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Brown bear feeding habits in a poor mast year where supplemental feeding occurs

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Abstract: The diet of free-ranging bears is an important dimension regarding their ecology, affecting their behavior, population structure, and relation with humans. In Croatia, there has been no recent study on the natural food habits of brown bears (*Ursus arctos*) or the influence of artificial feeding sites on their diet. During 2017, we collected 53 brown bear stomachs from bears in 2 regions of Croatia—Gorski Kotar and Lika—to assess their diet. Plants—*Allium ursinum,* the *Poaceae* family, *Cornus mas,* berries (i.e., *Prunus avium, Rubus plicatus*), beechnuts (*Fagus* spp.)—and various plant parts (i.e., dry leaves, buds, conifer needles, and twigs), as well as mushrooms, made up 80% of the percentage of the volume (%V) of all consumed items. Corn (*Zea mays*) from the feeding sites made up 37% of the bears' diet (%V), whereas 20% (%V) was meat and 14% (%V) was pome fruits. Scavenged or preyed animal species, such as wild boar (*Sus scrofa*), horse (*Equus caballus*), domestic pig (*S. scrofa domesticus*), cattle (*Bos taurus*), roe deer (*Capreolus capreolus*), and small mammals comprised >66% of %FO (frequency of occurrence), but only 20% of %V. Our results showed that food resources (i.e., livestock such as horses, cattle, and pigs, and corn) found at supplemental feeding sites were more frequently chosen by bears than natural food in 2017, a year characterized by almost no beechnut crop. The results showed that subadult bears obtained most food from feeding sites. These 2 patterns suggested that bears may focus on artificial feeding sites to find food in years when natural food sources are depleted, although this should be tested using diet and food availability data collected from several years.

Key words: artificial feeding, brown bear, Croatia, diet, mast, natural food, supplemental feeding, *Ursus arctos*

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Feeding behavior influences many relevant traits of a species' ecology and population dynamics (Braga et al. 2012), from habitat preference (Wetherbee and Cortés 2004) to predation (Martin et al. 2005, Frid and Marliave 2010), prey selection (Swenson et al. 1999, Motta and Wilga 2001), foraging behavior and social dominance (Gende and Quinn 2004), morphological traits (e.g., body mass), and reproduction success (Beeman and Pelton 1980, Beckmann and Berger 2003, Swenson et al. 2007, Bojarska and Selva 2011). Understanding animals' diet is important to understanding ecological adaptations, and therefore of great value when developing conservation strategies and management plans for species and ecosystem protection (Braga et al. 2012).

The brown bear (*Ursus arctos*) is a good species model for studying the effect of environmental and geographical variables on feeding behaviors because of the species' widespread distribution and broad diet range (Krechmar 1995, Bojarska and Selva 2011). The patterns of food availability and consumption have a direct influence on population size (Balestrieri et al. 2011), reproductive success (e.g., Hilderbrand et al. 2000), prey–predator relationships (Wachter et al. 2012), movement (e.g., Barnes 1990) and habitat use patterns (Nomura and Higashi 2000), feeding habits (Paralikidis et al. 2010), and the type and extent of bear–human conflicts (Rigg and Gorman 2005). Thus, determining diet composition is a valuable

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and crucial tool for bear management and conservation (Balestrieri et al. 2011, Kavčič et al. 2015).

The influence of food availability on brown bear feeding habits is well-documented in the literature. For example, in northern Spain (Cantabrian Range), Rodríguez et al. (2007) found a change in bear diet between 1974 and 2003, associated with changes in the availability of one main food item (alpine fruits, such as *Vaccinium*). As a result of climate change, the availability of this fruit-producing plant was reduced; bears had to move to lower altitudes searching for alternative foods, and therefore began including other fruits in their diet. Bear food choices are also influenced by the availability of anthropogenic food, mainly obtained through artificial feeding (defined by Inslerman et al. [2006] as the act of intentionally placing any food for the use of wildlife on an annual, seasonal, or emergency basis; sometimes called supplementary feeding), implemented as a diversionary feeding strategy to reduce bear–human conflicts (Rigg and Gorman 2005), or as bait to increase the success of hunting.

In Croatia, artificial food is generally available at feeding sites, set up by hunters to attract bears that can be legally hunted (Knott et al. 2014, Reljić et al. 2018). The hunting season ranges from 16 February to 15 May and from 16 September to 15 December. Periods when feeding sites are active start as early as 15 days prior to the beginning of hunting season (Bišćan et al. 2014). After hunting has ceased, the uneaten food is not removed and leftovers remain available for wildlife (Vranković et al. 2017). Grains (corn, oats [*Avena sativa*], and barley [*Hordeum vulgare*]), fodder beets (*Beta vulgaris*), sugar, various fruits (apples [*Malus* spp.], pear [*Pyrus* spp.]), and meat, including slaughterhouse waste from monogastric animals (e.g., domestic pigs [*Sus scrofa domesticus*], poultry, fish, and parts of wild game species) are common supplemental food added to such feeding sites (Bišćan et al. 2014, Vranković et al. 2017). However, artificial feeding is still a controversial issue that has raised concerns regarding its potential negative effects on bears, as well as on other wildlife (Kavčič et al. 2015). One of the effects is the shifting of bear feeding behavior and their increasing dependency on anthropogenic food, which can exacerbate human–bear conflicts (Kavčič et al. 2013, 2015). Thus, understanding the importance of artificial feeding on bear diet, in regions where this wildlife management strategy is implemented, can improve our knowledge of bear ecological adaptation to changing environments and contribute to a more effective and successful management of this endangered and emblematic large carnivore.

