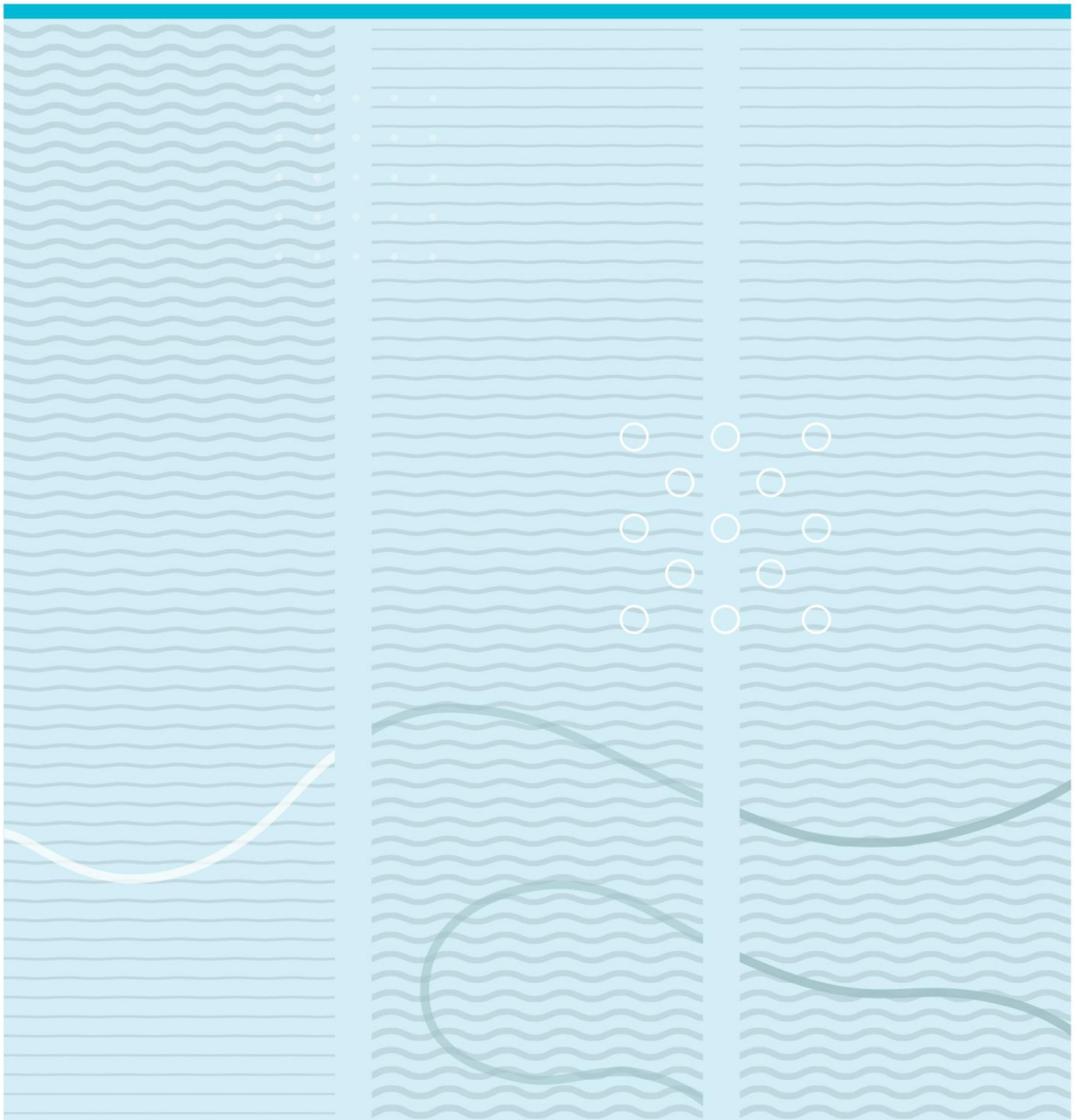


Simona Klamárová

# Dietary analysis of the brown bear (*Ursus arctos*) in Sweden 2015-2018



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This thesis is worth 60 study points

