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University of Natural Resources
and Applied Life Sciences, Vienna

Linking brown bear diet to habitat use

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Submitted by: Bogdan Kraft

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Institute of Wildlife Biology and Game Management (IWJ)

Department for Integrative Biology and Biodiversity Research (DIB)

Supervisors:

Associate Prof. Dr. Klemen Jerina

Assistant Prof. Dr. Miha Krofel

University of Ljubljana, Biotechnical Faculty, Department for Forestry

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Declaration in lieu of oath

I herewith declare in lieu of oath that this thesis has been composed by myself without any inadmissible help and without the use of sources other than those given due reference in the text and listed in the list of references. I further declare that all persons and institutions that have directly or indirectly helped me with the preparation of the thesis have been acknowledged and that this thesis has not been submitted, wholly or substantially, as an examination document at any other institution.

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Abstract

Brown bears (*Ursus arctos*) are animals of large body size and great strength. They potentially can cause conflicts in human dominated landscapes, mainly related to their feeding behaviour. Therefore understanding the link between their habitat use and diet is important and can be useful to improve their conservation and the management. To monitor the diet in relation to the habitat use of such elusive animals as brown bears is a task that can be achieved by coupling traditional scat analysis with global positioning system (GPS) telemetry. Searching for scats at locations soon after an animal with GPS-collar was there makes it possible to associate the sample with an individual, to estimate the defecation time more accurately than just by the appearance of randomly found feces (e.g. how dry it is) and to look for scats efficiently in various habitats, including those where habitat structure reduces detection by random sampling. Three bears were fitted with GPS-collars and monitored from June to August 2016 in the Snežnik region in southern Slovenia. 105 scat samples were collected at 152 surveyed daybed locations and their content analysed according to the method developed by Korschgen (1980). Binary logistic regression was used to estimate the probability of a particular food type to occur in a bear scat in relation to the habitat type and habitat characteristics (e.g. distance to the closest settlement or feeding spot) of bear locations 3-16 hours (gut retention periods) before the defecation. It was demonstrated that brown bear diet and habitat use are linked. The probability to find corn in a bear scat was higher if it used habitats closer to feeding sites beforehand, fruit was more likely to be found if habitats closer to settlements were used, insects if habitats with a higher conifer coverage were used and vertebrates if more grasslands were used before. Individual differences between the diets of the three bears in this study were relatively large.

Key words: brown bear, Ursus arctos, GPS telemetry, scat analysis, habitat use, Slovenia, human-dominated landscape, conflict species

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1 Introduction

The brown bear (*Ursus arctos* Linnaeus, 1758) is a solitary, non-territorial species (Craighead et al. 1995, Steyaert et al. 2012) of large size and omnivorous foraging behaviour. Usually bears have large over-lapping home ranges and occur in low population densities. In human-dominated landscapes most bears exhibit nocturnal and secretive behaviour and regular use of densely vegetated habitats, like forests (Ordiz et al. 2011). Because of these circumstances, global positioning system (GPS) telemetry is the most useful way to monitor the habitat use of brown bears. It has become even more practicable over the past decades as the accuracy has improved (up to a few meters, depending on the terrain characteristics; Frair et al. 2004) as well as the battery capacities, which leads to the possibility to record higher number of more precise locations (over a longer period of time or in much shorter time intervals). Thus habitat use data at a finer spatiotemporal scale can be obtained. Using this method in combination with classic scat analyses to simultaneously record habitat use and food consumption of bears has potential to give further insights into the foraging strategies of this cryptic species. By visiting bear locations scat samples can be efficiently collected (Elfström et al. 2014b). If done shortly after the visit of the animal, problems to link individuals correctly to the collected scat samples, one of the major weaknesses of standard scat collection can be reduced. Freshly collected scats can also be used for genotyping intestine epithelial cells that stick to it in order to confirm individual identity (Lesmerises et al. 2015). Using GPS-monitoring to increase success in finding scats also reduces other pitfalls of traditional scat analysis, such as bias introduced by different habitat structures and compositions. This could otherwise result in the oversampling of individuals using more open areas, where scats are easier to find (Lesmerises et al. 2015).

The habitat use of brown bears is usually affected by three general factors (Elfström et al. 2014b; Apps et al. 2004). First there are intraspecific interactions: Dominant bears scare away other bears or may occasionally even predate on them. Especially females with cubs avoid large males because of possible infanticide and all subdominant bears might use human settlements as a shield to escape aggressions (Elfström et al. 2014a, b; Steyaert et al. 2013a, 2016). The second strong factor in human-dominated landscapes is anthropogenic disturbances like traffic, hunting, tourism and similar land uses. But some land use forms like agriculture or settlements with anthropogenic food sources might attract bears and are somewhat connected to the third main factor, the food availability (Steyaert et al. 2013b). How the habitat use by brown bears is connected with their food use has not yet been sufficiently studied, although Elfström et al. (2014b) compared the quality of ingested food close to settlements to the quality in habitats further away from settlements. Improving the understanding of the connection between bear diet and their habitat use and testing the above mentioned method is the main aim of this master thesis. The hypothesis is that the diet of brown

bears is linked to their habitat use. In order to forage for certain food items they exhibit a higher use of specific habitat types. To verify this thesis, two assumptions were expected to be true:

1. Corn occurrence in scats decreases when the habitat use prior to defecation was within larger distance to feeding spots.
2. Fruit occurrence in scats decreases when the habitat use prior to defecation was within larger distance to settlements.

If this link is confirmed, it would be possible to predict bear diet from their use of habitats and the other way around. Understanding this connection could also be useful for the management of brown bears by helping to identify habitat types with abundant food sources. Protection of most important foraging areas may play an important role as part of conservation measures and conflict management. Higher availability of natural food sources or artificial food sources (feeding sites) might reduce the probability that they are drawn close to humans and their property, and trying to forage on anthropogenic food sources like crops, livestock or waste. Because of their awe of people most of these animals would preferably use food sources far from humans instead of those close to humans, if such are available (Ordiz et al. 2011).