This short-term study was based on samples collected throughout 2017, which was an exceptionally poor beechnut (*Fagus sylvatica*) mast year. The study aimed to gather information on brown bear diet in Croatia (Cicnjak et al. 1984, Vranković et al. 2017) by analyzing stomach contents collected in 2 regions with permanent bear presence and where supplemental feeding sites are abundant and used for hunting (Lika, 40 feeding sites; Gorski Kotar, 51 feeding sites [Huber et al. 2008]).

The use of stomach content analysis facilitates the identification of most of the partially digested food remains at the species level, improves the accuracy of prey item volume when compared with scat-based studies (Balestrieri et al. 2011), and eliminates scat misidentification, which is common in predator species (e.g., Monterroso et al. 2013). Furthermore, it can provide information on individual characteristics (i.e., age, sex, body weight), which are rarely known from fecal samples (Litvaitis 2000). In addition to assessing the current diet of Croatian bear populations, we also aimed to evaluate, for the first time, the diet importance of food available on supplemental feeding sites for Croatian bears. We hypothesized that anthropogenic food would be a major component in bear diet where supplemental feeding is a common practice (Kavčič et al. 2015).

Materials and methods

Study area

The study was carried out in Croatia, in south-central Europe (Fig. 1). All brown bear habitats in Croatia are located within the Dinaric Mountain Range, which runs parallel to the Adriatic Sea and ranges from Slovenia to North Macedonia, from the northwest to the southeast. Consequently, Croatia shares part of the Dinara–Pindos bear population with those countries and is home to 1 of 10 bear populations in Europe, with an estimated country population size of 1,000 bears (Skrbinšek et al. 2017). The current bear range in Croatia extends over 11,800 km^2, which represents 20% of the country's area and 34% of its forests. Within this range, bears permanently occupy 9,250 km^2, whereas 2,600 km^2 has only occasional bear presence (Huber et al. 2008, 2019). Altitudes in the Croatian part of the Dinara Mountains vary from sea level to 1,831 m. Forest covers about 70% of the mountain range, which is dominated by a mixture of beech, fir (*Abies alba*), and Norway spruce (*Picea abies*), although depending on elevation and exposure, other tree communities may be present. Depending on elevation, average monthly temperatures range from −2.6°C in January, when snow may be present for 60–165 days

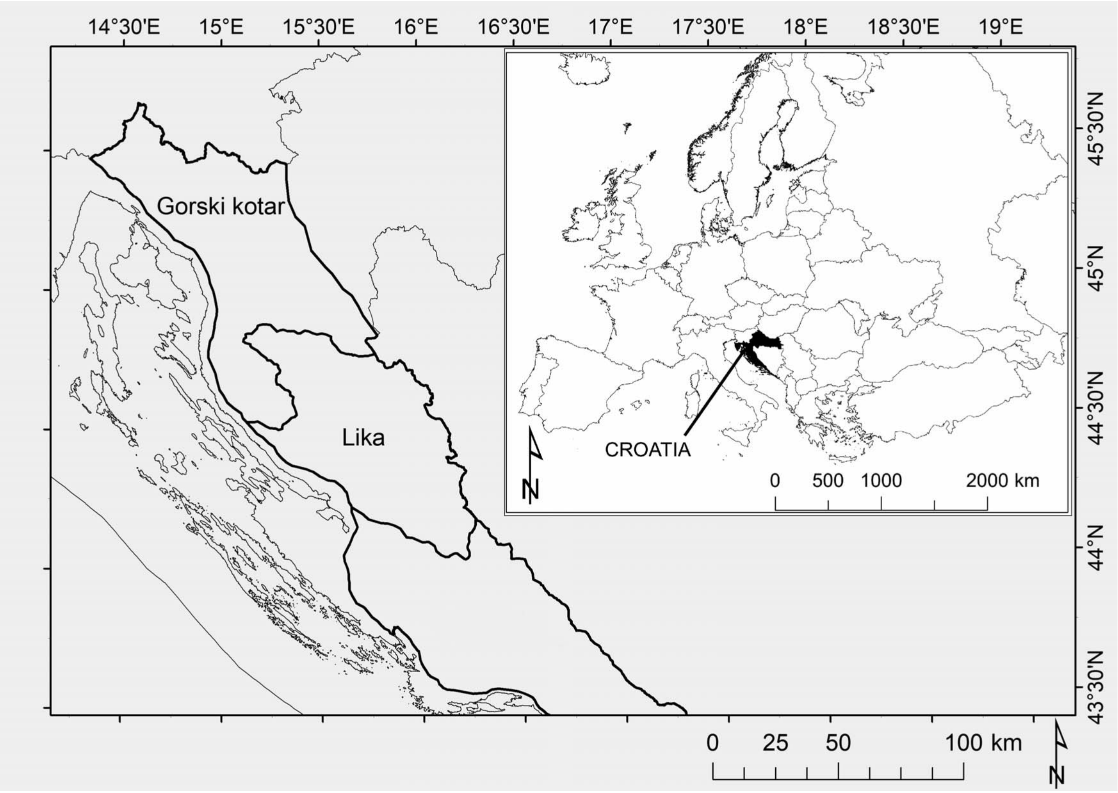

Fig. 1. The study areas Gorki Kotar and Lika in Croatia, where we examined influence of artificial feeding sites on food habits of brown bears (*Ursus arctos*) during 2017.

