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Master thesis:

Effects of diversionary feeding on life history traits of brown bears

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Impressum

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Abstract

All around the globe, many animal species have access to anthropogenic food sources. Several are provided unintentionally, others intentionally as with diversionary feeding, which is used as an instrument for human-bear conflict mitigation in Slovenia, but its side effects are still unclear. It is known, that food availability is a main driver that affects life history traits. In Slovenia brown bear (*Ursus arctos*) population densities and reproduction rates are extremely high, which may be the result of intensive feeding. Therefore we analysed the effects of food availability in the form of diversionary feeding and natural food availability on the life history traits body weight and litter size. Here we used spatial and biometric data of 663 shot bears from 2004 to 2012 (body weight analysis) and 615 litter size observations from 2004 to 2013 (litter size analysis) for the entire bear range (6.231 km²) of Slovenia. For both analyses, we included major factors that could affect food availability (e.g. forest cover, proportion of mast producing tree species). We developed set of basic models with all combinations of variables and selected the best models based on AIC-scores. Only forest cover showed an effect on body weight, although with an $R^2 < 0.005$, this effect is most likely biologically unimportant. None of the tested variables affected the litter size. Usually one would expect annual fluctuations in the life history traits due to variations in natural food availability, e.g. annual variability in beech mast production, one of the key natural food sources of bears in Slovenia. But no such effect was observed and we assume that intensive additional feeding buffers temporal and spatial variability in natural food availability. Supplemental feeding also considerably increases total habitat carrying capacity, which may also be explanation for the very high reproduction rates (19 – 22%/year) and population densities (up to 40 bears/100 km²) observed for Slovenian brown bears. The high reproductive potential and low natural mortality are triggering the demand of population control (up to 25% of population culled annually), with the goal of stabilizing the population. Finally we conclude that the two important factors that are driving evolution of brown bears in Slovenia – reproduction and mortality, are mainly controlled by humans, which could be seen as a kind of semi-domestication of bears, similarly as already described for ungulates.

Keywords: *Ursus arctos*, diversionary feeding, supplemental feeding, body weight, litter size, life history traits, Slovenia

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1 Introduction

In many animal species food availability has been recorded as one of the key factors affecting life history traits. It is one of the main drivers of inter- and intraspecific competition, which leads to natural selection and results in evolution (Darwin 1859). The food availability, for example, affects an individual's body weight (Harestad & Bunnell 1979, Hilderbrand et al. 1999a), body size (Beckmann & Berger 2003, Cellina 2008, Dahle & Swenson 2003b, Robbins et al. 2004, Welch et al. 1997), litter size (Cellina 2008, Hilderbrand et al. 1999a) and life expectancy (Jezierski 1977), as well as home-range size (Bjornlie et al. 2014, Boutin 1990, Burt 1943, Cederlund & Sand 1994, Cooper et al. 2006, Harestad & Bunnell 1979) and population density (Dahle & Swenson 2003a, Jerina et al. 2013).

All around the world, numerous animal species have access to anthropogenic foods due to the increasing habitat fragmentation, agriculture and human settlement expansion (Conover 2002). Food can be provided unintentionally (e.g. garbage, orchards, livestock, agriculture) or intentionally (i.e. by supplemental or diversionary feeding). This additional feeding is provided for numerous terrestrial and aquatic species worldwide. Feeding is performed for multiple purposes: tourism (Orams 2002), hunting (supplemental feeding and baiting; higher reproduction and bigger trophies (Milner et al. 2014)) and also human-wildlife conflict mitigation (diversionary feeding (Milner et al. 2014)). But scientists are often worried about possible side effects (Orams 2002, Milner et al. 2014, Dunkley & Cattet 2003) of additional feeding.

Brown bears (*Ursus arctos*) have huge home-ranges and are able to move long distances, which allows them to feed on many different feeding places. Highly intelligent, they're able to remind feeding times and their well-developed sense of smell enables them to discover new food sources over long distances. As a super-predator in a landscape without natural enemies, interspecific competition is low, which enables brown bears to monopolize feeding sites (Partridge et al. 2001). All these attributes make brown bears a good model species for studying possible effects of additional feeding on their life history traits.

It is relatively little known about the effects of additional feeding on life history traits in bears. Most of the studies were done on black bears (*Ursus americanus*) in Northern America and analysed primarily the effects of supplemental feeding during mast failures on reproduction success (Rogers 1976) and the suitability of diversionary feeding as an instrument of human-bear-conflict mitigation, in order to prevent damages on managed conifer stands (Partridge et al. 2001, Rogers 2011, Ziegler 1994, 2008). Food supplied bears had higher reproduction rates (Rogers 1976, 2011) and body weights (Partridge et al. 2001, Rogers 1987) than bears feeding only on natural food sources. Other studies similarly conclude that additional feeding increases the carrying capacity (Penteriani & Melletti 2010) and compensates lacks in natural food availability (e.g. mast (Gray et al. 2004, Ziegler 1994, 2008)). Except for mast production, no other environmental factors were considered in these studies. Additionally, these studies only research feeding effects on black bears in North America. No similar study has been conducted on brown bears in Europe yet. Hence, this will be the first study that analyses feeding effects on European brown bears, considering important environmental parameters.

In Slovenia, brown bears have been supplied with additional food for several purposes. The main purpose is the mitigation of human-bear-conflicts (Klenzendorf 1997). As an opportunistic omnivore, the brown bear utilizes all easily accessible food sources (Robbins et al. 2004). Bears are very dependent on the food supplied by their natural environment, so changes in the food availability (i.e. due to additional feeding) may affect their vitality (Boutin 1990, Costello et al. 2003, Iverson et al. 2001, Nielsen et al. 2013). Diversionary feeding in Slovenia is very intensive and provides food all year long. Kavčič et al. (2014) estimated an annual content of 34% additional food in Slovenian brown bear diet. It may be more efficient for bears to feed at feeding places than foraging on natural food sources

(Jerina et al. 2012, Kavčič et al. 2014). Compared to surrounding natural habitats, they are able to gain 3.9-times more energy at feeding places in the same amount of time (Kavčič et al. 2011). Possible side effects could be reflected by changes in several life history traits, e.g. in body weight and litter size. For Slovenia, one of the highest reproduction rates (19 – 22%/year, Krofel et al. 2012) and population densities (up to 40 bears/100km², Jerina et al. 2013) in brown bears worldwide have been reported.

Under natural conditions the availability of energetic rich food sources like hard and soft mast (main natural food source in autumn) in combination with population density is a main environmental factor that affects a bear's body weight and litter size (Boutin 1990, Costello et al. 2003, Iverson et al. 2001, Nielsen et al. 2013; Elfstrom et al., 2014a). But mast production varies in space and in the years, which results in inter-annual and spatial changes of habitat carrying capacity. In case of a lack in mast production, diversionary feeding could play an important role by buffering lower natural food availability. Without diversionary feeding, fluctuations/variations in life history traits are to be expected over the years and in space.

The goal of this study is to analyse the effects of diversionary feeding on the life history traits body weight and litter size of brown bears in Slovenia. We've set the following 3 hypotheses: (0) *Diversionary feeding has no effect on brown bear's life history traits*, (I) *Diversionary feeding directly affects a brown bear's life history traits*, or even, (II) *Diversionary feeding is everywhere and all the time so abundant, that it completely saturates the ecosystem with food*. Hypothesis (0) will be accepted, when diversionary feeding has no significant effect on brown bear body weight and/or litter size. Besides, at least some environmental factors that typically affect natural food availability (e.g. proportion of forests producing mast) and competition (density of bears) should cause spatial and yearly variations in the life history traits. Hypothesis (I) will be accepted, if diversionary feeding is significantly affecting body weight and/or litter size but some yearly fluctuations may be observed, because lacks in natural food availability are not necessarily completely compensated by diversionary feeding. Hypothesis (II) is accepted, when diversionary feeding and also no other variable has no biologically meaningful effects on the life history traits neither in space nor in time, so no yearly fluctuations and temporal variations in body weight and/or litter size will be observed, i.e. the population is in space and time ideally free distributed (Fretwell & Lucas 1970, Fretwell 1972, Stephens & Krebs 1987).