2 Material & Methods

2.1 Study area

The study area covered approximately 446 km² of southwest Slovenia, Central Europe (45°30'-45°47'N and 14°15'-14°36'E; Figure 1). It lies within the Slovenian core bear area and one of the least humanly populated regions of Slovenia, the Snežnik region. The Snežnik plateau and Javorniki cover approximately 500 km² and form the largest Slovenian forest complex (Jerina et al. 2012), which extends uninterruptedly across the border into Croatia. This mountainous karst landscape is part of the northern range of the Dinaric Mountains, which ranges from about 400 m to close to 1800 m above sea level and is characterised by rugged relief with steep slopes, rocks and dolines. There are no surface water streams, because of the karst nature of the plateau. The subcontinental climate, with some Mediterranean influence from the west-east direction, has mean annual air temperatures ranging from 2° to 10° C in different parts of the area (National Meteorological Service of Slovenia 2014) and average annual rainfall up to 3000 mm (temperate zone). The uneven-aged forest structures within the study area are composed mainly by European beech (*Fagus sylvatica*), silver fir (*Abies alba*), Norway spruce (*Picea abies*) and sycamore maple (*Acer pseudoplatanus*) (Bončina et al. 2002, Sommerfeld 2015), intermixed with small settlements and agricultural land. From late April to late October the region is within the vegetative growth period.

The brown bears occurring in the study area form the north-western part of the larger transboundary Dinaric–Pindos brown bear population, which continues uninterrupted into the adjoining country Croatia to the south (Krofel et al. 2012). Brown bear density is high in the region, ranging from 7 to 20 bears per 100 km², and locally over 40 bears per 100 km², with considerable overlaps in home ranges of different bears (Jerina et al. 2013). Estimated mean home range size of bears in Slovenia (male home ranges are about 4 times larger than female home ranges) is 350 km². Home ranges are in general smaller when local bear densities are high (e.g. in population core area) as well as in areas with a higher density of feeding sites (Jerina et al. 2012, Krofel et al. 2010).

Supplemental feeding in Slovenia is often carried out at the same spot for several wildlife species like red deer, wild boar and brown bear. This management tool is either used for monitoring reasons, for eco-tourism, as bait for hunting or as diversionary feeding to keep bears (also wild boar) from human settlements and agricultural land. The density of supplemental feeding sites is 16 feeding sites per 100 km² in the Snežnik region (Kavčič et al. 2015, verified for the study area by own calculations) with an estimated amount of 70-280kg maize provided per km² per year (Kaczensky 2000, Adamič 2005).

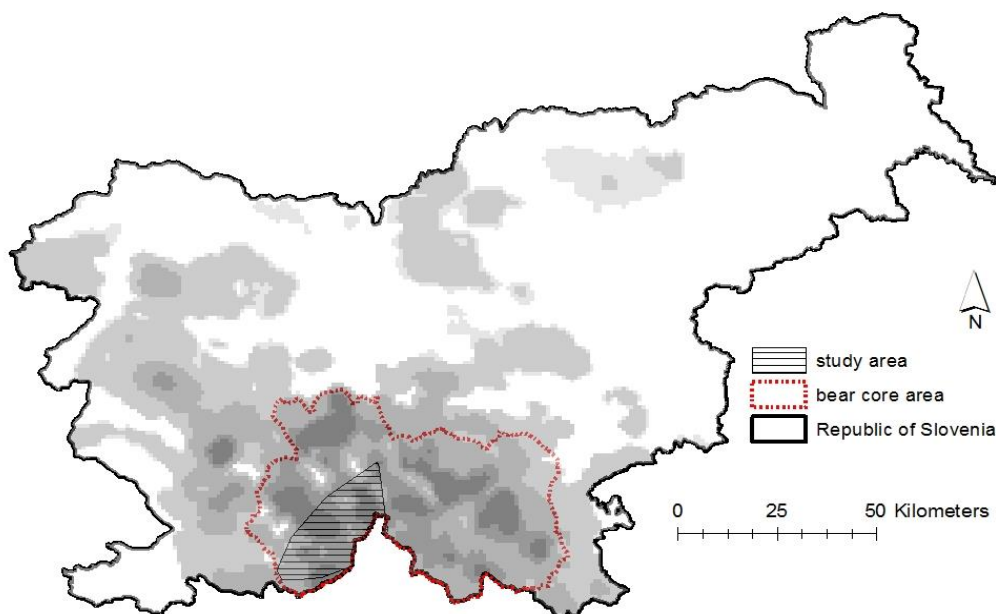


Figure 1. Map of Slovenia with the study area in the south. Dark hatched area represents 100% Minimum Convex Polygon (MCP) of three bears monitored with telemetry (plus a 500m buffer; without the part in Croatia). Dotted red line marks the bear core area of Slovenia. Underlying map shows distribution and local population densities of brown bears in Slovenia (from Jerina et al. 2013). Darker areas indicate higher density. Maximum population densities are approximately 40 bears / 100 km²

2.2 GPS collaring of bears and scat collection

The field work for this survey took place from May to August 2016. Three bears were captured by the Slovenian Bear Emergency Team by darting from a high stand (Tab.1). Two animals were fitted with GPS telemetry collars and one with a GPS telemetry collar plus an additional video camera (Lotek GPS Collars WildCellM5/MG, Lotek Wireless Inc., Newmarket, Canada). The first two collars were programmed to receive a GPS fix every hour (24 locations/day), the third one every 30 minutes. The collars sent a mortality signal if there was no activity recorded for more than 24 hours which meant either that the collar had dropped off or the animal had died. As long as a GSM network was available the recorded data (time and date, GPS coordinates, elevation, temperature and battery status) was sent regularly every 7 acquired GPS fix attempts via a text message to a terminal at the office in Ljubljana and processed with the software GPS Plus (Vectronic Aerospace GmbH, Berlin, Germany).

Tab.1 Information about the three bears fitted with GPS telemetry collars for this study

collar_ID	collar type	sex	estimated age	weight (kg)	date of capture	remarks
41110	Lotek-GPS-GSM, WildCellM5	female	6	120	1/6/2016	bear removed the collar on 1/8/2016
41111	Lotek-GPS-GSM, WildCellM5	female	13-15	131	3/6/2016	collar is still active on the bear; no cubs
41112	Lotek video-GPS-GSM, WildCellMG	male	10-15	175	16/6/2016	collar dropped off as scheduled on 21/7/2016

The bear movement was visualised and examined in Google Earth (Version 7.1.8.3036, Google Inc., Mountain View, United States of America) to find clusters, where bears had stayed for a longer period of time (more than 3 hours) around the midday. These indicated possible daybed locations (opposed to night clusters, which are commonly feeding spots), which were then visited in the field and searched in spirals for up to 30 minutes to find the daybed and fresh bear scats (daybeds were visited 1-4 days after use by the bears). Whenever several fresh scats were found at the same location, one was chosen randomly. The whole scat was collected in ziplock-bags and labelled. They were stored at minus 20° C until further analysis.