(Bertović and Martinović 1981), to 17.0°C in July (Makjanić 1971/1972). Geographically, the bear range can be divided in 2 subregions: Gorski Kotar (GK) and Lika (LI; Table 1). Rough estimates are that overall bear densities are higher in Gorski Kotar (≥10 bears/100 km^2) than in Lika (≤10 bears/100 km^2; Huber et al. 2019). Relevant habitat descriptors of both regions are presented in Table 1.

Stomach collection, processing, and dietary items identification

We collected 53 stomachs opportunistically from bears legally killed by hunters at artificial feeding sites ($N = 43$), animals killed in train ($N = 2$) and car ($N = 5$) accidents, and in control actions ($N = 3$; i.e., injured or problematic bears that were killed when the security of people and/or their property was at risk). The stomachs were collected from within the main bear core regions in Croatia—Lika (LI; $N = 20$) and Gorski Kotar (GK; $N = 33$)—throughout the 2 established periods of 2017's hunting season, from 31 March until 5 May (Spring;

Table 1. Characteristics and habitat descriptors of the Gorski Kotar and Lika study areas, Croatia, and the brown bear (*Ursus arctos*) populations inhabiting both areas (Huber and Roth 1986, Kusak and Huber 1998, Huber et al. 2008a, Skrbinšek et al. 2017).

Descriptor	Gorski Kotar	Lika
Area (km^2)	1,796	8,183
Supplemental feeding	Yes	Yes
Permanent bear presence area (km^2)	1,495	8,077
Approximate bear population (both regions)[a]	937 (846–1,072)	
Estimated adult sex ratio (F:M)	58%:42%	
Average elevation (m)	737.3	848.5
Average temp (°C)	7.6/yr	9.3/yr
Average precipitation (mm)	3,770/yr	1,360/yr
Estimated natural vegetation cover (%)	66	75
Road density (km/km^2)	1.91	[b]

[a] Information regarding bear population numbers are only available for entire Croatian population because the bear population is continuous (not fragmented), so only the overall densities may be compared.

[b] Denotes unknown.

Table 2. Summary table of brown bear (*Ursus arctos*) stomach contents collected throughout 2017 in Croatia, grouped into 8 food categories (V = volume [mL], M = mass [g], %F0 = percent of frequency of occurrence, %V = percent of volume, %mV = percent mean volume).

Items[a]	Frequency	Total V	Total M	%FO	%V	%mV
Meat[b]	35	6,602	10,170	66.03	19.50	12.87
Forbs*	30	9,550	9,789	56.60	28.20	15.96
Gramineae spp.*	20	4,104	4,426	37.72	12.12	4.57
*Allium ursinum**	10	5,446	5,363	18.88	16.08	3.04
Other plant material[c,*]	20	155	102	37.74	0.46	0.17
Cereals	29	12,402	12,965	54.72	36.62	20.04
Corn (*Zea mays*)	28	11,402	11,765	52.83	33.67	17.79
Rice (*Oryza sativa*)	1	1,000	1,200	1.88	2.95	0.06
Beech nuts*	2	135	117	3.77	0.40	0.01
Wild fruits (*Cornus mas*)*	2	300	744	3.77	0.89	0.03
Pome fruits (apple, pear)	15	4,696	5,766	28.30	13.87	3.92
Mushrooms*	4	25	59	7.55	0.07	0.01

[a] The wild dietary items are indicated with an asterisk (meat is not because we could not discriminate between meat from wild and domestic prey).

[b] Within this category, we identified the presence of wild boar and roe deer, and of domestics such as horses, pigs, or cattle, using some hair found in some samples (only few samples contained hair, so we could not estimate the frequency, Total V, and Total M for each individual mammalian prey.

[c] Bark, twigs, dry leaves, tree buds, conifer needles.

