,000,000 km^2 of their former range in North America alone (Woodroffe et al. 2005). Deforestation and fragmentation of the Atlantic Forest biome of South America is the foremost threat of the now severely endangered jaguar (*Panthera onca*) (Cullen Jr. L. 2005; De Angelo 2009; Haag T. et al. 2010). Fragmentation can isolate wildlife populations, decrease their genetic variability, and eventually lead to local extinctions (Pertoldi et al. 2001).

When anthropogenic processes destroy habitat, it typically results in two main components; i.e., habitat fragmentation and habitat loss (Fahrig 1997). Fragmentation of habitat is usually an effect of anthropogenic activity and implies the breaking up of a continuous landscape into smaller patches, transforming the landscape in a mosaic of patches with different habitat or land cover types (Bender et al. 1998; Buskirk 2000). Habitat loss means the actual removal of habitat from the landscape, i.e., being destroyed to such an extent that all of its natural occurring species and ecological communities no longer can be supported by it, leading to their disappearance and possibly extinction (Bender et al. 1998; Pimm & Raven 2000). Other effects caused by these components are; increased isolation of habitat patches, reduced interpatch connectivity, changes in ecological processes, reduced population sizes, but also the increase of new habitat (Burkey 1995; Buskirk 2000; Wilcove 1985).

Habitat fragmentation is a major problem for large carnivores, because they typically have large home ranges, occur at low densities, and are often involved in human-wildlife conflicts (Swenson 2003), such as livestock and wildlife depredation (Woodroffe et al. 2005). Rytwinski (2012) showed that wide-ranging large mammals with low reproductive rates are more susceptible to negative fragmentation effects at the population level. Overall, populations of large carnivores suffered a major decline historically, at different rates all over the world (Linnell et al. 2001). However, they have now increased again and have stable populations in some places thanks to protective legislation and the generally improved public opinion about large carnivores (Chapron et al. 2014).

This study will focus on the Scandinavian brown bear (*Ursus arctos*) and their selection of denning habitat in relation to human encroachment and fragmentation. In Scandinavia, brown bears were persecuted for centuries, almost leading to extinction, with only 130 individuals left in the 1930s (Swenson et al. 1995). However, they were protected in the early 20th century, resulting in a population increase (Swenson et al. 1995). By 1940, the population had increased sufficiently in Sweden for hunting to be reinstated (Swenson 2003). The population increased to about 1000 individuals (800-1300) in 2000, in spite of the ongoing hunt. In 2008 the population was estimated to be at about 3,298 (2,968-3,667) individuals, with a yearly increase of 4.5% from 1998-2007 (Kindberg 2010).

Most bears hibernate as an adaptation to strong seasonality when food is scarce (Rogers 1999; Sahlén et al. 2011). Therefore, they spend about 5-7 winter months in a den, usually dug into the ground, into abandoned anthills, under tree roots, or in natural cavities and caves (Linnell et al. 2000; Sahlén et al. 2011). Before denning in autumn, their diet in central Sweden mainly consists of berries, which is the most important food source for brown bears during this period. The most important of these berries are bilberries (*Vaccinium myrtillus*) and crowberries *(Empetrum hermaphroditum)* (Dahle et al. 1998; Opseth 1998; Stenset et al. 2016). In central Sweden, ants, mostly red forest ants (*Formica* spp.) and carpenter ants (*Camponotus herculeanus*), also make up about 20% of the brown bear’s diet and annual energy intake (Johansen 1997; Stenset et al. 2016; Swenson et al. 1999).

While hibernating, bears’ locomotive activities are reduced, and they become mostly inactive (Evans 2016; Friebe 2014). They do not drink, eat, urinate, or defecate, and they survive on the energy saved up in the summer when they were active (Evans 2016; Friebe 2014). They do this by displaying torpor over a longer period of time (Friebe 2014; Libal et al. 2011), a process defined as a controlled decrease of physiological functions (Friebe 2014; Nowack 2015). This means that they decrease their metabolic rate and oxygen consumption. According to Hellgren (1998), hibernating brown bears decrease their basal metabolic rate and oxygen consumption by 40% and 50%, respectively, compared to normal levels. In addition, their resting heart rate drops dramatically. When it comes to body temperature, the brown bear is different from other true hibernators. Their body temperature stays near normal (37-38 °C), ranging from 31,2 to 36 °C during hibernation (Evans 2016; Hellgren 1998). In addition to the obvious energy conserving benefits of hibernating, there also seems to be other benefits, such as prolonged life span (Lyman et al. 1981) or predator avoidance (Bieber et al. 2014; Friebe 2014; Turbill et al. 2011).

Brown bears spend almost half of their life time hibernating (Elfström & Swenson 2009), making the choice of site and den type extremely important, especially for pregnant females (Elfström & Swenson 2009; Friebe 2014; Nowack 2015). Den disturbance leads to arousal from hibernation and den abandonment which is extremely costly in terms of energy loss and offspring survival (Elfström & Swenson 2009). Human disturbances near the den area causing den abandonment include hiking, hunting, skiing and operating heavy machinery nearby (Swenson et al. 1997). The effects of den disturbance can vary, and the severity of such disturbances depends on factors like the degree of disturbance and the timing. Possible effects can be den abandonment, increased mortality risk, increased activity inside the den and change in body temperature or heart rate (Evans 2016; Linnell et al. 2000; Schoen et al. 1987). Anecdotal events show that bears can move up to 30 km before finding a new den after being disturbed (Swenson et al. 1997). Appropriate den site selection thus appears to be important to minimize disturbance risk, and constrain den site selection to more secluded areas (Evans 2016). For example, Sahlèn et al. (2011) showed that bears use dens that are more concealed or located in more rugged terrain when closer to roads and settlements that have potential for high human activity. They also found that human activity affects choice of den sites and their characteristics, such as cover and terrain (Sahlén et al. 2011). Taking into consideration that male bears can lose up to 20% and females 40% of their body mass (Kingsley et al. 1983; Swenson et al. 1997), they are also likely to prefer a den site close to areas with good food sources at den emergence in spring (Libal et al. 2011).

Female bears spend significantly more time in their den (especially pregnant females) than males, which emerge earlier (Friebe et al. 2001; Manchi & Swenson 2005; Oli et al. 1997). Females give birth to multiple altricial young in their winter den (Linnell et al. 2000; Steyaert et al. 2012), and pregnant females also spend relatively more energy than other reproductive classes, because reproduction is costly in terms of energy use (Elfström & Swenson 2009; Friebe 2014). According to the study of Linnell (2000), females with cubs tolerate greater levels of disturbance without abandoning the den compared to other classes of bears, because abandoning the den with young cubs that are not yet fully mobile, increases cub mortality risk through thermal stress and infanticide (Elfström & Swenson 2009). After females give birth, the cost of den abandonment is thus much higher compared to solitary conspecifics (Linnell et al. 2000). Swenson et al. (1997) provided evidence for larger cub mortality for females that abandoned their den versus those that did not. Thus, because den abandonment can be extremely costly in general, and specifically for females with dependent young, it is very important that bears choose denning sites far away from possible disturbances, such as anthropogenic activity (Elfström & Swenson 2009; Sahlén et al. 2011).

Scandinavian brown bears use four main types of dens; i.e., excavated anthills (hereafter ‘anthill dens’), excavated soil dens, rock dens, and nest dens (Nowack 2015) (Figure 1.). Excavated anthill dens are probably the most insulating and beneficial for female bears to hibernate in compared to soil, rock, and nest dens, because of their thick, airy walls, stability due to the root system of overgrowing bilberries (Nowack 2015), and radiating heat from the earth ((Folk Jr & Folk 1967) as cited by (Tietje & Ruff 1980)). The soft walls also allow the bear to shape the inside to fit it’s body size easily, in contrast to a rock den, which cannot be adjusted (Nowack 2015). The easy shaping of an anthill den results in minimum space around the bear’s body, decreasing loss of warmth and increasing energy conservation (Nowack 2015). Insulating the den with nest materials further helps reducing heat loss from the bear to the ground (Tietje & Ruff 1980). Nest dens are used primarily by large males and insulated by a closed snow cover only. A soil den is different from an anthill den in regards to wall composition, having walls that are made of tightly packed soil, with less insulation properties (Nowack 2015).

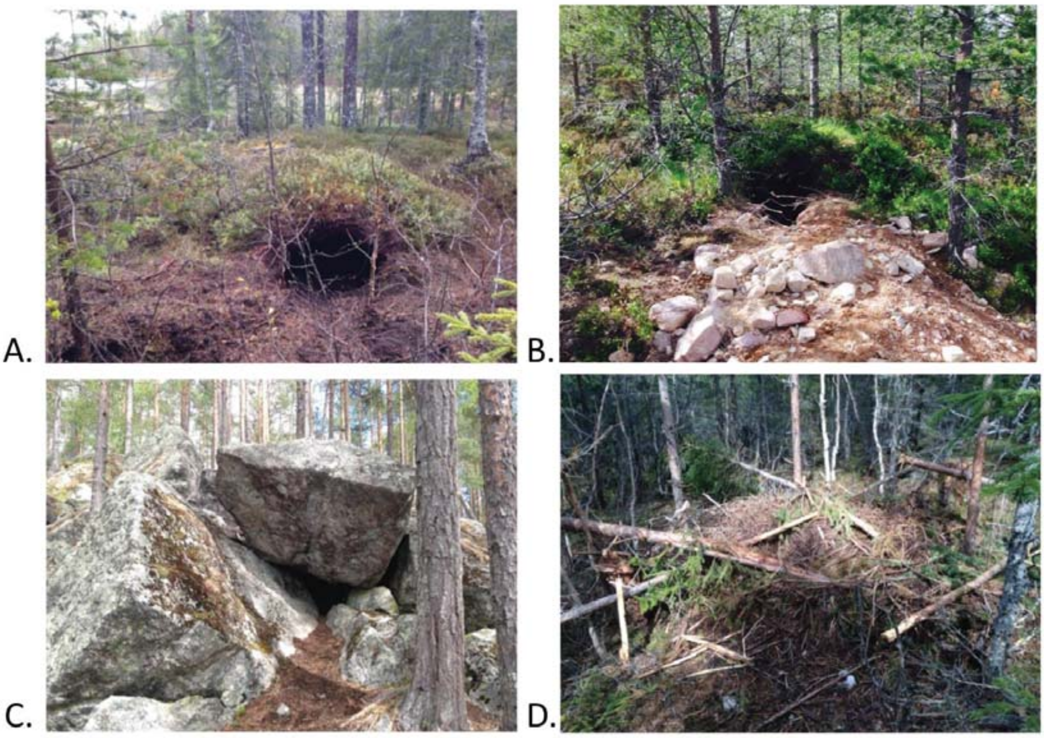

Figure 1. The four main den types used by the Scandinavian brown bear. A: anthill den, B: soil den, C: rock den, D: nest den.

Dens built in anthills (mound building ants (*Formica* spp.)) appear to be the most common den type in Scandinavia (Manchi & Swenson 2005; Nowack 2015; Swenson et al. 1999), especially among females. Females are probably more selective than males in den type selection, considering that they have greater costs related to disturbance during hibernation (Elfström & Swenson 2009; Nowack 2015). Nowack (2015) found that anthill denning, although not affecting the probability of having offspring, does result in bigger litters and litters containing a higher proportion of male cubs. Therefore, anthill denning must save the mother bear a significant amount of energy in comparison to other den types. Also, there appears to be a decline in the use of anthill dens by brown bears in our study area, which might indicate a decline in the availability of anthills. As our study area is affected by forest management (Friebe et al. 2001), habitat fragmentation and loss might be a reason for the possible anthill decline. Anthills need time to grow to the dimensions needed for denning, therefore they are probably more commonly found in older forests. Clearcuts are probably destroying anthills and therefore potential dens.

