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Use of feeding sites by brown bears (*Ursus arctos*) before, during and after the hunting season

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Abstract

"Landscape of fear" describes how an animal perceives it´s environment and illustrates the trade-off between foraging and predation risk in a specific area. The main factor implicating an animal's "landscape of fear" is direct and perceived predation risk. Human disturbance, especially hunting, can have strong impact on wildlife behaviour. For many top predators such as large carnivores, which do not have natural enemies, hunting and human persecution represents a major reason for adult mortality. In Slovenia, brown bears (*Ursus arctos*) are intensively fed and hunted at feeding sites. For this reason, monitoring of bears at feeding sites provides an excellent opportunity to investigate the trade-off between foraging and predation risk. I investigated feeding site use of bears by using camera traps at n = 22 feeding sites continuously throughout the year for the duration of two years (2016 and 2017). I calculated Generalized Liner Models (GLM´s) to evaluate if there are differences in feeding site use during consecutive days, the month and the interaction between those two variables during and outside of the hunting season. I ran separate models for different social units, including females with cubs, which are protected from hunting, and solitary bears, which are not protected. I predicted differences in the use of feeding sites for the social units, in particular that solitary bears should use feeding sites less during the hunting season, while females with cubs should respond to the hunting season to a lesser extent. Indeed, solitary bears used feeding sites less during the hunting season. Females with cubs showed also differences in feeding site visitation but these differences where less pronounced. I also investigated whether bears changed their circadian feeding site use in response to the hunting season, with the prediction that visitation peaks where shifted more to the night. However, I could not observe such patterns as circadian feeding site use was independent of the hunting season. In summary, my findings may indicate a response of the different social units and their respective hunting pressure. However, more research is needed to determine the influence of other factors on bear behaviour, e.g. avoidance of feeding sites by females with cubs due to the risk of infanticide.

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1 Introduction

1.1 Background

The term "landscape of fear" refers to the way an animal perceives its environment based on a trade-off between foraging and safety in its available area (Brown et al. 1999). The main factor implicating an animal's "landscape of fear" is direct and perceived predation risk (Laundre et al. 2001). Human disturbance, especially hunting, can have strong impact on wildlife behaviour, it may for example cause increased vigilance, which can in turn result in spending less time on foraging (Benhaiem et al. 2008). In areas where large, natural predators were extirpated, hunters have filled their role in the food chain (Marantz et al. 2016). In a study investigating the impact of humans on spatial behaviour of white-tailed deer (*Odocoileus virginianus*), the results showed that the deer recognized threats from humans and altered their behavioural strategies by minimizing their movement and exhibiting high residency times in well established ranges (Little et al. 2016, Marantz et al. 2016). Ciuti et al. (2012) also showed that in human-dominated landscapes, human disturbance had higher impacts on elk (*Cervus canadensis*) behaviour than habitat or natural predators. The behavioural changes in elk were expressed in increased vigilance and decreased foraging. A study from south-eastern Norway showed that roe deer (*Capreolus capreolus*) responded stronger to human persecution than lynx (*Lynx lynx*) predation (Lone et al. 2014). Similarly, Proffitt et al. (2009) found that GPS-collared elk reacted stronger to humans, when facing the risk of getting shot by hunters and the risk of getting killed by wolfs (*Canis lupos*). Due to the higher temporal predictability of human hunting pressure it makes it easier and more cost-efficient to respond to, than to natural predators (Proffitt et al. 2009)

For many top predators such as large carnivores, which do not have natural enemies, hunting and human persecution is a major cause for adult mortality (Woodroffe & Ginsberg 1998). This is also the case for brown bears (*Ursus arctos*) in Slovenia, where 12% of the bear population is hunted every year (average of the period from 1998-2017, Jerina et al. 2018). Thus, hunters may generate a "landscape of fear" for bears. Several studies have shown behavioural changes in bears linked to hunting; for example, a study by Ordiz et al. in (2012) showed that bears changed their activity patterns during the hunting season and became more nocturnal. However, females with cubs changed their behaviour much less than solitary bears, likely because they are protected from hunting. A temporal analysis of habitat selection of brown bears in Scandinavia revealed that bears avoid disturbed areas and select

more likely slopes during periods of high human activities (Martin et al. 2010). Moreover, changes in heart rate and heart rate variability of Scandinavian brown bears suggest that they face a human-induced landscape of fear (Støen et al. 2015). Notably, a study from Van de Walle (2018) showed that hunting even changed life history traits in female bears. In their study, they found evidence that cubs stay longer with their mothers because of the hunting legislation that females with cubs are protected from hunting.

In Slovenia bears are usually hunted at feeding sites (Krofel et al. 2012) and artificial feeding of brown bears has a long history in Slovenia and is practiced since over 100 years in some regions (Kavčič et al. 2013). Feeding sites were typically supplied with maize and carrion and Kavčič et al. (2011) showed that artificial food represents even 1/3 of the bears' yearly food intake. Moreover, bears are able to gain 3.9 times more energy per time unit as compared to surrounding natural habitats (Kavčič et al. 2011), which makes feeding site use an efficient way to gain weight. For this reason, monitoring of bears at feeding sites provides an excellent opportunity to investigate the trade-off between foraging and predation risk in the form of hunting. The hunting season also covers hyperphagia, an important foraging period for bears in which they have to consume a lot of food to accumulate enough fat for surviving the denning phase over winter (Oct-Dec till Mar-May) (Barboza et al. 1997, Swenson et al. 2007). Feeding sites may thus be particularly attractive to bears during this time.

In this study, I will examine data gathered from camera traps continuously throughout the year for the duration of two years, to investigate bear presence at feeding sites before, while and after the hunting season (Oct-May). Furthermore, I will examine differences in feeding site use of social units (females with cubs, solitary bears) and investigate whether feeding sites are used during different time frames within the hunting season. Females with cubs are protected from hunting and may thus not perceive feeding sites as dangerous as solitary bears. This allows for investigating the trade-off between foraging and survival with respect to the according risk of a certain social unit.

To see if hunting induces a landscape of fear to bears using artificial feeding sites, I formulated the following hypotheses:

- Females with cubs show less changes in their feeding site use because they are protected from hunting and may be aware of that.
- Solitary bears react to the hunting season and change their feeding site use with the prediction, that they use feeding sites less during the hunting season, due to the risk they face because of hunting.

- To avoid hunters, bears change their circadian use of feeding sites and visit feeding sites mainly at night-time during the hunting season.

This study aims to determine whether human persecution alters bear behaviour, to which extent, and if such behavioural changes are adaptive according to the different social units. In the light of the rapid expansion of the human population, which is paralleled by an increased impact on wildlife and its habitat, such research is critically important.

1.2 Bear - Management in Slovenia

Under the European Union Council Directive on the Conservation of Natural Habitats and of Wild Fauna and Flora the brown bear is protected as a priority species and is listed in Annex 2 of the Bern Convention on the Conservation of European Wild Fauna and Flora. According to this, the species and its natural habitats are strictly protected in Europe (Dick, 2006). Brown bear management in Slovenia has the main goal to minimize the number of conflicts with men, with hunting or regulating the bear population being part of this management. As a result, Slovenia negotiated a reservation to Appendix II for the brown bear in line with the provision in paragraph 1 of Article 22 and in relation to Article 6 of the Bern Convention (MOP 2007).

The brown bear was never extinct in Slovenia, although at the end of the 19th and the beginning of the 20th century the bear population was quite low with an estimated size of 30 - 40 bears (Simonič 1992). Until 2004, the brown bear was a game species in Slovenia but it always received the status of a specially protected species which was implemented through hunting legislation (MOP 2007). In 2004, a new protection measure was implemented (Decree on protected wild animal species), since then the brown bear is a protected species only. Since 2005, the Ministry of the Environment and Spatial Planning has the main power for brown bear management (MOP, 2007).

