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Source: Wildlife Biology, 21(1):1-8.
Published By: Nordic Board for Wildlife Research
DOI: http://dx.doi.org/10.2981/wlb.00013
URL: http://www.bioone.org/doi/full/10.2981/wlb.00013

Wildlife Biology 21: 1–8, 2015
doi: 10.2981/wlb.00013

Subject Editor: Andreas Zedrosser. Accepted 23 August 2014

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Distribution, quantity and quality of food resources affect the diet and several other life-history traits of large mammals. Supplemental feeding of wildlife has high potential for influencing the behaviour and diet of opportunistic omnivores, such as bears. Supplemental feeding of brown bears *Ursus arctos* is a common practice in several European countries, but the effects of this controversial and expensive management measure on bear diet and behaviour are poorly understood. We analysed 714 brown bear scats collected throughout the year in three regions of Slovenia with different densities of supplemental feeding sites. Supplemental food was the most important food category in the bear diet and represented 34% of the annual estimated dietary energy content (maize: 22%, livestock carrion: 12%). The proportion of supplemental food in the diet varied with season and region, being highest in spring and in the region with the highest density of feeding sites. However, considerable seasonal changes in bear diet, despite year-round access to supplemental food, suggest that bears prefer high-energy natural food sources, particularly insects, fruits, and hard mast, when available. Despite high availability and use of supplemental food, human–bear conflicts are frequent in Slovenia. In addition, evidence from earlier studies suggests that changes in diet and foraging behaviour due to supplemental feeding may affect several aspects of bear biology and in some cases increase the probability of human–bear conflicts. Thus, we caution against promoting unconditional supplemental feeding as a measure to prevent or reduce human–bear conflicts.

Anthropogenic foods are used by omnivorous mammals throughout the world and have high potential for affecting the ecology of wildlife (Fedriani et al. 2001). Such food sources have been documented to affect wildlife behaviour (e.g. movement patterns, reproductive strategies), demography (e.g. population growth) and life history (e.g. reproduction), as well as to alter community structure (e.g. species diversity) (Boutin 1990, Putman and Staines 2004, Robb et al. 2008). Anthropogenic foods used by wildlife are often obtained through supplemental feeding, which was defined as the act of intentionally placing any food for use by wildlife on an annual, seasonal, or emergency basis (see Inslerman et al 2006 for full definition). Here we consider supplemental feeding to include also baiting (i.e. feeding for the purpose of attracting or/and capturing wildlife), since in many areas (especially in Europe) feeding is often used simultaneously for several purposes (Kavčič et al. 2013, Selva et al. 2014). Supplemental feeding is commonly used in wildlife management and conservation. However, increased availability of anthropogenic food sources may have several undesired side effects on wildlife and habitats (Boutin 1990, Robb et al. 2008, Penteriani et al. 2010, Jerina 2012, Sorensen et al. 2014).

Brown bears *Ursus arctos* are typical opportunistic omnivores that feed on a variety of food sources, including anthropogenic foods (Bojarska and Selva 2012). The distribution, availability and quality of food resources are known to influence bear reproductive success (Rogers 1976, Blanchard 1987, Beckmann and Berger 2003) and several other life history traits (Hilderbrand et al. 1999, McLellan 2011), denning chronology (Beckmann and Berger 2003), as well as bear population density (Hilderbrand et al. 1999, Rode et al. 2001) and human–bear conflicts (Mattson et al. 1992). Knowledge of bear feeding behaviour and the effects of different food sources is therefore necessary for a solid understanding of their ecology and for effective management.

Bears are capable of shifting feeding behaviour and taking advantage of a variety of available food sources (Bojarska and Selva 2012). Because of the high local variation in bear diet, it is difficult to generalize about dietary patterns of bears across regions. Although the diet of brown bears has been extensively studied, most studies have been carried out in the northern part of the species' range and in areas with low human impact (reviewed by Bojarska and Selva 2012).