I hypothesize (H1) that there has been a decrease in the probability of female bears denning in an anthill den in my study area over the years 1986-2014. Secondly, I hypothesize (H2) that the probability of denning in an anthill den is positively related to (H2a) old growth forests and (H2b) to areas far from human disturbance (e.g., settlements and roads). I also predict (H2c) that anthill dens occur less frequently in clearcuts than random. Thirdly, I hypothesize (H3) that habitat loss and fragmentation has negatively affected the availability of good-quality denning sites during the study period. I tested my hypotheses based on a long-term dataset (years 1986-2015) collected by the Scandinavian Brown Bear Research Project in south central Sweden. The role of anthill dens seems to be important in the Scandinavian brown bear's reproduction, and decrease in use of anthill dens could have negative effects on the population. My results will contribute to more knowledge about the use of anthills, which is important for the efficient conservation and management of the brown bears in Scandinavia.

Materials and methods

This research is part of the Scandinavian Brown Bear Research Project (SBBRP), which has been a Swedish-Norwegian collaboration since 1987. The goal of the SBBRP is to provide management authorities and the public with knowledge on the ecology of the Scandinavian brown bear (SBBRP).

Study area

The study was conducted in south-central Sweden (~ 61°N, 15°E) in the counties Dalarna and Gävleborg (Figure 2), with the research station located in Tackåsen. Elevation in the study area ranges between 200 to 1000 m above sea level (Ordiz et al. 2014). The dominating tree species in this 13,000 km^2 area of boreal forest are Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), lodgepole pine (*Pinus contorta*) and birch species (*Betula pendula*, *B. pubescens*) (Moe et al. 2007). On the forest floor, the vegetation mostly consists of lichens, mosses, heather (*Calluna vulgaris*), and several berry species (bilberry, crowberry, lingonberry *(V. vitis-idaea)*) (Friebe et al. 2001; Moe et al. 2007). The area is characterized by intensely managed forest, and lakes and bogs (Friebe et al. 2001; Swenson et al. 1999), and has a dense network of gravel roads (Friebe et al. 2001). Forest management resulted in a patchy landscape with various age cohorts of forest and a median patch size of 22,500 m^2 (Moe et al. 2007). The population density is 4-7 inhabitants/km^2 with a few villages located in the north and south of the area. Cabins are spread throughout the area (Sahlén 2013) and are mostly inhabited in the summer and fall, when activities like hunting, fishing, and berry and mushroom picking are common

(Nellemann et al. 2007; Sahlén 2013). The bear population density in the study area was approximately 30 individuals per 1000 km^2 (Moen et al. 2012).

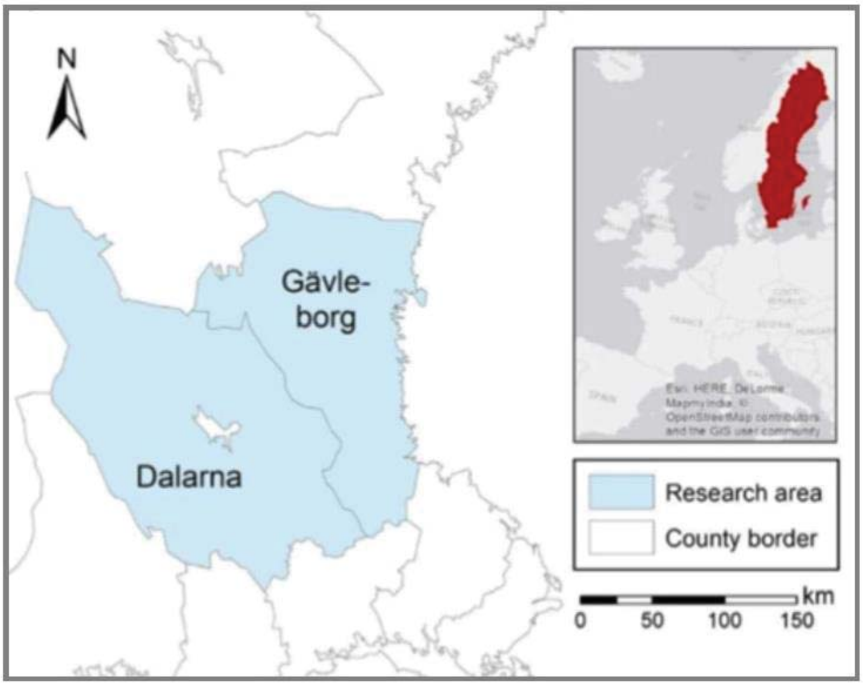

Figure 2. Map highlighting the location of the two counties (Dalarna and Gävleborg) (blue) in which within lie the study areas of the SBBRP in Sweden (red). Source: (Spitzer et al. 2016).

Data collection

The Scandinavian Brown Bear Research Project has been monitoring brown bears and collecting data on winter dens since 1985 (Nowack 2015). Both already marked and new, unmarked individuals of all age classes, have been captured by SBBRP (Sahlén 2013). Exceptions are females with cubs-of-the-year, which are not captured (SBBRP). Marking is done by darting the bears with a sedation drug from a helicopter and collaring them with a GPS (Global Positioning System, GPSPlus, Vectronic Aerospace GmbH, applied in the SBBRP since 2003) or a VHF collar (Telonics ®, Model 500). The bears are mostly captured and handled in spring. See Arnemo & Fahlman (2011) for further detailed information on handling and capturing bears. Because many of the bears in the project have been followed since they were born, the year of birth of most bears is known. For bears that were captured at an unknown age, the age has been estimated by counting cementum annuli in a molar tooth (Dahle & Swenson 2003; SBBRP).

I used the already existing den data from the SBBRP from winters 1986-2014 as a base for my thesis. In addition, I used den data that I collected myself from May to August 2015. Collecting den-specific and microhabitat data at winter den sites is routine data collection of the SBBRP. I visited 43 den sites from winter 2014, adding up to a total of 946 den registrations between 1986 and 2015. I used den site location, bear identity, den type (anthill, soil, rock, and nest den), and year from the annual den site registrations as input data to test my hypotheses.

I extracted the following environmental predictor variables from digital spatial data layers in a geographical information system (GIS): elevation (m), slope (˚), cardinal direction (4 categories; N, E, S, W), distance to roads (km), distance to railroads (km), distance to villages (km), distance to houses (km) and habitat type (old forest, mid-aged forest, young forest, bogs and clearcuts), and the normalized difference vegetation index (NDVI). These variables were extracted from a 50*50 m digital elevation model (DEM), satellite imagery (Resourcesat, 23.5 * 23.5 m, July 2014) and the Swedish land cover database (Svenska Marktäckedata, SMD-data). The maps were also updated annually for land cover types, human encroachment, and road construction. The SMD data was annually updated (2003-2014) for clearcuts and young forests based on data obtained at the Swedish Forest Agency (www.skogsstyrelsen.se). I digitalized satellite imagery mosaics (2000-2015) to obtain annually updated road networks. All data was referenced to SWEREF 99 TM.

Ethics

All capturing and handling of bears was in accordance with the Swedish legislation (Arnemo & Fahlman 2011). The collar belts are fitted with a break-away zone, a strap of cotton fabric that rots and weakens over time. This ensures that the collar will eventually fall off the bear in case we lose contact with it. The young bears that are still growing are fitted with a new collar each year.

Statistical Analysis

Is there a temporal decline in the use of anthill dens?

I first calculated the proportion anthills used by all bears, and females alone (from my original dataset), to look for a preference in anthill dens. After merging this dataset with a dataset containing the reproductive information for each bear, some of the observations ($N_{dens} = 28$) were taken out due to lack of needed reproductive information. Next, I used a logistic mixed effect regression model to predict the probability for a bear to use an excavated anthill as a den. I dummy-coded den types, with anthill dens being 1 and all other den types as 0. This binary variable served as the response variable. I considered year (continuous), sex, age, and the sex*age interaction as fixed effects in the models. I included bear identity as a random effect on the intercept, because of repeated measures for bears that were monitored over several years, and to account for individual, bear-specific den type preferences (Zuur et al. 2009). I ran all possible model combinations using the ‘dredge’ function in the MuMIn package (Bartoń 2009) in R (R Development core team 2015). I ran these analyses for all bears together, and separately for adult pregnant females (< 3 years) and adult females (< 3 years) that entered the den with cubs that were 1 year and older. I fitted the models using the lme4 package (Bates et al., 2015) in R.

Den site selection

I used the resource selection function (RSF) modeling approach to evaluate spatial patterns in den site selection by comparing resource ‘use’ with resource ‘availability’ with a logistic regression model (Manly et al. 2007). Resource use is represented by animal relocation sites (here ‘den sites’), whereas resource availability is sampled with random locations. The landscape covariates represent the resources. An RSF is often considered as an index of habitat suitability (Boyce et al. 2002). For each used and random location, I used ArcGIS 10.2. to extract the following habitat characteristics from digital spatial data layers in a GIS: elevation (m), land cover (old forest, mid-aged forest, young forest, water, clearcuts, bogs and other), distance to roads (m), distance to villages (m), distance to houses (m), and NDVI.

The scale of sampling resource availability is crucial in resource selection modeling (Boyce et al. 2002). I chose to sample resource availability on the landscape scale (2nd order resource selection), assuming that all bears could physically reach all locations in the entire study area. I sampled resource availability in a 1:1 use - availability ratio. Therefore, I constructed a 90% kernel density range over all den sites collected by the SBBRP. I set the kernel radius at 11 km, as this is the average home range radius for female brown bears in Scandinavia (Dahle et al. 2003). Within the kernel, 691 den sites (for all den types and all bears) of the total 909 (years 1986-2014) were included (not using the 218 outlying dens). I then made some small adjustments in this dataset, combining the den type categories ‘uprooted tree’ and ‘nest’ with the category ‘other’ to simplify the data. In total, from the 691 dens, 109 nest dens and 24 uprooted tree dens were merged into the category ‘other’. I extracted all landscape covariates for all den sites and an equal number of random locations with ArcGIS 10.2, resulting in a combined total of 1382 locations. From these I removed all dens with habitat type category ‘water’, as no dens are found in water, and ‘other’, as these were not relevant, resulting in a total of 1349 locations in the final dataset. Temporal gaps in the road data occurred in 2002, 2003, 2004 and 2006, and no good quality road data was available before 2000. Therefore, all the dens registrations before the year 2000 were linked with the extracted road data from 2000, the den registrations from year 2003 and 2004 with the road data from 2005, and the den registrations from 2006 with the road data from 2007.

I tested for collinearity between the numerical variables in the data before proceeding (Zuur et al. 2009; Zuur et al. 2010), and set the threshold for correlation at r = 0.70 (O’brien 2007). I compared the used locations with the random locations, using mixed effect logistic regression models to evaluate how certain landscape variables affect den site location. I used mixed effect models with “bear ID” as a random effect on the intercept and all landscape characteristics as fixed effects. I ran all possible model combinations using the ‘dredge’ function in the MuMIn package (Bartoń 2009) in R. I repeated the analyses including only females that used anthills, as I was especially interested in that group. The criteria for choosing the best model was the model with the lowest number of parameters (degrees of freedom, df) and a second-order Akaike Information Criterion difference score (ΔAICc) below 2 (Arnold 2010).

Changes in habitat quality

I mapped the model output of the most parsimonious model of the RSF models to assess den site selection for all dens, and for anthill dens alone (used by females of all age classes) to visualize general denning and anthill den habitat suitability in the study area. I made these maps for the years 2005, 2008, 2011, and 2014 to assess changes in the availability of habitat suitability for denning over time. I used «raster calculator» in ArcGIS 10.2 to do this. A relative probability value of 0 represents unsuitable habitat, whereas 1 represents perfect habitat (Kusak & Huber 1998).