2.3 Scat analysis

The scats were analysed according to the procedures and techniques used by Korschgen (1980). Frozen scat samples were defrosted and then rinsed under tap water through a set of two sieves (mesh sizes 10 and 1 mm). The food items were identified (if necessary using a stereo microscope (7-50x; Olympus, Tokyo, Japan)) and grouped into the following categories: corn (*Zea mays*), fruit, other plant material, insects, vertebrates, hard mast and mushrooms (for specifics see Appendix 1). In cases that more than one food item was present in a sample, a percent volume was estimated visually for each item (rounded to predefined 5% values). The Person estimating volumes (B.K.) was previously trained with known percentages. This visual method has been shown to achieve values comparing well to exact measures (Mattson et al. 1991).

2.4 Data preparation

Microsoft Excel (2016), ArcGIS 10.4.1 for Desktop (ESRI 2015) and SPSS Statistics for Windows, Version 21.0 (IBM 2012) were used for data management and all statistical analyses.

The 100% Minimum Convex Polygon (MCP) of the three bears monitored with GPS-telemetry was taken to define the study area. A 500-m-wide buffer surrounding it was added because the bear's exact path between two consecutive GPS-locations was not known and because the nearby forest edge, road or settlement could have been positioned outside the MCP but still influenced the bears habitat use. One bear crossed the border to Croatia several times and although scat samples from that area were recovered, they had to be excluded because not all necessary environmental data (see below) could be gained.

The Euclidean distances between each bear GPS location to the nearest feeding site, forest edge, settlement and regional road were extracted from geographic information system (GIS) data layers. Locations of feeding sites were obtained from a national register maintained by the Slovenian Forest Service and the Hunters Association of Slovenia (Jerina 2012). All other data layers for independent variables were prepared from GIS layers obtained from the Surveying and Mapping Authority of the Republic of Sloveniav (GURS).

Feeding sites were expected to have a strong effect on the bears habitat use and diet due to high availability of provided food (Kavčič et al. 2015). The distance to the closest forest edge might have an influence on the bears because of the cover provided by the forest and the availability of different types of food at varying distances to the forest edge. Settlements and roads might be avoided by bears because of human activity or attract them because of anthropogenic food sources. Minor forest roads were excluded, only the main forest road (915) through Snežnik forest, which is classified as a regional road and is not paved, was included. The reason for that is that logging teams often build their roads as they go and no completely accurate and up to date map was available. Also does the use of these forest roads differ a lot (intensively when the logging takes place, then possibly not at all for years). Railways were supposed to be included for the reason that roadkill and the spill of agricultural products like corn and grain might have an influence on the bears feeding behaviour. But the closest railway did not touch the final (buffered) study area, so it was left out. The conifer coverage was calculated as the mean conifer coverage of the 50 meters surrounding a location in agreement with accuracy of conifer data layer. This variable indicates differences in habitat use and food intake of bears within the forest. Although the study area is generally covered with mixed forest, there are patches which could be categorised as pure conifer forest (e.g. spruce plantations) or broadleaf forest. The distance to the nearest road and settlement, elevation and coniferous forest have already been shown to be important factors for the habitat suitability for brown bears (Güthlin et al. 2011).

Habitat types were taken in account by specifying the type of habitat every recorded GPS point was located in. The habitat types from the land-use data layer were combined into the following eight categories: forest, grassland, orchards, build-up land, abandoned farmland, wetland, dry open land and brush. These categories represent the general differences between all the highly specific habitats that were used in the data layer (e.g. the categories “swamp” and “other marshy land” were combined to “wetland”).

2.5 Habitat use analyses

Experiments with brown bears in captivity have shown that their defecation rates range between approximately 7 defecations / 24 hours for a diet of mostly plants or fruit to 4 defecations /24 hours for meat diet (Elfström et al. 2013; Roth 1980). Their gut retention time (GRT) ranges from around 3 to 16 hours, with a median GRT 50% (i.e. when 50% of all scats containing experimental food had been defecated) of 5 h and 47 min for berries and 14 h 30 min for meat (Elfström et al. 2013). The approximate transit time for corn is 8 hours (K. Bojarska, Institute of Nature Conservation, Polish Academy of Sciences, pers. communication). Following this, the habitat characteristics from the

recorded GPS-locations were analysed corresponding to 3-16 hours prior to the daybed location where the scat was found.

2.6 Statistical analyses

Table 2 summarizes the variables that were used to build the models. The data were distributed bimodally, with one peak at value 0 and other with value close to 100%. The response variables (food items in the scats) were therefore reclassified to binary (present (1) or not present (0) for each food type for each scat sample) and 0 volume percent (vol%) was taken as the cut value.

The food category “mushrooms” was omitted because no evidence of mushrooms was found in any scats. “Hard mast” appeared in 4 scats and below 5 vol%. Only very few beechnuts were discovered and even so it is possible that bears feed on beechnuts in spring, especially after a year with good beech masting (which was not the case in 2015), because of the very low occurrence this category was taken out as well.

The habitat type categories were reduced to *forest* and *grassland* because the occurrences of others were too low (very low means in the descriptive statistics: orchards = 0.001, build-up land = 0.003, abandoned farmland = 0.017, wetland = 0.001, dry open land = 0.007, brush = 0.031).

Binary logistic regressions were used to analyse the ingested food corresponding to the habitat used before defecation. Hosmer and Lemeshow (1989) showed that this method is robust and has relatively few assumptions regarding the data distribution. This binary logistic regression models predict the likelihood that the response variable will take one of the two possible binary values for given values of explanatory variables. The models adjusted to the data set of this study predict the likelihood that a specific food category will be present in a scat by taking into account the beforehand visited habitats.

Backward eliminations starting from the full set of variables (Table 2) were done. This backward stepwise selection with removal testing based on the probability of the Wald statistic was chosen to reduce the variables in the models to those most meaningful in order to find the most parsimonious models. Every model was run once with CollarID included as a categorical explanatory variable and once without to examine the effects on individual variability.