The culling quota is based on integral monitoring and is structured by sex, weight (up to 100 kilograms, 100 – 150 kg, over 150 kg) and spatial distribution. Most of the regular culled bears are in the first weight category, involving young, immature animals, most often involved in conflict situations (MOP 2007). Moreover, the quota is divided among individual hunting grounds, with priority of those hunting grounds and areas where conflicts between humans and bears have occurred. A problem bear can be shot within the legal harvest limit if

a conflict occurs during the hunting season, outside of the hunting season, a special permit has to be issued (Klenzendorf, 1997). Every hunted bear is monitored and gets checked by hunting inspectors (MOP, 2007). Using this quota system, about 12% of the bears are harvested annually during the hunting season, which lasts from October to April (Jerina et al. 2018, Kaczensky 2004). However, the permits for culling have to be issued on an annual basis, which in some years led to a delayed start of hunting (see Table 1).

Table 1: Occurrence of bear cullings during the regular hunting season (Oct-Apr) in Slovenia from 1994 to 2018.

Season	Oct	Nov	Dez	Jan	Feb	Mar	Apr
1994/95	X	X	X				X
1995/96	X	X	X		X	X	X
1996/97	X	X	X	X	X	X	X
1997/98	X	X	X	X		X	X
1998/99	X	X	X		X	X	X
1999/00	X	X	X	X	X	X	X
2000/01	X	X	X	X		X	X
2001/02	X	X	X		X	X	X
2002/03	X	X		X	X	X	X
2003/04	X	X	X			X	X
2004/05	X	X			X	X	X
2005/06	X	X	X				X
2006/07	X	X				X	X
2007/08	X	X	X			X	X
2008/09	X	X				X	X
2009/10	X	X	X				X
2010/11	X	X	X		X	X	X
2011/12	X	X	X	X	X	X	X
2012/13	X			X	X	X	X
2013/14			X	X	X	X	X
2014/15	X	X		X	X	X	X
2015/16	X	X	X	X	X	X	X
2016/17				X	X	X	X
2017/18				X	X	X	X

2 Material and Methods

2.1 Study area

The study area for monitoring the feeding sites is located within in the bear core area in Dinaric Alps of Southern Slovenia (Figure 1). This area is the main habitat of 95% of the Slovenian brown bear population and covers 3855 km^2, which represents 19 % of the countries territory (Jerina et al. 2013).

The elevation in this area ranges between 740 and 1350 m above sea level. Precipitation levels are high with 2166 mm per year. The average temperature in the area is 6.5°C, in July the temperature reaches the mean monthly maximum of 16.4°C and the mean monthly minimum is reached in January with -3.4°C. Snow cover often lasts until late spring with an average duration of 90 days (122 days maximum). The bedrock is formed of carbonate, mainly limestone and to a lesser extent dolomite. The dominant species, accounting for 50% of the total growing stock is fir (*Abies spp.*), followed by beech (*Fagus spp*., 26%), spruce (*Picea spp*, 18%) and sycamore (Acer pseudoplatanus L.) with 2% (Klopčič et al. 2010).

Slovenia has one of the highest bear population densities worldwide, with an estimated population size of 975 individuals (spring population estimate, ranging from 875-1130), and local densities up to 80 bears per 100km² (Jerina et al. 2018). In the bear core area densities approximate 13 bears per 100km² on average (Jerina et al. 2013). The high bear population densities may result from successful conservation management, a high natural carrying capacity (Jerina & Adamič 2008) and/or the intense supplemental feeding habits (Jerina et al. 2013). The supplemental food consists mainly of maize, which is high in energy and is available to bears throughout the whole year and in high quantities (on average 12,500 kg/100 km² per year). In Slovenia, feeding sites densities are high with an average of 19 feeding sites/100 km² (Jerina et al. 2013).

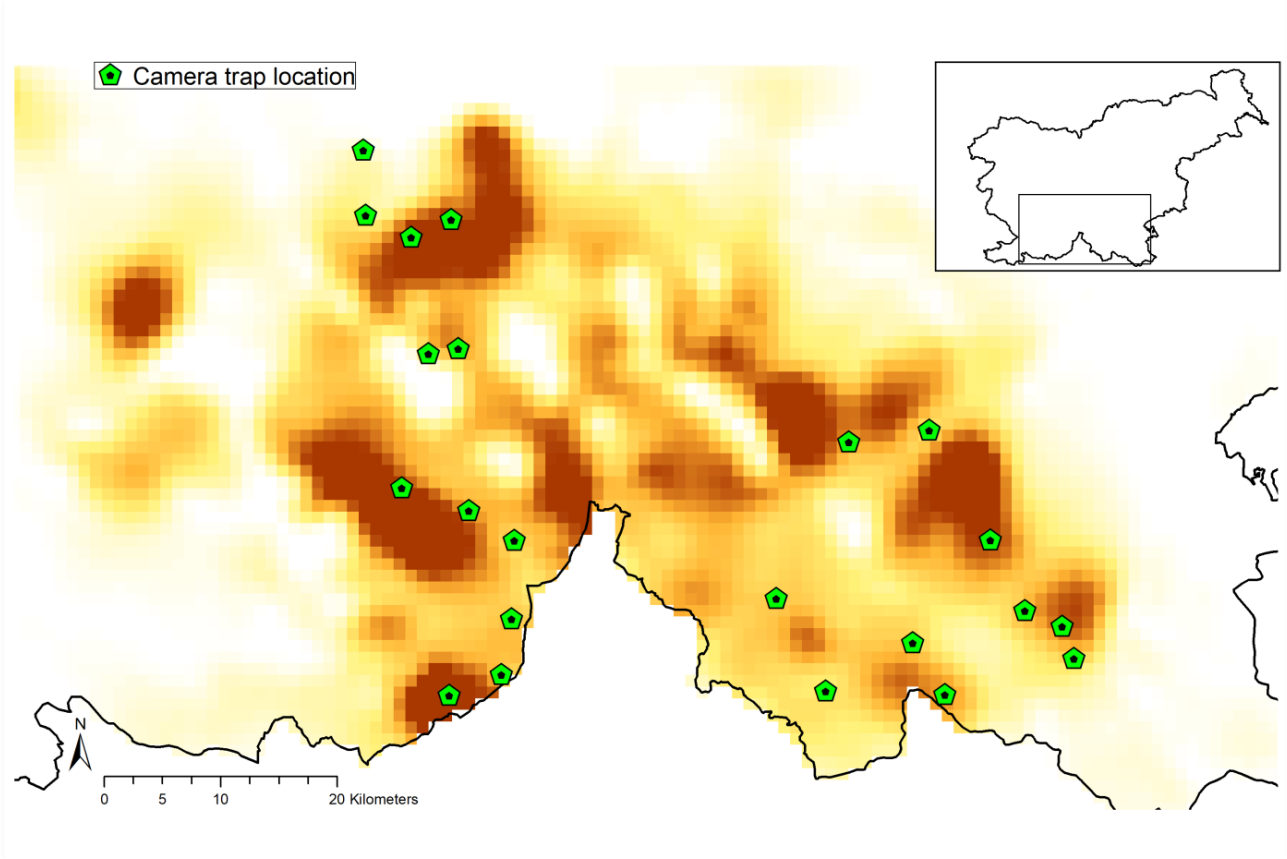


Figure 1: Feeding sites used in this study (95% of all bears of Slovenia live in the shown area). The shades from yellow to brown illustrates the bear density, darker colours imply higher densities.