One of the potentially important anthropogenic effects on bear diet is supplemental feeding. This controversial management measure is currently practised in several countries throughout Europe, including Bosnia and Herzegovina, Croatia, Finland, Romania, Serbia, Slovakia and Slovenia (reviewed by Kavčič et al. 2013). Supplemental feeding of bears is used for various purposes, including hunting and eco-tourism (i.e. as baiting), but probably the most controversial use is for the prevention of human–bear conflicts. By providing food in remote areas, managers aim to divert bears away from settlements and reduce damage to human property such as livestock (Landers et al. 1979, Kaczensky 1999, Huber et al. 2008, Krofel and Jerina 2012). Experts have contrasting views on the effectiveness of supplemental feeding for conflict mitigation; some report it can reduce damages and conflicts (Partridge et al. 2001, Mason and Bodenchuk 2002, Ziegltrum 2008), while others believe that supplemental feeding creates problem bears, increases the level of conflicts (Herrero 1985, Gray et al. 2004), and is ineffective in the long term to reduce bear–human conflicts (Fersterer et al. 2001, Kavčič et al. 2013).

Supplemental feeding is an expensive measure, and there is growing concern among experts worldwide about the potential negative side effects on bears and other wildlife. These include habituation to people and conditioning to anthropogenic food, which have been shown to increase the probability of human–bear conflicts, including bear attacks on people (Herrero 1985, Gunther and Hoekstra 1998, Gray et al. 2004). The constant availability of anthropogenic food at feeding sites could shorten the hibernation period (Špacapan 2012), disrupt movement patterns (Penteriani et al. 2010), and change reproductive behaviour (Craighead et al. 1995, Steyaert et al. 2012) and reproductive success (Gray et al. 2004), as well as increase population density above the local carrying capacity (Gray et al. 2004, Jerina et al. 2013). When feeding sites are used for baiting, hunting at these sites can alter sex ratio (Bischof et al. 2008). Concern has also been expressed about the possible exposure to bio-accumulative contaminants in supplemental food (Penteriani et al. 2010) and that concentrating wildlife at feeding sites could increase transmission of diseases and parasites (Sorensen et al. 2014, Putman and Staines 2004), increase aggressive intra- and inter-specific encounters and affect scavenger communities (Penteriani et al. 2010, Selva et al. 2014).

Surprisingly, however, the impacts of supplemental feeding on ursid ecology, including its effects on bear diet, have been poorly studied. To our knowledge, only three studies have been published in the scientific literature that mention the nutritional importance of maize *Zea mais* as a supplemental feed for bears (Landers et al. 1979, Rigg and Gorman 2005, Vulla et al. 2009), and none have examined the use of livestock carrion, although supplemental feeding with carrion is still practised in many countries, especially in southern Europe (reviewed by Kavčič et al. 2013).

To improve our understanding of the effects of supplemental feeding and use of food resources in human-dominated landscapes, we studied the diet of brown bears in Slovenia. Here bears live mainly in areas with high human density and high availability of anthropogenic food sources (Jerina et al. 2012, 2013). Moreover, bears have been intensively supplied with maize and carrion year-round at several hundred feeding sites, in some areas for over 100 years (Simonič 1994). Supplemental feeding is officially used as a conflict mitigation measure that aims to divert bears away from human settlements (i.e. diversionary feeding) and reduce livestock depredation, but feeding sites are also used for bear hunting, eco-tourism and monitoring the bear population (e.g. trends in population size and fecundity; Krofel et al. 2012a, Kavčič et al. 2013).

We used scat analysis to determine the frequency of two kinds of supplemental food (maize, livestock carrion) in the bear diet and their energetic contribution compared to natural food sources. Due to intensive supplemental feeding and the long history of this practice, we expected that anthropogenic food would represent a major component of the bear diet in the region. To gain a better understanding of bear preferences for supplemental food versus natural food and possibilities for altering anthropogenic food intake by adjusting management practices, we also studied the effects of supplemental feeding intensity on bear diet patterns. We tested the predictions that the use of anthropogenic food would be 1) lower in seasons with higher natural forage availability and 2) higher in areas with a higher density of feeding sites.