As model diagnostics the chi-square (χ^2), the -2 Log Likelihood (-2LL), the Nagelkerke pseudo r-square (Nagelkerke R^2), the classification accuracy and the Hosmer and Lemeshow goodness of fit test (Hosmer and Lemeshow Test) were looked at. The Hosmer and Lemeshow goodness of fit test is especially well suited for models like these, with continuous explanatory variables and rather small sample size. If the test is not statistically significant it means that the model fit is good.

To detect and avoid multicollinearity between continuous explanatory variables ($> \pm 0.8$) correlation matrices and scatter plots were used. The correlation matrices showed a highly significant ($p < 0.05$)

correlation between *grassland* and *forest* (-0.909) and between *dist_settl* and *elev* (0.865). Because of the high biological relevance of all of these variables the decision was made to leave them in the set of starting variables for the backward elimination. Only when those variables became variables of interest, meaning the pair appeared together in the outcome of the final model, the starting set of variables was reduced by one of the correlated variables because the multicollinearity makes the coefficients unstable and interferes in determining the precise effect of each predictor. The idea was to remove the variable that was less bivariate correlated to the dependent variable of the model but the results showed that it made in fact no difference which one of the two correlated variables was excluded in these cases.

The significance level for hypothesis testing was set to level of $\alpha = 0.05$.

Tab.2 Names / abbreviations and descriptions of the variables used in the models

Variable name / abbreviation	Description
<i>Response variable (one for each model)</i>	
Corn	maize; Binary: 0 or 1
Other plant material	graminoids, forbs, etc.; Binary: 0 or 1
Fruit	apple, cherry, Cornelian cherry, checker tree fruit; Binary: 0 or 1
Insects	ants, wasps, bees, dung beetles; Binary: 0 or 1
Vertebrates	red deer, roe deer, wild boar, rodents, sheep; Binary: 0 or 1
<i>Categorical explanatory variables</i>	
CollarID	Specific ID for each of the three bears with collars
<i>Continuous explanatory variables</i>	
dist_frste	Distance to the nearest forest edge in m
dist_feed	Distance to the nearest feeding site in m
dist_road	Distance to the nearest regional road in m
dist_settl	Distance to the nearest settlement in m
cnfr_prct	Mean of the conifer percentage coverage in a 50m radius
elev	Elevation in m above sea level
Forest	Percentage of the use of the habitat type “forest” over a specific period of time
Grassland	Percentage of the use of the habitat type “grassland” over a specific period of time

3 Results

A total of 4484 GPS locations of the three bears were analysed (41110: 1434; 41111: 1667; 41112: 1615). 273 GPS locations in Croatia, all from bear 41112, were excluded beforehand because some of the needed GIS strata were not available. Mean GPS fix success rate was 98.5%.

Overall 152 clusters (potential daybeds) from the 3rd of June to the 13th of August 2016 were surveyed in the field and 105 scat samples were collected and analysed in the lab (plus 3 samples from Croatia which were discarded).

Tab.3 Distribution of surveyed clusters and collected / analysed scats among bears and the time they were monitored

CollarID	Surveyed clusters	Scats collected / analysed	Time monitored
41110	60	45	60 days and 6 h
41111	63	42	71 days and 17 h
41112	29	18	33 days and 21 h

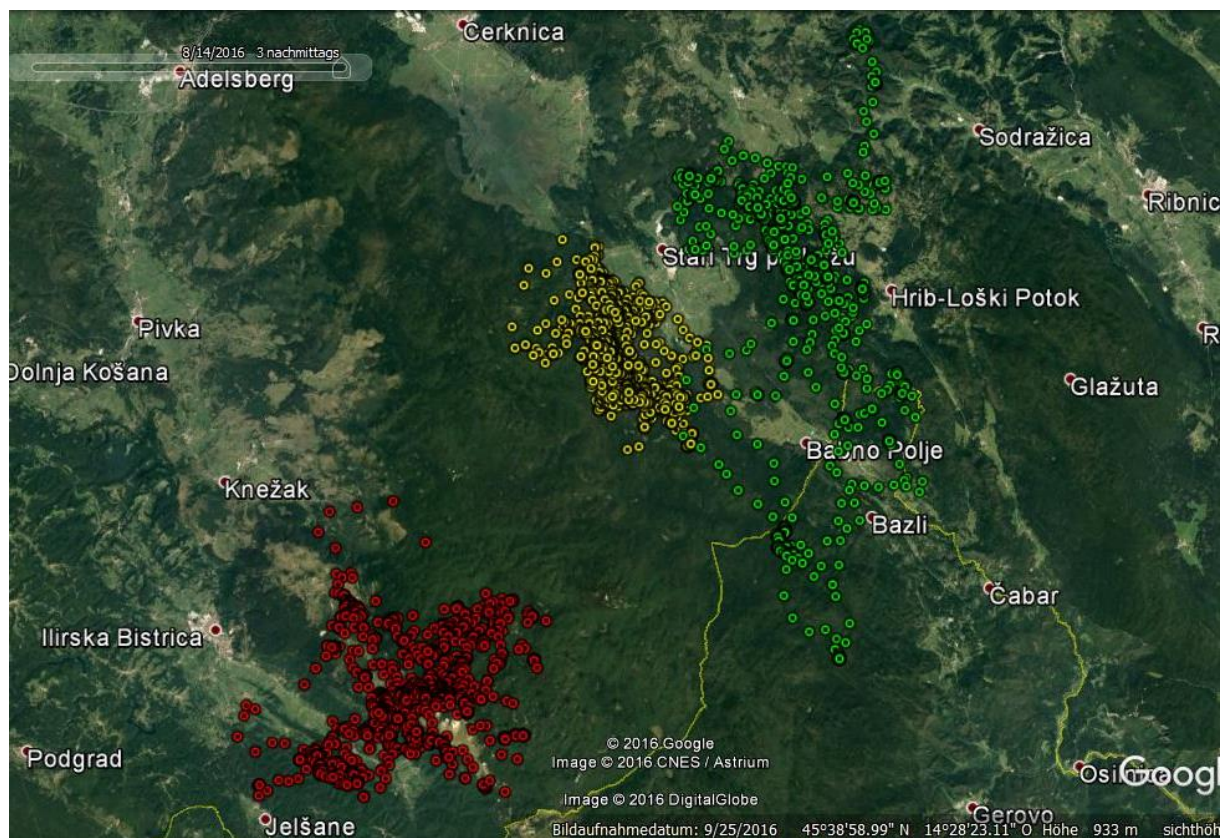


Fig. 2 All GPS locations collected for this study (yellow: 41110; red: 41111; green: 41112). Yellow line indicates the national border with Croatia.