2.2 Study animal

The study animal is the European brown bear (*Ursus arctos*). Brown bears are omnivorous but in the first place eat vegetarian foods. This depends highly on environmental conditions and the availability of food (Brown 2013). Generally they live solitary, only during the mating season they form short alliances. The exact duration of the mating season in Slovenia is hard to define, but most copulations take place between early May until mid of June (Krže 1988, Jonozovič 2003). The brown bear is also known as an animal which commits infanticide (of unrelated cubs), to increase it's mating opportunities (Bellemain et al. 2006). The litter size of female brown bears ranges normally from 1 to 5 cubs (1-3 in Slovenia). How long the cubs stay with their mother highly depends on the available habitat and food sources; for example in Montana the cubs stay with their mother from 1 to 3 years, whereas in the Arctic the cubs stay from 2 to 4 years with their mother (Brown 2013). Brown bears hibernate

during the hard winter months (Oct-Dec until Mar-May). During hibernation, they reduce their body temperature, heartbeats per minute and their metabolic rate in order to minimize their energy demand during the winter (Nelson et al. 1983). In this time they do not eat and they also do not defecate in order to use the nutrients, which they eat before the winter, in the best way (Skuban 2011).

Bears have big home ranges and the size of it depends highly on the available food, population density and other environmental factors. The mean home range size of brown bears in Slovenia was estimated at 350 km² (Jerina et al. 2012), which is similar to other populations with comparable environments. It is notable, that the male home ranges are on average 4 times larger than the females home ranges in Slovenia (Jerina et al. 2012). Relatively to their body size, bears possess the biggest brains of all carnivora. Due to this, scientists believe that they may be able to memorize and learn from many events, e.g. even from a single gunshot (Brown 2013).

2.3 Camera traps

In total, n = 22 feeding sites were equipped with camera traps in the years 2016 and 2017. For comparing bear presence at feeding sites before, during and after the hunting season, I used data collected one month before the beginning of the hunting season (September), which I compared to the first month within the hunting season (October). Moreover, I used data from the last month during the hunting season (April) and compared it with the first month after the end of the hunting season (May). I did not have data from all the feeding sites for the abovementioned months and thus had to exclude some locations from analysis. I analysed data from n = 17 feeding sites for spring 2016, and data from n = 14 feeding sites for spring 2017. For autumn, I analysed data from n = 14 feeding sites in 2016 and n = 16 feeding sites in 2017.

Three different models of the digital surveillance camera trap UO Vision IR Plus (Fototrappolagio/Italy) were used to monitor bears at feeding sites; the model UV565 was the most utilised one, while at feeding sites were camera traps were stolen they were replaced with the successor model UV595. At feeding sites were a wider angle was useful, the model UV572 was used. Cameras were triggered by a high sensitive passive infrared motion sensor to capture a picture and/or record a video clip. The cameras were

programmed to take a photo every 5 min in the presence of a moving object. After every picture, a 30-second video was taken, which was checked when the object on the picture was unidentifiable.

2.4 Statistics

In total, approximately 200.000 camera trap pictures were evaluated to determine which animal species was visiting the feeding site, and, if possible, of which sex. In the case of bears, I distinguished between solitary bears, females with cubs in their first year of life and females with cubs in their second year of life based on the body size of the cubs. For analysis, I just used two categories and pooled females with cubs (both in their first and second year) because females with cubs are generally protected from hunting. The group I used for comparison were solitary bears (both sexes) which are not protected from hunting. There was a small percentage of pictures that only showed cubs, in this case I treated them as follows: if the picture showed cubs in their first year of life, I counted them to the group "Females with cubs", because it was very likely that the female was around but just not on the picture. I excluded pictures showing cubs in their second year of life without a female, because at this age, I could not be sure whether they were still accompanied by their mother or not. If they were with their mother, all of them would be protected from hunting, but if the cubs were on their own, they would not hold this protection status.

I used a Generalized Linear Model (GLM) with Poisson distribution and logit link to evaluate whether there are differences in the visitation rates before, during and after the hunting season. I ran separate models for solitary bears and females with cubs where I used bear presence as response variable (= number of bears). The response variable bear presence was modelled either as absolute number of bear pictures, or as daily proportion of females with cubs within all bears. The independent variables used in all models were the month (April & October = hunting, May & September = non-hunting), the consecutive day in the year (continuous) and the interaction between these two variables, to test whether the slopes of feeding site use differed between the two months. Initially, I also used year as independent variable and found that there was a difference in bear presence between the years. Thus, I created separate models for 2016 and 2017. I also ran separate models for spring and autumn hunting seasons (start and end of the hunting period). I corrected for differences in the number of camera trap days by setting the model weights to the according number of

days for each camera and month. Lastly, I investigated whether bears used feeding sites at different times of the day in the hunting and non-hunting period.

To determine the best model, I used a backward model selection procedure based on the Akaike information criterion (AIC) (Burnham et al. 2010; Wagenmakers & Farrell 2004). For models with AIC differences between 0 and 2, I selected the simpler model, which means that I choose the model with lesser parameters. Model parameters were considered as informative, if they did not include 0 in their 95% confidence interval (Arnold 2010). I used Access 2010 and Excel 2010 to evaluate the camera trap data, for my illustrations and tables, I used Excel 2007 (Microsoft Inc., USA). For calculating the models I used R (R Development Core Team) and R Studio (RStudio, Inc.).

3 Results

In general, feeding site use was highest during the summer months (for further information see Appendix 1). The number of bear pictures taken at all analysed feeding sites within a month differed between the hunting and non-hunting season (Table 2). These differences were more pronounced in solitary bears than in females with cubs (Table 2), apart from the autumn season 2017, where there were only minor differences for both social units. It also has to be considered that the different months and years had different camera trap working days (CTD, pooled for all cameras). In April 2016 cameras were working for 363 days where there was a visit ratio (bear pictures per day) of 0.99, in May 2016 the cameras worked for 453 days with 1.90 bear pictures per day, in September 2016 for 377 days with the visit ratio of 1.84, in October 2016 for 385 days with 0.82 bear pictures per day, in April 2017 for 309 days with a visit ratio of 1.12, in May 2017 for 338 days with 2.09 bear pictures per day, in September 2017 for 431 days with a visit ratio of 1.81 and in October 2017 the cameras were working for 394 days with 1.62 bear pictures per day.

Table 2: Absolute number of bear pictures during hunting months (April & October) and non-hunting months (May & September) in the years 2016 and 2017.

Year	Other/solitary bears				Females with cubs			
	April	May	September	October	April	May	September	October
2016	318	837	648	283	42	24	45	34
2017	311	685	641	503	34	20	141	137

3.1 Females with cubs

In spring 2016, the only informative variable in the most parsimonious model for feeding site presence of females with cubs was the day in the year (Table 3). Thus, the differences within the days were larger than the differences between the two months April and May. This means that females with cubs used the feeding sites the same way independent of the hunting season, although the number of bear pictures was higher in April (42 pictures during the hunting season) than in May (24 pictures outside of the hunting season) (Table 2). In spring 2017, feeding site use of females with cubs was lower in May than in April (Table 3). As in 2016, there was a decline in the bear pictures from hunting to non-hunting season, with the numbers decreasing from 34 in April 2017 to 20 in May 2017. In autumn 2016, the interaction between month and day was informative, which shows that the slopes of the

visitation rates were different within these two months. In particular, daily bear presence decreased in September 2016, while the slope for bear presence increased in October 2016 (Figure 2). This shows that females with cubs used feeding sites more along the consecutive days in the month October, i.e. in the regular hunting season. The number of bear pictures decreased from 45 in September 2016 to 35 in October 2016 (Table 2). In autumn 2017, there was also an interaction between month and day for predicting feeding site use of females with cubs. In September 2017, feeding sites were equally used during the consecutive days, whereas in October 2017, the slope of feeding site use was increasing. There was only a minor difference in the number of bear pictures between the two months, with 141 pictures in September 2017 and 137 pictures in October 2017.