Material and methods

Study area

The study was carried out between 1993 and 1998 in three regions with different intensities of supplemental feeding: Snežnik (southwestern Slovenia, 352 km^2), Menišija (central Slovenia, 177 km^2) and Kočevsko (southeastern Slovenia, 685 km^2). Together these study areas cover 40% of the core brown bear area in Slovenia (45°30′–46°15′N, 13°30′–15°15′E; Fig. 1). Brown bear densities in all three regions were high, ranging from 7 to 20 bears 100 km^{-2}, and locally over 40 bears 100 km^{-2} (Jerina et al. 2013). Human density ranged from 28 to 42 inhabitants km^{-2} (Perko and Orožen Adamič 1998). All three regions had similar habitat characteristics. Forests were dominated by silver fir *Abies alba* and common beech *Fagus sylvatica* associations and intermixed with agricultural fields and small settlements; the average distance to the nearest house in the study area was ~ 1 km. Annual precipitation is 1500 mm, and average annual temperatures are 7–8°C with monthly temperatures ranging from –3 to 0°C in January and 15 to 20°C in June. Snow cover lasted from 50 days at 500 m and up to several months at higher elevations. The vegetative growth period lasts from late April to late October. The main difference among the three study regions was the intensity of supplemental feeding due to the density of feeding sites, which was higher in Menišija and lower in Snežnik and Kočevsko (34 vs 16 feeding sites 100 km^{-2}; Table 3). Another distinction was the availability of orchards, which was higher in Kočevsko and lower in Menišija and Snežnik.

Supplemental feeding of bears in Slovenia is used simultaneously for several purposes, including as diversionary feeding to divert bears from human settlements and as baiting for hunting, eco-tourism and monitoring purposes. The same feeding sites are also often used simultaneously for several wildlife species (e.g. brown bear, wild boar, red deer). During the study period (1993–1998), the national brown bear management strategy demanded at least one carrion feeding site per every 60 km^2 of bear habitat. In addition, bears had access to maize feeding sites (intended

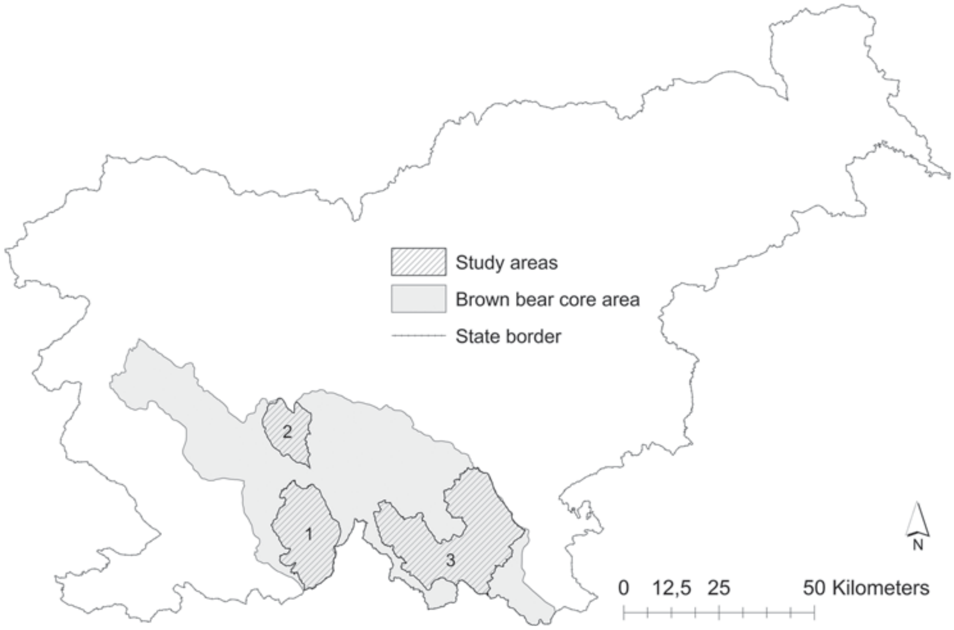

Figure 1. Locations of the three study regions in Slovenia: 1 - Snežnik, 2 - Menišija, 3 - Kočevsko. The shaded area represents the core area of the brown bear population in Slovenia.

for bears and wild ungulates) at average densities of one site per every 5.6 km². The amount of maize provided per year was estimated at 70–280 kg km^{-2} and the amount of livestock carrion at 33–146 kg km^{-2} (Kaczensky 2000, Adamič 2005). Approximately two-thirds of feeding sites were supplied with food throughout the year, including winter. Carrion from wild ungulates was also available in nature from gut piles left at hunter kill sites, from the prey remains of gray wolves *Canis lupus* and Eurasian lynx *Lynx lynx* (Krofel et al. 2012b) and from animals that died due to other causes, cumulatively estimated to amount to another 60–120 kg km^{-2} year^{-1} (data from Stergar et al. 2009). Average red deer *Cervus elaphus* and roe deer *Capreolus capreolus* densities in the study area were 6.7 and 1.7 km^{-2}, respectively (Adamič and Jerina 2010). In 2004, supplemental feeding of bears with livestock carrion was forbidden due to the adoption of EU veterinary legislation (Kavčič et al. 2013). Previous carrion feeding sites have remained active and have been supplied with maize only since the ban. Otherwise, supplemental feeding practices have remained similar. The ban on supplemental feeding with livestock carrion did not affect bear visitation rates to feeding sites (Kavčič et al. 2013).