2 Material and Methods

2.1 Study area

Slovenia has a total land area of 20,273 km². As already mentioned, bear population densities exceed 40 bears per 100 km², but these densities are only found in a relatively few small and fragmented areas. The region that consists 95% of all Slovenian bears has an area of 3,855 km² (19% of the Slovenian territory) and a mean density of 13 bears per 100 km² (Jerina et al. 2013). For whole Slovenia, 2,193 feeding places (appropriate for bears) are irregularly distributed and provide 1,716,974 kg food per year. The average bear home-range in Slovenia is 350 km² (Jerina et al. 2012).

In the whole bear range (6,231 km²), 935 feeding places provide 457,836 kg food per year. This results in 15 feeding places per 100 km². The mean amount of food provided is 7347kg food per year and per 100 km².

2.2 Hunting and feeding in Slovenia

In Slovenia, feeding sites are used to attract red deer, wild boar and brown bears for hunting purposes (Jerina 2012, Krofel et al. 2012) and as an attempt to mitigate human-bear conflicts (Kavčič et al. 2013), so both types of feeding (supplemental and diversionary feeding) are used. Huge amounts of maize (as well as wheat and apples, but their quantities

are much smaller) have been used to supply bears all year long, in some parts of Slovenia, for more than 100 years (Simonič 1994). Its goal was/is to reduce livestock-bear problems, by keeping the bears in the core area (away from human settlements) of their spatial distribution and to bait bears facilitating selective harvesting and annual population counts (Klenzendorf 1997) as a part of the bear monitoring.

All regular hunting of bears occurs from elevated stands at feeding sites (Jerina 2012, Krofel et al. 2012). Hunting season for bears starts on 1st October and ends on 30th April. Harvest quota is distributed in 3 body mass categories: < 100 kg (min. 75% of quota), 100 – 150 kg (max. 15% of quota) and > 150 kg (max. 10% of quota) (Krofel et al. 2012). Management hunting (e.g. removal of problem bears) is allowed all year and not only limited at supplemental feeding places. 81.7% bears were regularly hunted, 17.4% were removed due to management purposes. Annual harvest rate during the years 1998 – 2008 was 20% (Krofel et al. 2012) and has increased significantly due to the increasing trend in damages caused by bears (Jerina & Adamič 2008). 59% of the removed bears were male and 78% of all bears had an age of < 4 years (Krofel et al. 2012). All killed bears have to be examined by personally trained employees of the Slovenia Forest Service, following standardised procedures, to check if regulations have been followed and to gather exact biometric data for further analysis and monitoring activities.

2.3 Data on feeding

Slovenian hunters have to report their feeding places, with the yearly amount of food to the Slovenian forest service. The feeding places can be controlled by inspectors and possible misinformation will be penalised. For this study, a dataset with locations of all feeding places and their amounts of food has been provided by the Slovenian forest service. For the locations, information about hunting ground and cadastral parcels are given. Cadastral parcels are usually very small (most of them are smaller than 1 ha), which allowed us to reconstruct the exact feeding location by analysing maps of hunting grounds and cadastral parcels. Due to the obligation of reporting correct information about the feeding places, dataset on feeding that is used in this research should be accurate enough for the purposes of our study.

This dataset contains all feeding places for Slovenia, so not only feeding places for brown bears. Therefore we first extracted the data on feeding places which are appropriate for bears. In the end, our dataset comprises 2,193 supplemental feeding places. An average amount of 783 kg (natural-log transformed: mean = 6.11, sd = 1.05) food is provided all year long per feeding place.

2.4 Environmental data

In order to consider all possible factors that could affect food availability and distribution, several environmental parameters are taken into account. These parameters have been recorded for the national monitoring of ungulates (Adamič & Jerina 2010) and several research projects leaded by the supervisor of the present thesis in a 1×1 km square grid for the whole surface of Slovenia. A dataset with data on several environmental parameters for every cell of this grid has been provided for our analyses. The following parameters have been chosen to be considered in the analyses: percentage of forest cover (forest as usual brown bear habitat with natural food availability, Kobler & Adamič 2000), carrion (ungulates as natural food source; Kavčič et al., 2013), distance to nearest settlement (anthropogenic food sources like garbage, fruits or livestock, agriculture), proportion of mast trees (mast as important food sources in autumn, Rogers 1976), average yearly temperature (correlates with altitude and duration of hibernation: represents the duration of the growing season, where many important natural food sources are being produced) and the bear density (reflects the potential of intraspecific).

2.5 Biometric data

A dataset containing biometric data of 1,121 bears that have been removed from 1994 to 2012 is available. For most of the bears ($n = 663$), coordinates of the exact location of removal have been recorded. For the other bears (bears shot before 2004, $n = 458$), only information about the hunting ground was available. So here we took the centroid of the hunting ground as place of harvest. Sex, body weight, date of death and age represent the biometric data, available for every bear. The age of 877 bears was estimated by the tooth-cross-section-method (at the Matson's lab, United States of America), the age of the remaining 225 bears (mostly cubs of the years and other sub adults) was estimated based on the body weight, sex and season with a regression tree method (Jerina & Krofel 2012). About 80 % of the samples were classified with the exact age.

Due to strict regulations, all the data was collected by well-trained experts, we believe that this dataset, covering the entire brown bear range of Slovenia, provides excellent base rock for the studying selected research questions.

2.6 Data on reproduction

For analysing the effects on the reproduction, we used counts of litter size. The dataset contains litter size counting from the years 2004-2013 in the entire brown bear range of Slovenia. This monitoring was standardized and the counting was conducted from elevated stands at 167 fixed feeding places every year, by hunters and volunteers (Kavčič et al. 2013). Monitoring is performed in two main periods per year (Spring: May/June, Autumn: August/September/October). The monitoring was always performed by teams of two persons and similarly at the feeding places on the same predefined day and time. These strict requirements are necessary, to ensure a proper data collection, which flows into the national bear monitoring and management program. Brown bear dispersal starts at an age of 1.5-2 years (Jerina et al. 2003), so they recorded the cubs of the year (< 1 year old) and the yearlings. To avoid errors in the analyses, only the numbers of cubs of the year have been considered in this study, due to possible losses in litter size after one year. Litter sizes ranged from a minimum of 1 to a maximum of 4 in $n = 615$ counts (mean = 1.84, sd = 0.67). 148 counts were done in spring and 467 in autumn.

2.7 Data preparation

For further analyses, data on feeding and environmental parameters are needed for every bear, respectively litter size counting. Most logical method would be, to get this data by analysing the home-range of a bear, so the area where he's foraging. But the place where a bear was shot or a litter size counting was performed probably doesn't reflect the centre of the bear's home range. Therefore we had to reconstruct a potential home-range of the killed/observed bear, which reflects the environment he most likely lived in. These spatial analyses were done in ESRI ArcGIS 10.2.2. For each location (place where bear was hunted or litter sizes were counted), a circle with radius of 10,555 meters and area of 350 km² (mean annual home-range of Slovenian bears) was built by using the "Buffer"-function (for litter size counts only 7,356 meters radius, because the mean home-range size for females is 170 km² (Jerina et al. 2012)). These circles represent a purely theoretical home-range polygon layer. But not all areas in these polygons are suitable for bears. Therefore we clipped this layer by a habitat suitability layer for brown bears in Slovenia (Jerina et al. 2003), so that only suitable areas of the theoretical home-range layer are remaining (Fig. 1).

Secondly, the 1×1 km raster grid, containing the environmental parameters and the feeding places, was added as a point layer, the points represent the centroids of the before described 1×1 km raster cells. Points with less than 4% of forest cover have been excluded, because we believe that bears don't use, respectively avoid these areas (Ordiz et al. 2011). Finally we added the points (environmental parameters and feeding data) that were covered by the suitable home-range areas to the bears/observations they belong to. In Excel (MS

Office) we summarized the values of all points for each parameter and calculated the average values for every bear/observation. For the data, we summarized the number of feeding places and the amount of food for each bear/observation and weighted these values by the area size of the bear's/observation's suitable home-range area.