## Abstract

Understanding dietary variation is crucial for a better understanding of a species' ecology as well as for its effective management and conservation. Here I investigate the dietary variation of brown bears (*Ursus arctos*) in south-central Sweden in relation to year, season, sex and age based on the analysis of 958 bear scats, collected from 2015-2018. The diet of brown bears varied significantly among the seasons and years. Insects and vegetative materials were important food items during the spring/summer season. The most important group of insects were ants, especially *Formica* spp., with EDEC of 45.06%. The consumption of ungulates was stable between years, but was higher in spring/summer, in accordance with the calving season of moose (*Alces alces*). Berries (in order of importance: bilberries, lingonberries, crowberries) represented the most important food items (estimated dietary energy content (EDEC): 98.22%) during the pre-denning period in fall. The preference for berries in the fall season was stable between years, but the proportion of species changed, indicating that bears switched between species in relation to environmental conditions. The diet of bears varied also between the sexes, with males consuming comparatively less berries than females, but also more vegetative material compared to females. I found only little effect of age (adult/subadult) on diet choice. The present study is important for the documentation and understanding of feeding habits of brown bears, to understand the potential responses and adaptations of bears to climatic changes, and ultimately, for the effective management and conservation of the species.

*Key words: brown bear, diet, fecal analysis, Sweden, Ursus arctos*

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# Foreword

I thank chiefly to my supervisor Andreas Zedrosser, for his patience and support not only with the statistics and writing; to all students and volunteers who devoted their time and effort to collecting and analysing scats; Clayton Creed for his great help with the laboratory analysis; my family and friends for their patience and support during hard writing times.

Bø i Telemark, 05.05.2019

Simona Klamárová

# 1. Introduction

Energy and nutrients (“food”) are inevitable for all living organisms and have a major effect on the life history of species (Stearns 1992). They affect, amongst other things, body mass, body size, movement, habitat selection, litter size, breeding interval, and home range size and selection (Blanchard 1987, Mattson *et al.* 1991, Welch *et al.* 1997, Zedrosser *et al.* 2006, Bojarska and Selva 2012, Kavčič *et al.* 2015, Stenset *et al.* 2016). Feeding is commensurate in the long term with fitness and, thus, it is a target for natural selection (Schoener 1971, Bojarska and Selva 2012). Documentation and understanding of the variations in the diet and food habits of a species are crucial for understanding the ecology of a species as well as its effective management and conservation, for example to minimize or avoid human-animal conflicts (Frąckowiak and Gula 1992, Paralikidis *et al.* 2010, Bojarska and Selva 2012, Kavčič *et al.* 2015, Stenset *et al.* 2016). Variations in the diet of a species can be a result of annual and seasonal variations due to weather conditions and climatic change, but also due to human-induced habitat changes (Bojarska and Selva 2012, Stenset *et al.* 2016).

Brown bears (*Ursus arctos*) are flexible and opportunistic omnivores with a highly variable diet (Bacon 1987, Bojarska and Selva 2012). Due to their life cycle with an active period during the warm parts of the year and hibernation during the cold winter months, bears must acquire fat reserves during the pre-denning (hyperphagia) period in fall (Swenson *et al.* 2007). Bears are able to hibernate for up to 6 months without the need for food, water, urination, or even defecation. In addition to this, female bears give birth during hibernation in their dens (Evans 2016). The amount of body fat directly affects reproduction, because the fertilized eggs of females bears do not implant until hibernation (Hellgren 1998, Friebe 2014), and females with a body fat content below 17% at the onset of hibernation are not able to successfully implant and reproduce in that winter (López-Alfaro *et al.* 2013).

In spite of the fact, that bears morphologically and taxonomically possess all the traits of carnivores (Robbins *et al.* 2004, Bojarska and Selva 2012), they are an omnivorous (Robbins *et al.* 2004, Stenset *et al.* 2016) and monogastric species that cannot digest fiber effectively (Welch *et al.* 1997, Naves *et al.* 2006). However, plant materials play an important role in their nutrition. The ecological flexibility of brown bears determines their wide dietary niche (Krechmar 1995, Bojarska and Selva 2012). Brown bears usually consume insects, ungulates and various vegetative material, such as grasses, fruits and berries (Beeman and Pelton 1980, Welch *et al.* 1997, Stenset *et al.* 2016).

Especially bears living in areas where energy-rich foods (such as salmonids) are not available, are reliant on grazing and wild fruits (Welch *et al.* 1997). The demand for formation of fat layers necessary for hibernation lead bears to spend a significant part of their daily activity on feeding (Stelmock and Dean 1986, Naves *et al.* 2006).