For the females (all age classes) that used anthill dens, I calculated the percentage of improved and decreased habitat suitability from the years 2005-2014. Improved habitat meaning pixels where the probability of denning in an excavated anthill increased over time, and habitat that had become less suitable, meaning habitat where the probability of anthill denning had decreased. I report the percentage of terrestrial pixels that improved and decreased in denning habitat quality, respectively.

Results

Is there a temporal decline in the use of anthill dens?

I started with a dataset that had a total of 933 den observations (all den types) ($N_{\text{female bear}}$ = 695, $N_{\text{male bear}}$ = 238) whereof 53% were anthill dens, and 78% of these were used by female bears (all age classes) (55.4% anthill den use within this group). This indicated a preference for anthill dens. The best model to assess a temporal trend in the probability that bears (N_{bears} = 196, N_{dens} = 905) used an anthill as a winter den included year and bear age as fixed effects (df = 4, ΔAICc = 0, AICcw = 0.43). The second- (df = 5, ΔAICc = 0.13, AICcw = 0.4) and third- (df = 6, ΔAICc = 1.84, AICcw = 0.17) ranked models had ΔAICc below 2, but were more complicated in model formulation and therefore discarded. The probability of using an anthill den has declined over time (β = -0.099, se = 0.006, p value < 0.001) (Table 1, Appendix Figure A1), and increased with bear age (β = 0.108, se = 0.026, p value < 0.001) (Table 1, Appendix Figure A2) for all bears. Sex had no significant effect (Appendix Figure A3, Appendix table A1), and there was no significant sex*age interaction (Appendix Table A1). Rerunning the model for females only (pregnant females and females with cubs) yielded somewhat similar results. The best model to assess a temporal trend in the probability that pregnant female bears (N_{bears} = 63, N_{dens} = 187) used an anthill as a winter den included only age as fixed effects (df = 3, ΔAICc = 0.92, AICcw = 0.37). The second-ranked model (df = 4, ΔAICc = 0.00, AICcw = 0.59) had ΔAICc below 2, but was more complicated in model formulation and included both age and year. The probability of pregnant females using an anthill den increased with age (β = 0.164, se = 0.064, p value = 0.01) (Figure 3.), but was not affected by year. The best model to assess a temporal trend in the probability that female bears with cubs (1 year and older) (N_{bears} = 48, N_{dens} = 149) used an anthill as a winter den included only year as a fixed effect (df = 3, ΔAICc = 0.00, AICcw = 0.57). The second-ranked model (df = 4, ΔAICc = 1.8, AICcw = 0.23) had ΔAICc below 2, but was more complicated in model formulation and included both age and year. The probability of females with cubs using an anthill den declined over time (β = -0.139, se = 0.018, p value < 0.001) (Figure 4.), but was not affected by age. The explained variance of the random component was 2.632, 2.604, and 3.586 for the models, respectively.

Table 1. Results for fixed effects from the best glmer model to assess a temporal trend in the probability that the Scandinavian brown bear (including all bears) (N_{bears} = 196, N_{dens} = 905) used an excavated anthill den as a winter den (1986-2014) in south central Sweden.

Fixed effects:

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
Intercept	198.083	11.586	17.097	< 0.001 ***
Age	0.109	0.026	4.162	< 0.001 ***
Year	-0.099	0.005	-17.119	< 0.001 ***

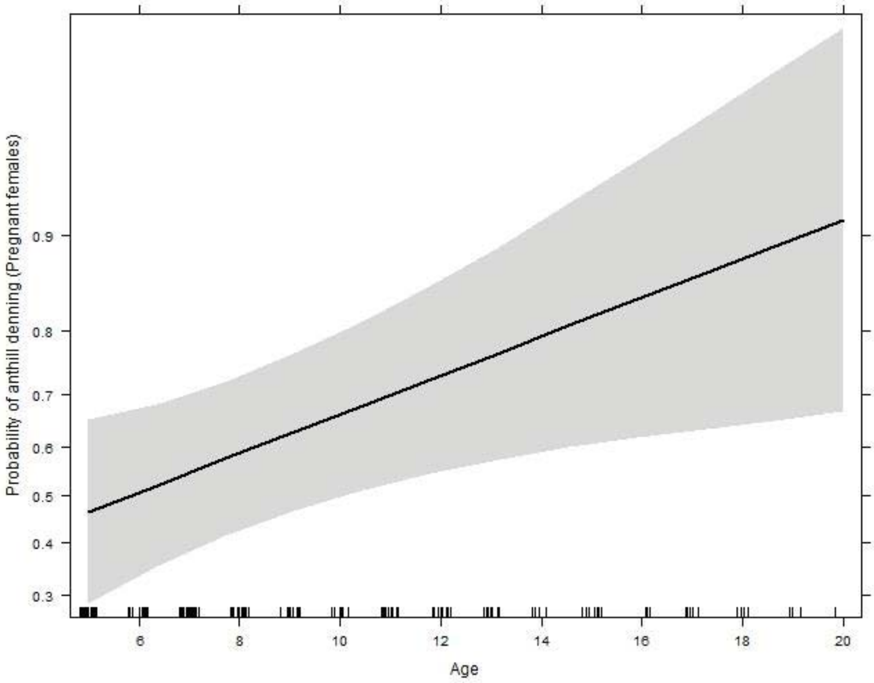

Figure 3. The predicted likelihood of pregnant female bears (> 3 years) (N_{bears} = 63, N_{dens} = 187) using an anthill den as a winter den between 1986 and 2014 in south central Sweden, in relation to age. Den type as response variable; 1 = anthill, 0 = no anthill.

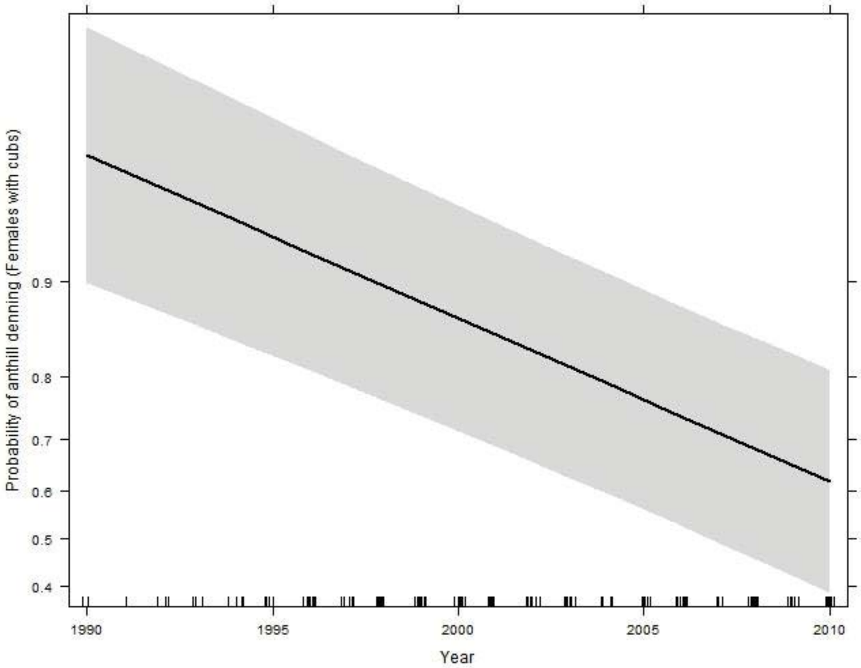

Figure 4. The predicted likelihood of female brown bears (> 3 years) with cubs (1 year and older) (N_{bears} = 48, N_{dens} = 149) using an anthill den as a winter den between 1985 and 2014 in southcentral Sweden, in relation to age. Den type as response variable; 1 = anthill, 0 = no anthill.

Den site selection

I observed no collinearity between the landscape variables (Appendix Figure A4.). The glmer for the full model did not converge, because there were no registered used anthill dens in clearcuts in the entire dataset, whereas there *were* random points located in clearcuts. This resulted in perfect separation, explaining the convergence issue. Complete separation occurs because the explanatory variable ‘clearcut’ perfectly predicts both zeros (no anthill den) and ones (anthill den) in the binary observations (Rainey 2015). Mathematically, the maximum likelihood estimate for a clearcut having a response variable of 1 (anthill den) does not exist. Because of this problem of separation, I removed the clearcut category from the analysis, as this did not result in data loss of ‘used’ locations.

Running the models with (Appendix Table A3) or without (Appendix Table A2) ‘bear ID’ as a random effect had little effect on the parameter estimates of the landscape variables. Therefore, I decided to remove the random effect from the model, to improve model fit and simplicity. The best model to assess den site selection (all den types) of bears (N_{bears} = 161, N_{dens} = 1323), included habitat type (old forest, mid-aged forest, young forest and bogs), elevation, slope, and distance to houses, railroads, roads and villages as fixed effects (df = 9, ΔAICc = 0, AICcw = 0.57). The second-ranked model (df = 10, ΔAICc = 1.65, AICcw = 0.25) had ΔAICc below 2, but was more complicated in model formulation and therefore discarded. The probability of denning for all bears increased with increased distance to roads (β = 0.0006, se = 0.00014 , p value = < 0.001), villages (β = 0.00004, se = 0.000008, p value < 0.001) and houses (β = 0.0002, se = 0.00008, p value = 0.01). The probability of denning decreased with increased distance to railroads (β = -0.00003, se = 0.000007, p value < 0.001) and with increased elevation (β = -0.002, se = 0.0005, p value < 0.001) (Appendix Table A2). Bogs had a strong negative effect on denning probability (β = -1.34, se = 0.2363, p value < 0.001), whereas old forest (β = 0.172, se = 0.144, p value = 0.23), mid-aged forest (β = 0.104, se = 0.25, p value = 0.675) and young forest (β = 0.238, se = 0.152, p value = 0.117) had no real effects on denning probability (Appendix Table A2). Note that negative parameter estimates for the ‘distance to’ variables indicate selection, whereas positive values indicate avoidance. The best model for females of all age classes that used anthills (N_{bears} = 128, N_{dens} = 519), included distance to roads, railroads and villages, habitat type (old forest, mid-aged forest, young forest and bogs) and elevation (df = 8, ΔAICc = 0.63, AICcw = 0.230). The second-ranked model (df = 9, ΔAICc = 0.00, AICcw = 0.315) had ΔAICc below 2, but was again more complicated in model formulation and therefore discarded. Running the best model for only females (all age classes) that used anthills yielded similar results as before; i.e., the probability of a female bear using an anthill den in an area increased with increased distance to roads (β = 0.00047, se = 0.0002 , p value = 0.016) and villages (β = 0.00004, se = 0.000013, p value < 0.001). The probability of denning in an anthill also increased with increased elevation (β = 0.0023, se = 0.00088, p value = < 0.001) and decreased with increased distance to railroads (β = -0.00007, se = 0.00001, p value < 0.001). The bogs (β = -1.532, se = 0.4, p value = < 0.001) and mid-aged forest (β = -1.006, se = 0.4, p value = 0.011) had negative effects on anthill denning probability, whereas old forest (β = 0.276, se = 0.233, p value = 0.235) and young forest (β = 0.05, se = 0.254, p value = 0.846) had no real effects on anthill denning probability (Table 2, Figure 5, Figure 6).

Table 2. Results from the best model to assess den site selection including only female brown bears (all age classes) (N_{bears} = 128, N_{dens} = 519) that used anthills as a den in southcentral Sweden.