Table 3: Informative predictors in the GLM models for females with cubs for spring and autumn periods in the years 2016 and 2017. β = beta coefficient, σ = standard error, LL & UL = lower and upper limit of the 95% confidence interval

Response/predictors	**β**	**δ**	**LL**	**UL**
Females with cubs in spring 2016				
day*	-0.033	0.007	-0.048	-0.019
Females with cubs in spring 2017				
month5*	-0.685	0.282	-1.254	-0.142
Females with cubs in autumn 2016				
month10:day*	0.116	0.029	0.061	0.173
Females with cubs in autumn 2017				
month10:day*	0.044	0.014	0.018	0.072

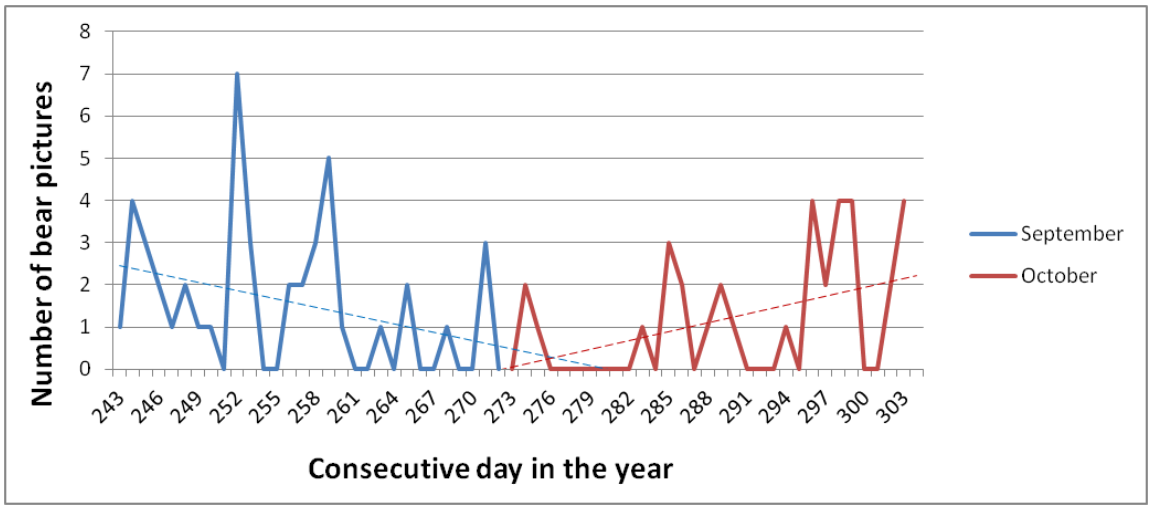


Figure 2: Feeding site use (= number of bear pictures) for females with cubs during the consecutive days in the year in September 2016 and October 2016. The trend line for each month represents the informative interaction between month and consecutive day in the GLM model.

3.2 Other bears/solitary bears

In spring 2016, the most parsimonious model included the informative variable month, with a higher presence of solitary bears in May 2016. The overall numbers of bear pictures raised from 318 in April 2016 to 837 in May 2016 (Table 2, Figure 3). In spring 2017, the interaction between month and day was informative. In April 2017, there was an increase of the use of feeding sites within the consecutive days especially at the end of the hunting season and a decrease of the use within the consecutive days in May 2017. However, the total number of bear pictures raised from 311 in April 2017 to 685 in May 2017 (Table 2). In autumn 2016, both, the month and the day were informative variables (Table 4), but not their interaction. In particular, in October 2016 feeding sites were less used than in September 2016. The total number of bear pictures decreased from 648 in September 2016 to 283 in October 2016 (Table 2). In addition, the consecutive day in the year was an informative variable, which suggests that daily feeding site use was fluctuating during both months. In autumn 2017, the interaction between month and the consecutive day in the year was also informative, which shows that the slopes for feeding site use were different in the two months. In September 2017, the slope was increasing with the consecutive days, and in October 2017, the slope was decreasing. The total number of bear pictures decreased from 641 in September 2017 to 503 in October 2017.

Table 4: Informative predictors in the GLM models for solitary bears for spring and autumn periods in the years 2016 and 2017. β = beta coefficient, σ = standard error, LL & UL = lower and upper limit of the 95% confidence interval

Response/predictors	**β**	**δ**	**LL**	**UL**
Other bears in spring 2016				
month5*	0.565	0.066	0.437	0.695
Other bears in spring 2017				
month5:day*	-0.075	0.008	-0.092	-0.059
Other bears in autumn 2016				
month10*	-0.648	0.137	-0.918	-0.379
day*	-0.008	0.004	-0.016	-0.001
Other bears autumn 2017				
month10:day*	-0.020	0.007	-0.034	-0.007

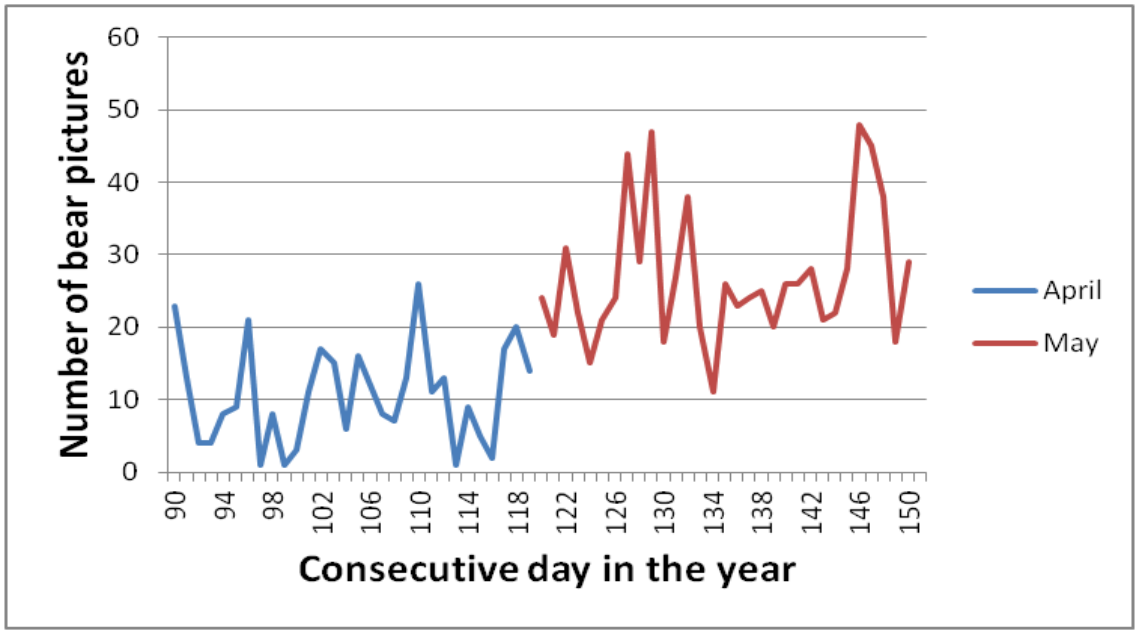


Figure 3: Number of bear pictures for solitary bears during the consecutive days in the year in April 2016 and May 2016.