Here I investigate the interannual and seasonal variation in the diet of brown bears from south- central Sweden. At the beginning of the 20th century, the population of brown bears in Scandinavia was almost exterminated due to overhunting (Swenson *et al.* 1997, Sæther *et al.* 1998). However, during the last 60 years, a strong population growth and range expansion were recorded in this area (Swenson *et al.* 1997, Sæther *et al.* 1998). Brown bears in Scandinavia inhabit a landscape heavily affected by forest management and practices (Hertel *et al.* 2016). In the Swedish boreal forest, the bilberry (*Vaccinium myrtillus*) covers more than 17% of the forest floor (Kardell 1979, Hertel *et al.* 2016), and serves as the most important food source for brown bears (Stenset *et al.* 2016). Other important food sources in Scandinavia are lingonberries (*Vaccinium vitis-idaea*) and crowberries (*Empetrum spp.*) during the fall; fungi, fruits and insects (mainly ants (*Camponotus spp.*, *Formica spp.*) and larvae) during the summer; and grasses and carrion during the spring (Dahle *et al.* 1998, Swenson *et al.* 1999, Persson *et al.* 2001, Hertel *et al.* 2016, Stenset *et al.* 2016).

My research is based on scat analysis and aims at understanding the interannual and seasonal variations in the feeding habits of brown bears in south-central Sweden. I investigate the following questions: 1) Is there annual variation in the diet of bears? 2) Is there seasonal variation in the diet of bears? 3) Is there a dietary difference between male and female bears? 4) Is there a dietary difference between subadult and adult bears?

## 2. Methods

### 2.1 Study area

The study area was located in Dalarna and Gävleborg counties in south-central Sweden (Figure 1). The size of the study area was approximately 6,000 km<sup>2</sup> around the village of Tackåsen. The annual mean temperature ranges from -7°C in January to +15°C in July and the snow cover typically lasts from late October to early May (Zedrosser *et al.* 2006). The area is a rolling landscape with elevations from 175m to 725m above sea level (Elfström *et al.* 2008). The landscape is covered by forests interspersed with lakes and bogs, and is on a large scale influenced by human activities, such as wood extraction and forestry roads. The main tree species in the study area are Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). Broad-leaved trees, such as birch (*Betula pubescens*) and Eurasian aspen (*Populus tremula*), generally dominate in the clear-cuts of various ages. The most common ground layer species are juniper (*Juniperus communis*), bilberry, lingonberry, and crowberry (Elfström *et al.* 2008, Stenset *et al.* 2016). The bear density is about 30 bears per 1000 km<sup>2</sup> (Bellemain *et al.* 2005).

### 2.2 Scat collection

Scats from GPS-collared bears (Vectronic Aerospace, Berlin, Germany) were collected from late May until late September 2015-2018, as a part of the field activities of the Scandinavian Brown Bear Research Project ([www.bearproject.info](http://www.bearproject.info)). For more information on capturing and radio-collaring of bears see Arnemo *et al.* (2012). In 2015, a scat of every GPS-collared individual was collected on a weekly basis, and from 2016-2018 a scat from every GPS-collared individual was collected on a bi-weekly basis.

GPS locations from radio-collared bears were downloaded remotely and visualized in the software ArcGIS (Geographic Information System) 9.0 (2004; Environmental Systems Research Institute, Redlands, CA, USA). Based on the observed movement data, cluster sites corresponding to bed sites of bears were located (Rauset *et al.* 2012). A cluster site was defined as a minimum of three consecutive locations within a circle of 30-m radius, i.e. an area where bear spent  $\geq 1.5$  hour, suggesting resting time (Ordiz *et al.* 2011). The locations of bed cluster sites were downloaded into a handheld GPS (Garmin GPSMAP 64) and then visited in the field. A bed site was defined as bear bed only if it contained bear hairs (Ordiz *et al.* 2011). Scat of bears was only collected if only



one bed was present at a site, to avoid collecting samples from unknown individuals accompanying a radio-collared bear during the mating season. Whenever possible, the scat closest to the bed site was collected. Scats were stored individually in plastic bags, marked with a unique identification number, and stored frozen at  $-19^{\circ}\text{C}$  for later analyses.



**Figure 1.** Location of the study area for the collection of scats of GPS-collared brown bears in south-central Sweden.