Coefficients:

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
Intercept	-1.006	0.3963	-2.538	0.011 *
Distance to roads	0.000468	0.000196	2.388	0.016 *
Elevation	0.002296	0.000878	2.613	< 0.001 **
Distance to railroads	-0.00007	0.000011	-5.960	< 0.001 ***
Distance to villages	0.000036	0.000013	2.727	< 0.001 **
Old forest	0.2765	0.2331	1.186	0.235
Bog	-1.532	0.3994	-3.835	< 0.001 ***
Young forest	0.0493	0.2539	0.194	0.846

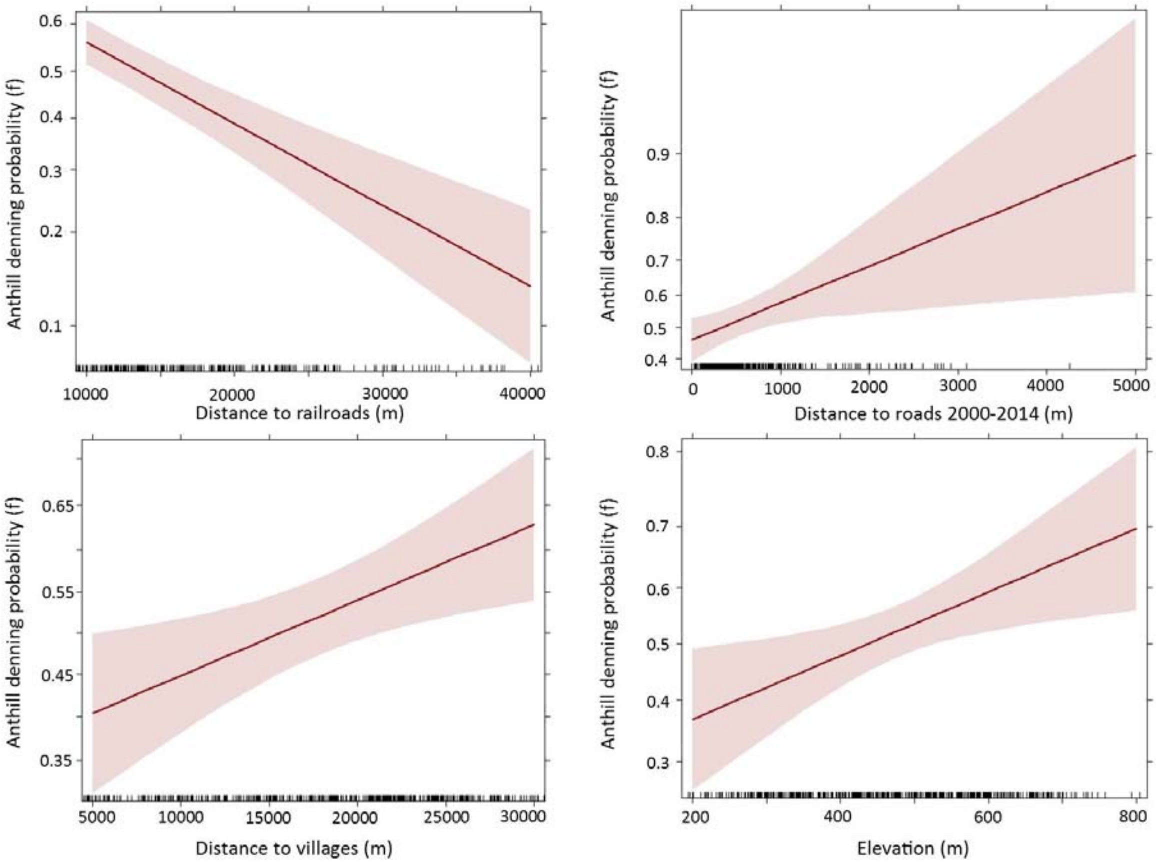

Figure 5. Relationships between a particular landscape variable (x-axes) and the probability of a female brown bear (all age classes) (N_{bears} = 128, N_{dens} = 519) denning in an anthill (y-axes) in southcentral Sweden. These variables are elevation (in meters), and distance (in meters) to railroads, roads (year: 1986-2014) and villages. Den type as response variable; 1 = anthill, 0 = no anthill.

Changes in habitat quality

I choose to use maps for the years 2005 and 2014 to examine changes in anthill denning habitat for females (all age classes) over time (Figure 7). For the comparison of maps for years 2005, 2008, 2011, and 2014 together, see Appendix Figure A5. For the distribution of all dens compared to anthill dens only, see Appendix Figure A7. Pixel counts for negatively and positively changed habitat indicated that 16% of the denning habitat has decreased in suitability, whereas only 2% has improved in suitability (Figure 8).

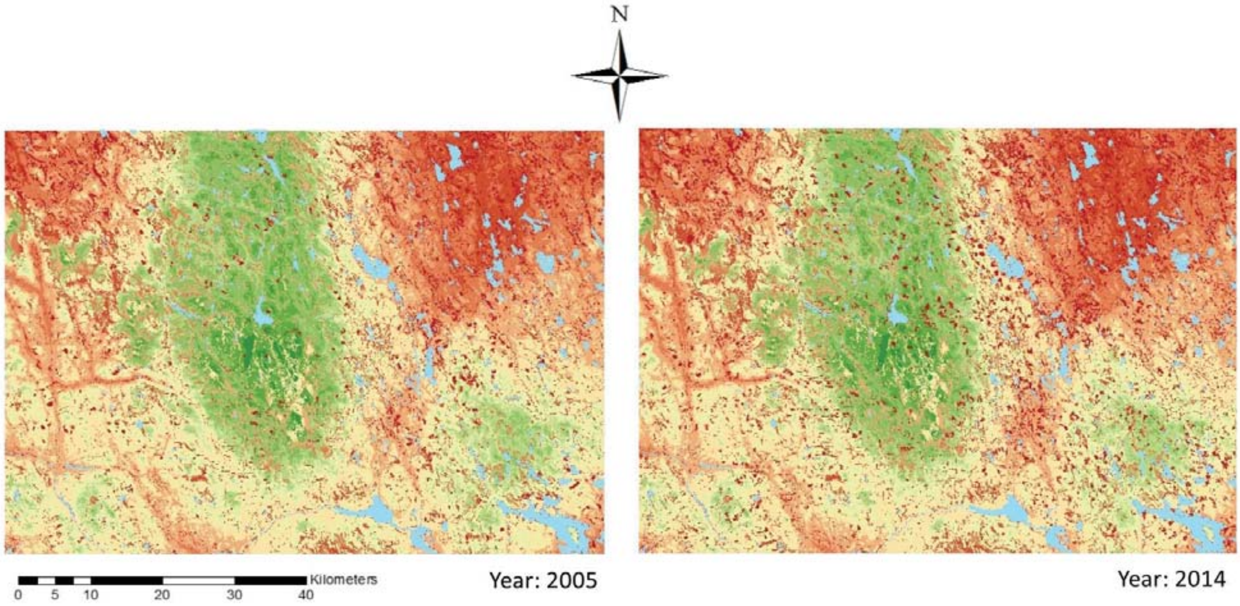

Figure 6. Relative probability of anthill den occurrence for the female Scandinavian brown bears (all age classes) (N_{bears} = 128, N_{dens} = 519) in the study area in southcentral Sweden for year 2005 and 2014, to examine changes in anthill denning habitat. The greener the pixels, the more suitable the habitat, and the higher the probability of occurrence. The more red the pixels, the less suitable the habitat, and the lower probability of occurrence. Water is marked with a blue color.

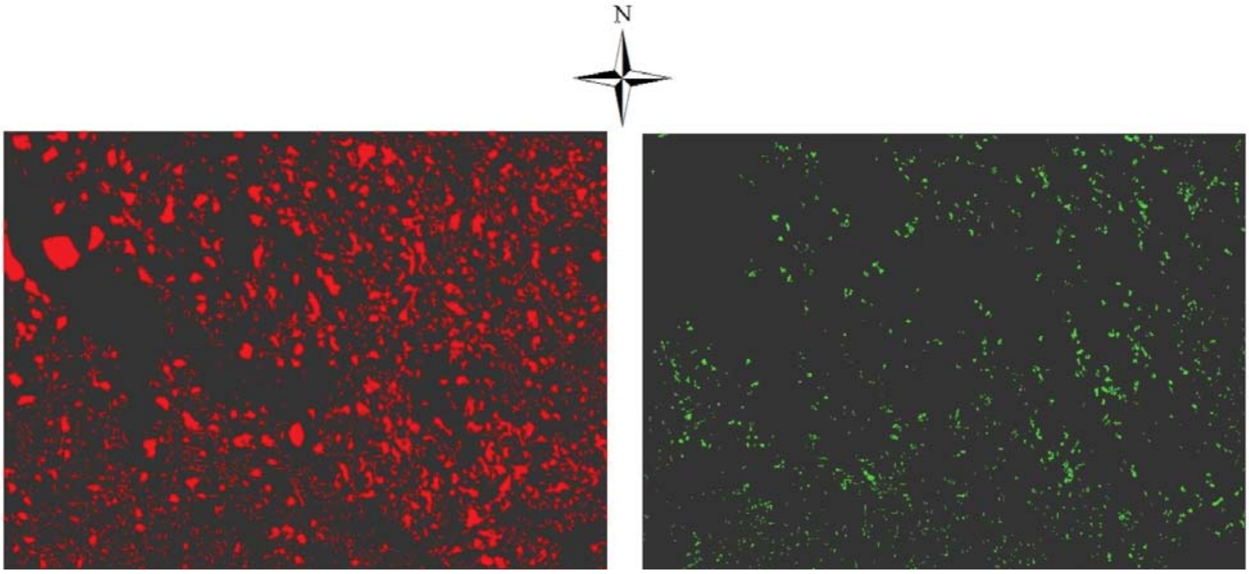

Figure 7. Maps indicating the negative (left, red) and positive (right, green) changes in habitat quality for anthill denning by female brown bears (all age classes), from 2005 to 2014 in southcentral Sweden, to highlight changes in anthill denning habitat.

Discussion

My results produced three key findings. First, as predicted, there was a temporal decline in the use of anthill dens by all bears, and by female bears with cubs, in the study area (H1). Second, denning probabilities (all den types and anthills alone) were not affected by old forest (H2a), but did increase with distance to houses, villages, and roads (H2b). Bears never used anthill dens in clearcuts (H2c). Third, the availability of good-quality denning habitat in the study area decreased over time (H3).

Temporal decline in the use of anthill dens

The results showed (Appendix Figure A1) that the probability to use an excavated anthill as a winter den for all bears in the study area has declined since 1986, and the same trend was shown for females with cubs. However, no trend was found for pregnant females. A possible explanation could be that this group of bears has the highest cost related to reproductive success, which probably makes anthill dens the most important to this group. This might result in them showing the highest degree of selection for anthills. Age also had an effect on the probability of using an anthill den. My results showed that the older the bear, the more likely that it used an excavated anthill as a winter den (Figure 3), except for females with cubs (no age effect). The finding of an age effect suggests competition for anthills among bears, with the older bears more often winning the competition, as brown bears' size and age matter in their hierarchy (Stonorov & Stokes 1972). It could also be that older bears have more experience in finding anthills, and because of their knowledge are more successful in it. My results support the conclusion that anthills are important in the denning ecology of the brown bear, and indicate that anthills indeed are preferred over other den types. The importance of winter den-type choice to reproductive success has already been investigated in studies on the American black bear (*Ursus americanus*) (Klenzendorf et al. 2002). Some of these studies suggest that bears increase their reproduction by denning in tree dens over other dens (Klenzendorf et al. 2002; Oli et al. 1997), as they provide more protection against disturbance and predation, and provide thermal insulation, which increases energy savings (Johnson et al. 1978; Oli et al. 1997).