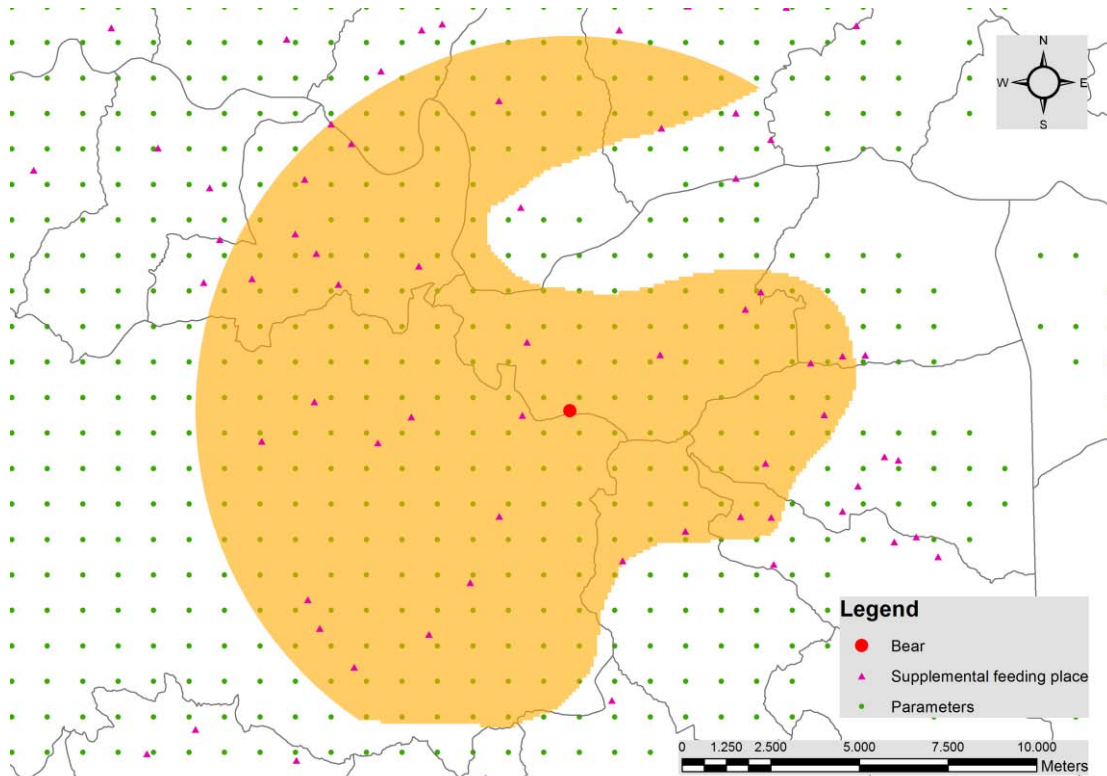


Fig. 1. Suitable home-range (orange circle) of a bear (red dot, place of harvest/litter size observation). Supplemental feeding places are marked as triangles and the environmental parameters as green dots. Black lines represent the hunting grounds. The used diameter for the circle corresponds to the average home-range diameter of Slovenian bears (10,555 meters).

2.8 Analysis of body weight

Brown bear body weight is affected by the age (Nielsen et al. 2013), sex (Kingsley et al. 1988), season (Hilderbrand et al. 1999b) and external (environmental) factors, such as food availability (Rogers 1976). Basically the environmental parameters (Table 1) could be used in the same statistical model than the biometric (age, sex) and chronological (season) data, but in order to avoid confounding factors that could affect later results, the analysis has been divided into two parts. So we first wanted to explain how age, season and sex affect the body weight in a basic model. Age has been used as continuous variable (*age_cont*), by considering end of January as date of birth to get a more exact age, where body weight is also explained by season. Body weight by age differs strongly between both sexes ($p < 0.001$, $R^2 = 0.68$, non-linear regression). Therefore we tried to get the pure effect of *age_cont* on body weight independent of sex by calculating the predicted values of the non-linear (generalized additive model: GAM, “mgcv”-package in “R 3.2.0”) relationship of body weight (natural log transformed: *ln_brutto* = gross body weight with fur and entrails) with the interaction of age and sex (*gam(ln_brutto~te(age_cont,sex))*). The new variable is named *predict_age_sex* and represents the linear part of the model, because its curve is already fitted. To include seasonal effects on body weight (food availability/distribution varies during the year), we created the variable “day of the year” (*doy*), which summarizes all days,

beginning on 1st January to the end of the year. The variable *doy* is used with *sex* as a factor, in order to consider seasonal foraging differences between both sexes. Cubs of the year and yearlings are still with their mother, which could influence their foraging behaviour. Therefore we created an interaction between *age_cont* and *doy*, also with *sex* as a factor. The variables *doy* (by sex) and *doy* × *age_cont* (by sex) represent the non-linear part of the model. With all these variables we've built the following basic model:

$$ln_brutto \sim predict_age_sex + s(doy, by = sex) + te(doy, age_cont, by = sex)$$

For the next analyses (testing for effects of environmental and feeding variables on body weight) we extracted the residuals of this basic model, which reflect the pure effect of sex, age and season on brown bear body weight. That way we avoided possible covariations of one or more individual variable (which are essential for the analyses) with environmental parameters, which would cause problems when using all variables in a single model. For better understanding, the results of this basic model are already presented here and not in the results chapter: the explained deviance of the generalized additive model is $R^2 = 0.793$. Visual diagnostics showed that the extracted residuals are perfectly normally distributed; there are no trends over age, season and sex, which confirms the model's robustness.

In the next step, we checked for outliers in the relationships of the residuals with feeding and environmental parameters. Here we took the residuals as dependent variable, in relation with each single environmental parameters in a linear regression model and finally checked the hat-values (function: `hatvalues()` of the "car"-package). We've searched for patterns in all environmental variables, noted the ID's of bears with abnormally high hat-values and excluded them, when they occurred more than 2 times. In total, we classified 19 bears as outliers and removed them of the dataset, so $n = 1,102$ (660 males, 442 females).

Table 1. Environmental parameters

Variable	Explanation
year	Year of harvest
ageclass	Age classes of table 2
avg_places_quadrant*	Number of supplementary feeding places per km ²
avg_places_forest*	Number of supplementary feeding places by forest cover
avg_amount_quadrant*	Amount of supplementary food supplied per km ²
avg_amount_forest*	Amount of supplementary food supplied by forest cover
forest_percent	Percentage forest cover
carrion	Average amount of carrion provided
bear_dens	Average bear density
dist_settlement	Average distance to next settlement
prop_mast_trees	Average proportion of mast trees (broadleaf trees >40 cm breast height diameter)
temp	Average annual temperature

*** = supplemental feeding variable**

Before we launched the final statistics, we decided to remove all bears from our dataset, where we have no exact removal location. For these bears only the name and code of the registered hunting ground where they were hunted was available. Only way to fix this issue, would have been using hunting ground centroids as their removal location. But several hunting grounds are much larger than brown bear home-ranges, which dramatically decreases the accuracy and distorts data on feeding and environmental parameters. Especially in the bear core are, where a lot of bears were hunted, this problem would get

reinforced: all bears with no exact removal location and hunted in the same hunting ground will get the same values of environmental parameters, because they will all have the same removal location. Finally, this would lead to disturbances in the statistics (e.g. leverage effects). In the end, we reduced our dataset to all the bears removed from 2004 to 2012 ($n = 663$).

For the final analyses and also for biological reasons, we categorized the individuals into age classes (Table 2).

Table 2. Categorization of age classes

Age class	Age	Sex	n	Body mass (in kg)
1	0 – 1.5	m/f	97	44.31 (sd = 15.32)
2	1.5 – 4	f	180	76.75 (sd = 20.13)
3	> 4	f	60	109.93 (sd = 22.11)
4	1.5 – 5	m	268	101.24 (sd = 28.32)
5	> 5	m	58	203.57 (sd = 52.71)

Males and females are kept together in age class 1 because they are at least until an age of 1.5 with their mother before dispersal (Jerina et al. 2003). From the age of 1.5 years on, sexes are separated, because of sexual dimorphism: 1st – males are growing faster and get higher body weight, 2nd – old strong males monopolize feeding places and scare away weaker males and females (Elfström et al. 2014b, Fretwell & Lucas 1970). So the access to the feeding sites might be age and sex specific. Females age > 1.5 are categorized in age class 2 and 3, divided by the age of first reproduction when 4 years old (Švigelj 1961, Jerina et al. 2003), where mass gain is reduced, respectively culminates (Fig. 2). Males age > 1.5 are categorized in age class 4 and 5, divided by the age of 5 years, which is the point of inflection/culmination in mass gain (Fig. 2).