Scat collection and analysis

In the current study we combined scats collected and analysed in the laboratory within two previous studies, i.e. Adamič (2005) and Grosse et al. (2003). In both studies most of the brown bear scats in all three regions were collected opportunistically by local hunters, students, volunteers and researchers, and stored at –20°C. Only fresh scats (i.e. a few days old) were considered in the analysis. Scats were collected during 1993–1998, from March to November when most bears are active (Jerina et al. 2012). A small number of scats were also gathered in the winter period, but these scats were only analysed for food content and not included into further analyses due to the small sample size. Analysis of scats followed procedures and techniques described by Korschgen (1980). Scats were rinsed under tap water through a set of two sieves (mesh size 4 and 0.8 mm). After 20 min of straining, all food items were sorted and identified to the lowest taxonomic level possible using a stereoscope (7–50×). When more than one food item was present in a scat, the per cent volume of each food item was estimated visually and rounded to predefined 5% intervals. Lab personnel had been previously trained with known volumes of different food items. Mattson et al. (1991) showed that visual estimates of per cent volume correspond well to exact measures.

The remains of mammals in scats were analysed by two different approaches. In the first approach (Adamič 2005) mammal remains were separated into two food categories: livestock carrion (mainly cattle and some horse carcasses) provided at brown bear feeding sites and wild ungulates (mainly cervids) scavenged or killed by bears. Ingested hair was used to distinguish between wild and domestic ungulates. In the second approach, there was no differentiation between livestock and wild ungulate remains in the scats (Grosse et al. 2003). For these samples, we used the season-specific ratios between livestock and wild ungulates from the samples analysed with the first approach (Adamič 2005). Preliminary analysis showed that livestock-wild ungulate ratios are very similar between regions, but change considerably between seasons.

Data analysis

Food items were grouped into the following seven food categories: maize, livestock carrion, wild ungulates, insects, fruits, hard mast and other plant material (e.g. graminoids, forbs). To analyse seasonal differences and to enable comparison with other studies (Mattson et al. 1991, Dahle at al. 1998), the year was divided into three equidistant seasons:

spring (March–May), summer (June–August) and autumn (September–November). Unfortunately, we were not able to include the year the samples were collected in the analysis, as these records were lost when databases were merged several years ago. Although interannual variability in natural food availability can affect the diet of bears, the samples were collected over a relatively long period (six years) and homogenously over time and space (the sample size was comparable between the years in each of the study areas), which likely buffers the effect of interannual variations in the availability of natural food items to a certain degree.

For each season and region we calculated the frequency of occurrence (FO; proportion of samples containing a given food item) and faecal volume (FV; average of percent volumes for a given food item) for each food category in a given season and region. Different foods differ in their digestibility and nutritional composition. Consequently, highly digestible and energy rich food items tend to be underestimated in scat-based diet studies based only on FO or FV. To avoid these biases, we used two groups of correction factors. The first group of correction factors (CF1) was used to estimate originally ingested matter (estimated dietary content; EDC, in per cent) from faecal matter (FV) for each food item (Hewitt and Robbins 1996, Dahle et al. 1998). We used a second group of correction factors (CF2) to translate EDC values into estimated dietary energy content (EDEC, in per cent), which represents the digestible energy of the ingested matter available for the bear (Dahle et al. 1998).

The CF1 used were maize and hard mast 1.18 (Bojarska and Selva 2013), livestock carrion 2.0, wild ungulates 1.5, insects 1.1, fruits 0.93, and other non-animal material 0.24 (Hewitt and Robbins 1996). The CF1 for meat depend on the amount of hair and skin consumed together with the meat and viscera (Hewitt and Robbins 1996). We used a correction factor of 2.0 for livestock carrion from feeding sites, assuming 50% of skin and hair consumed, and a correction factor of 1.5 for wild ungulates scavenged by bears, assuming 67% of skin and hair consumed (Hewitt and Robbins 1996).