$N = 15$) and from 29 September until 15 November (Fall; $N = 38$). We extracted stomachs in situ and stored them at −18°C in a freezer prior to analysis. We recorded the bear's sex, body weight, and collection site. We determined age in Matson's Laboratory (Manhattan, Montana, USA) by counting the cementum annuli on the teeth radix (Matson et al. 1993). For 2 bears, we could not determine sex and age because of the advanced deterioration of the carcass or lack of structures that allow such determination (e.g., region of the genitalia or teeth was already missing on collection). In the lab, we thawed the stomachs and flushed food contents through a sieve of 1.5-mm mesh width, after which we sorted them by hand and identified the undigested items, when possible, to the species level. We observed all hairs using a microscope and identified them by comparison with the available identification keys (Teerink 1991) and personal collections from the Department of Anatomy, Histology and Embryology at the University of Zagreb, Faculty of Veterinary Medicine. In many cases, there was just meat, free of hairs, so it was impossible to identify the prey species. The detected bone fragments were also assigned only to a group of animals (e.g., rodents, other small mammals). We identified the remaining items using a magnifying lens and field identification guides (Lakušić 1982; Šilić 1983, 1984). Items found more than once in the stomachs were organized into 8 main categories (Table 2) that included the following items: cereals (rice, corn), forbs (*Gramineae* spp., *Allium ursinum*), pome fruits (domestic apple, pear), beechnuts, wild fruits (*Cornus mas*), other plant material (e.g., bark, twigs, dry leaves, tree buds, conifer needles), mushrooms, and meat (e.g., bones, hairs, tissues, fat). In addition, we found a single occurrence of anthropogenic garbage—3 plastic packages of rabies vaccines. We found garbage only once; garbage had no energetic value for bears, so we excluded it from further analysis. We weighed (in grams) dietary items identified in each stomach and measured their volume by water displacement in a glass container, to the nearest milliliter.

Data analysis

We expressed the results of stomach analysis as suggested by Kruuk and Parish (1981). We have used the following diet indices:

(1) Frequency of occurrence, expressed as a percentage (%FO)

$$\%\mathrm{FO} = \frac{\text{number of samples containing a food item}}{\text{total number of samples}} \times 100$$

(2) Percent volume (%V)

$$\%\mathrm{V} = \frac{\text{total estimated volume of each food item}}{\text{total estimated volume of all samples}} \times 100$$

(3) Percent mean volume, which outlines the proportional contribution of each food item to the overall diet (%mV).

$$\%\mathrm{mV} = \frac{\%\mathrm{FO} \times \%\mathrm{V}}{100}$$

We assessed the differences in consumption of the 8 predefined food categories with the Kruskall–Wallis test (Zar 2010) for volumes. The correlation between the proportions of volume of the different categories was tested by Spearman´s correlation test. We also built 3 general linear models (GLM) with %V as response variable for each main food category (i.e., with a %V >20%; one different model for forbs, meat and cereals; Gaussian family and identity link function); and another 3 models with presence–absence as response variable for each food category (1 different model for forbs, meat and cereals; Binomial family, logit link function). The metric %Vol is the most informative regarding the actual importance of each food item in bear diet. Nevertheless, the presence–absence of an item in the diet provided us with information about patterns of food use. The 6 models had, as independent variables, the region where the stomach was collected (Region; LI, GK), the period of collection (Season: Spring, Fall), the age of the animal (Age; Subadult [≤3 yr], Adult [>3 yr]), its sex (Sex: Male, Female), and weight (Bear weight: ≤100 kg, >100 kg; using weight categories suggested by Frkovic et al. 1987). The 6 models, in addition to having 5 main variables, also included the interactions "Season × Sex" and "Season × Region," which could be influential on both dependent variables. First, we tested collinearity between the independent variables with the Variance Inflation Factor (VIF; Zuur et al. 2007). We considered the variables with VIF >5 to be significantly correlated and excluded them from the GLM analysis (Zuur et al. 2007). We based model selection criterion on Akaike´s Information Criterion, corrected for a small sample size (AIC_c), where the best selected models followed a $\Delta\mathrm{AIC}_c < 2$ criterion (i.e., the difference between each model AIC_c and the smaller AIC_c value was <2; Burnham and Anderson 2002). We used Relative Importance (RI) to identify models with non-informative parameters (Arnold 2010). Lastly, we assessed the variation in consumption of items consumed at feeding sites versus those not found at feeding sites using Mann–Whitney's test (U; Zar 2010) for the %V and chi-squared test (χ^2) for binomial presence–absence. For the latter, we excluded those items that registered a %V >2.5%, to avoid the overestimation of food traces and the devaluation of items substantially present in the stomachs (Kavčič et al. 2015). For both tests we applied Bonferroni's Sequential Technique to calculate the respective levels of significance. Additionally, we built 2 more GLM models, following the procedure described above, to test whether the same 5 descriptive variables and interactions between the 2 variables could influence the %V of ingested food from feeding sites and non-feeding sites. We followed a more conservative approach, excluding all items where we could not be certain about the source (fruits, unidentified meat, hare, and wild boar [*Sus scrofa*]; the latter was due to possible identification confusion with the domestic counterparts). We considered domestic animals (such as horse [*Equus caballus*], cattle [*Bos taurus*], and domestic pig) as being present at feeding sites, whereas we included wild prey species (such as roe deer [*Capreolus capreolus*], rodents, and small mammals) in the non-feeding sites category.

Results

Collected samples

During the spring and fall of 2017, we collected 53 brown bear stomachs, 25 (47%) from female bears and 28 (53%) from males. Adults (>3 yr) comprised 57% ($N = 30$) and subadults (≤3 yr) 43% ($N = 23$), with 51% ($N = 27$) from bears weighing ≤100 kg and 49% ($N = 26$) >100 kg (overall range = 40–291 kg). The average stomach mass was 794 g (range = 107–2,000 g) and the average stomach content volume was 785 mL (range = 50–2,400 mL).