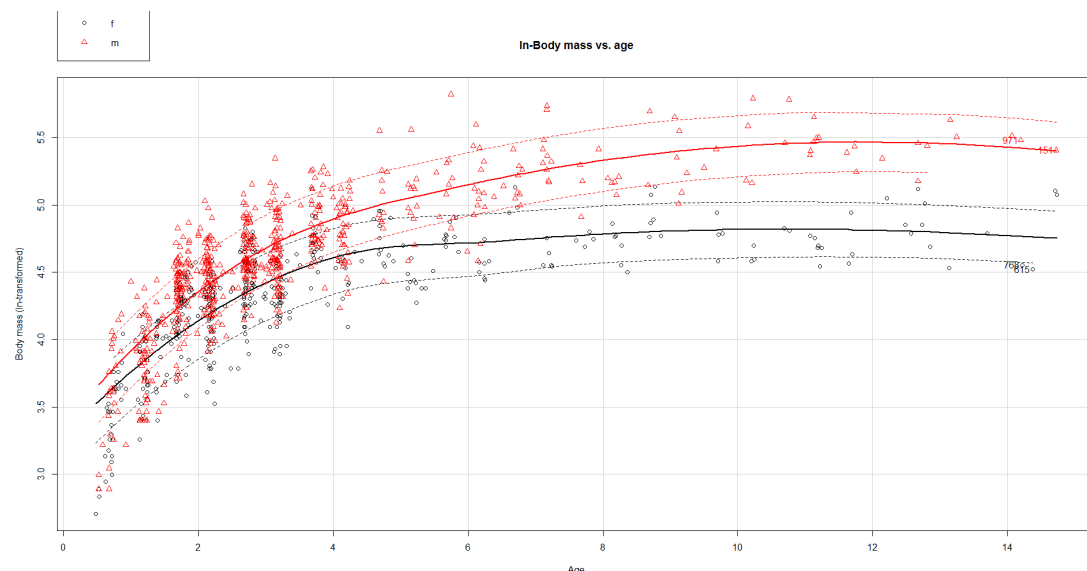


Fig. 2. Natural log transformed body mass of male (red triangles, mean = 4.58, sd = 0.49) and female (black circles, mean = 4.30, sd = 0.43) bears in relation to their age.

In the final step we analysed the effects of the environmental and feeding variables on the residuals that have been extracted from the basic model. Here we used linear models (LM) and linear mixed models (LMM, “lme4”-package, version 1.1-7). Before we could build an

optimal model, we had to select the most important variables. Therefore we performed a model selection for which we first constructed models containing all environmental variables. These models were always used with one feeding variable (Table 3). In the LMM, we tested the same variables with *year* as a random factor. Additionally we included the interaction of a feeding variable with *ageclass*, to consider different behaviours between the age classes.

Table 3. Models before model selection.

Model	Variables
LM	<i>[feeding_variable]</i> +year+forest_percent+carrion+bear_dens+dist_settlement+prop_mast_trees+temp)
LM	<i>[feeding_variable]*ageclass</i> +forest_percent+carrion+bear_dens+dist_settlement+prop_mast_trees+temp)
LMM	<i>[feeding_variable]*ageclass</i> +(1 year)+forest_percent+carrion+bear_dens+dist_settlement+prop_mast_trees+temp)

Dependent variable is always *residuals*, the residuals extracted from the basic model. *[feeding_variable]* represents one of the four feeding variables *avg_places_quadrant*, *avg_places_forest*, *avg_amount_quadrant* or *avg_amount_forest*.

2.9 Analysis of litter size

For the litter size, we used the number of cubs (*nr_cubs*) as the dependent variable and additionally to *season* (counting periods: spring and autumn) the same independent variables as for the body weight analysis (Table 4). We've built generalized linear models (GLM) and generalized linear mixed models (GLMM, "lme4"-package, version 1.1-7) for the analyses. The litter size dataset is poisson-distributed (Fig. 3), so a poisson-GLM/GLMM (family = "poisson") was used. *Season* was implemented as a factor, because it has to be considered that some cubs could disappear during the year due to mortality. An interaction of the feeding variable with *year* was added to the GLM, due to yearly fluctuations in natural food availability. In the GLMM *year* was used as a random factor.

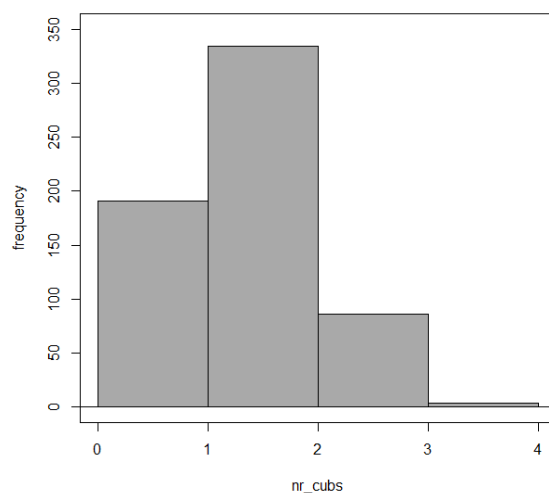


Fig. 3. Poisson distributed litter size in dataset.

Table 4. Models before model selection.

Model	Variables
GLM	<i>[feeding_variable]*year+factor(season)+forest_percent+carrion+bear_dens +dist_settlement+prop_mast_trees+temp)</i>
GLMM	<i>[feeding_variable]+(1 year)+factor(season)+forest_percent+carrion+bear_dens +dist_settlement+prop_mast_trees+temp)</i>

Dependent variable is always *nr_cubs*. *[feeding_variable]* represents one of the four feeding variables *avg_places_quadrant*, *avg_places_forest*, *avg_amount_quadrant* or *avg_amount_forest*.

Model selection

For the body weight and litter size analyses, model selection of the linear models (LM/GLM) was done by the stepwise model selection (forward/backward) tool “stepAIC” of the “MASS”-package (version 7.3-35). Model selection of LMM/GLMM’s was performed by the “drop1”-tool of the “stats”-package (version 3.1.2).

Finally, the models were ranked by their Akaike-Information-Criterion-Score (AIC, “stats”-package, version 3.1.2).

All statistical analyses were done in “R 3.2.0”, and significance level is set as $p < 0.05$.

3 Results

3.1 Body weight

In the best model, resulting from the stepwise model selection, only the variable *forest_percent* is remaining. Its effect is negative and significant ($p < 0.04$). The explained deviance is only $R^2 = 0.005$ (Table 5).

The 2nd best model only includes the feeding variable *avg_amount_forest*. Here the explained deviance is $R^2 = 0.004$. The effect is negative, but not significant ($p = 0.07$). In the 3rd model, *avg_amount_forest* and *forest_percent* are remaining. Both variables have a negative effect, but are not significant ($p = 0.37$, respectively $p = 0.17$).

The best linear mixed model (*lmer(residuals~(1|year)+avg_places_forest+forest_percent)*) had an AIC-score of only -96.01, therefore it isn’t listed anymore in our ranking. Both variables *avg_places_forest* and *forest_percent* had a negative effect, but none of them was significant. It’s explained deviance was $R^2 = 0.007$ (R^2 for LMM calculated with the *r2.corr.mer*-function by Jarrett Byrnes).

Table 5. Best models for the bears with exact removal location ($n = 663$), resulting from the stepwise model selection

Model	AIC-Score	R ² *	Nr.
lm(residuals~forest_percent)	- 101.69	0.005	1
lm(residuals~avg_amount_forest)	- 100.62	0.004	2
lm(residuals~forest_percent+avg_amount_forest)	- 100.50	0.005	3

The best models ranked by their AIC-scores. Lowest means best model.