Tab.4 Diet of brown bears based on the scats collected for this study (n = 105). Percent frequency of occurrence (FO) and average percent faecal volume (FV) are given for every food category.

Food category	FO (%)	FV (%)
Corn	55.2	65.5
Other plant material	89.5	48.7
Fruit	21.0	39.4
Insects	43.8	7.4
Vertebrates	35.2	27.1
Hard mast	3.8	< 5.0

3.1 Corn

In the initial model the correlated variable pair *elev* and *dist_settl* was included, therefore the variable *elev* was excluded and the model rerun.

The results (Table 5) show a significantly higher probability of corn in a scat sample, when *dist_feed* is smaller. If *dist_road* is larger, the probability also increases (not significant). When *CollarID* is included in the full model the same effects can be observed but *dist_feed* is not significant anymore. The bear with the CollarID 41110 had a higher probability to have corn in the scats than the other two bears after controlling for *dist_feed* and *dist_road*. Both models have a significant chi-square so they are better than the ones a step before (with more variables left; Tab. 3). The Hosmere and Lemeshow Test is not statistically significant for any of the two models, so the model fits are good. The model including *CollarID* is more accurate (less unexplained information) than the one without (-2 log likelihood of 53.4 compared to 127.3). It also explains the variance of the outcome better (77.6% compared to 20.1%, see Nagelkerke R² in Tab. 3) and correctly classifies the outcome for 87.6% of the cases instead of 62% as the model without *CollarID*.

Tab.5 Binary logistic regression model for the response variable corn, without and with the explanatory variable CollarID (contrasts with the CollarID 41110, the bear with the most scat samples). B = regression coefficients; SE = Standard error; Sig. = Significance ($\alpha = 0.05$); OR = Odds ratio

Variable	model corn				model corn with CollarID			
	B	SE	Sig.	OR	B	SE	Sig.	OR
Constant	,736	,597	,218	2,087	20,819	5786,203	,997	1100262549,116
Collar ID (reference class: 41110)							,441	
COLLAR_ID(1) (41111)					-22,150	5786,203	,997	,000
COLLAR_ID(2) (41112)					-23,248	5786,203	,997	,000
dist_feed	-,001	,000	,001	,999	-,001	,001	,159	,999
dist_road	,000	,000	,062	1,000	,001	,000	,054	1,001
chi-square	$\chi^2 = 17,112$; df = 2; Sig. < 0,000				$\chi^2 = 90,974$; df = 4; Sig. < 0,001			
-2LL			127,294				53,433	
Nagelkerke R ²			,201				,776	
Hosmer and Lemeshow Test, Sig.			,178				,597	
classification accuracy, %			61,9				87,6	

3.2 Other plant material

In the outcome of the first models the correlated variable pair *elev* and *dist_settl* was included, so the variable *elev* was excluded and the models rerun.

The results of both models (Table 6) show that no variables remain in the final models. There is no improvement by inclusion of any variables to the null model and the addition of *CollarID* as a categorical explanatory variable does not alter the outcome either.

Tab.6 Binary logistic regression model for the response variable other plant material, without and with the explanatory variable CollarID (contrasts with the CollarID 41110, the bear with the most scat samples). B = regression coefficients; SE = Standard error; Sig. = Significance ($\alpha = 0.05$); OR = Odds ratio

Variable	model other plant material				model other plant material with CollarID			
	B	SE	Sig.	OR	B	SE	Sig.	OR
Constant	2,145	,319	,000	8,545	2,145	,319	,000	8,545
-2LL			70,439				70,439	
Nagelkerke R ²			,000				,000	
classification accuracy, %			89,5				89,5	

3.3 Fruit

The initial model with *CollarID* included the correlated variable pair *forest* and *grassland*, therefore the variable *grassland* was excluded and the model rerun.

The results of the model for the response variable *fruit* (Table 7) show that a shorter *dist_settl* increases the probability significantly that bears fed on fruit.

Shorter *dist_settl* increases the probability significantly that bears fed on fruit also when *CollarID* is included in the model. The variable *dist_feed* is included in that model and a higher probability to find fruit in a scat sample is observed when it was smaller (not significant). The collared bear 41111

fed on fruit significantly more than the reference bear, the bear with the CollarID 41112 less (not statistically significant) after controlling for *dist_settl* and *dist_feed*. The chi-square values are significant for both models, so they are an improvement to former ones. The model for fruit has a good fit, but the other one has not (Hosmer and Lemeshow goodness of fit Test value <0.05), meaning that results are not robust. Including *CollarID* makes the model more accurate (-2 Log Likelihood of 65.4 opposed to 81.8), explains more of the variance (51.8% with CollarID, 27% without) and makes the classification more accurate as well (85.7% instead of 80%).

Tab.7 Binary logistic regression model for the response variable fruit, without and with the explanatory variable CollarID (contrasts with the CollarID 41110, the bear with the most scat samples). B = regression coefficients; SE = Standard error; Sig. = Significance ($\alpha = 0.05$); OR = Odds ratio

Variable	model fruit				model fruit with CollarID			
	B	SE	Sig.	OR	B	SE	Sig.	OR
Constant	1,422	,749	,058	4,145	2,273	1,430	,112	9,705
Collar ID (reference class: 41110)							,007	
COLLAR_ID(1) (41111)					2,493	,791	,002	12,098
COLLAR_ID(2) (41112)					-18,073	8242,989	,998	,000
<i>dist_feed</i>					-,001	,001	,087	,999
<i>dist_settl</i>	-,002	,000	,001	,998	-,002	,001	,001	,998
chi-square	$\chi^2 = 19.959$; df = 1; Sig. <0,001				$\chi^2 = 42.421$; df = 4; Sig. <0,001			
-2LL				81,81			65,378	
Nagelkerke R ²				,270			,518	
Hosmer and Lemeshow Test, Sig.				,306			,003	
classification accuracy, %				80,0			85,7	