The CF2 used were 16.8 kJ g^{-1} for maize and hard mast (Gray 2001), 19.3 kJ g^{-1} for livestock carrion and wild ungulates (Mealey 1980), 17.7 kJ g^{-1} for insects (Swenson et al. 1999), 11.7 kJ g^{-1} for fruits, and 6.3 kJ g^{-1} for other non-animal material (Dahle et al. 1998).

We considered EDEC to be more important for the interpretation of our results than FO, FV, or EDC, because the energy contribution of a food item was assumed to best reflect the real importance of that food item for the bears (Persson et al. 2001).

In general, compositional analysis (Aitchison 1986) can be considered most suitable for analysing proportions of different categories in a sample, as it takes into account that proportions are not independent and it can handle finite value sets. However, our data on food category proportions had a pronounced zero-one inflated bimodal distribution with the first modus at 0% (zeroes represented 58–91% of all values for individual food categories, on average 75% for all food categories) and the second modus at 100% (range 2–17% of all values for individual food categories, average 10%). The distribution of our data was thus close to binary. Therefore, we used logistic regression to explore the effects of season and region on brown bear diet. We used the presence or absence of the main food items in each scat as a dependant variable, and region (Kočevje, Menišija, Snežnik), season (spring, summer, autumn) and the interaction season × region as explanatory variables. Because we focused on the presence or absence of food items, traces would be analysed in the same way as a food constituting a substantial portion of the scat. To avoid this, we only considered food items that occurred at a volume $> 2.5\%$. We built the final model by the backward removal procedure and used Bonferroni correction to adjust for multiple comparisons on partially dependent samples (in compositions the value of each component always depends on the sum of proportion of other components; DF for our six comparisons is 5; Bonferroni corrected entry probability in backward regression was therefore $p = 0.04$) (Rice 1989).

To analyse the effects of supplemental feeding intensity on the use of supplemental food by bears, we used logistic regression. For this we joined data from two regions (Snežnik and Kočevsko) with the same feeding site density (16 per 100 km^2) and used region (Menišija and Snežnik + Kočevsko) as a binary dependent variable, and the proportion of maize (EDEC) in the bear diet, season, and interaction between proportion of maize × season as independent variables. We used weighting to balance the sample sizes between the two regions for each season. We built the final model by the backward removal procedure (entry probability $p = 0.05$). We did not distinguish between feeding sites intended for bears or ungulates, because bears used maize from both types of feeding sites. In this analysis we did not use data on carrion consumption, since it was not originally separated into livestock carrion and wild ungulates for most samples from Menišija.

Average FO, FV, EDC and EDEC values for the whole study area were calculated as arithmetic means of regional FO and FV, weighted by the proportion of bears living in each region (data from Jerina et al. 2013) to account for unequal sampling intensity (collected faeces/bear) between regions. The total amount of carrion in the annual diet for the entire study area was calculated for all faeces using extrapolations and also only from samples in which carrion from livestock and wild ungulates were distinguished in the lab.

The differences in EDEC values between food categories for the whole study area on an annual basis were analysed by the resampling method (bootstrapping). The method and results of the analysis is presented in the Supplementary material Appendix 1 Table A1.

Results

In total, we analysed 714 scats from subsamples of 153–313 scats per season, 220–260 per region, and 42–118 per season × region. We also obtained results from 12 scats from winter. All taxa found in bear scats are listed in Supplementary material Appendix 2 Table A2.

Annually, maize and insects were the most important foods, based on EDEC (Table 1). Graminoids and forbs (i.e. other plant material) were the most frequent food item ingested annually, but due to their low energy content, this category was of minor importance from an energetic perspective (Table 1). Livestock carrion was less important than

Table 1. Diet of brown bears based on the analysis of scats collected in Slovenia, 1993–1998 (n = 714). Average annual percent frequency of occurrence (FO), percent faecal volume (FV), percent estimated dietary content (EDC), and percent estimated dietary energy content (EDEC) values for the entire study area are given. The minimum and maximum annual values of the three regions (Kočevsko, Snežnik and Menišija) are given in parenthesis. Values for each region separately are given in Supplementary material Appendix 3 Table A3.1, A3.2, A3.3, A3.4.