### 2.3 Analysis of food items

The methods described by Hamer and Herrero (1987), Dahle *et al.* (1998), and Stenset *et al.* (2016) were used for dietary analysis of the collected scat samples. A sample was defrosted and the weight (in g) and volume (in ml, as measured by water displacement) was recorded. Then each sample was homogenized and 3-5 subsamples of ~6ml were taken for further analysis. Each subsample was placed in a 0.8 mm mesh and thoroughly rinsed with water. Then the food items left in the mesh were visually sorted, classified, and the percent volume of the following taxonomic categories was estimated: berries, insects, vertebrates, vegetative material, and miscellaneous (see Table 1 for further details). According to Mattson *et al.* (1991), visual estimates of percent volume correspond well with those based on exact volumes. Scat analyses were carried out by different volunteers in each year, however, all volunteers were trained and supervised by the same project supervisor.

For statistical analyses, I calculated the mean percent volume of each food item from the subsamples for each scat. I also calculated the frequency of occurrence (FO) and percent of fecal volume (FV) for each food item (Dahle *et al.* 1998, Stenset *et al.* 2016). However, not all food items are digested the same, and food items more difficult to digest might be overestimated, and *vice versa*, easily digestible food items might be underestimated (Hewitt and Robbins, 1996). To prevent such as bias, I used correction factors ( $CF_D$ ) for main food categories, to calculate the estimated dietary content (EDC) for each food item using the following formula (Hewitt and Robbins 1996, Stenset *et al.* 2016):

$$EDC [\%] = \frac{CF_D \times FV}{\sum CF_D \times FV \text{ for all food items}} \times 100.$$

These correction factors are derived from and are related to the amount of the residues in feces in relation to the amount of the food items ingested (Hewitt and Robbins 1996, Stenset *et al.* 2016). Based on Hewitt and Robbins (1996) and Stenset *et al.* (2016), I used the following correction factors: *Vaccinium* spp. and *Empetrum* spp.: 0.54; ants (*Formica* spp. and *Camponotus* spp.) and other insects: 1.1; bones and hairs: 2; graminoids and other vegetation: 0.24; oats: 0.26; and miscellaneous food items: 0.99. To convert dry matter to digestible energy (i.e., the energy available for assimilation), I used another group of correction factors ( $CF_E$ ) to calculate estimated dietary energy

content (EDEC) using the following formula (Hewitt and Robbins 1996, Stenset *et al.* 2015):

$$EDEC [\%] = \frac{CF_E \times EDC}{\sum CF_E \times EDC \text{ for all food items}} \times 100.$$

Based on Dahle *et al.* (1998) and Stenset *et al.* (2016), I used the following  $CF_E$ : *Vaccinium* spp. and *Empetrum* spp.: 11.7 (kJ/g); ants (*Formica* spp. and *Camponotus* spp.): 17.7 (kJ/g); other insects: 11.3 (kJ/g); bones and hairs: 18.8 (kJ/g); graminoids and other vegetation: 6.3 (kJ/g); oats: 8.4 (kJ/g); and miscellaneous: 0.99 (kJ/g). For the category hairs and bones, I used the same correction factor as for small mammals (Dahle *et al.* 1998). Category ants unidentified was measured during year 2018 only.

## 2.4 Statistical analysis

To analyze seasonal dietary differences, I divided the annual scat collection period (i.e., May to September) into two seasons: summer (from start of collection in late May to 31 July, n = 632 scats) and fall (from 1 August to end of collection in September, n = 326 scats) (Dahle *et al.* 1998, Stenset *et al.* 2016). I used non-parametric statistics (chi-square tests) to compare differences in FO between the years and seasons.

I used general linear models (GLM) (Zuur *et al.* 2009) to understand the variation in the consumption of main food items (bilberries, lingonberries, crowberries, insects, vertebrates, vegetation and miscellaneous material) between years, seasons (as categorical variable: summer, fall), sex (categorical: male, female), and age classes (categorical: subadult, adult). Because scats from several individuals were sampled multiple times, I also evaluated the use of generalized linear mixed models, with the same response and explanatory variables, and by including bear ID as random variable (Zuur *et al.* 2009). However, the results were almost identical (not presented) to results obtained with a GLM, and therefore only the results of the simpler GLM models are presented in the results section. Non-significant variables were removed in a backwards selection procedure, until the model only contained significant or suggestive terms (Zuur *et al.* 2009). The level of significance was set at  $p \leq 0.05$ , and p-values  $> 0.05$  and  $< 0.10$  were considered as suggestive. All statistical tests were conducted in RStudio 1.1.463 ([www.r-project.org](http://www.r-project.org)).

### **3. Results**

#### ***Is there annual variation in the diet of bears?***

An overall sample of 958 scats was collected and analyzed (328 in 2015, 164 in 2016, 160 in 2017, and 306 in 2018) (Table 1). The mean scat volume was  $754 \pm 484$  ml (SD) (range: 25-3200ml), and the mean scat weight was  $620 \pm 452$  g (range: 17-2634g).