3.4 Insects

The results of the model for the response variable *insects* (Table 8) show a significantly higher likelihood of insects being in the scats when *dist_feed* is higher and *dist_road* is smaller. With every percent that *cnfr_prct* rises, the odds that a bear ingests insects are over 9-times increased (OR = 9.254; not statistically significant). *Dist_feed* and *dist_road* have the same meaning for the model which includes *CollarID* with the exception that *dist_road* has no statistical significance. *Cnfr_prct* is not included in the most meaningful set of variables anymore. The bear with CollarID 41111 had five times (OR = 5.39) higher odds to feed on insects, while 41112 had less than half the odds to feed on insects (OR = 0.46) compared to the bear of the reference class after controlling for *dist_feed* and *dist_road*. Both models have an acceptable goodness of fit (Hosmer and Lemeshow Test values > 0,05) and improved from their models one step before (χ^2 values are significant for both of them). The addition of *CollarID* reduces the amount of information unexplained by the model (-2LL from 122.66 to 107.59), it has a higher Nagelkerke pseudo r^2 (39.2% instead of 24.6%) and classification accuracy (80% instead of 67.6%).

Tab.8 Binary logistic regression model for the response variable insects, without and with the explanatory variable CollarID (contrasts with the CollarID 41110, the bear with the most scat samples). B = regression coefficients; SE = Standard error; Sig. = Significance ($\alpha = 0.05$); OR = Odds ratio

Variable	model insects				model insects with CollarID			
	B	SE	Sig.	OR	B	SE	Sig.	OR
Constant	-1,531	,733	,037	,216	-1,329	,692	,055	,265
Collar ID (reference class: 41110)							,000	
COLLAR_ID(1) (41111)					1,685	,518	,001	5,393
COLLAR_ID(2) (41112)					-,773	,721	,283	,462
dist_feed	,001	,000	,001	1,001	,001	,000	,003	1,001
dist_road	-,001	,000	,017	,999	-,001	,000	,074	,999
cnfr_prct	2,225	1,268	,079	9,254				
chi-square	$\chi^2 = 21,286$; df = 3; Sig. <0,001				$\chi^2 = 36,359$; df = 4; Sig. <0,001			
-2LL				122,7				107,588
Nagelkerke R ²				,246				,392
Hosmer and Lemeshow Test, Sig.				,513				,151
classification accuracy, %				67,6				80,0

3.5 Vertebrates

The results of the model for the response variable *vertebrates* (Table 9) show that only the variable *grassland* is left in the most parsimonious model and the use of that habitat by a bear prior to defecating makes it more likely to find vertebrate remains in bear scats (19.7-times higher odds for every percent of higher use of that habitat prior to defecation). These Odds Ratios increase to the factor 29.5 when *CollarID* is included in the model (both times the values are statistically significant). The bear with the CollarID 41111 was less likely to consume vertebrates (not statistically significant) while the bear with the CollarID 41112 was significantly more likely to consume vertebrates than the reference bear 41110 after controlling for *grassland*. Both models pass the threshold value of > 0.05 for the goodness of fit test and have significant chi-square values. The accuracy of the model increases with the introduction of *CollarID* (-2LL of 131.91 before; 118.12 after), as does the explanation of the variance of the outcome (5.6% before; 21.8% after) and the correct classification of the outcome (65.7% of the cases before; 74.3% of the cases after).

Tab.9 Binary logistic regression model for the response variable vertebrates, without and with the explanatory variable CollarID (contrasts with the CollarID 41110, the bear with the most scat samples). B = regression coefficients; SE = Standard error; Sig. = Significance ($\alpha = 0.05$); OR = Odds ratio

Variable	model vertebrates				model vertebrates with CollarID			
	B	SE	Sig.	OR	B	SE	Sig.	OR
Constant	-1,011	,291	,001	,364	-1,287	,409	,002	,276
Collar ID (reference class: 41110)							,002	
COLLAR_ID(1) (41111)					-,339	,498	,496	,713
COLLAR_ID(2) (41112)					1,868	,636	,003	6,475
Grassland	2,982	1,476	,043	19,729	3,384	1,568	,031	29,495
chi-square	$\chi^2 = 4,365$; df = 1; Sig. = 0,037				$\chi^2 = 18,148$; df = 3; Sig. <0,001			
-2LL				131,9				118,122
Nagelkerke R ²				,056				,218
Hosmer and Lemeshow Test, Sig.				,282				,593
classification accuracy, %				65,7				74,3

4 Discussion

The results of the study confirm a connection between the diet and the habitat use of brown bears in Slovenia. Indications about which type of food bears utilize in different habitats can be drawn from those results.

The most obvious connection can be found between the use of corn and the average distance to the feeding sites. Corn is the most prominent food type provided at feeding sites and the three bears payed regularly visits to feeding sites in their home ranges. So the probability of corn in the scats of a bear is higher the more time it spent close to feeding places. Ecologically it means that with a shorter distance to feeding sites the probability that bears visit these sites and feed on corn is elevated. The observation that distance to roads increases the likelihood of corn in the scats is also not surprising. Although roads are necessary to get to the feeding sites, these are usually placed well off regional roads with regular traffic and just minor forest roads lead to them. Those have been excluded from the study (see "2.4 Data preparation" for reasons).

The models for *other plant material* indicate that bears have access to other plant material in the forest as well as on grasslands and their feeding on that type of food is not linked to any of the other variables used for the analysis. They seem to consume other plant material everywhere, which is also indicated by high occurrence of that food type in all the scats that were analysed for this study (other plant material was found in 94 of 105 scat samples).

Fruit is more often present in bear scats when they used habitats closer to settlements. That was expected, because in the rural parts of Slovenia people often have little orchards right beside their houses. If those are not properly fenced and bordering to cover, which is often the reality around the

Snežnik area, they are frequent feeding grounds for bears during the weeks the fruits are ripe. The fact that a shorter distance to feeding spots enhances the chances to find fruit in bear scats might be connected to the fact that feeding sites are also supplied with fruits and bears do feed on them there.

The model for *insects* shows a strong positive relation between the conifer coverage and insects in a bear scat. They are more likely to occur with each percent of conifers more. Ants were the most common insects found in the scats (in 45 out of 46 samples with insects). In the temperate climate zone ants build their anthills usually from conifer needles, so they are often located within coniferous patches of the forest and bears feed on them there. Große et al. (2003) showed that during summer ants are an important food source for brown bears in Slovenia. That the use of insects increases with shorter distances to roads could be the result of correlations between the distance to roads and factors like the openness of the forest and habitat productivity. For example the vegetation at the side of roads can be an habitat (usually similar to unfertilised dry meadows) that is especially well suited for some species of insects. A greater distance to feeding spots as a factor that enhances the chances to find insects in bear scats could be based on behavioural elements. It seems, when a bear visits a feeding spot, it will feed on corn and therefore not search for insects in the same feeding bout.