Due to the importance and preference of anthills, the declined use of them is an alarming cause of concern. It could be assumed that the ongoing and heavy forestry in the study area, which has greatly affected Swedish flora and fauna (Berg et al. 1994), is directly destroying anthills and the habitat needed for them (Domisch et al. 2008; Punttila 1996). Clearcutting causes anthill abandonment by ants and increases the anthills' exposure to precipitation, making it hard for the ants to keep the dry and porous structure of the anthill (Punttila 1996). Anthills are built up of organic material from the surrounding forest floor and is dominated by needle litter in coniferous boreal forests (Domisch et al. 2008), such as in Sweden. Without the trees needed to create this litter, such as in clearcuts, anthills cannot be built. Also, the anthills can become as much as a 100 years old (Domisch et al. 2008) and probably take a long time to be built and to become of a size useful for a bear den. Therefore, if an anthill is destroyed, it will likely not be replaced quickly. If forestry management destroys big and suitable anthills for denning faster than the ants can build them up again, it could partially explain the decrease. Another explanation could be that the recent increase in the bear population (Kindberg 2010) has reduced the availability of old, suitable anthills for denning, especially because bears rarely reuse an excavated anthill den (Linnell et al. 2000). It is possible that the effects (reduced reproductive success in female bears) of this declining number of suitable-sized anthills for denning will be delayed. Perhaps the effects on the bear population will not become apparent until a significant amount of these anthills have disappeared. If this is the case, then there might already have been great losses, which we are just now seeing some effects of (declined use of anthills as dens). Further effects later on could possibly be a reduced population growth in the Scandinavian brown bear.

Den site selection

Anthropogenic activity affects den site selection of brown bears in the study area, as my results show that bears avoid villages, houses, and roads. However, as bears denned closer to railroads than other anthropogenic variables, although the likelihood increased only slightly with increasing distance, making the effect of railroads very small. When it comes to habitat types, it was clear that clearcuts and bogs were avoided, showing strong negative effects on anthill den site selection. This is as predicted, as both bogs and clearcuts are ill suited for denning. As mentioned before, anthills likely are destroyed in clearcuts, and materials to rebuild them are hard to find in such habitat. The unsuitability could also partially be explained by the fact that bogs and clearcuts can have free-flowing surface water, which reduces the bear's insulation (Elfström et al. 2008; Schoen et al. 1987). In addition, bogs and clearcuts lack vegetation that provides enough cover and concealment for a bear during denning, which leaves a bear exposed and easily detected by humans. Forestry has also been shown to have negative effects on the breeding success in other species, such as the goshawk *(Accipiter gentilis)*, black grouse *(Tetrao tetrix)* and capercaillie *(T. urogallus)*. Crocker-Bedford (1990) states that the goshawk's nestling production decreased by an estimated 97% after partial harvesting around nesting areas. Also, a negative correlation was found between breeding success, and degree of fragmentation and decreasing percentage of older forests in both of the species of forest grouse (Kurki et al. 2000).

The probability for denning seems to be higher at lower altitudes. Slope, on the other hand, was excluded from my models by model selection, although it has shown to have an effect in other studies (Elfström et al. 2008; Schoen et al. 1987). There was no difference between males and females in den site selection, both choosing to den away from anthropogenic activity. This was also shown in the study of Elfström (2008), suggesting that both are negatively affected by such disturbance (Kurki et al. 2000).

For the remaining habitat types, old, mid-aged and young forest, my results showed no significant effect on denning (except for mid-aged forest, which showed a slight negative effect on anthill denning in females). This was not expected, as other studies did find a preference for older forest by bears (Elfström et al. 2008; Schoen et al. 1987). I assumed that, because anthills probably take a long time to reach the dimensions needed for denning, it was more likely for them to be found in older forests, which could result in a preference. I also assumed that young forests could be preferred for their dense vegetation, providing cover.

Changes in habitat quality

On a landscape scale, it is clear that the Scandinavian brown bear shows preference for specific habitat types for denning. The influence of human activity on bears' choice of den type and site is significant, and has become increasingly significant over the years (Figure 7, Appendix Figure A5.). Bears avoid denning close to anthropogenic structures such as roads and houses (Elfström et al. 2008; Sahlén et al. 2011), and are therefore likely affected by indirect habitat loss by not using the entire available habitat in the study area (Swenson 2000). Based on my results, anthropogenic structures and human encroachment have a negative effect on the quality of denning habitat for brown bears in the study area (Figure 8). This indicates that anthropogenic disturbance during denning can be costly for bears.

The proportion of anthills used as den type has decreased since this study started in 1986, supporting my third hypothesis, which stated that the availability of good quality denning sites, having anthills, has declined over the years. It appears that most dens are located in the parts of the study area with the most suitable habitat (green color), especially anthills (Appendix Figure A7). This gives even more reason to believe that these habitats are extremely important for the population of brown bears in the area, as females have greater reproductive success when they give birth in anthills (Nowack 2015). On the maps (Figure 7, Appendix Figure A5) one can clearly see where the clearcuts are, as they are small, distinct patches of land marked brightly red. The red color indicates that the habitat has decreased in suitability and has a decreased probability of anthill den occurrence for females. Lacking a lot of vegetation and cover, due to harvesting and plowing (Mannerkoski et al. 2005), they are also very open areas, which brown bears avoid (Swenson 2000). However, there are some positive effects, as some recent studies (Moe et al. 2007; Nielsen et al. 2004) have shown that brown bears select clearcuts during the active period. In Sweden, they do this in spring during crepuscular hours, likely foraging on ants (especially carpenter ants) that inhabit the dead wood lying around in a clearcut (Nielsen et al. 2004; Swenson et al. 1999). These ants are an important food source for bears in Sweden (Frank et al. 2015; Swenson et al. 1999).

When the quality of a habitat has declined in an area with no clearcut, I assume that this was due to the effects of surrounding roads and increased human activity in the area. The road network in the study area has been extended significantly throughout the years (based on my updating of road maps in ArcGIS) and has left most of the area influenced by humans and mechanized forestry. Trains and motor vehicles (traffic) can increase traffic mortality of bears (Huber et al. 1998). However, the roads, being public, have likely also lead to an increased amount of human activity, as it provides more access to the area. According to a study in Norway, secondary traffic and people hiking into the woods from the roads, present an important disturbance to the bears (Elgmork 1978). This increased accessibility to this formerly remote bear habitat brings mushroom and berry pickers, hunters and poachers, tourists, and fishers, all contributing to the human disturbance (Swenson 2000). It may interfere with the bears' foraging behavior, causing them to become more nocturnal and avoid areas with much human activity, leading to possible nutritional stress, as suggested by Swenson (2000). It also means that, other than the direct loss of habitat by destruction, more bear habitat is lost in terms of avoided human–influenced areas (Swenson 2000). In a study of Swenson et al. (1997) as much as 67% of den abandonments were likely related to human activity found close to the den, which again leads to possible reduced survival and reproductive success (Linnell et al. 2000). Also, Kaal (1976) states that increased human activity in forests restricts dispersal and reproduction of the bears in Estonian SSR (Kaal 1976).

All in all, habitat fragmentation, forestry and other anthropogenic activity reduces connectivity between habitats, causes disturbance, and directly destroys important anthills and denning habitat. This can all cause limited distribution, den abandonment, possible decreased reproductive success (less anthills for denning), and possible reduced population growth in the Scandinavian brown bear population. According to Elfström et al. (2008), den abandonment seems to be caused primarily by human disturbance, and not habitat choice. This might make habitat a secondary factor, and indicate the greater importance of human activity close to the den site (Elfström et al. 2008). The availability of good denning sites with anthills, has shown to be important to the bears, and have an effect on the females’ reproductive success (Nowack 2015).

Conclusion

My results show that forestry could indirectly be affecting the bears' reproductive success through loss of anthills, as they seem to have become less available over the years. This again may affect the bears' population dynamics. Especially clearcuts and bogs have a negative effect on the probability of female bears denning in an anthill; loss of cover (for denning and human avoidance), likely direct destruction of anthills and the habitat needed for the ants to build them. Forest management should take these effects in consideration when making management decisions, in order to conserve as many anthills as possible, and avoid further destruction by forestry. Also, research should be conducted on how fast inactive old large anthills are created, and how fast they are being destroyed by bears in order to find a natural equilibrium. This should then be used to evaluate effects of forestry in relation to it. In addition, further research should be conducted on what kind of habitat contains most anthills, and are best suited for bears to den in. To determine this, and as a mitigating action, one could map the location of anthills, over a certain size, in the study area. I would recommend that management take some measures to conserve the remaining anthills in the areas suitable for denning. Other human disturbance also has a negative effect on bears; leading to den abandonment, stress, indirect habitat loss (avoidance of areas with much activity), direct habitat loss (forestry and roads), fragmentation of habitat, increased traffic-mortality. My results, showing the distribution of good quality habitat (largest probability of anthill den occurrence) for female bears to den in an anthill, should be used as a guide to which areas should be avoided by humans and human activity during the denning period.

Acknowledgments

First I would like to thank my supervisor Sam Steyaert. This thesis would not have been possible without all the help and advice I got from him, for which I am so very grateful. He has been patient with answering all of my questions and guiding me through this whole process, and encouraged me at the times I thought everything was going wrong. He taught me how to use the programs R and GIS, which was anything but easy, and introduced me to using the habitat protocols in the field. I was very lucky to have a supervisor who had such an interest and enthusiasm for my thesis himself, and who always answered my questions promptly and came up with solutions when I ran into statistical problems.

I thank Sven Brunberg for everything he does in Tackåsen, and the guidance and help in the field. And of course for reassuring me by saying that he would come and pull me out if one day I would get stuck in a bear den and not return from fieldwork. I also thank Andrea Friebe for the help in the field and the introduction to using the den protocols. Also a big thanks to Per Martin Lokholt and Bente Lokholt for their hospitality, support and help in finding the remaining dens when I had to do the last part of my fieldwork in Fulufjellet. I also thank Jon Swenson for reading through my thesis in the very end and giving me some much appreciated final advice.

For all the support and belief in me from my nearest at home, I am also deeply grateful. They have put up with all my complaining when I was down or stressed, and helped me through by encouraging me and rooting me on. Thanks to all of you who helped me with reading through my thesis and giving me advice. And thanks to my fellow master students who also answered my questions when I was stuck, and who encouraged me.

Finally, I would like to thank the Scandinavian brown bear research project, not only for giving me the opportunity to write a master thesis on such a great and interesting topic as the Scandinavian brown bear, and providing the funding which allowed me to do the fieldwork, but also for giving me the opportunity to meet so many interesting people. My fieldwork in Tackåsen and the people who were there, is something I won’t soon forget. It was a great experience of which I learned a lot, and I was lucky to spend my time of fieldwork in the company of such a great bunch of motivating and supporting people.

Literature cited

Arnemo, J. M. & Fahlman, Å. (2011). Biomedical protocols for free-ranging brown bears, gray wolves, wolverines and lynx. *Hedmark University College, Evenstad, Norway and Swedish University of Agricultural Sciences, Umeå, Sweden*.Arnemo, J. M. & Fahlman, Å. (2011). Biomedical protocols for free-ranging brown bears, gray wolves, wolverines and lynx. *Hedmark University College, Evenstad, Norway and Swedish University of Agricultural Sciences, Umeå, Sweden*.

Arnold, T. W. (2010). Uninformative Parameters and Model Selection Using Akaike's Information Criterion. *The Journal of Wildlife Management*, 74 (6): 1175-1178.

Bartoń, K. (2009). *MuMIn: multi-model inference. R package, version 0.12. 2*.

Bender, D. J., Contreras, T. A. & Fahrig, L. (1998). HABITAT LOSS AND POPULATION DECLINE: A META-ANALYSIS OF THE PATCH SIZE EFFECT. *Ecology*, 79 (2): 517-533.

Berg, Å., Ehnström, B., Gustafsson, L., Hallingbäck, T., Jonsell, M. & Weslien, J. (1994). Threatened plant, animal, and fungus species in Swedish forests: distribution and habitat associations. *Conservation biology*, 8 (3): 718-731.

Bieber, C., Lebl, K., Stalder, G., Geiser, F. & Ruf, T. (2014). Body mass dependent use of hibernation: why not prolong the active season, if they can? *Functional Ecology*, 28 (1): 167-177.