Bear diet description

We found an average of 2.0 ± 0.8 standard deviation food items per stomach, with 84% of the food volume consisting of 3 main categories: cereals (37%), forbs ('herbs';28%), and meat (20%; Fig. 2), having a proportional contribution (%mV) of 20%, 16%, and 13%, respectively (Table 2). The %mV did not differ across food categories ($F = 0.22$, $P = 0.80$, 2 df). The remaining food items comprised a negligible importance in bear diet, with a %mV = 1, except for pome fruits, which reached 4%. However, we detected meat in 66% of samples (%FO; Table 2), and we only managed to collect hair in 39% of all samples, and bone fragments in 6%. The microscopical analysis of prey hairs allowed us to identify several mammalian species, some wild (such as wild boar and roe deer), and others from domestic animals (such as horses, pigs, and cattle). Unfortunately, we were unable to identify some prey species, which we only identified as "rodents," "other small mammals," or "unidentified mammals" (Fig. 3). Lastly, we detected a significant correlation between the ingestion of forbs and cereals and between forbs and meat (Table 3). The consumption of forbs was inversely and significantly related to the ingestion of cereals and meat, but we detected no significant correlation between meat and cereals (Table 3).

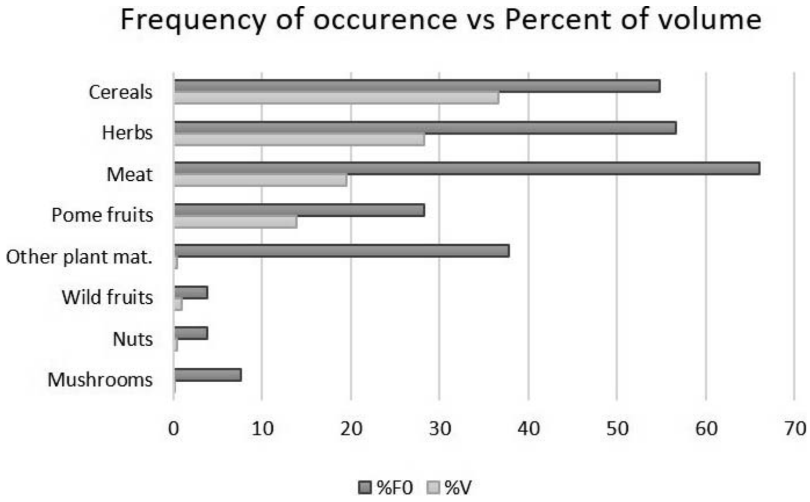

Fig. 2. Frequency of occurrence (%FO) and percent of volume (%V) for the 8 main food categories ingested by brown bears (*Ursus arctos*) during 2017 in Croatia.

Diet variation drivers

We detected no collinearity between the independent variables (i.e., all VIF <5); thus, we used all variables as candidates for both regression models. Considering the %V of meat, we included 3 variables (sex, season, and region) in 4 models that achieved an AIC$_c$ <2 and were considered the highest ranked models (Table 4). Sex was the only variable whose 95% confidence interval (CI) did not include 0, and thus was the only one for which we could assess the direction of its influence (Table 4), indicating a greater ingestion of meat by males ($\%V_M = 26\%$, $\%V_F = 7\%$). For the %V of cereals, 4 variables (season, age, region, and bear weight) were selected in the 6 highest ranked models; however, we could not estimate the direction of their influence because the 95% CI of all variables included 0 (see Supplemental material, Table S1). The same occurred for the %V of forbs, where just one best model and one variable (season) were selected, but the 95% CI included 0 (see Supplemental material, Table S2). However, when considering the %FO of forbs, the seasonal variation explained some of the change in forbs consumption, with forbs being more frequently ingested during spring ($\%FO_{Spring} = 86\%$, $\%FO_{Fall} = 30\%$; Table 5). The contrary was shown for the %FO of meat—bears consumed less meat in spring than in fall ($\%FO_{Spring} = 10\%$, $\%FO_{Fall} = 35\%$; Table 6). For %FO of cereals, 4 models were selected as the highest ranked models, including 3 variables (sex, season, and region). All the variables' 95% CI included 0, so we could not make conclusions about their influence (see Supplemental material, Table S3). Supplemental food was more frequently chosen by bears than natural food ($\chi^2 = 8.36$, 1 df, $P = 0.004$), especially by subadults, which consumed a greater %V of items coming from these sites (Table 7). For the model including %V natural resources as dependent variable, the variables season (spring) and the interaction season × region had 95% CIs that did not include 0 in the averaging best model (Table 8).