Food item	FO (%)	FV (%)	EDC (%)	EDEC (%)
Maize	31.7 (13–50)	13.9 (5–35)	19.7 (9–48)	21.7 (10–52)
Livestock carrion	9.1 (6–11)	4.0 (3–5)	9.6 (8–10)	12.2 (11–13)
Wild ungulates	7.4 (6–8)	3.2 (2–4)	5.7 (4–7)	7.3 (5–9)
Insects	33.3 (31–42)	13.8 (11–16)	18.2 (14–19)	21.1 (15–22)
Fruits	29.0 (22–31)	18.1 (12–20)	20.3 (13–23)	15.5 (10–19)
Hard mast	15.9 (4–19)	11.6 (2–13)	16.5 (3–21)	18.1 (3–25)
Other plant material	62.9 (58–70)	34.6 (27–48)	10.0 (7–16)	4.1 (3–7)
Other	4.5 (3–13)	0.8 (0–2)	/	/

natural animal foods (wild ungulates and insects) (Table 1). The EDEC value for livestock carrion on an annual basis was 12.2% when using extrapolated values, and 12.3% when based only on samples in which carrion from livestock and wild ungulates was distinguished in the lab.

We noted high variation in the frequency of occurrence of food items between seasons and regions (Supplementary material Appendix 3 Table A3.1), as well as the interaction season × region. Region affected four out of seven food categories with the strongest influence on maize. Season affected all food categories except maize, with the strongest influence on insects (Table 2). The interaction season × region was significant for maize, insects and fruits (Table 2, Supplementary material Appendix 3). In spring, maize and carrion were the most important food items, representing 27% and 26% of the EDEC, respectively. In summer, insects represented more than 50% of the EDEC. In autumn, hard mast and fruits (beechnuts, apples, pears and plums) were the most important foods, representing 32% and 31% of the EDEC, respectively (Fig. 2). Livestock carrion was available to the bears at feeding sites in all seasons, but it was used mainly in spring (3- and 7-times more often compared to autumn and summer, respectively). The most important food category was maize (52% EDEC) in Menišija, insects (22% EDEC) in Kočevsko, and hard mast (25% EDEC) closely followed by insects (22% EDEC) in Snežnik (Supplementary material Appendix 3 Table A3.4).

Supplemental food (maize and livestock carrion) contributed to 18% of FV and 34% of EDEC in the annual diet of bears (Table 1). It was most important during spring, when it represented 53% of the EDEC, and less important in summer and autumn with 26% and 25% EDEC, respectively (Supplementary material Appendix 3 Table A3.4). In the Menišija region, maize also was the most important food in autumn, while in the other two regions, the autumn diet was dominated by fruits and hard mast. The twelve scats found in winter consisted entirely of supplemental food (maize 95%, livestock carrion 5%). Among the three regions, use of supplemental food varied between 22 and 63% annual EDEC (Table 3). The proportion of maize in the bear diet (EDEC) was positively related to the density of feeding sites in the region over entire year and in all seasons (Table 4).

Discussion

Similar to other temperate zones (Bojarska and Selva 2012), bears in Slovenia frequently feed on hard mast, fleshy fruits and insects, when they are available. However, besides natural food items, bears in Slovenia also consumed large amounts of anthropogenic foods. In our study, more than one third of the total annual estimated dietary energy content was derived from supplemental food, and the seasonal extreme in one region was as high as 70%. This is among the highest amounts of supplemental food in the bear diet reported so far (Rigg and Gorman 2005, Vulla et al. 2009). Use of supplemental food in Slovenia coincided with the density of feeding sites in the three regions. This suggests that the effects of supplemental feeding on bear diet can be regulated by controlling the number of feeding sites.

The overall high use of supplemental food by bears in Slovenia is likely a result of its high availability and the long tradition of this practice (> 100 years in some parts of Slovenia; Simonič 1994). The longevity of supplemental

Table 2. Logistic model with region, season and the interaction region × season as an explanatory variables for the occurrence of major food items in brown bear diet in Slovenia, 1993–1998 (n = 714). Models were produced by the backward removal procedure. Parameter estimates, standard errors and other test statistics are presented in the Supplementary material Appendix 4 Table A4.