Boyce, M. S., Vernier, P. R., Nielsen, S. E. & Schmiegelow, F. K. A. (2002). Evaluating resource selection functions. *Ecological Modelling*, 157 (2–3): 281-300.

Burkey, T. V. (1995). Extinction Rates in Archipelagoes: Implications for Populations in Fragmented Habitats. *Conservation Biology*, 9 (3): 527-541.

Buskirk, S. W. (2000). Habitat fragmentation and interspecific competition: Implications for lynx conservation [Chapter 4].

Cartwright, Samantha J., Nicoll, Malcolm A. C., Jones, Carl G., Tatayah, V. & Norris, K. (2014). Anthropogenic Natal Environmental Effects on Life Histories in a Wild Bird Population. *Current Biology*, 24 (5): 536-540.

Chapron, G., Kaczensky, P., Linnell, J. D., von Arx, M., Huber, D., Andrén, H., López-Bao, J. V., Adamec, M., Álvares, F. & Anders, O. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science*, 346 (6216): 1517-1519.

Cohen, J. E. (1995). Population growth and earth's human carrying capacity. *Science*, 269 (5222): 341-6.

Cullen Jr. L., A. K. C., Sana D. & Nava A. F. . (2005). Jaguars as landscape detectives for the upper Paraná River corridor, Brazil. *The Brazilian Journal of Nature Conservatio*, 3: 161.

Dahle, B., Sørensen, O., Wedul, E. H., Swenson, J. E. & Sandegren, F. (1998). The diet of brown bears Ursus arctos in central Scandinavia: effect of access to free-ranging domestic sheep Ovis aries. *Wildlife biology*, 4 (3): 147-158.

Dahle, B. & Swenson, J. E. (2003). Home ranges in adult Scandinavian brown bears (Ursus arctos): effect of mass, sex, reproductive category, population density and habitat type. *Journal of Zoology*, 260 (4): 329-335.

De Angelo, C. D. (2009). *The Upper Parana Atlantic Forest landscape and its effects on jaguar (Panthera onca) and puma (Puma concolor) distribution and population structure.* . Buenos Aires, Argentina: Universidad de Buenos Aires, Facultad de Ciencias Exactas y Naturales 507-508 pp.

Domisch, T., Ohashi, M., Finér, L., Risch, A., Sundström, L., Kilpeläinen, J. & Niemelä, P. (2008). Decomposition of organic matter and nutrient mineralisation in wood ant (Formica rufa group) mounds in boreal coniferous forests of different age. *Biology and Fertility of soils*, 44 (3): 539-545.

Elfström, M., Swenson, J. E. & Ball, J. P. (2008). Selection of denning habitats by Scandinavian brown bears Ursus arctos. *Wildlife Biology*, 14 (2): 176-187.

Elfström, M. & Swenson, J. E. (2009). Effects of sex and age on den site use by Scandinavian brown bears. *Ursus*, 20 (2): 85-93.

Elgmork, K. (1978). Human impact on a brown bear population (Ursus arctos L.). *Biological Conservation*, 13 (2): 81-103.

Evans, A. L. (2016). *Ecophysiology of Brown Bears. Basic physiology and effects of hibernation, pregnancy, body mass, and capture.* PhD in Applied Ecology: Hedmark University College, Faculty of Applied Ecology and Agricultural Sciences.

Fahrig, L. (1997). Relative Effects of Habitat Loss and Fragmentation on Population Extinction. *The Journal of Wildlife Management*, 61 (3): 603-610.

Folk Jr, G. E. & Folk, M. A. (1967). PHYSIOLOGICAL OBSERVATIONS ON SUBARCTIC BEARS UNDER WINTER DEN CONDITIONS: DTIC Document.

Frank, S. C., Steyaert, S. M., Swenson, J. E., Storch, I., Kindberg, J., Barck, H. & Zedrosser, A. (2015). A “clearcut” case? Brown bear selection of coarse woody debris and carpenter ants on clearcuts. *Forest ecology and management*, 348: 164-173.

Friebe, A., Swenson, J. E. & Sandegren, F. (2001). Denning Chronology of Female Brown Bears in Central Sweden. *Ursus*, 12: 37-45.

Friebe, A. (2014). *Winter ethology of free-ranging brown bears (Ursus arctos) in central Sweden.* Doktorgrades der Naturwissenschaften. Frankfurt: der Goethe-Universität in Frankfurt am Main, Biowissenschaften. 93 pp.

Haag T., Santos A. S., Sana D. A., Morato R . G., Cullen Jr. L., Crawshaw Jr. P. G., De Angelo C., Di Bitetti M. S., M., S. F. & E., E. (2010). The effect of habitat fragmentation on the genetic structure of a top predator.

Hellgren, E. C. (1998). Physiology of hibernation in bears. *Ursus*: 467-477.

Huber, D., Kusak, J. & Frkovic, A. (1998). Traffic kills of brown bears in Gorski kotar, Croatia. *Ursus*: 167-171.

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

Johnson, K., Johnson, D. & Pelton, M. (1978). *Simulation of winter heat loss for a black bear in a closed tree den*. Proceedings of the Eastern Workshop on Black Bear Research and Management. 155-166 pp.

Kaal, M. (1976). Ecology, protection and prospect of utilization of the brown bear in the Estonian SSR. *Bears: Their Biology and Management*: 303-306.

Kindberg, J. (2010). *Monitoring and management of the Swedish brown bear (Ursus arctos) population*. Doctoral Thesis Umeå: Swedish University of Agricultural Sciences Department of Wildlife, Fish and Environmental Studies 45 pp.

Kingsley, M. C. S., Nagy, J. A. & Russell, R. H. (1983). Patterns of Weight Gain and Loss for Grizzly Bears in Northern Canada. *Bears: Their Biology and Management*, 5: 174-178.

Klenzendorf, S. A., Vaughan, M. R. & Martin, D. D. (2002). Den-type use and fidelity of American black bears in western Virginia. *Ursus*: 39-44.

Kurki, S., Nikula, A., Helle, P. & Lindén, H. (2000). Landscape fragmentation and forest composition effects on grouse breeding success in boreal forests. *Ecology*, 81 (7): 1985-1997.

Kusak, J. & Huber, D. (1998). Brown Bear Habitat Quality in Gorski Kotar, Croatia. *Ursus*, 10: 281-291.

Libal, N. S., Belant, J. L., Leopold, B. D., Wang, G. & Owen, P. A. (2011). Despotism and risk of infanticide influence grizzly bear den-site selection. *PloS one*, 6 (9): e24133.

Linnell, J. D., Swenson, J. E., Andersen, R. & Barnes, B. (2000). How vulnerable are denning bears to disturbance? *Wildlife Society Bulletin*: 400-413.

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

Lyman, C. P., O'Brien, R. C., Greene, G. C. & Papafrangos, E. D. (1981). Hibernation and longevity in the Turkish hamster Mesocricetus brandti. *Science*, 212 (4495): 668-670.

Manchi, S. & Swenson, J. E. (2005). Denning behaviour of Scandinavian brown bears Ursus arctos. *Wildlife Biology*, 11 (2): 123-132.

Manly, B., McDonald, L., Thomas, D., McDonald, T. L. & Erickson, W. P. (2007). *Resource selection by animals: statistical design and analysis for field studies*: Springer Science & Business Media.

Mannerkoski, H., Finér, L., Piirainen, S. & Starr, M. (2005). Effect of clear-cutting and site preparation on the level and quality of groundwater in some headwater catchments in eastern Finland. *Forest Ecology and Management*, 220 (1–3): 107-117.

Moe, T., Kindberg, J., Jansson, I. & Swenson, J. (2007). Importance of diel behaviour when studying habitat selection: examples from female Scandinavian brown bears (Ursus arctos). *Canadian Journal of zoology*, 85 (4): 518-525.

Moen, G. K., Støen, O.-G., Sahlén, V. & Swenson, J. E. (2012). Behaviour of solitary adult Scandinavian brown bears (Ursus arctos) when approached by humans on foot. *PLoS One*, 7 (2): e31699.

Nellemann, C., Støen, O.-G., Kindberg, J., Swenson, J. E., Vistnes, I., Ericsson, G., Katajisto, J., Kaltenborn, B. P., Martin, J. & Ordiz, A. (2007). Terrain use by an expanding brown bear population in relation to age, recreational resorts and human settlements. *Biological Conservation*, 138 (1–2): 157-165.

Nielsen, S. E., Boyce, M. S. & Stenhouse, G. B. (2004). Grizzly bears and forestry: I. Selection of clearcuts by grizzly bears in west-central Alberta, Canada. *Forest Ecology and Management*, 199 (1): 51-65.

Nowack, L. (2015). *Reproductive performance of Scandinavian female brown bears (Ursus arctos) in relation to the use of den-type.* . Master thesis. Vienna: University of Natural Resources and Apllied Life Sciences, Vienna, Department for Integrative Biology and Biodiversity Research. 21 pp.

O'brien, R. M. (2007). A Caution Regarding Rules of Thumb for Variance Inflation Factors. *Quality & Quantity*, 41 (5): 673-690.

Oli, M. K., Jacobson, H. A. & Leopold, B. D. (1997). Denning ecology of black bears in the White River National Wildlife refuge, Arkansas. *The Journal of wildlife management*: 700-706.

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

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

Pertoldi, C., Loeschcke, V., Madsen, A. B., Randi, E. & Mucci, N. (2001). Effects of habitat fragmentation on the Eurasian badger (Meles meles) subpopulations in Denmark. *Hystrix, the Italian Journal of Mammalogy*, 12 (1).

Pimm, S. L. & Raven, P. (2000). Biodiversity: extinction by numbers. *Nature*, 403 (6772): 843-845.

Punttila, P. (1996). Succession, forest fragmentation, and the distribution of wood ants. *Oikos*: 291-298.

R Development core team. (2015). *R Studio: integrated development for R. RStudio, Inc., Boston, MA*.

Rainey, C. (2015). Dealing with Separation in Logistic Regression Models: Working paper. Latest version at https://github. com/carlislerainey/priors-for-separation.

Rogers, L. (1999). Bear center conducts hibernation study *North American Bear Center Newsletter* 3(4): 1-3.

Rytwinski, T. (2012). *The effects of species behavioural responses to roads and life history traits on their population level responses to roads*: Carleton University Ottawa.

Sahlén, E., Støen, O.-G. & Swenson, J. E. (2011). Brown bear den site concealment in relation to human activity in Sweden. *Ursus*, 22 (2): 152-158.

Sahlén, V. (2013). *Encounters between brown bears and humans in Scandinavia—contributing factors, bear behavior and management perspectives*: Doctorate thesis. Norwegian University of Life Sciences, Department of Natural Resource Management, Ås.

SBBRP. *The Scandinavian Brown Bear Research Project*. Available at: http://bearproject.info/.

Schoen, J. W., Beier, L. R., Lentfer, J. W. & Johnson, L. J. (1987). Denning ecology of brown bears on Admiralty and Chichagof Islands. *Bears: Their Biology and Management*: 293-304.

Stenset, N. E., Lutnæs, P. N., Bjarnadóttir, V., Dahle, B., Fossum, K. H., Jigsved, P., Johansen, T., Neumann, W., Opseth, O. & Rønning, O. (2016). Seasonal and annual variation in the diet of brown bears Ursus arctos in the boreal forest of southcentral Sweden. *Wildlife Biology*, 22 (3): 107-116.

Steyaert, S. M., ENDRESTØL, A., Hacklaender, K., Swenson, J. E. & Zedrosser, A. (2012). The mating system of the brown bear Ursus arctos. *Mammal Review*, 42 (1): 12-34.

Stonorov, D. & Stokes, A. W. (1972). Social Behavior of the Alaska Brown Bear. *Bears: Their Biology and Management*, 2: 232-242.