*** Adjusted R-squared**

3.2 Litter size

The model selection resulted in only 3 different models (Table 6).

Table 6. Best models, resulting from the stepwise model selection

Model	AIC-Score	R ² *	Nr.
glm(nr_cubs~1)	1680.1	0.001**	1
glm(nr_cubs~avg_amount_quadrant)	1681.9	0.001**	2
glmm(nr_cubs~avg_amount_quadrant+(1 year))	1683.9	0.000***	3

The five best models, ranked by their AIC-scores. Lowest means best model.

*** Adjusted R-squared**

**** McFadden's pseudo-R² ("BaylorEdPsych"-package, function "PseudoR2", version 0.5).**

***** R² for LMM calculated with the r2.corr.mer-function by Jarrett Byrnes.**

The best model had an AIC-score of 1680.1 and an R² of 0.001. The model selection excluded all variables; none of them explains any effect on *nr_cubs*, only a constant is remaining. In the second best model, only *avg_amount_quadrant* remains as an independent variable. Its effect on *nr_cubs* is positive, but not significant ($p = 0.64$). Also the 3rd model showed no significant effects.

4 Discussion

Before starting this study, we've expected relations between the life history traits and food availability, expressed as habitat structures (environmental parameters), population density and artificial feeding intensity. Our expectations were in agreement with several studies that report effects of food availability on population density, leading to changes in intraspecific competition and resulting in effects on life history traits of mammal species. For example, decreases in body weight of wild reindeers (*Rangifer tarandus*) due to increasing population densities have been observed (Skogland 1990). Similar results have been recorded for moose (*Alces alces*), where body mass is density dependent (Hjeljord & Histøl 1999). In bighorn sheep (*Ovis canadensis*), low resources availability due to high population densities caused reductions in body mass gain and reproductive success (Festa-Bianchet et al. 2000). Of course some variation in body mass and litter size is also driven by genetics, but food availability still plays an important role in determining body weight and litter size: high food

availability positively affects reproduction (Gray et al. 2004, Schwartz et al. 2006) and body weight/size (Partridge et al. 2001, Welch et al. 1997) in black bears and grizzlies (*Ursus arctos horribilis*). In brown bears, Zedrosser et al. (2006) report positive effects of food availability on population density, resulting in a negative correlation of population density with adult female body size. Natural food availability is dependent on many environmental parameters (Bojarska & Selva 2012). For several mammal and bird species, mast is an important food source. But mast production varies over the years (Övergaard et al. 2007), which in many tree species is assumed to be a strategy for preventing seed predation (Silvertown 1980). Black bear reproduction, survival and growth are affected by these inter-annual changes in mast production (Rogers 1976, 1987). The mast abundance positively correlates with body mass in black (Seeger et al. 2013) and brown bears (Nielsen et al. 2013). Losses of more than 60% in black bear natality following years with mast failure have been reported (Costello et al. 2003).

In contrast, our study reports no effects of food availability on body weight or litter size. Following our results neither habitat variables, density of the bears nor time (*year*) are playing an important role. In the body weight analysis, only a significant effect of *forest_percent* was found. For the litter size analysis, no effects of any variable were reported. For both analyses, the explained deviance was always very low ($R^2 < 0.005$), therefore the biological importance of the factors in the model are likely negligible. With other words, the first two hypotheses (*Hypothesis 0* and *Hypothesis 1*) can be rejected. As a result, only *Hypothesis II* could be accepted, because no clear effects of feeding, neither the environmental parameters nor the temporal (*year*) variables were detected. There are also no indices for density dependence although population densities of the bears are one of the largest reported worldwide. It appears that the bear population is ideally free distributed in space and time.

Although Slovenia is a small country, there are huge differences in the landscape structures, as well as in the bear population densities. In some areas, Slovenia hosts one of the World's highest brown bear population densities (up to 40 bears/100 km², Jerina et al. 2013). Forests, the usual habitat of European brown bears (Ordiz et al. 2011), are irregularly distributed and cover 60% of the Slovenian landscape (Statistical Office of the Republic of Slovenia); 44% of the forest area is covered with beech- (*Fagus sp.*), 15% with beech-fir- (*Abies alba*) and 11% beech-oak-forests (*Quercus sp.*) (Perko 2004). So beech forests represent a majority of the forest area, which makes beeches the most important mast producers for Slovenia (Jerina et al. 2015). In Slovenian bear diet, the estimated dietary energy content of hard mast is 18.1% (Kavčič et al. 2014), which identifies mast as an important natural food source. But the availability of mast in Slovenian beech forests fluctuates from year to year (Kryštufek & Zavodnik 2003). Considering these fluctuations, mast production is an important driver of natural food availability and one would expect temporal and spatial differences in the bears' life history traits.

Given previous facts the most possible explanation for our observed patterns is the impact of extra strong artificial feeding. High amounts of anthropogenic supplied food might buffer spatial and temporal differences (especially lacks) in natural food availability. Our study showed that the average Slovenian brown bear has access to a mean yearly amount of 50 tons (s.d. 17.5 tons, mean home-range size of 350 km²) of artificial food in its home-range (for females (litter size): 26.80 tons (170 km²), s.d. 10.2 tons). In some areas a seasonal percentage of 70% of anthropogenic food in bear scats has been detected (Kavčič et al., 2015). The mean estimated dietary energy content of supplemental/diversionary feeding in brown bears represents 34% (Kavčič et al. 2014); bear foraging on feeding places gain 3.9 times more energy per time unit than feeding on the surrounding natural food sources. Artificial feeding doesn't totally replace natural food availability, in years with good mast productivity, bears use feeding places for 36% less than in years with poor mast production (Jerina et al. 2015), so actually the use of anthropogenic food is negatively related to the

natural food availability (Kavčič et al. 2014). These facts somehow indicate that the carrying capacity of brown bear habitat in Slovenia might be enhanced by additional anthropogenic food. Our results point out that the population density hasn't already reached the level of its carrying capacity. In agreement with this, a possible explanation for the highest reproduction rates found worldwide in Slovenian brown bears is given (19 – 22%/year, Krofel et al. 2012). Given extra high population densities of bears in Slovenia this appears as unusual, but can be explained by highly elevated carrying capacity with intensive additional feeding.

The results of this study could be also the artefact of poor used methodology, but we believe that this is rather unlikely. Based on results of similar studies, we've tried to cover all probable and available key variables that are affecting natural habitat carrying capacity – in space and time (e.g. proportion of mast producing trees (Nielsen et al. 2013), year (Rogers 1976), population density (Zedrosser et al. 2006), distance to settlement (Elfström et al. 2014a, Gütthlin et al. 2011), percentage of forest cover (Boitani et al. 1999, Knauer 2000)). We used a dataset with relatively big sample size; the data has been collected by experienced and trained personal. The data gathering was done systematically following strict rules and undergoing quality controls. We filtered all data out, where we weren't sure they are exact (check for logical inconsistency). Furthermore we only used methods that are best adapted to our data. Here for example we first summarized the non-linear relationship of sex, age and season on body weight (factors affecting body weight independent of food availability) into a new variable, before testing for linear effects of environmental parameters and feeding in order to consider only factors that affect the food availability. We've tried several approaches to achieve the best models explaining body weight and litter size.

Officially, feeding is primarily used for human-bear conflict mitigation in Slovenia, i.e. damages on livestock, agriculture, beehives and human properties. Considering livestock depredation, a previous study showed that feeding with carrion has no mitigation effect (Kavčič et al. 2013). On the other hand, damages are positively correlated with the increasing bear population size (in time) and density (in space) (Jerina et al. 2015). There are some indices that feeding decreases conflicts per capita, especially in agriculture (Jerina et al. 2015). But previous studies confirm that food availability plays an important role in determining population densities and since supplemental/diversionary feeding probably buffers lacks in natural food availability and increases the total food availability, one could also assume that it is an important factor influencing population densities. As a consequence of increasing population densities the potential of more frequent human-bear conflicts might increase.