3.3 Proportions of pictures of females with cubs to all bear pictures

In general the proportions of females with cubs were always higher in the hunting season compared to the non-hunting season (Table 5). In all models, the interaction between month and the consecutive day in a year was informative (Table 6)

In spring 2016, the daily proportions of females with cubs using the feeding site was rather equally distributed along the consecutive days in April, whereas the slope for the proportion of females with cubs decreased in May (Figure 4). Interestingly, the mean proportions of females with cubs dropped from 0,126 in April 2016 to 0,031 in May 2016 (Table 5). In April 2017, the slope for the proportions of females with cubs present was decreasing along the consecutive days, whereas in May 2017 the proportion of females with cubs was equally distributed along all days. From April to May 2017, mean proportions of females with cubs dropped from 0,116 in April 2017 to 0,028 in May 2017. While in September 2016 the slope for the proportion of females was decreasing along the consecutive days, it increased in October 2016. Also, the mean monthly proportion increased from 0,078 in September 2016 to 0,123 in October 2016. For autumn 2017, the slope for the proportion of females was decreasing in September and increasing in October. Surprisingly, the difference in the mean

proportions of females with cubs was not very pronounced; it raised from 0,179 in September 2017 to 0,210 in October 2017.

Table 5: Mean monthly proportions of females with cubs to all bears in the different seasons and years.

	Month	2016	2017
Spring	4	0.126	0.116
	5	0.031	0.028
Autumn	9	0.078	0.179
	10	0.123	0.210

Table 6: Informative predictors in the GLM models for the daily proportions of females with cubs to all bears for spring and autumn periods in the years 2016 and 2017. β = beta coefficient, σ = standard error, LL & UL = lower and upper limit of the 95% confidence interval

Response/predictors	**β**	**δ**	**LL**	**UL**
Proportions spring 2016				
month5:day*	-0.071	0.032	-0.136	-0.010
Proportions spring 2017				
month5:day*	0.075	0.033	0.010	0.141
Proportions autumn 2016				
month10:day*	0.109	0.031	0.050	0.171
Proportions autumn 2017				
month10:day*	0.064	0.015	0.034	0.094

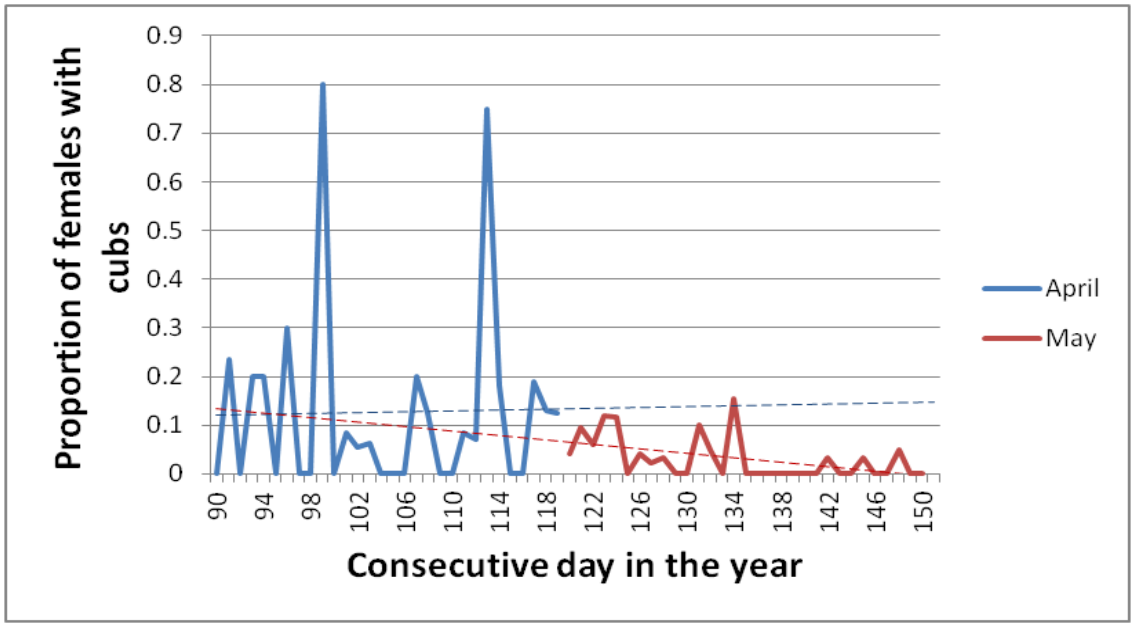


Figure 4: Proportion of females with cubs to all bears during the consecutive days in the year in April 2016 and May 2016. The trend lines depict the informative interaction.

3.4 Visitation times

3.4.1 Solitary bears

In spring, the daily visitation time peaked between 10 and 11 pm (Figure 5). In general, bears used the feeding sites mostly during night time. In addition, a smaller peak occurred also in 2016 between 4 and 5 pm. There was no obvious change in visitation time during the hunting season, only the total number of bear pictures differed between the years. Similarly, the visitation time peaked in autumn between 9 and 10 pm, with the exception of October 2017, were the most bear pictures were taken between 8 and 9 pm (Figure 6). In line with the results for spring, bears used the feeding sites mostly during night time.

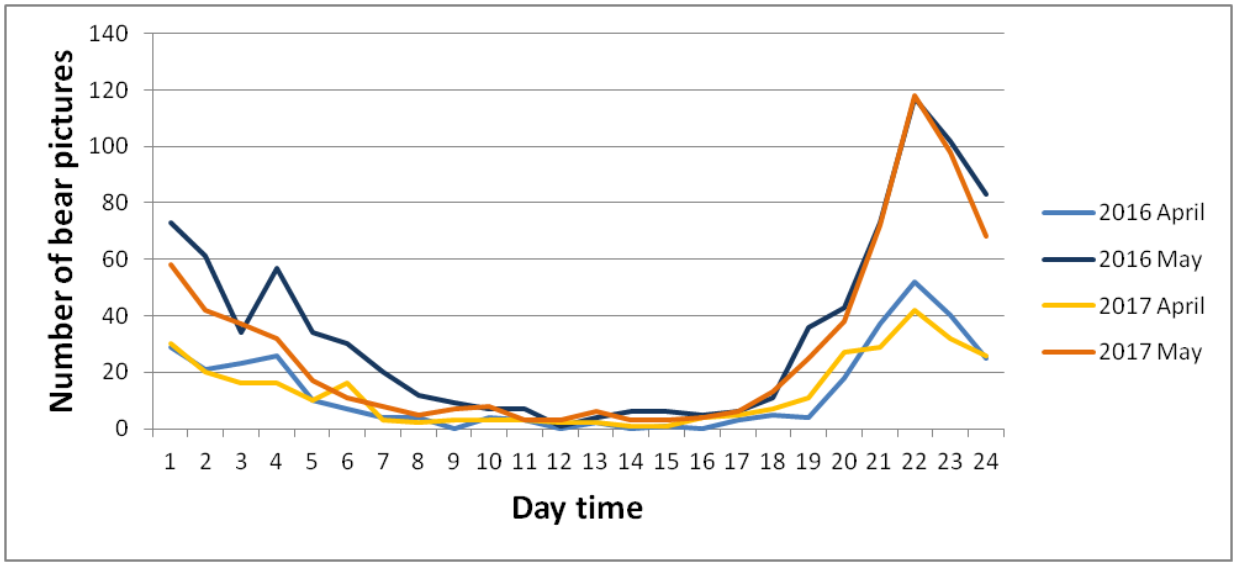


Figure 5: Daily visitation time of the solitary bears in spring. The different colours represent the different months and years.