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

Swenson, J. E., Sandegren, F., Brunberg, S. & Wabakken, P. (1997). Winter den abandonment by brown bears Ursus arctos: causes and consequences. *Wildlife Biology*, 3 (1): 35-38.

Swenson, J. E., Jansson, A., Riig, R. & Sandegren, F. (1999). Bears and ants: myrmecophagy by brown bears in central Scandinavia. *Canadian Journal of Zoology*, 77 (4): 551-561.

Swenson, J. E. (2000). *Action plan for the conservation of the brown bear in Europe (Ursus arctos)*: Council of Europe.

Swenson, J. E. (2003). *The ecology of an increasing brown bear population: managing a successful recovery*: na.

Tietje, W. D. & Ruff, R. L. (1980). Denning behavior of black bears in boreal forest of Alberta. *The Journal of Wildlife Management*: 858-870.

Turbill, C., Bieber, C. & Ruf, T. (2011). Hibernation is associated with increased survival and the evolution of slow life histories among mammals. *Proceedings of the Royal Society of London B: Biological Sciences*, 278 (1723): 3355-3363.

Wilcove, D. S. (1985). Nest predation in forest tracts and the decline of migratory songbirds. *Ecology*, 66 (4): 1211-1214.

Woodroffe, R., Thirgood, S. & Rabinowitz, A. (2005). *People and wildlife, conflict or co-existence?*: Cambridge University Press.

Zuur, A., Ieno, E., Walker, N., Saveliev, A. & Smith, G. (2009). Mixed effects models and extensions in ecology with R; Gail M, Krickeberg K, Samet JM, Tsiatis A, Wong W, editors. *New York, NY: Spring Science and Business Media*.

Zuur, A. F., Ieno, E. N. & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1 (1): 3-14.

Appendix

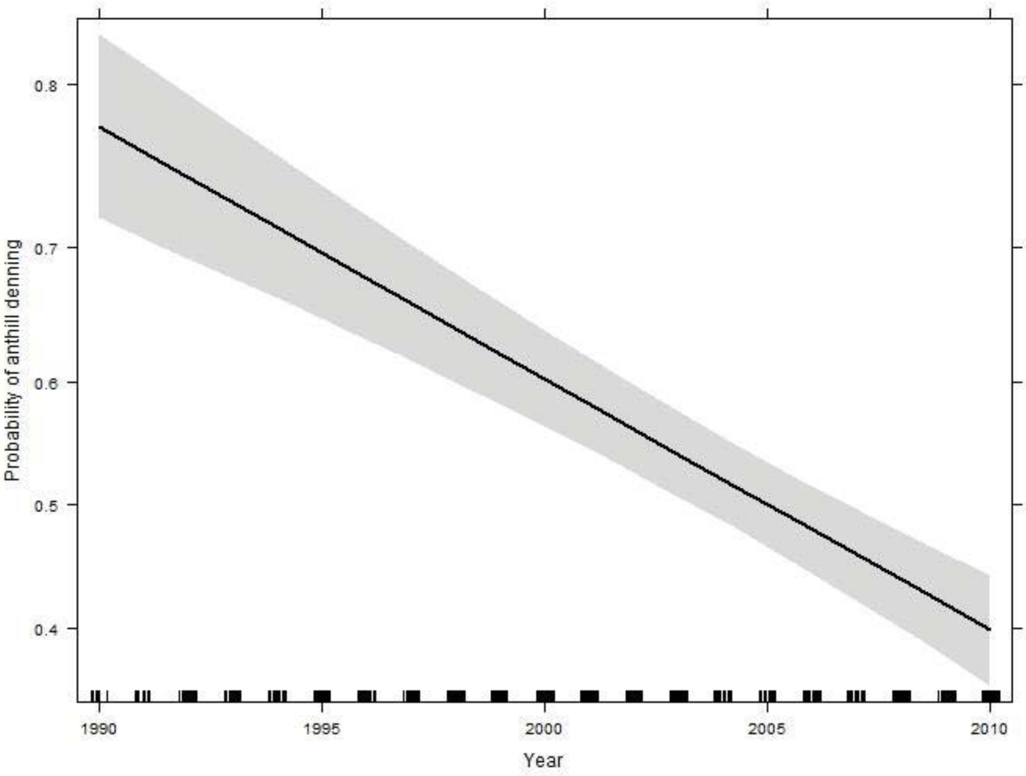

Figure A1. The predicted likelihood of all bears (N_{bears} = 196, N_{dens} = 905) using an anthill den as a winter den between 1986 and 2014 in south central Sweden. Den type as response variable; 1 = anthill, 0 = no anthill.

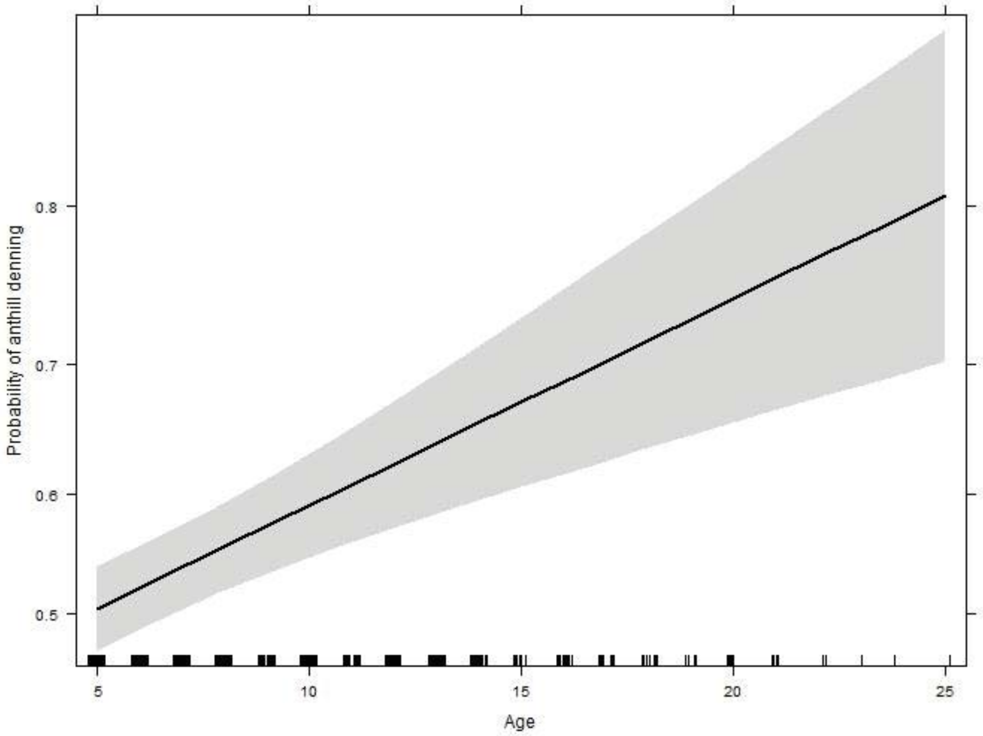

Figure A2. The predicted likelihood of all bears (N_{bears} = 196, N_{dens} = 905) using an anthill den as a winter den (1985 and 2014) in southcentral Sweden, in relation to age. Den type as response variable; 1 = anthill, 0 = no anthill.

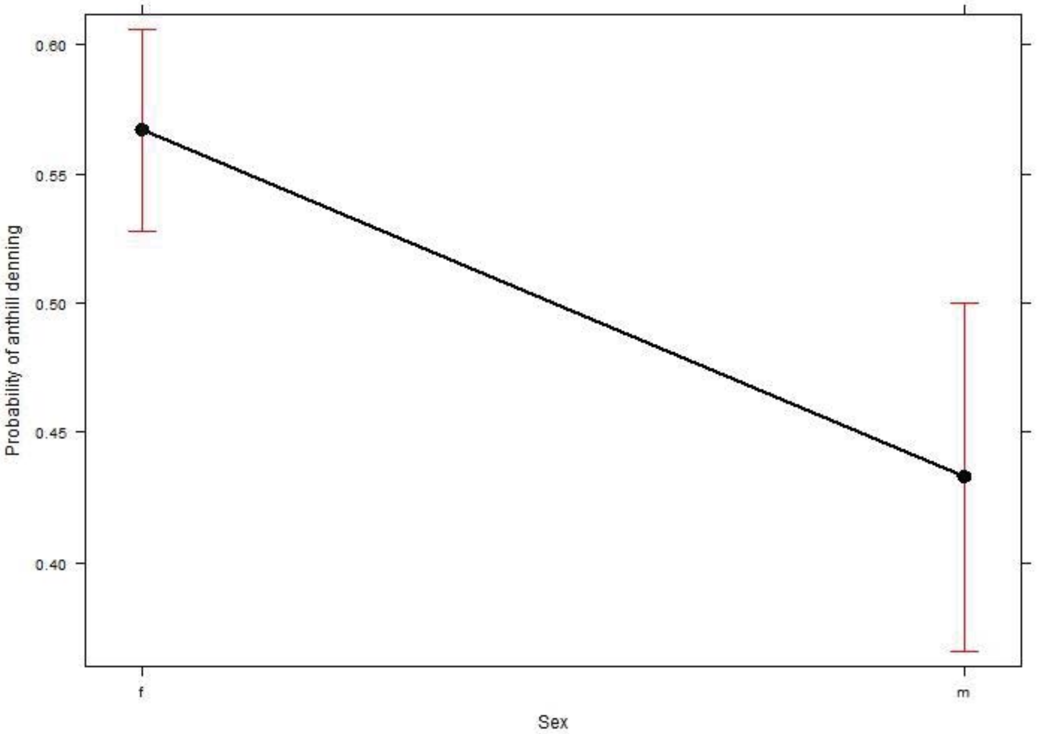

Figure A3. The predicted likelihood for each sex of all bears using an anthill den as a winter den (1985 and 2014), in southcentral Sweden. Den type as response variable; 1 = anthill, 0 = no anthill. Sex: m = male, f = female.

Table A1. Results for fixed effects from the best glmer model to assess a temporal trend in the probability that the Scandinavian brown bear (including all bears) (N_{bears} = 196, N_{dens} = 905) used an excavated anthill den as a winter den (1986-2014) in southcentral Sweden.

Fixed effects:

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
Intercept	203.27113	10.92725	18.602	< 0.001 ***
Age	0.11680	0.02966	3.937	< 0.001 ***
Sex – male vs. female	-0.27795	0.45693	-0.608	0.543
Year	-0.10166	0.00546	-18.618	< 0.001 ***
Age:sex – male vs. female	-0.03284	0.05817	-0.565	0.572

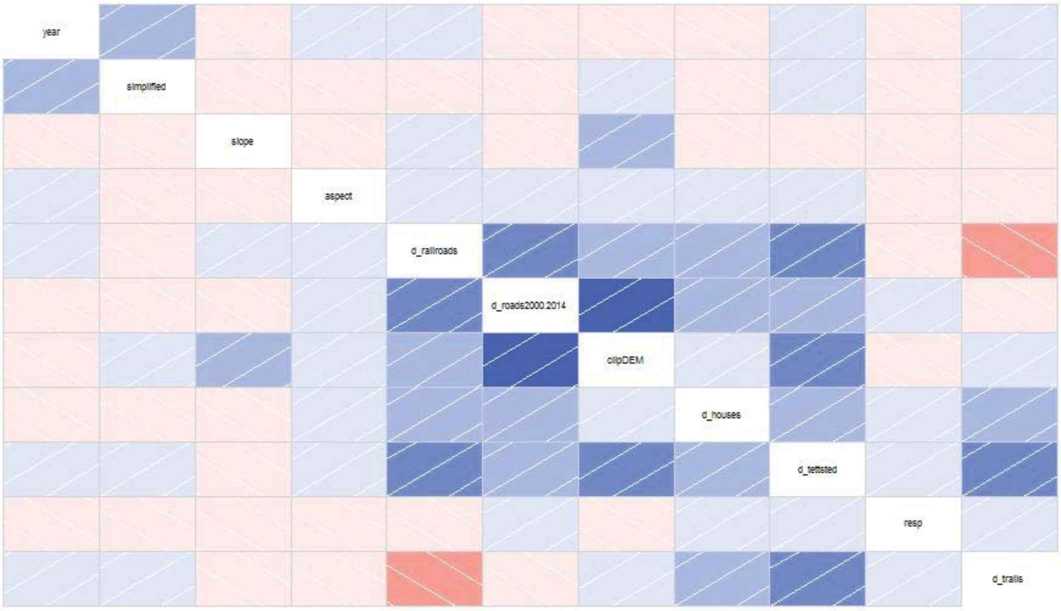

Figure A4. Correlogram showing the degree of collinearity between all landscape variables. Red = negative correlation. Blue = positive correlation. Light/dark = degree of correlation, the darker the stronger.