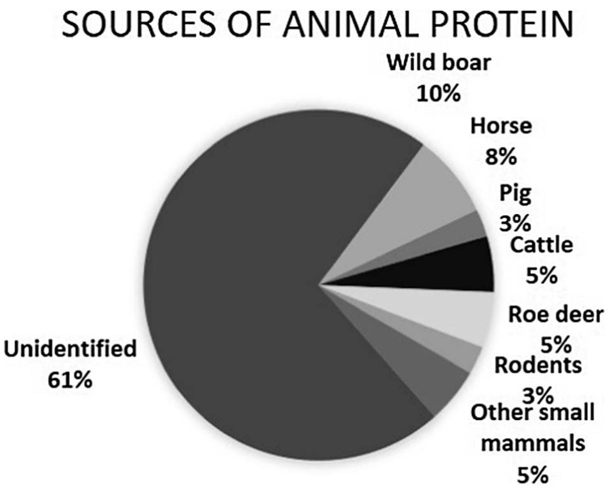

Fig. 3. Frequency of occurrence of animal food sources in brown bear (*Ursus arctos*) diet throughout 2017 in Croatia.

Table 3. Relationship between the percent of volume (%V) of 8 main food categories collected from brown bear (*Ursus arctos*) stomach contents throughout 2017 in Croatia, assessed by Spearman´s correlation coefficient.[a]

	Cereals	Forbs	Meat	Other plant material	Pome fruits	Beech nuts	Wild fruits
Forbs	– 0.44**						
Meat	– 0.21	– 0.30*					
Other plant material	– 0.12	0.12	– 0.16				
Pome fruits	– 0.19	– 0.19	– 0.18	– 0.18			
Beech nuts	– 0.11	0.13	– 0.08	0.22	−0.07		
Wild fruits	– 0.11	– 0.02	0.02	– 0.08	−0.08	−0.03	
Mushrooms	– 0.10	0.19	– 0.07	– 0.06	−0.04	−0.03	−0.03

[a] Correlation significance: * $P < 0.05$, ** $P < 0.001$.

Discussion

Stomach content analysis from 2017 showed that the Croatian bear population fed on 3 broad food categories: cereals, forbs, and meat. This reflects the omnivorous and generalist feeding patterns of bears, which consume both plant and meat material (Cicnjak et al. 1984), as has been described for the European populations of this carnivore (Robbins et al. 2004, Paralikidis et al. 2010). Furthermore, our results fit the Vulla et al. (2009) model that found a positive correlation of animal prey consumption with latitude (i.e., southern European populations, such as bears in Croatia were more omnivorous). Meat was the most frequent food item in their diet, but reached a lesser %mV due to a lower %V. Such a pattern can be related to greater and quicker digestibility of meat in the stomach, when compared with other food components that are harder to digest (e.g., plant proteins are less digestible; Clauss et al. 2010). A greater digestibility may also explain the absence of invertebrates such as insects (e.g., Diptera larvae) because their presence would be expected according to other Dinaric bear-population diet studies (e.g., Cicnjak et al. 1984, Große et al. 2003, Rigg and Gorman 2005, Kavčič et al. 2015). However, we cannot discard the possibility that the non-consumption of adult insects or their larval form (e.g., ants, wasps) may be linked to a local preference of the

Table 4. Characteristics of the highest ranked models explaining variation in the percentage of volume (%V) of meat ingested by brown bears (*Ursus arctos*) throughout 2017 in Croatia, ordered by increasing $\mathrm{AIC_c}$ values. The highest ranked model-averaging parameters (indicated by an asterisk) are presented at the bottom.

Models	df[a]	LogLik[b]	AIC_c[c]	$\Delta\mathrm{AIC}_c$[d]	*w*[e]
Sex	3	−11.81	30.1	0.00	0.33
Sex + Season	4	−10.69	30.3	0.12	0.31
Sex + Season + Site	5	−9.98	31.3	1.18	0.18
Sex + Site	4	−11.23	31.4	1.21	0.18
Null model	1	−14.07	32.1		

Model-averaging coefficients

	β[f]	SE[g]	*t*-value	*P*-value	95% CI[h]	RI[i]
Intercept	0.08	0.07	1.16	0.25	[−0.06, 0.23]	
Sex (males)*	0.18*	0.09*	1.99*	0.05*	[0.002, 0.36]*	1.00*
Season (spring)	−0.07	0.10	−0.71	0.48	[−0.34, 0.05]	0.49
Site	0.04	0.08	0.49	0.63	[−0.09, 0.30]	0.36

[a] df, degrees of freedom.

[b] LogLik, log-likelihood of the linear model.

[c] $\mathrm{AIC_c}$, Akaike Information Criteria for small sample sizes.

[d] The difference between each model $\mathrm{AIC_c}$ and the smaller $\mathrm{AIC_c}$ value.

[e] w, Akaike weight.

[f] β, variable coefficient.

[g] SE, standard error.

[h] CI, confidence interval.

[i] RI, relative importance.

Table 5. Characteristics of the highest ranked models explaining variation in the presence or absence of forbs ingested by brown bears (*Ursus arctos*) throughout 2017 in Croatia, ordered by increasing AIC$_c$ values. The highest ranked model-averaging parameters (indicated by an asterisk) are presented at the bottom.