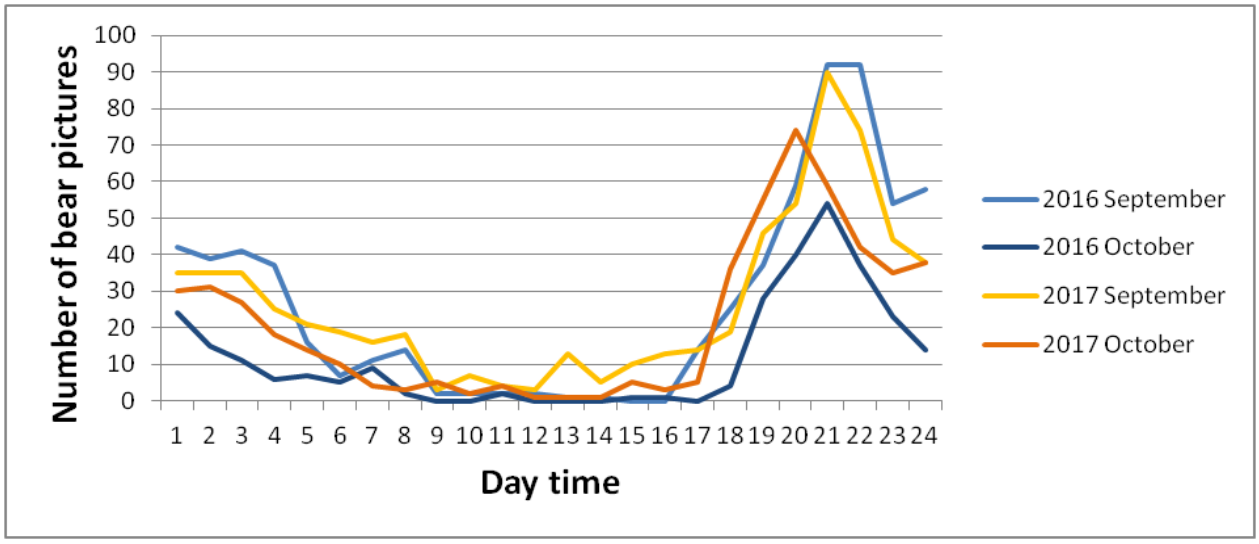


Figure 6: Daily visitation time of solitary bears in autumn. The different colours represent the different months and years.

3.4.2 Females with cubs

Due to the relatively small sample size of females with cubs in spring, visitation times during the day in spring were very scattered with no obvious peaks. As no inference can be drawn from these data, I do not include an illustration here. On the other hand, data from the autumn months showed different peaks; In September 2016, most of the pictures were taken between 9 and 10 pm. When compared to solitary bears, the number of pictures of females with cubs already started to increase during the late afternoon (Figure 8). In October 2016, the peak visitation time was between 7 and 8 pm. In September 2017, most pictures of females with cubs were taken between 7 and 8 pm, whereas in October 2017 the first peak was between 6 and 7 pm and a second peak occurred between 8 and 9 pm (Figure 7).

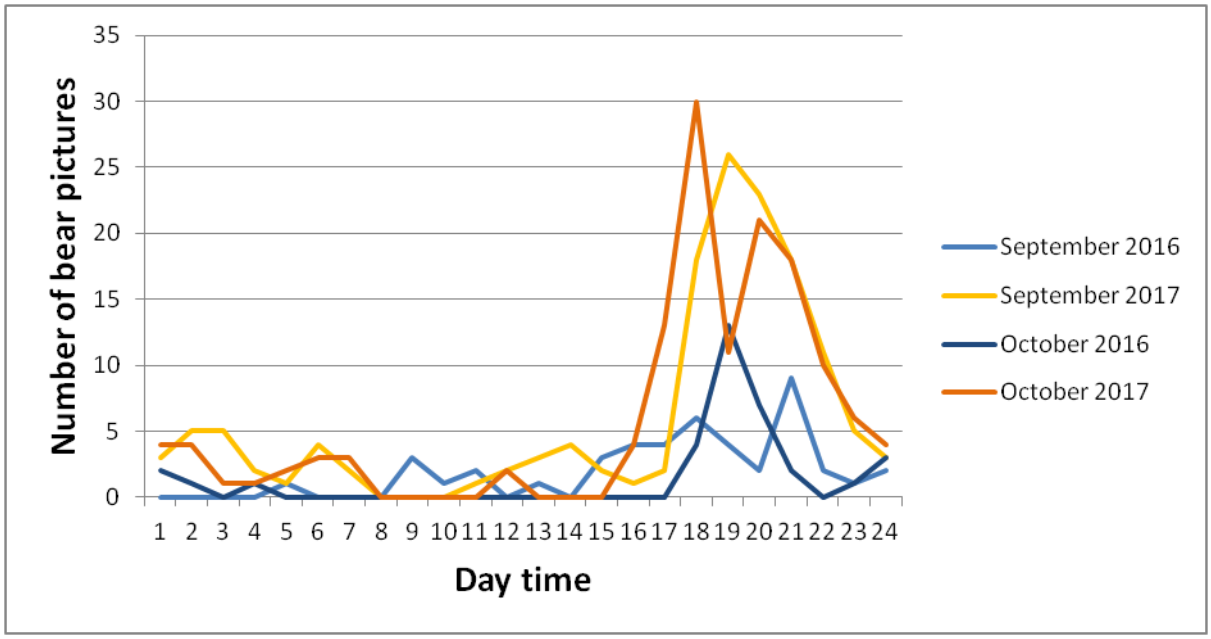


Figure 7: Daily visitation time of females with cubs in autumn. The different colours represent the different months and years.

4 Discussion

Feeding site use of bears differed during and outside of the hunting season. Solitary bears, in particular, used feeding sites less during the hunting season than in non-hunting periods. In females with cubs, differences in feeding site use during and outside of the hunting season were less pronounced, especially during autumn. In spring, there was a slight difference in the feeding site use of females with cubs, with a higher presence of female with cubs during the hunting season. The proportions of females with cubs to all bears were always higher in the regular hunting season compared to non-hunting periods. While this was particular pronounced in spring, the differences in autumn were smaller. The daily visitation peaks for solitary bears in spring were between 10 and 11 pm and in autumn between 9 and 10 pm, with an exception of October 2017 were it was between 8 and 9 pm. The daily visitation peaks of females with cubs showed greater variation, but with an overall trend to come during sunset in the evening. In comparison, females with cubs came earlier than solitary bears.

4.1 Spring hunting

The feeding site use of females with cubs differed in the spring months. Feeding site use of females with cubs was higher during the hunting season and was going down after the end of the hunting season. This may be a response to hunting, since females with cubs face no danger of getting shot during the hunting season. This is interesting because generally, the number of bear pictures at feeding sites was increasing within these two spring months, this was not the case for females with cubs. On the contrary, solitary bears used the feeding sites in spring much less during the hunting season than in non-hunting season. Clevenger et al. (1990) showed that bear activity is quite high in the post-denning period, when compared to other periods. This would suggest that both females with cubs as well as the solitary bears should visit the feeding sites more often during spring. Thus, the observed lower presence of solitary bears at feeding sites during the hunting season may indeed result from hunting pressure. Another explanation for the differences between the two social units could also be that females with cubs are avoiding the feeding sites in May because the numbers of solitary bears are raising in this month. Infanticide male brown bears pose a great threat to cubs (Ben-David et al. 2004), therefore, females with cubs may avoid places with high food availability which also attract male bears. A further explanation for the lower numbers of

females with cubs in May could be that the mating season also starts in May and the males more likely commit infanticide (Bellemain 2008) also due to a higher movement of males in the mating season (Jerina et al. 2013). Furthermore the cubs are still very vulnerable at this time of the year (Sellers & Aumiller 1994). When looking at the proportions of females with cubs to all other bears during the two spring months, there is a big difference between the hunting and the non-hunting season in both years. The proportions of females with cubs was always higher during the spring hunting season, which may also suggest a response to hunting. In this way, the proportions-model underlines the differences which were also found in the separate models for solitary bears and females with cubs.