Vertebrates are more likely to be consumed when bears used grasslands. This could be explained by the fact that domestic animals are mostly kept on grasslands, although just 2 of 37 scat samples containing vertebrates included a domestic animal (sheep). But deer numbers are also generally higher in areas including more grasslands. And roe deer for example leave their fawns hidden in the long grass of meadows as long as they are not able to follow their mother and are an easy prey for bears. Hooves of roe deer fawns were found in the feces samples several times. Another possibility for the cause of that outcome could be that rodents are easier to dig out of the ground on grassland than on other more rugged terrain in this study area with its karst nature. Bones from rodents were also found in several scats. But this does depend on the rodent species, for example dormice (*Glis glis*) are expected to be connected to forests instead of grasslands.

The models including *CollarID* show that there are rather large individual differences between the food use of the three bears in this study (*CollarID* was significant for fruit, insects and vertebrates). It could be suggested that a reason for this is that they are all different types of bears (young female with cubs / older female without cubs / older male) but firstly that cannot be determined with samples from such few bears and secondly Steyaert et al. (2014) showed that individual variation among brown bears is rather large and dilutes population-wide patterns. The inclusion of *CollarID* improved the model diagnostics in general, because the bears exhibit differential foraging behaviour. However, the corn was used by all of them quite similarly.

A restriction of this study is the limited sample size of just three bears, among which only 18 scat samples were obtained from one of them. This was due to the fact that not more bears could be captured within the time of the study. So increasing both, the number of individuals and the number of scats collected per individual, would make the study more reliable and it would enable to study variation between different groups of bears (age, sex, reproductive stage). A bigger sample size would also lower the problems of multicollinearity this study had. Possibly more variables could have stayed in the model and the outcome would have been more distinguishable (e.g. higher number of habitat types). But the study was of preliminary nature in order to test the developed method, so the small sample size was expected beforehand.

Nevertheless, the gains of using GPS data from collared bears to find their scats was demonstrated, especially if the clusters are surveyed shortly after the use by the bear in order to reduce the possibility that another bear came along and defecated at the same location. Another point is that apart from females with offspring and during mating season, brown bears are solitary. But the survey time included the peak in the mating period (from early May to mid-June in Slovenia; Krofel et al. 2010) during which a female bear is often accompanied by a male. Frequently more than one fresh scat was found at a visited cluster (up to 4) and one was chosen randomly, although bears are actually able to have such high defecation rates. But even if a pair of bears was sampled, they would most likely also have foraged together and the habitat analysis would still be connected to a fitting scat sample. Genotyping intestine epithelial cells would prove the correct association between bear and scat, but is expensive. DNA metabarcoding of the feces, which would make the diet analyses more thorough (like Elfström et al. did in 2014b) is also costly.

It also has to be kept in mind that the food items were easier to be visually identified in the scats when they occurred aggregated and made up a high percentage of the volume in the sample. For example, cherries and apples were found in large amount in the bears scats after visits to orchards or feeding sites while fruit of the checker tree was only found in low percentages, maybe because those fruits are not as abundant at one place as cherries and apples at an orchard. Fruits of the checker tree also do not seem to be brought to feeding places in large amounts. The gut retention time is another possible source of error, which was met by taking into account known values of gut retention time for brown bears from other studies. It could be minimized further by feeding bears in captivity with exactly the food items available to bears in the study area.

Probably the major source for error was the fact that the exact time when a bear defecated could not be determined. The bears spent from 3 up to a maximum of 11 hours at the clusters that were examined. They could have drop the scats anytime, from the instant before they laid down the first time over the moments when they swapped into another daybed a few meters away right to the time as they were just about to leave the cluster. For the analyses of this survey the locations for the

time interval from 3 to 16h before the cluster were selected because they should cover the food intake best that could be represented in the scats according to the known gut retention times. But obviously the variance of the in fact analysed time interval before defecation can be quite large. Usually animals avoid lying near their excrements (possible seat of disease) and would defecate when they leave their daybeds. But maybe bears would switch to another daybed (was often the case over the course of the day) a few meters away after defecating or move away a few meters to defecate and return after. To confirm those possibilities and specify the time of defecation would only be possible by visual observation, what is most likely only possible with habituated bears.

Another improvement could be made by increasing the rate of GPS fixes. The lower the intervals between the locations, the better the habitat use is displayed. But bears are usually quite stationary when they feed on something, so all major foraging behaviour should be included.

The diagnostics for the models for corn were better compared to those of the other dependent variables, probably because the exact locations where corn was available were known (feeding sites). For the other food types the availability was linked to an area (e.g. coniferous patches to insects or orchards right beside settlements to fruit) not a specific point and no data layers specifically for them were used. This might have diluted the effects those habitat characteristics had.

To extend this study over a whole year would make changes in the food and habitat use of brown bears over the course of a year more obvious. Besides fruits hard mast does play an important role in the nutrition of bears during autumn (Kavčič et al. 2015), especially in a mast year, and corn from feeding places does lose some importance. It can be expected that this would result in a higher use of the habitat type broadleaf forest.

Another interesting approach would be to check whether because of the varying gut retention times of diverse food types different time intervals before the defecation, each specific for a given food type, should be analysed. To test this the averages for two more datasets were calculated from the data of this study. The dataset 3-9 hours before the defecation was expected to represent the habitat use for the intake of the components fruit and other plant material (softer, easier to digest) especially well and the dataset for the 10-16 hours timeframe for the components corn, insects and vertebrates (harder to digest). But no advancement in the models could be shown (see Appendix 2). Possibly it would be a more useful approach to first determine the diet via scat analysis, then determine the time period that predicts the gut retention time best for each sample and based on this information choose the most suitable time frame for the habitat use analysis also for each sample separately.