Models	df[a]	LogLik[b]	AIC$_c$[c]	ΔAIC$_c$[d]	*w*[e]
Season	2	−27.90	60.1	0.00	0.50
Season + Age	3	−27.42	61.4	1.31	0.26
Season + Sex	3	−27.50	61.5	1.47	0.24
Null model	1	−36.13	76.3		

Model-averaging coefficients

	β[f]	SE[g]	*t*-value	*P*-value	95% CI[h]	RI[i]
Intercept	−0.82	0.48	1.67	0.093	[−1.78, 0.14]	
Season (spring)*	2.63*	0.85*	3.01*	0.002*	[0.915, 4.34]*	1.00*
Age (subadult)	−0.17	0.45	0.37	0.709	[−2.00, 0.70]	0.26
Sex	0.14	0.42	0.34	0.736	[−0.76, 1.94]	0.24

[a] df, degrees of freedom.
[b] LogLik, log-likelihood of the linear model.
[c] AIC$_c$, Akaike Information Criteria for small sample sizes.
[d] The difference between each model AIC$_c$ and the smaller AIC$_c$ value.
[e] w, Akaike weight.
[f] β, variable coefficient.
[g] SE, standard error.
[h] CI, confidence interval.
[i] RI, relative importance.

bear population or to the availability of more profitable items.

The meat remains found in bear stomachs belonged to animals that were mostly, or only, scavenged. We assumed they were not, in fact, killed by the bears because this species is known to be a limited active predator (Bojarska and Selva 2011). Brown bears are known to be highly dependent on wild fruits and nuts (Štofik et al. 2013), which in Croatia are predominantly beechnuts because of their large availability during late summer and

Table 6. Characteristics of the highest ranked models explaining variation in the presence or absence of meat ingested by brown bears (*Ursus arctos*) throughout 2017 in Croatia, ordered by increasing AIC$_c$ values. The highest ranked model-averaging parameters (indicated by an asterisk) are presented at the bottom.

Models	df[a]	LogLik[b]	AIC$_c$[c]	ΔAIC$_c$[d]	*w*[e]
Season	2	−28.05	60.4	0.00	0.71
Season + Sex	3	−27.82	62.2	1.79	0.29
Null model	1	−31.34	64.8		

Model-averaging coefficients

	β[f]	SE[g]	*t*-value	*P*-value	95% CI[h]	RI[i]
Intercept	−0.40	0.41	0.99	0.323	[−1.20, 0.40]	
Season (spring)*	−2.22*	1.09*	1.99*	0.047*	[−4.42, −0.03]*	1.00*
Sex (male)	0.45	0.65	0.67	0.503	[−0.86, 1.75]	0.29

[a] df, degrees of freedom.
[b] LogLik, log-likelihood of the linear model.
[c] AIC$_c$, Akaike Information Criteria for small sample sizes.
[d] The difference between each model AIC$_c$ and the smaller AIC$_c$ value.
[e] w, Akaike weight.
[f] β, variable coefficient.
[g] SE, standard error.
[h] CI, confidence interval.
[i] RI, relative importance.

Table 7. Characteristics of the highest ranked models explaining variation in the percentage of volume (%V) consumed from supplemental feeding sites by brown bears (*Ursus arctos*) throughout 2017 in Croatia, ordered by increasing AIC_c values. The highest ranked model-averaging parameters (indicated by an asterisk) are presented at the bottom.

Models	df[a]	LogLik[b]	AIC_c[c]	ΔAIC_c[d]	w[e]
Age	3	−25.15	56.8	0.00	0.64
Age + Season	4	−24.55	58.0	1.17	0.36
Null model	1	−34.66	71.3		

Model-averaging coefficients

	β[f]	SE[g]	*t*-value	*P*-value	95% CI[h]	RI[i]
Intercept	0.23	0.08	2.73	0.006	[0.07, 0.40]	
Age (subadults)*	0.34*	0.12*	2.88*	0.004*	[0.11, 0.58]*	1.00*
Season (spring)	−0.14	0.13	1.04	0.299	[−0.40, 0.12]	0.36

[a] df, degrees of freedom.

[b] LogLik, log-likelihood of the linear model.

[c] AIC_c, Akaike Information Criteria for small sample sizes.

[d] The difference between each model AIC_c and the smaller AIC_c value.

[e] w, Akaike weight.

[f] β, variable coefficient.

[g] SE, standard error.

[h] CI, confidence interval.

[i] RI, relative importance.

fall (Kusak and Huber 1998, Vranković et al. 2017). However, the importance of beechnuts during the sampled year was negligible. The low frequency of beechnuts was probably due to an assumed irregular annual production in 2017, which resulted in a shortage of beechnut availability (Cicnjak et al. 1984). Slobodyan (1976) mentioned that in a beechnut shortage period (1972–1973), the opportunity for Carpathians bears to build up a layer of fat

Table 8. Characteristics of the highest ranked models explaining variation in the percentage of volume (%V) consumed from natural food sources by brown bears (*Ursus arctos*) throughout 2017 in Croatia, ordered by increasing AIC_c values. The highest ranked model-averaging parameters (indicated by an asterisk) are presented at the bottom.