4.2 Autumn hunting

Generally, the differences in feeding site use before and during the autumn hunting period were less pronounced than in spring. For females with cubs, in both years the slopes for the interaction between month and consecutive day in the year were increasing during the hunting season. For solitary bears, in autumn 2016 there was a pronounced difference with a lower bear presence at feeding sites during hunting, which may represent a response to hunting. In autumn 2017, however, the differences were less obvious, even though there was a decreasing slope for the feeding site use of solitary bears. The smaller differences in feeding site use of solitary bears before and during the hunting season in autumn 2017 may be connected to the bad food availability in this year, which means that the bears likely used the feeding sites also during the hunting season to gain weight to survive the denning phase. Moreover, the large difference in feeding site use of solitary bears in autumn 2016 may also be attributed to the availability of food, since bear activity and movement have been shown to be linked to the availability of food (Jonkel 1971, Amstrup & Beecham 1976). In the year 2016, there was a big beech mast in Slovenia, which means that the bears could feed anywhere in the forest and build up their fat reserves without facing the risk to get shot at feeding sites. Only in autumn 2016, the number of pictures of females with cubs declined marginally during the hunting season, however, the difference was not informative. Similarly to the other models, the models using proportions of females showed differences in feeding site use, although these differences were again less pronounced than during spring (in particular during autumn 2017). Again, this may be also be explained with the poor availability of natural food. Furthermore, the hunting season did not actually start in October that year (as well as in 2016), which could mean less disturbance by hunters, which may in

turn be perceived by bears and result in a rather normal feeding site use and more activity (Clevenger et al. 1990) even during the hunting season.

4.3 Circadian feeding site use

A study by Ordiz et al. (2012) showed that brown bears in Sweden showed differences in their activity patterns during the day because of hunting. After the onset of the hunting season, bears shifted their activity more into the night hours, while this effect was particularly obvious in males and other solitary bears (Ordiz et al. 2012). In this study, bears showed no such shift in feeding site use. Generally, feeding sites were mainly used during the night, both during and outside of the hunting season. However, solitary bears came 1 hour earlier to the feeding sites in October 2017, which could be explained by the differences in sunset between the two months, which was approximately one hour. Interestingly, this shift did not occur in 2016. In females with cubs, there was a two hour difference in the peak feeding site use only in 2016. However, for this year the sample size was rather small, which could in turn result in a higher influence of individual behaviour of bears than general patterns. It is suggested that the nocturnality originates from the long history of bear hunting and the resulting fear of humans (Kaczensky et al. 2006). In general, females with cubs came earlier than solitary bears, which may also be explained by avoidance effects. This means that due to the increased risk of infanticide (Ben-David et al. 2004), females with cubs may avoid time periods during which higher numbers of solitary bears are present.

4.4 Conclusion and outlook

My hypothesis that "Females with cubs show less changes in their feeding site use" can be partly confirmed, because I found differences in feeding site use between the hunting and non-hunting seasons, but they were not as obvious as in solitary bears. The second hypothesis that" Solitary bears react to the hunting season and change their feeding site use " can be confirmed. My last hypothesis that bears, in particular solitary individuals, become more nocturnal during the hunting season has to be rejected. However, I cannot exclude other factors which may have influenced feeding site use of the different social units. In my study, there were large differences in food availability between the years. In addition, due to a delay in issuing the permits, the hunting season did not start before spring during both

years. For future studies, I suggest to include more years of research to reduce the influence of year-effects on the results and get a more complete picture. Furthermore, the availability of food and other environmental factors of the specific years should be included in the analysis. Ideally, my findings should be compared to data from an area were bears are also fed artificially but not hunted. In this way, it would be possible to determine the extent to which other factors influence my observations on feeding site use, for example infanticide.

5 References

Amstrup S. C., & Beecham J. (1976). Activity patterns of radio-collared black bears in Idaho. The Journal of Wildlife Management, 340-348.

Anderson D. R. (2007). Model based inference in the life sciences: a primer on evidence. Springer Science & Business Media.

Arnold T. W. (2010). Uninformative parameters and model selection using Akaike's Information Criterion. The Journal of Wildlife Management, 74(6), 1175-1178.

Barboza P. S., Farley S. D. and Robbins C. T. (1997). Whole-body urea cycling and protein turnover during hyperphagia and dormancy in growing bears (Ursus americanus and U. arctos). Canadian Journal of Zoology 75:2129–2136.

Bellemain E., Swenson J. E., Taberlet, P. (2006). Mating strategies in relation to sexually selected infanticide in a non-social carnivore: the brown bear. Ethology, 112(3), 238-246.

Ben-David M., Titus K., Beier L. R. (2004). Consumption of salmon by Alaskan brown bears: a trade-off between nutritional requirements and the risk of infanticide?, Oecologia, 138(3), 465-474.

Benhaiem S., Delon M., Lourtet B., Cargnelutti B., Aulagnier S., Hewison A. M., Morellet N., Verheyden, H. (2008). Hunting increases vigilance levels in roe deer and modifies feeding site selection. Animal Behaviour, 76(3), 611-618.

Brown JS., Laundr´e JW, Gurung M. (1999). The ecology of fear: optimal foraging, game theory, and trophic interactions. J. Mammal. 80:385–99

Brown G.(2013), The Bear Almanac, 2nd: A Comprehensive Guide to the Bears of the World, Lyons Press, 352 Pages

Burnham K. P., Anderson D. R., Huyvaert K. P. (2010). AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. Behavioral Ecology and Sociobiology, 65, 23–35.

Ciuti S., Northrup J. M., Muhly T. B., Simi S., Musiani M., Pitt J. A., Boyce M. S. (2012). Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. PloS one, 7(11), e50611.

Clevenger A. P., Purroy F. J., Pelton, M. R. (1990). Movement and activity patterns of a European brown bear in the Cantabrian Mountains, Spain. Bears: Their Biology and Management, 205-211.

Dick G. (2006). Slovenian hunting quota for Brown bear (Ursus arctos) exceeds sustainable levels, threatening the wider bear population of the region. WWF Position Paper: 1-6. For the 26th meeting of the Standing Commitee, Convention on the Conservation of European Wildlife and Natural Habitats, Strasbourg, 27-30

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

Gray R.M., Vaughhan M.R., McMullin S.L. (2004): Feeding wild American black bears in Virginia: a survey of Virginia bear hunters, 1998-99. - Ursus 152: 188–196.

Jerina K., Adamic M. (2008). Fifty years of brown bear population expansion: effects of sex-biased dispersal on rate of expansion and population structure. J. Mammal., 89, 1491–1501.

Jerina K, Krofel M, Stergar M, Videmšek U (2012). Factors affecting brown bear habituation to humans: a GPS telemetry study. Final report—summary for users. University of Ljubljana, Biotechnical Faculty, Ljubljana

Jerina K., Jonozovič M., Krofel M., Skrbinšek T. (2013). Range and local population densities of brown bear Ursusarctos in Slovenia. European Journal of Wildlife Research. 59, 459–467.

Jerina K., Polaina E., Huber Đ., Reljić S., Bartol M., Skrbinšek T. Jonozovič M. (2018) Reconstruction of brown bear population dynamics in Slovenia and Croatia for the period 1998-2018, prepared within C5 action of LIFE DINALP BEAR Project (LIFE13 NAT/SI/0005): 46 pp.

Jonkel C. J. (1971). The black bear in the spruce-fir forest. Wildlife monographs, (27), 3-57.