5 Conclusion

The purpose of this study was to test the used method and to find out if the habitat use of brown bears is linked to their diet and if they use specific habitat types more in order to forage for certain food items. It was shown that bears do use habitat close to feeding sites to forage on corn and habitat close to settlements and feeding sites to feed on fruit. The probability to find insects in a bear scat increased if habitats with a higher conifer coverage were used more and vertebrates if more grasslands were used before. This proves that there is in fact a link between the habitat use and the diet of brown bears in Slovenia, which can be proven by the applied method. Management authorities could make use of the knowledge that can be gained with this method to reduce the number of human-bear conflicts, for example by providing fruit for bears at feeding spots and advising the public to remove their ripe fruit directly during the time when bear would otherwise use the fruit in orchards close to human settlements. Conservation measures resulting from this study could be to protect patches of pure conifer forest in the Snežnik region, because ants are an important food source to bears in general and those insects depend on conifer needles.

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7 Appendix

Appendix 1: Data sheet used for the scat analysis

FOOD CATEGORIES:

VERTEBRATES

- wild ungulates (red deer, roe deer, wild boar, chamois)
- other wild vertebrates (carnivores, rodents, birds, reptiles, amphibians)
- domestic ungulates (sheep, cattle, pig, goat, horse, donkey)
- other domestic animals (cat, dog, poultry...)

INSECTS

- ants, wasps, bees, dung beetles, ...

HARD MAST

- beechnuts
- acorns
- other (hazelnuts, chestnuts...)

FRUITS

- wild (blueberry, raspberry, blackberry, wild cherry, Cornelian cherry, rowan, checker tree...)
- domestic (plums, apples, pears, cherry...)

OTHER PLANT MATERIAL

- graminoids (grasses, sedges and rushes)
- forbs
- moss
- other

MUSHROOMS

ANTHROPOGENIC FOOD

- Corn (*Zea mays*, L.)
- other cereals
- garbage

Appendix 2: Binary logistic regression models for alternative data sets

2.1 Data set 3-9h prior to the daybed location where the scat was found

Tab.10 Binary logistic regression model for the response variable fruit, without and with the explanatory variable CollarID (contrasts with the CollarID 41110, the bear with the most scat samples). B = regression coefficients; SE = Standard error; Sig. = Significance ($\alpha = 0.05$); OR = Odds ratio

Variable	model fruit (without elev)				model fruit with CollarID (without elev)			
	B	SE	Sig.	OR	B	SE	Sig.	OR
Constant	,876	,658	,183	2,401	,876	,658	,183	2,401
dist_settl	-,001	,000	,002	,999	-,001	,000	,002	,999
chi-square	$\chi^2 = 16.910$; df = 1; Sig. < 0,001				$\chi^2 = 16.910$; df = 1; Sig. < 0,001			
-2LL			90,888				90,888	
Nagelkerke R ²			,232				,232	
Hosmer and Lemeshow Test, Sig.			,642				,642	
classification accuracy, %			80,0				80,0	

Tab.11 Binary logistic regression model for the response variable other plant material, without and with the explanatory variable CollarID (contrasts with the CollarID 41110, the bear with the most scat samples). B = regression coefficients; SE = Standard error; Sig. = Significance ($\alpha = 0.05$); OR = Odds ratio

Variable	model other plant material				model other plant material with CollarID			
	B	SE	Sig.	OR	B	SE	Sig.	OR
Constant	2,1454	0,31867	1,7E-11	8,5454545	2,1454	0,318665	1,67E-11	8,5454545
-2LL			70,439				70,439	
Nagelkerke R ²			4,5E-16				4,54E-16	
classification accuracy, %			89,5238				89,52381	

2.2 Data set 10-16h prior to the daybed location where the scat was found

Tab.12 Binary logistic regression model for the response variable corn, without and with the explanatory variable CollarID (contrasts with the CollarID 41110, the bear with the most scat samples). B = regression coefficients; SE = Standard error; Sig. = Significance ($\alpha = 0.05$); OR = Odds ratio

Variable	model corn (without elev)				model corn with CollarID			
	B	SE	Sig.	OR	B	SE	Sig.	OR
Constant	,931	,633	,142	2,537	,931	,633	,142	2,537
dist_feed	-,001	,000	,002	,999	-,001	,000	,002	,999
dist_road	,001	,000	,006	1,001	,001	,000	,006	1,001
cnfr_prct	-2,151	1,126	,056	,116	-2,151	1,126	,056	,116
chi-square	$\chi^2 = 21.586$; df = 3; Sig. < 0,001				$\chi^2 = 21.586$; df = 3; Sig. < 0,001			
-2LL			122,821				122,821	
Nagelkerke R ²			,249				,249	
Hosmer and Lemeshow Test, Sig.			,221				,221	
classification accuracy, %			70,5				70,5	

Tab.13 Binary logistic regression model for the response variable insects, without and with the explanatory variable CollarID (contrasts with the CollarID 41110, the bear with the most scat samples). B = regression coefficients; SE = Standard error; Sig. = Significance ($\alpha = 0.05$); OR = Odds ratio

Variable	model insects				model insects with CollarID			
	B	SE	Sig.	OR	B	SE	Sig.	OR
Constant	-1,439	,393	,000	,237	,272	,758	,719	1,313
Collar ID (reference class: 41110)							,093	
COLLAR_ID(1) (41111)					-1,163	,537	,030	,313
COLLAR_ID(2) (41112)					-,645	,709	,363	,525
dist_feed	,001	,000	,000	1,001	,001	,000	,040	1,001
dist_road					,000	,000	,096	1,000
chi-square	$\chi^2 = 14,951$; df = 1; Sig. <0,001				$\chi^2 = 22,057$; df = 4; Sig. <0,001			
-2LL			128,996				121,891	
Nagelkerke R ²			,178				,254	
Hosmer and Lemeshow Test, Sig.			,349				,337	
classification accuracy, %			64,8				68,6	

Tab.14 Binary logistic regression model for the response variable vertebrates, without and with the explanatory variable CollarID (contrasts with the CollarID 41110, the bear with the most scat samples). B = regression coefficients; SE = Standard error; Sig. = Significance ($\alpha = 0.05$); OR = Odds ratio

Variable	model vertebrates				model vertebrates with CollarID			
	B	SE	Sig.	OR	B	SE	Sig.	OR
Constant	-,609	,204	,003	,544	-,609	,204	,003	,544
-2LL			136,271				136,271	
Nagelkerke R ²			,000				,000	
classification accuracy, %			64,8				64,8	