Models	df[a]	LogLik[b]	AIC_c[c]	ΔAIC_c[d]	w[e]
Season + Region + Season × Region	5	−21.92	55.2	0.00	0.55
Season	3	−24.53	55.6	0.38	0.45
Null model	1	−34.66	71.3		

Model-averaging coefficients

	β[f]	SE[g]	*t*-value	*P*-value	95% CI[h]	RI[i]
Intercept	0.24	0.08	3.00	0.002	[0.08, 0.39]	
Season (spring)*	0.44*	0.17*	2.52*	0.01*	[0.10, 0.79]*	1.00*
Region (LK)	0.08	0.13	0.60	0.55	[−0.14, 0.43]	0.55
Season × Region*	−0.32*	0.35*	0.91*	0.36*	[−1.11, −0.06]*	0.45*

[a] df, degrees of freedom.

[b] LogLik, log-likelihood of the linear model.

[c] AIC_c, Akaike Information Criteria for small sample sizes.

[d] The difference between each model AIC_c and the smaller AIC_c value.

[e] w, Akaike weight.

[f] β, variable coefficient.

[g] SE, standard error.

[h] CI, confidence interval.

[i] RI, relative importance.

was reduced and they change their feeding focus. The hypothesis that the negligible consumption of beechnuts must be related to availability is supported by the results of other diet studies in the Balkans, where bears showed a preference for natural foods (including hard mast, as nuts), when available (Kavčič et al. 2015). These authors also stated that bears often prefer to feed on natural foods (such as nuts) when available, instead of using resources that may promote their encounter with humans, such as those available at supplemental feeding sites. Such behavior led us to hypothesize that the lack of consumption of a natural food item commonly found in the bears' diet must be related to its lower availability in the wild during this year. Even though we did not find data on beechnut yield for 2017, there are records documenting that 2016 and 2018 were good mast years (Gavranović et al. 2018, Skrbinšeket al. 2019). Beechnuts have an inherent biennial masting pattern (Hilton and Packham 2003) and this pattern, together with our observations in the field, led us to assume a low availability of beechnuts during the study period (i.e., 2017). In addition, the absence of berries such as *Prunus avium* and *Rubus plicatus* (Cicnjak et al. 1984) was probably related to the fact that there were no stomachs collected throughout the summer when these fruits are highly available. Forbs were the most important (in terms of %mV) component of bear diet from April to May and also the main natural food available in this season (as mentioned for other areas where bears diet was assessed; Naves et al. 2006, Paralikidis et al. 2010). We did not evaluate food availability, so the ecological mechanism behind this distinct pattern is unknown.

Male bears seem to eat more meat than females, a pattern already seen in brown bears of North America and Asia (Mowat and Heard 2006, Nawaz et al. 2019). Sixty-seven percent of the identified prey was wild boar, horse, cattle and domestic pig, which are all common bait used by hunters at feeding sites; therefore, most of the meat found in bear stomachs was likely from carrion or gut piles and the skins of hunted game displayed at feeding sites. Furthermore, the most common supplemental food at the feeding sites is corn (Huber et al. 2008, Vranković et al. 2017), and therefore all, or at least most, of the cereal found in the sampled stomachs is likely from feeding sites. We found an inverse relationship between forb consumption and consumption of meat and cereals, suggesting that when bears feed mainly on forbs, they do not need to ingest much extra resources through supplemental feeding. Grasses are available through all seasons, but bear garlic (*Allium ursinum*) is mainly restricted to spring, when it is highly abundant. Additionally, subadults, as well as adult females with offspring, are the cause of more conflicts with humans (Inslerman et al. 2006, Jerina et al. 2015) than are adult males because they approach closer to human settlements as a strategy to avoid dominant bears (Elfström et al. 2014b), to overcome food shortage (McCullough 1982, Gunther et al. 2009, Rogers 2011), or even because they lack experience with humans as compared with older conspecifics (McLellan et al. 1999, Kaczensky et al. 2006, Elfström et al. 2014b). The subadult bear group showed more dependency on the feeding sites. It is risky for bears to visit supplemental feeding sites because they can be shot, are in exposed areas, and have a greater chance of meeting other bears. However, the reward is great—a feast (Pease and Mattson 1999, Inslerman et al. 2006, Elfström et al. 2014a, Kavčič et al. 2015).

Even though the results from this short-term assessment were restricted to one low-mast year, they helped to fill the knowledge gap about the brown bear's diet in Croatia, which is underrepresented in bear literature. We acknowledge that approximately 75% of the samples were collected from bear feeding sites. However, the frequent use of supplemental food sources in a period when natural foods were less readily available, as seen in our study, may indicate that in years where natural food sources are depleted, bears focus on artificial feeding sites to fulfil their energetic needs. Nevertheless, this pattern must be tested with data collected over longer temporal scales.

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Supplemental material

Table S1. Characteristics of the highest ranked models explaining variation in the %V of cereals ingested by brown bears throughout 2017 in Croatia, ordered by increasing AICc values. The highest ranked model-averaging parameters are presented at the bottom.

Table S2. Characteristics of the highest ranked models explaining variation in the %V of forbs (herbs) ingested by brown bears throughout 2017 in Croatia, ordered by increasing AICc values. The highest ranked model-averaging parameters are presented at the bottom.

Table S3. Characteristics of the highest ranked models explaining variation in the presence or absence of cereals ingested by brown bears throughout 2017 in Croatia, ordered by increasing AICc values. The highest ranked model-averaging parameters are presented at the bottom.