	Region			Season			Region × Season		
	Wald	DF	p	Wald	DF	p	Wald	DF	p
Maize	60.3	2	< 0.001	4.1	2	0.131*	39.8	4	< 0.001
Livestock carrion and wild ungulates				13.2	2	0.001			
Insects	3.6	2	0.169*	146.9	2	< 0.001	18.2	4	< 0.001
Fruits	3.2	2	0.200*	102.4	2	< 0.001	17.2	4	0.002
Hard mast	27.9	2	< 0.001	33.3	2	< 0.001			
Other plant material	29.7	2	< 0.001	83.0	2	< 0.001			

*main effect of variable is not significant

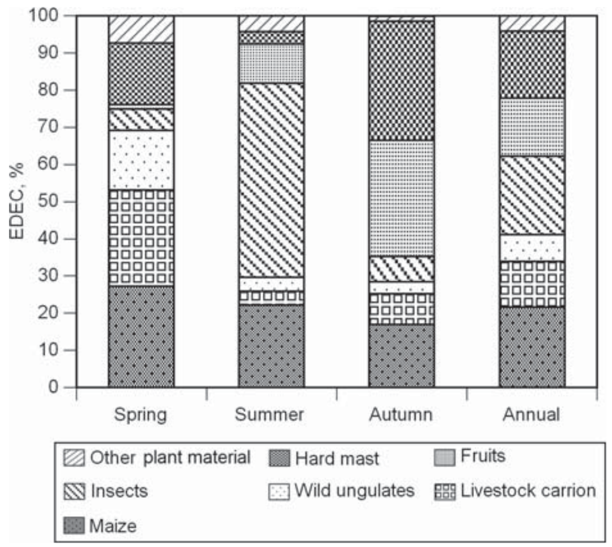

Figure 2. Seasonal and annual percent estimated dietary energy content (EDEC%) of food items in 714 brown bear scats in Slovenia, 1993–1998.

feeding has been shown to be an important factor influencing the use of feeding sites by ungulates (Van Beest et al. 2010, Jerina 2012). As a consequence, entire range and magnitude of effects of supplemental feeding practices may not become evident during short-term experimental supplemental feeding studies (e.g. the recent study in Scandinavia; Zedrosser et al. 2013). Thus, our results are important for predicting the effects of supplemental feeding on bear diet for other regions, where the (re-)introduction of long-term use of this measure is being considered.

The availability of natural food sources for bears in temperate regions is characterized by high seasonal and spatial variability (Bojarska and Selva 2012). In contrast, highly nutritious supplemental food was available at numerous predictable locations in Slovenia in large quantities throughout the year. Nevertheless, we observed seasonal variation in its use by bears. The proportion of energy gained from supplemental food was high in winter and spring, when it represented the majority of all ingested food. But bears shifted to natural forage when it became available in summer (insects) and autumn (hard mast and fruits). This suggests a preference for natural over supplemental food when both are available at the same time. Previous studies have shown that bears do not necessarily feed on the most available or energy-rich food items, but rather prefer a mixed diet to maximize energy intake and mass gain (Robbins et al. 2007). In addition, bears may preferentially feed on natural foods to avoid encounters with humans. Bears often adjust their behaviour to avoid people (Ordiz et al. 2011). Virtually all feeding sites have hunting towers nearby, which are frequently visited by hunters. Furthermore, 15% of the bear population is killed annually at feeding sites in Slovenia (Krofel et al. 2012a).

Table 3. Comparison of feeding site density and annual proportion of maize and supplemental food (maize and carrion) in the brown bear diet (estimated dietary energy content) for three study regions in Slovenia. The minimum and maximum values for the three seasons (spring, summer, autumn) are given in paranthessis.

Region	Feeding sites 100 km^{-2}	% maize in bear diet	% supplemental food in bear diet	n scats
Kočevsko	16	20 (10–32)	33 (17–57)	220
Menišija	34	52 (41–60)	63 (54–70)	260
Snežnik	16	10 (8–15)	22 (15–36)	234

Table 4. Parameter estimates and test statistics for the logistic regression model explaining differences in the use of supplemental food (maize) by bears between the two regions that differ in the intensity of supplemental feeding (Menišija vs Snežnik + Kočevsko) in Slovenia, 1993–1998 (n = 714). The proportion of maize in the bear diet (estimated dietary energy content - EDEC), season and interaction between EDEC and season were used as independent variables and region as binary dependent variables. The final model presented was selected using backward removal procedure. One level of each categorical variable served as contrast (estimate = 0.00) for the remaining levels of that variable. The model gives probabilities that a given sample originates from the region with higher supplemental feeding intensity. Estimated, standard errors and other test statisctics are presented in the Supplementary material Appendix 4.