In an ecosystem flooded with food, intraspecific food competition is likely low. Malnutrition and starving-caused mortality likely decrease – patterns of natural selection might be disturbed. As a result, natality and survival possibly increase. Natural mortality is low and in order to control the population densities, harvest rates are high in Slovenia (20% annually; Krofel et al., 2012). Adding traffic collisions, anthropogenic mortality is the highest cause of death (Krofel et al. 2012). In the end, two important factors driving to evolution, natality and mortality, are controlled by humans. For ungulates, it has been shown that year-round feeding could lead into a form of semi-domestication (Mysterud 2010). Our study indicates that this is likely also the case in a large carnivore species like the brown bear.

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6 Appendix

Map 1: Hunting grounds of Slovenia

Map 2: Forest percentage in a 1×1 km raster grid

Map 3: All feeding places appropriate for bears

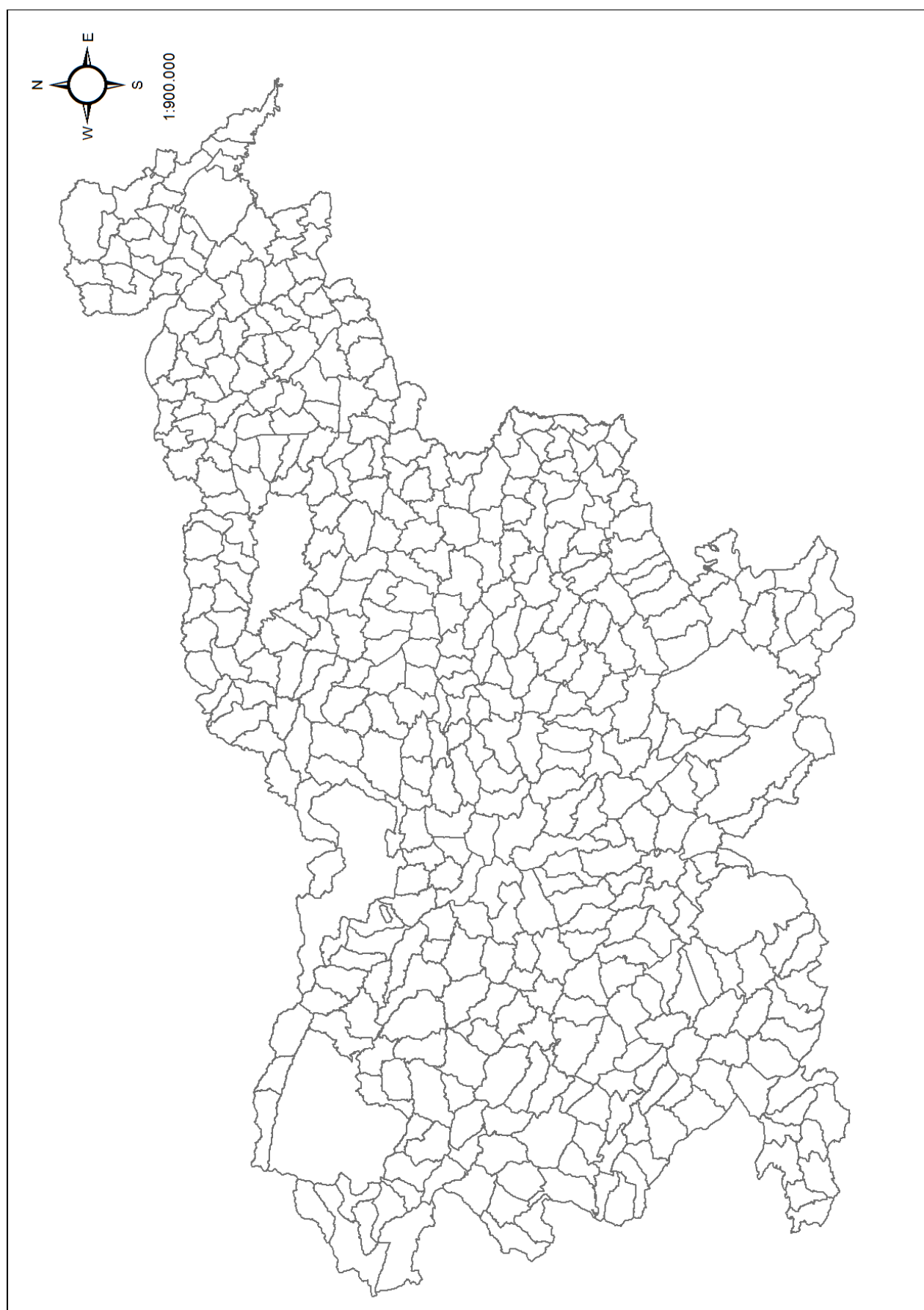
Map 4: Brown bear habitat suitability map and settlements

Map 5: Population densities

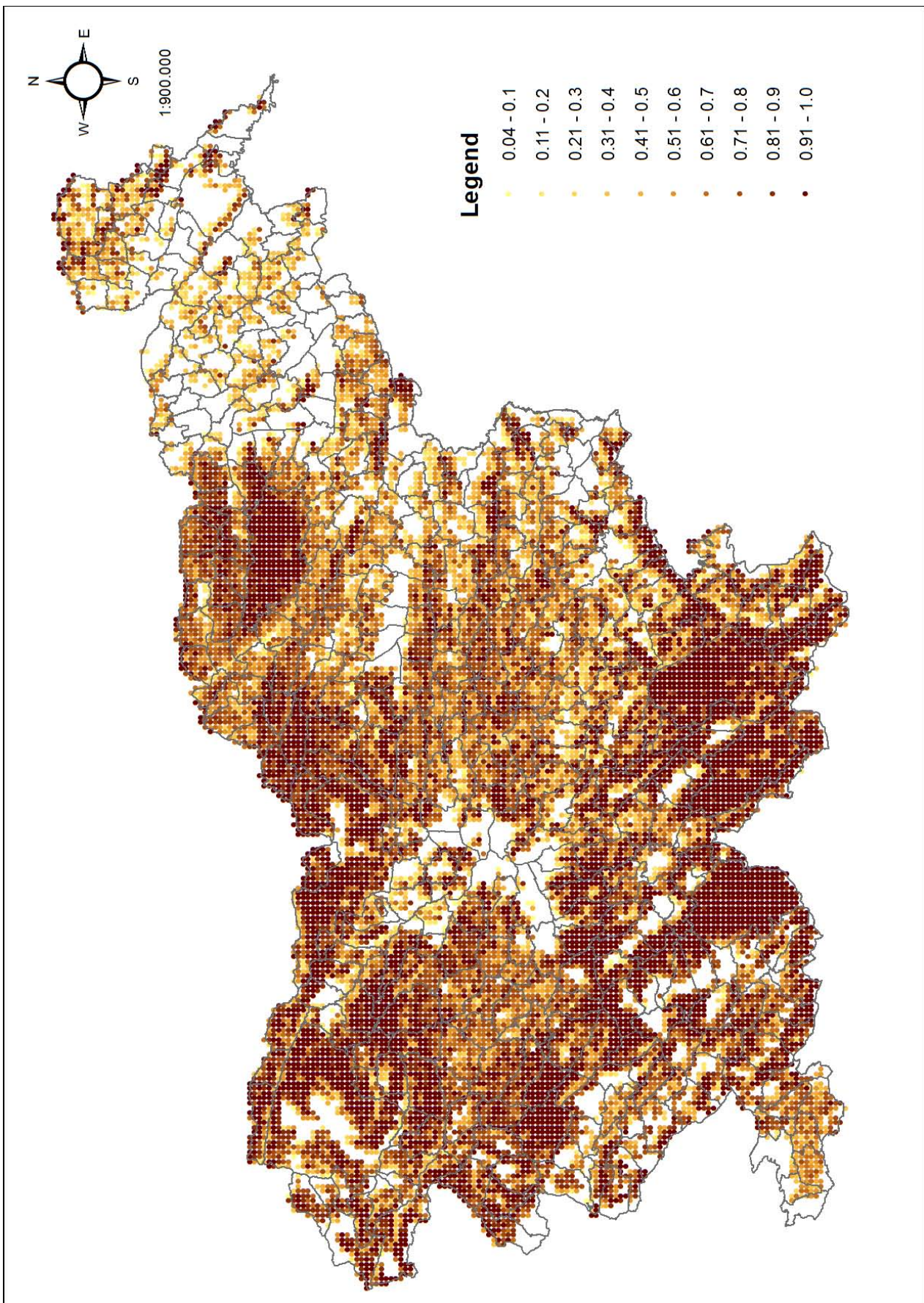
Map 6: Locations of hunted/removed bears and their theoretical activity range