Jonozovič M. (2003). Strokovna izhodisca za vzpostavl- janje omrezij Natura 2000 Agencija RS za okolje, Ljubljana, Slovenia, (in Slovenian)

Kaczensky P., Blazic M., Gossow H. (2004). Public attitudes towards brown bears (Ursus arctos) in Slovenia**.** Biological Conservation, 118, 661–674.

Kaczensky P., Huber D., Knauer F., Roth H., Wagner A., Kusak J. (2006) Activity patterns of brown bears (Ursus arctos) in Slovenia and Croatia. J Zool 269:474–485

Kavčič I., Adamič M., Krofel M., Jerina K., Kaczensky P. (2011) Brown bear food habits in human dominated landscapes of Slovenia: importance of intensive long-term supplemental feeding. 20th International conference on bear research and management, Ottawa, pp 162-163.

Kavčič I., Adamič M., Kaczensky P., Krofel M., Jerina, K. (2013). Supplemental feeding with carrion is not reducing brown bear depredations on sheep in Slovenia. Ursus, 24(2), 111-119.

Klenzendorf S. (1997). Management of brown bears (Ursus arctos) in Europe. Thesis, Virginia Polytechnic University, Blacksburg, Virginia, USA.

Klopcic M, Jerina K, Boncina A (2010) Long-term changes of structure and tree species composition in Dinaric uneven-aged forests: are red deer an important factor? European Journal of Forest Research, doi: 10.1007/s10342-009-0325-z

Krofel M., Jonozovič M., Jerina K. (2012). Demography and mortality patterns of removed brown bears in a heavily exploited population. Ursus 23:91–103.

Krže B. (1988). Rjavi medved Ursus arctos Linnaeus, 1758. Pages 23-62 in B. Krystufek, A. Brancelj, B. Krze, and J. Cop, editors. Zveri II. Lovska Zveza Slovenije, Ljubljana, Slovenia, (in Slovenian)

Laundre J.W., Hernandez L., Altendrof K.B. (2001). Wolves, elk, and bison: reestablishing the landscape of fear in Yellowstone National Park, USA. Canadian journal of zoology., 79, 1401–1409.

Little A. R., Webb S. L., Demarais S., Gee K. L., Riffell S. K., Gaskamp J. A. (2016). Hunting intensity alters movement behaviour of white-tailed deer. *Basic and applied ecology*, *17*(4), 360-369.

Lone K., Loe L. E., Gobakken T., Linnell J. D., Odden J., Remmen J., Mysterud, A. (2014). Living and dying in a multi-predator landscape of fear: roe deer are squeezed by contrasting pattern of predation risk imposed by lynx and humans. Oikos, 123(6), 641-651.

Marantz S. A., Long J. A., Webb S. L., Gee K. L., Little A. R., Demarais S. (2016). Impacts of human hunting on spatial behavior of white-tailed deer (Odocoileus virginianus). Canadian journal of zoology, 94(12), 853-861.

Martin J., Basille M., Van Moorter B., Kindberg J., Allaine D., & Swenson J. E. (2010). Coping with human disturbance: spatial and temporal tactics of the brown bear (Ursus arctos). Canadian Journal of Zoology, 88(9), 875-883.

Ministry of the Environment and Spatial Planning (MOP) (2007). The brown bear conservation and management in Slovenia. Ljubljana

Nelson R.A., Folk G.E., Jr., Pfeiffer E.W., Craighead J.J., Jonkel C.J., Steiger D.L. (1983). Behavior, biochemistry, and hibernation in black, grizzly, and polar bears. International Conference on Bear Research and Management 5:284–290.

Ordiz A. , Støen O.G., Sæbo S., Kindberg J., Swenson J.E. (2012). Do bears know they are being hunted? Biological Conservation, 152 (2012), pp. 21-28

Proffitt K. M., Grigg J. L., Hamlin K. L., Garrott R. A. (2009). Contrasting effects of wolves and human hunters on elk behavioral responses to predation risk. The Journal of Wildlife Management, 73(3), 345-356.

Sellers R. A., Aumiller L. D. (1994). Brown bear population characteristics at McNeil River, Alaska. Bears: Their Biology and Management, 283-293.

Simonič A., (1992). The legal protection of the brown bear in Slovenian territory—past and present, and some suggestions for the future. In: Zbornik posvetovanja o rjavem medvedu v deželah Alpe-Adria. Univerza v Ljubljani, Biotehniška fakulteta, Oddelek za gozdarstvo, Ljubljana, Slovenia, pp. 43–76.

Skuban M. (2011). Dem Braunbär auf der Spur ...: Lebensweise, Geschichte, Mythen; Stocker Verlag, Graz

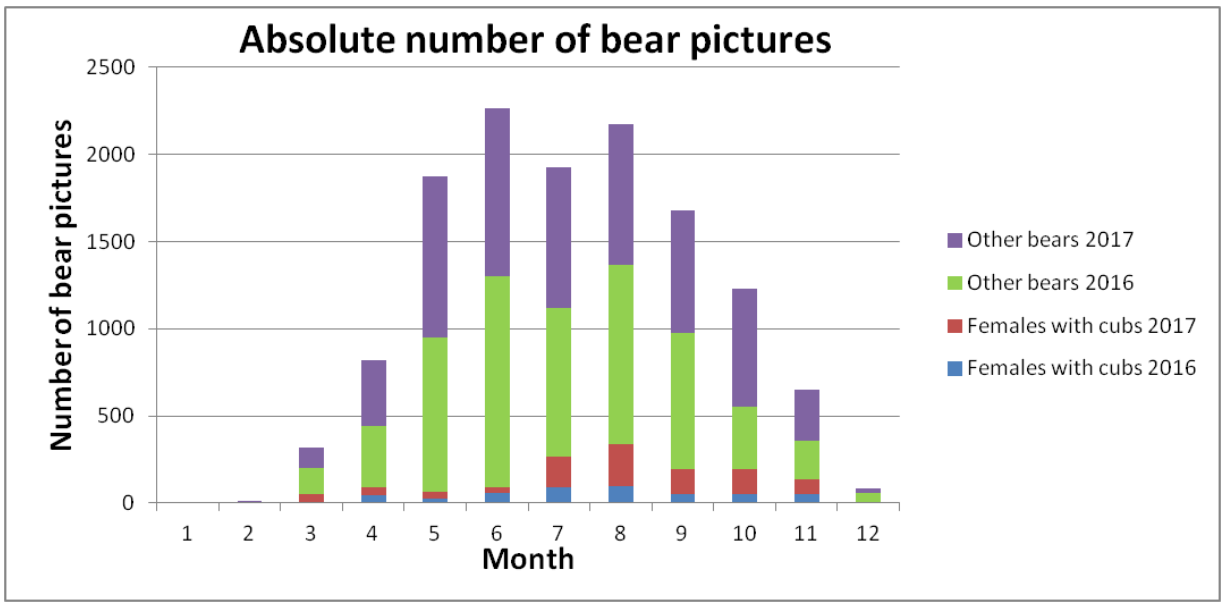
Swenson J.E., Adamic M., Huber D., Stokke S., 2007. Brown bear body mass and growth in northern and southern Europe. Oecologia 153, 37–47.

Van de Walle J., Pigeon G., Zedrosser A., Swenson J. E., Pelletier F. (2018). Hunting regulation favors slow life histories in a large carnivore. Nature communications, 9(1), 1100.

Wagenmakers E.-J., Farrell S. (2004). AIC model selection using Akaike masss. Psychonomic Bulletin & Review, 11, 192–196.

Woodroffe R., Ginsberg J. R. (1998). Edge effects and the extinction of populations inside protected areas. Science, 280(5372), 2126-2128.

6 Appendix



Appendix 1: Total number of bear pictures at feeding sites in the years 2016 and 2017. Colours correspond to different years and different social units (females with cubs and other bears/solitary bears).