Explanatory variables	Estimate	SE	Wald	p
Maize EDEC (%)	3.06	0.52	34.6	< 0.001
Season*			4.4	0.113
autumn	0.00			
spring	0.59	0.29	4.3	0.038
summer	0.20	026	0.6	0.431
Maize EDEC × season			7.4	0.025
maize – autumn	0.00			
maize – spring	−1.68	0.63		0.008
maize – summer	−0.65	0.59		0.275

*main effect of variable is not significant

Feeding on maize and livestock carrion at feeding sites is more effective than foraging on natural food sources (Jerina et al. 2012), and our diet analysis showed a high proportion of supplemental food in the bear diet. Thus, we expect that supplemental feeding affects the overall energy budget of bears and could consequently have important implications for bear ecology and management. Several studies have already shown that the population density and reproductive output of bears increase with availability of high quality food sources (Rogers 1987, Miller et al. 2003, McLellan 2011). The high content of supplemental food in the diet of bears in Slovenia may thus explain why Slovenia has one of the highest population densities (up to 40 bears 100 km^{-2}; Jerina et al. 2013) and reproductive rates (19–22% annually; Krofel et al. 2012a) reported for brown bears worldwide. Moreover, despite the high population density, no relation between body condition index and bear density was found among Slovenian bears (Elfström et al. 2014), suggesting a lack of food competition due to extra-abundant resources.

Use of supplemental food probably to certain extent affects consumption of natural food. This could affect some of the ecological functions that bears perform in the ecosystem, such as seed dispersal (Wilson and Gende 2004). Food availability can also influence denning behaviour (Schoen et al. 1987, Van Daele et al. 1990). In Slovenia, scats found during winter months consisted entirely of supplemental food. Such foraging at feeding sites in winter, when natural food sources are scarce, may explain why bears in Slovenia show a tendency for later den entry and earlier den emergence than bear populations in neighbouring regions without supplemental feeding (e.g. Trentino, Italy; Špacapan 2012).

Supplemental feeding in Slovenia is officially used to mitigate human–bear conflicts. However, the effects of this measure are not well understood and its effectiveness is questionable (Kavčič et al. 2013). For a long period, providing livestock carrion to bears in Slovenia was based on the common belief that by satisfying their need for animal protein, sheep depredations would be reduced (Štrumbelj 2006, Krofel and Jerina 2012). In the present study, we showed that bears used carrion from feeding sites mostly during spring, when sheep are mainly still indoors and thus not susceptible to depredation. On the other hand, in summer, when depredations are most frequent, our results show that bears do not use livestock carrion provided at feeding sites but cover most of their protein intake by feeding on insects. This explains why the ban on livestock carrion feeding in 2004 did not increase bear depredation rates on sheep (Kavčič et al. 2013).

Further studies are needed to fully understand the effects of supplemental feeding of bears in human-dominated landscapes. Despite the high availability of supplemental food, the intensity of human–bear conflicts in Slovenia is high (on an annual basis approximately 450 reported damages, 160 000 € paid in damage compensation, 200 reported cases of bears approaching human settlements, and lethal removal of 15 problem bears; Kragelj 2011, Krofel and Jerina 2012, Krofel et al. 2012a). Evidence from other studies suggests that supplemental feeding may increase reproduction and survival, resulting in high bear densities (Jerina et al. 2013), while year-round availability of high energy food may shorten the denning period, resulting in more bear movements in winter (Špacapan 2012). Both factors likely cause an increase in the rate of bear encounters with humans and their property, and thus the probability of human–bear conflicts. Therefore, we suggest caution in promoting supplemental feeding as a measure to prevent or reduce human–bear conflicts, at least until its effectiveness and potential side effects are better understood.

Acknowledgements – We are grateful to hunters from the Slovenian Hunting Association and students of the Univ. of Ljubljana for their help with the field work. Funding for the study was provided by the Ministry for Agriculture, Forestry and Food of the Republic of Slovenia, the Slovenian Research Agency (projects P4–0257-0404-93 and J4–7297-488-95) and the Austrian Science Foundation (FWF project 11529-BIO).

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Supplementary material (Appendix wlb.00013 at www.wildlifebiology.org/readers/appendix). Appendix 1–4.

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