Table A2. Results from the best model to assess den site selection (all den types) of all bears (N_{bears} = 161, N_{dens} = 1323) without the random effect (bear ID).

Coefficients:

	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	0.104	0.25	0.419	0.675
Distance to roads	0.0006	0.0001	3.862	< 0.001 ***
Elevation	-0.002	0.0005	-3.915	< 0.001 ***
Distance to houses	0.0002	0.00008	2.566	0.01 *
Distance to railroads	-0.00003	0.000007	-4.954	< 0.001 ***
Distance to villages	0.00004	0.000008	5.026	< 0.001***
Old forest	0.172	0.144	1.198	0.23
Bog	-1.34	0.236	-5.879	< 0.001 ***
Young forest	0.238	0.152	1.568	0.116

Table A3. Results from the best model to assess den site selection (all den types) of all bears (N_{bears} = 161, N_{dens} = 1323) including the random effect (bear ID).

Coefficients:

	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	0.105	0.25	0.422	0.672
Distance to roads	0.00056	0.0001	3.954	< 0.001 ***
Elevation	-0.002	0.0005	-4.129	< 0.001 ***
Distance to houses	0.0002	0.00008	2.621	0.008 **
Distance to railroads	-0.00003	0.000005	-5.918	< 0.001 ***
Distance to villages	0.00004	0.000005	8.260	< 0.001***
Old forest	0.172	0.144	1.2	0.23
Bog	-1.34	0.235	-5.904	< 0.001 ***
Young forest	0.238	0.152	1.569	0.116

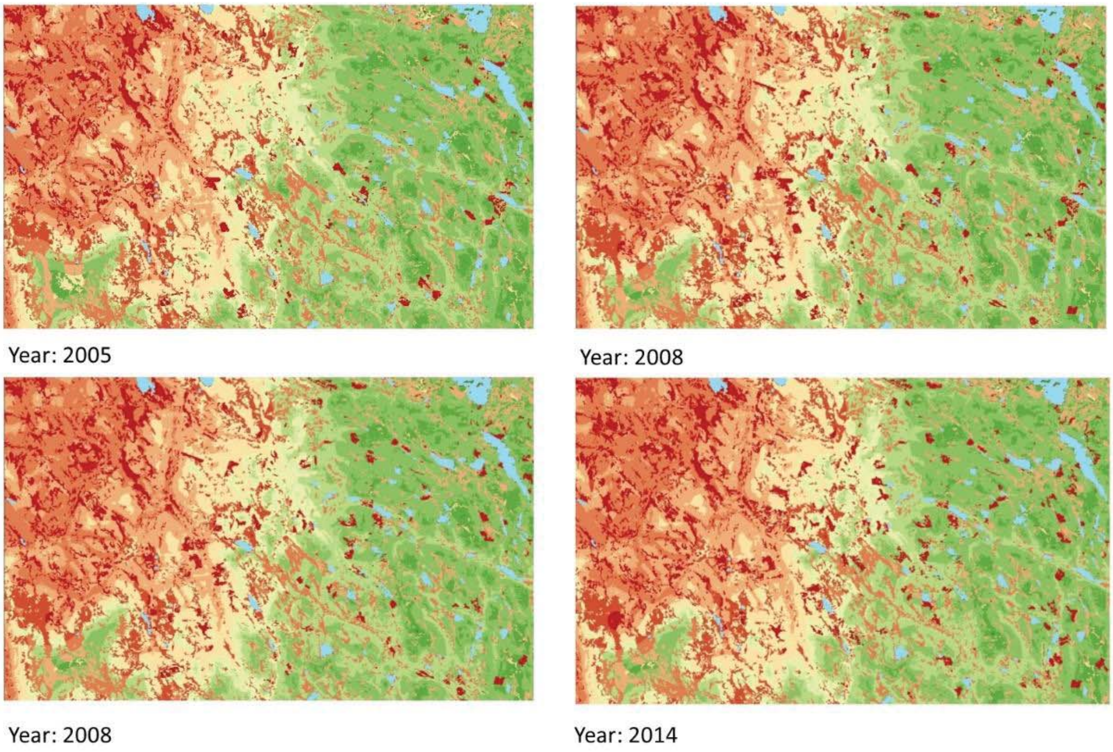

Figure A5. Relative probability of anthill den occurrence for females (all age classes) (N_{bears} = 128, N_{dens} = 519) in the study area for year 2005 and 2014, to highlight changes in anthill denning habitat. The greener the pixels, the more suitable the habitat, and the higher the probability of occurrence. Whereas the more red the pixels, the less suitable the habitat, and the lower probability of occurrence. Water is marked with a blue color.

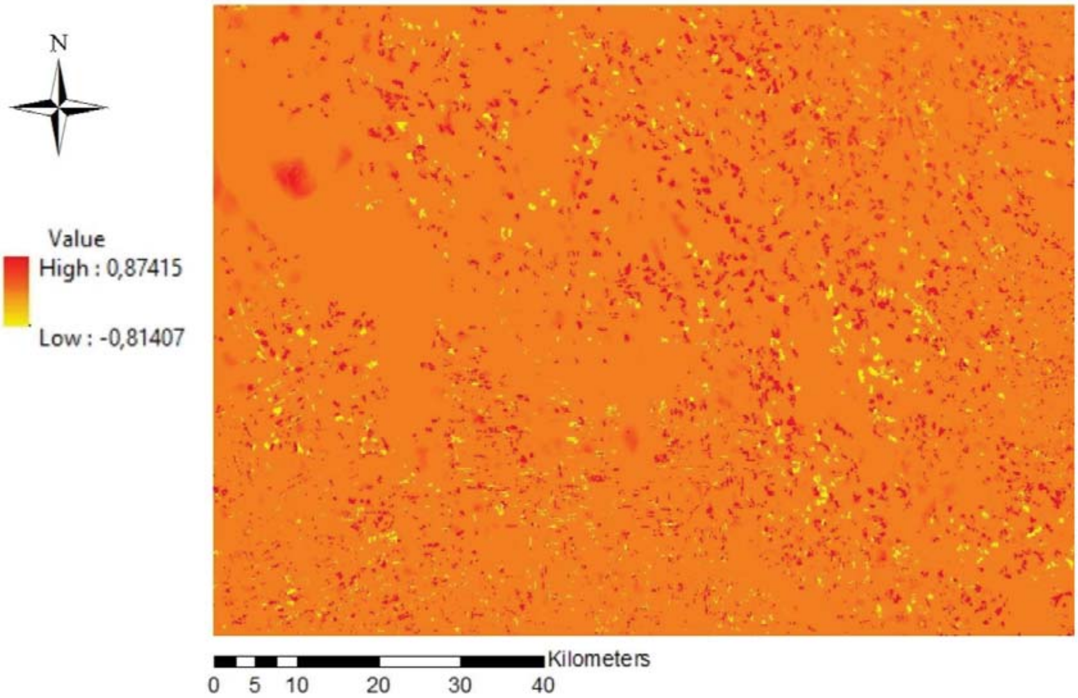

Figure A6. The distribution of negative and positive changes in suitability of habitat for anthill denning by the female Scandinavian brown bear (N_{bears} = 128, N_{dens} = 519), from 2005 to 2014. The more red, the more negative change in suitability. The more yellow, the more positive change in suitability.

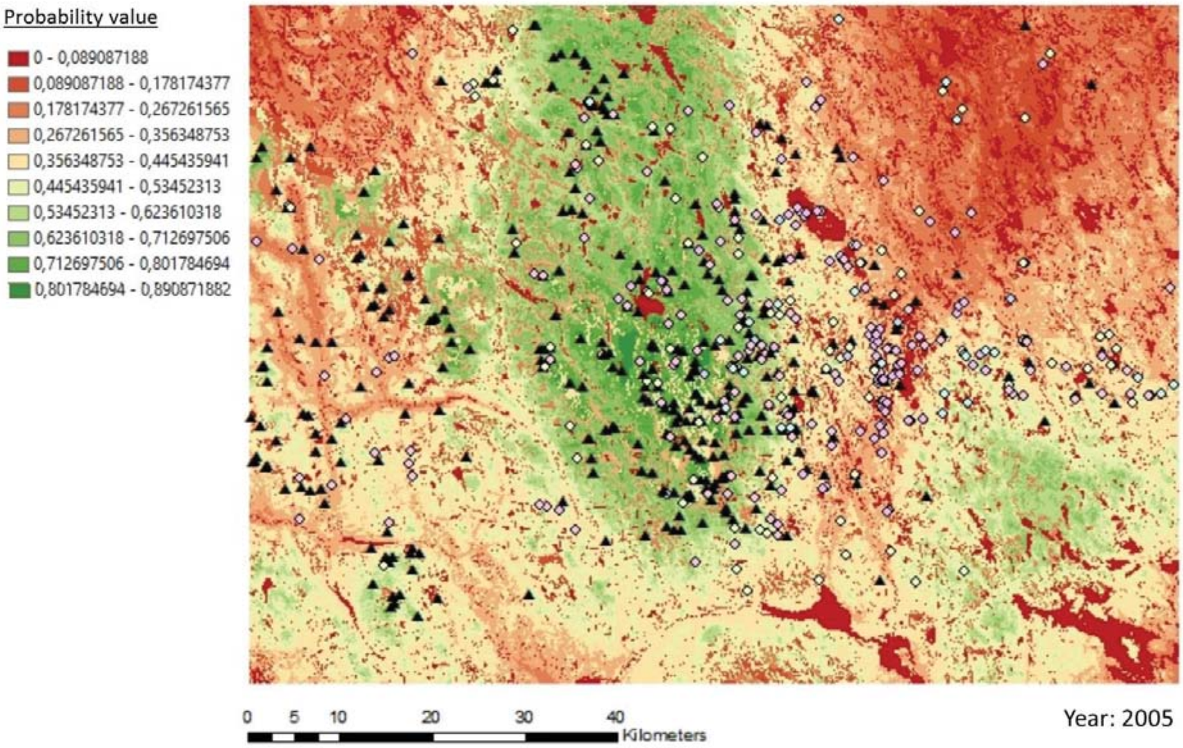

Figure A7. Distribution of anthill dens (marked with a triangle) and other dens (marked with a circle) (1986-2014) in the study area for year 2005, to highlight that the dens (especially anthill dens) are indeed found in the most suitable habitat in the area. Relative probability of anthill den occurrence for females (all age classes) ($N_{bears} = 128$, $N_{dens} = 519$) in the study area for year 2005 is also shown. The greener the pixels, the more suitable the habitat, and the higher the probability of occurrence. Whereas the more red the pixels, the less suitable the habitat, and the lower probability of occurrence. Water is marked with a blue color.

Norges miljø- og biovitenskapelig universitet
Noregs miljø- og biovitskapelege universitet
Norwegian University of Life Sciences

Postboks 5003
NO-1432 Ås
Norway