Map 7: Litter size observation locations (monitoring grid) and the theoretical activity range of females

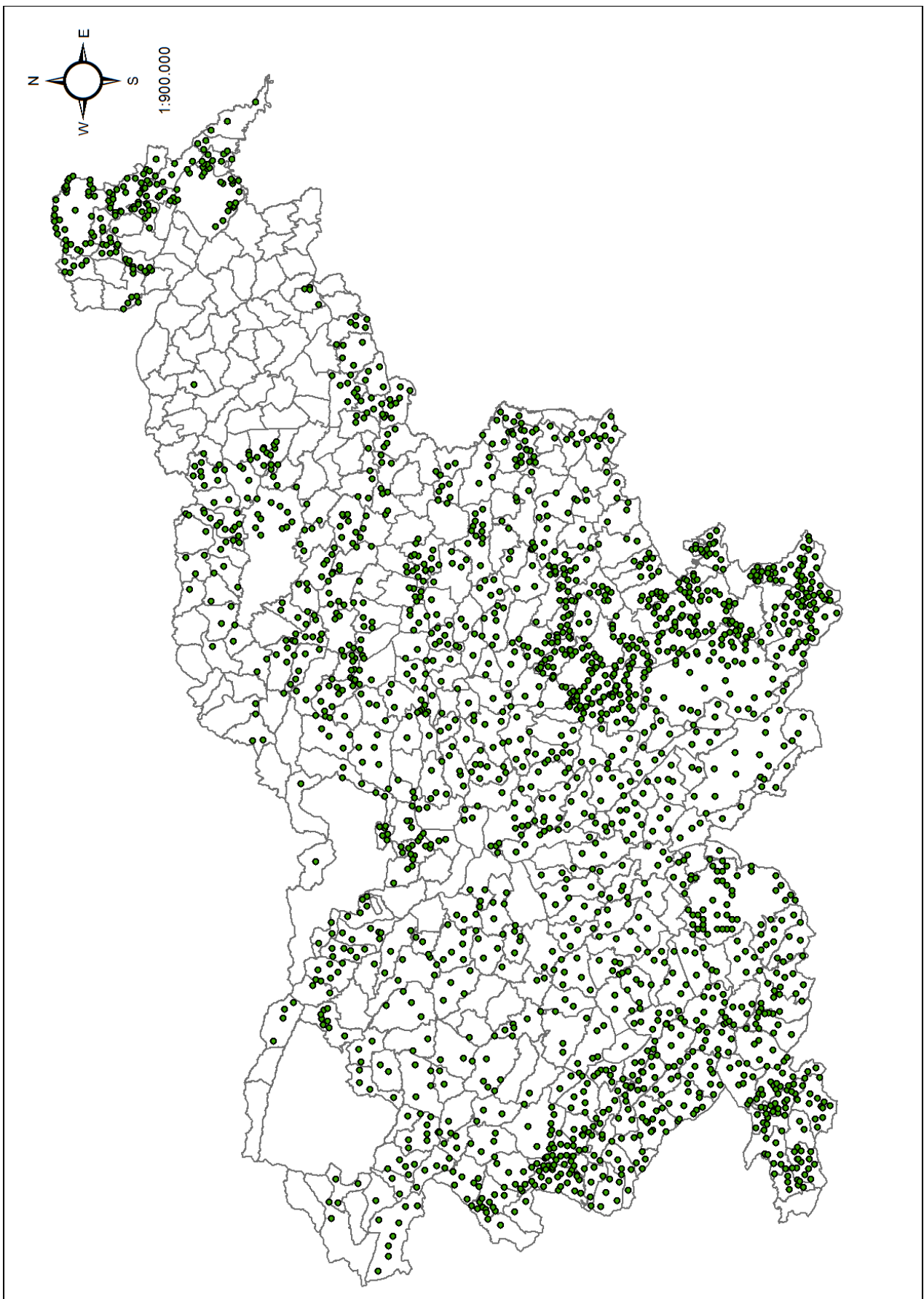
6.1 Map 1: *Hunting grounds of Slovenia*



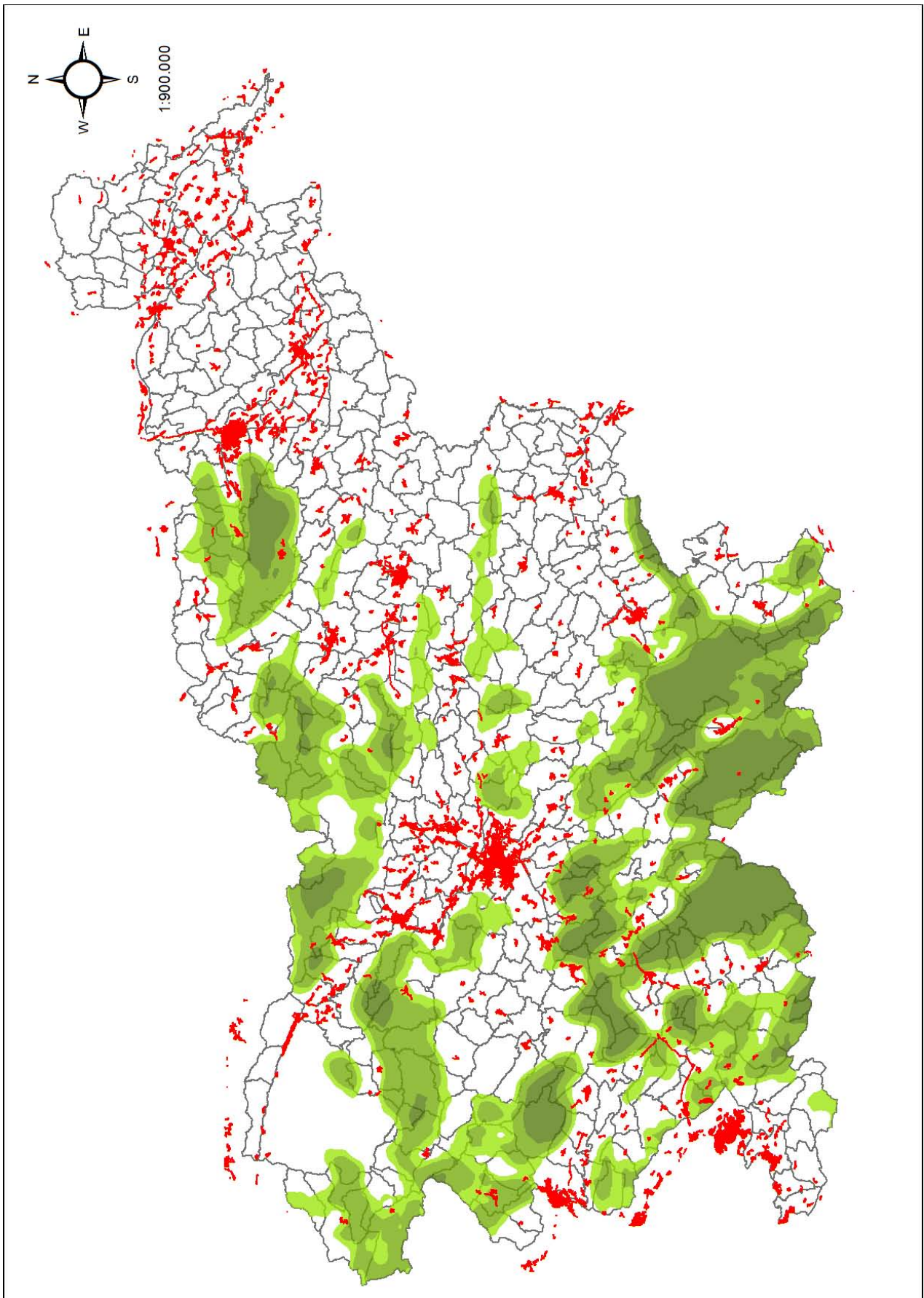
6.2 Map 2: Forest percentage in a 1x1 km raster grid