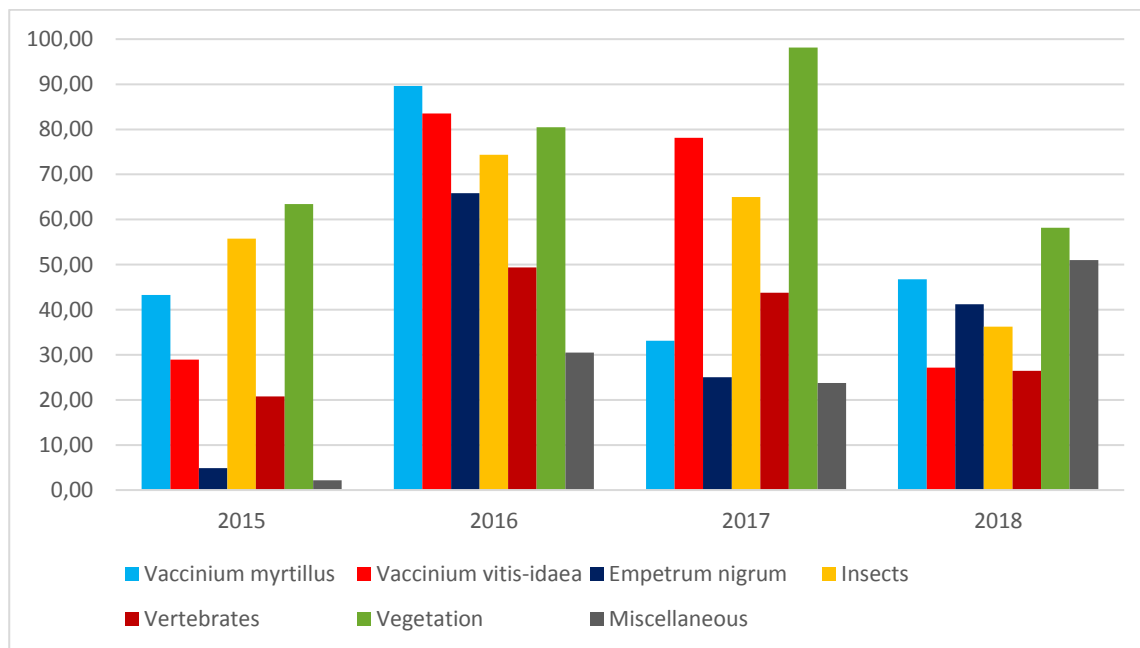
**Table 1.** Annual diet of brown bear in Sweden, 2015-2018. The food items are presented as frequency of occurrence (FO), fecal volume (FV), estimated dietary content (EDC) and estimated dietary energy content (EDEC). Food item: Ants unidentified was collected during year 2018 only.