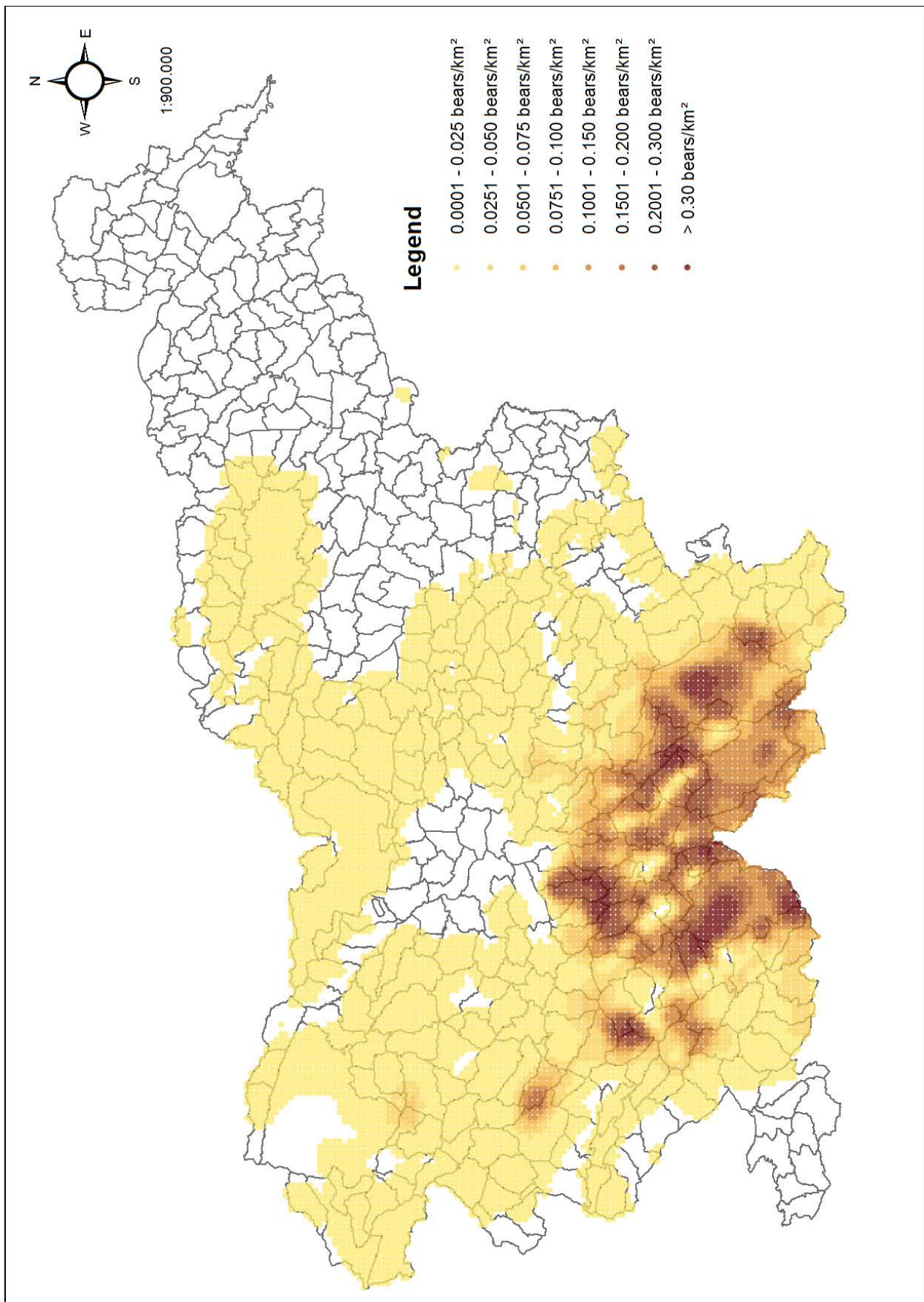
6.3 Map 3: All feeding places appropriate for bears



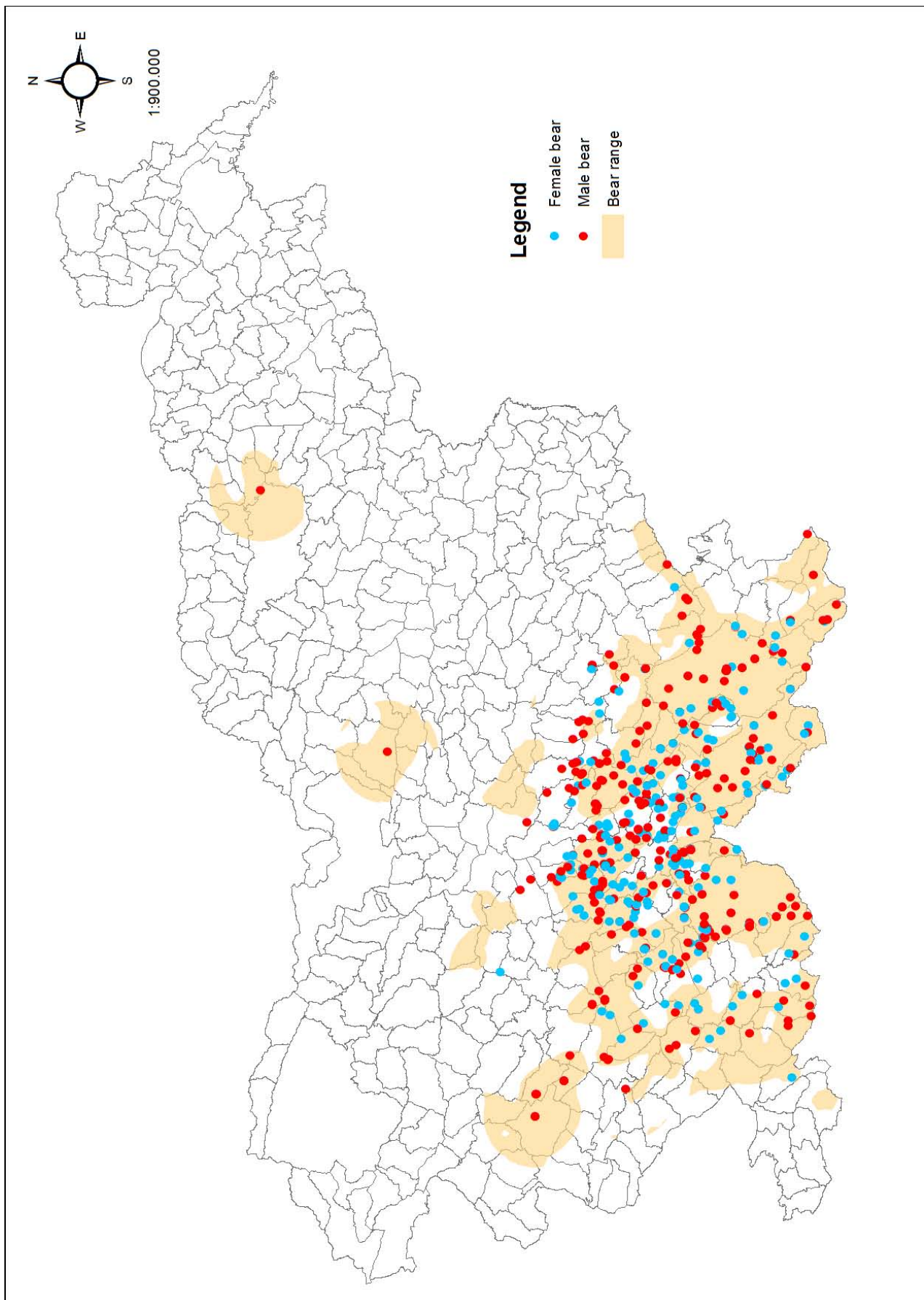
6.4 Map 4: Brown bear habitat suitability map and settlements



6.5 Map 5: Population densities



6.6 Map 6: Locations of hunted/removed bears and their theoretical activity range



6.7 Map 7: Litter size observation locations (monitoring grid) and the theoretical activity range of females