Food item	2015 (n=328)			2016 (n=164)			2017 (n=160)			2018 (n=306)						
	FO	FV	EDC	FO	FV	EDC	FO	FV	EDC	FO	FV	EDC				
<i>Vaccinium myrtillus</i>	43.29	35.87	30.11	25.41	89.63	43.29	35.33	32.02	33.13	12.89	13.45	13.31	46.73	29.58	26.1	23.68
<i>Vaccinium vitis-idaea</i>	28.96	1.78	1.50	1.26	83.54	12.38	10.11	9.16	78.13	14.26	14.88	14.72	27.12	5.10	4.49	4.9
<i>Empetrum nigrum</i>	4.88	0.33	0.24	0.24	65.85	8.2	6.55	5.93	25.00	7.19	7.50	7.42	41.18	17.95	15.78	14.37
<b>Berries</b>	<b>46.04</b>	<b>38.94</b>	<b>33.39</b>	<b>27.33</b>	<b>98.78</b>	<b>67.51</b>	<b>57.52</b>	<b>50.99</b>	<b>84.38</b>	<b>36.76</b>	<b>41.75</b>	<b>40.92</b>	<b>64.71</b>	<b>53.29</b>	<b>47.48</b>	<b>43.28</b>
<i>Formica spp.</i>	44.51	9.33	15.95	20.36	39.63	1.33	2.21	3.3	46.25	1.42	3.2	4.52	8.82	0.90	1.61	2.21
<i>Camponotus spp.</i>	28.66	4.56	7.80	9.96	31.10	0.70	1.16	1.59	30.63	0.97	2.5	3.7	12.75	1.32	2.36	3.25
Ants unidentified	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	21.90	3.37	6.3	8.30
Eggs/Larvae	28.96	3.37	5.76	4.70	58.54	1.45	2.41	2.11	18.75	0.43	0.92	0.88	3.92	0.18	0.32	0.28
Other insects	17.38	2.45	4.20	3.42	59.15	5.65	9.39	8.22	76.25	6.57	13.97	13.35	20.26	1.23	2.21	1.94
<b>Insects</b>	<b>55.79</b>	<b>17.69</b>	<b>30.90</b>	<b>38.26</b>	<b>74.39</b>	<b>3.69</b>	<b>6.40</b>	<b>8.58</b>	<b>65.00</b>	<b>3.2</b>	<b>6.98</b>	<b>10.35</b>	<b>36.27</b>	<b>5.83</b>	<b>10.59</b>	<b>14.59</b>
Bones	13.11	0.87	2.72	3.69	25.61	1.71	5.16	7.52	26.88	1.29	4.97	7.90	8.50	0.57	1.85	2.71
Hair moose	18.90	5.62	17.48	23.70	29.88	3.7	9.29	13.52	26.88	2.28	8.81	14.00	19.61	4.78	15.58	22.79
Hair other	1.22	0.05	0.17	0.23	17.68	2.46	7.43	10.82	10.00	0.98	3.80	6.3	7.19	1.12	3.66	5.35
<b>Vertebrates</b>	<b>20.73</b>	<b>6.71</b>	<b>21.32</b>	<b>28.4</b>	<b>49.39</b>	<b>7.67</b>	<b>24.21</b>	<b>34.49</b>	<b>43.75</b>	<b>4.87</b>	<b>20.47</b>	<b>32.25</b>	<b>26.47</b>	<b>6.56</b>	<b>21.64</b>	<b>31.69</b>
Graminoids	30.79	16.24	6.6	2.75	69.51	9.12	3.31	1.61	78.75	21.75	10.9	5.37	37.58	10.17	3.97	1.95
Oats	9.45	10.12	4.9	2.48	18.29	7.35	2.89	1.88	7.50	4.76	2.39	1.70	14.71	10.15	4.30	2.81
Other veg. material	37.50	9.5	3.38	1.53	3.5	0.37	0.13	0.07	85.00	23.51	10.90	5.81	37.91	8.23	3.22	1.58
<b>Vegetation</b>	<b>63.41</b>	<b>36.30</b>	<b>13.83</b>	<b>6.10</b>	<b>80.49</b>	<b>17.86</b>	<b>6.76</b>	<b>3.23</b>	<b>98.13</b>	<b>53.54</b>	<b>53.54</b>	<b>14.26</b>	<b>58.17</b>	<b>28.91</b>	<b>11.45</b>	<b>5.62</b>
<b>Miscellaneous</b>	<b>2.13</b>	<b>0.35</b>	<b>0.55</b>	<b>0.27</b>	<b>30.49</b>	<b>3.27</b>	<b>5.11</b>	<b>2.71</b>	<b>23.75</b>	<b>1.81</b>	<b>1.81</b>	<b>2.22</b>	<b>50.98</b>	<b>5.42</b>	<b>8.85</b>	<b>4.82</b>

Based on FO, the dominant food items in 2015 were *Formica* spp. (44.51%) and bilberry (43.29%); in 2016: bilberry (89.63%) and lingonberry (83.54%); in 2017: other vegetation (85%) and graminoids (78.75%); and in 2018: miscellaneous (50.98%) and bilberries (46.73%) (Table 2, Figure 2). All major food categories showed significant annual variation, with the exception of the category vertebrates (Table 3).

**Table 2.** The Frequency of Occurrence of the 5 most important food items in brown bear scats in Sweden, 2015-2018.

Rank	2015 (n=328)	2016 (164)	2017 (n=160)	2018 (n=306)
1	<i>Formica</i> spp.	<i>V.myrtillus</i>	Other vegetation	Miscellaneous
2	<i>V.myrtillus</i>	Graminoids	<i>V.vitis-idaea</i>	<i>V.myrtillus</i>
3	Other vegetation	<i>V.vitis-idaea</i>	Graminoids	<i>E.nigrum</i>
4	Graminoids	<i>E.nigrum</i>	Other insects	Other vegetation
5	<i>V.vitis-idaea</i> ,eggs/larvae	Other insects	<i>Formica</i> spp.	Graminoids

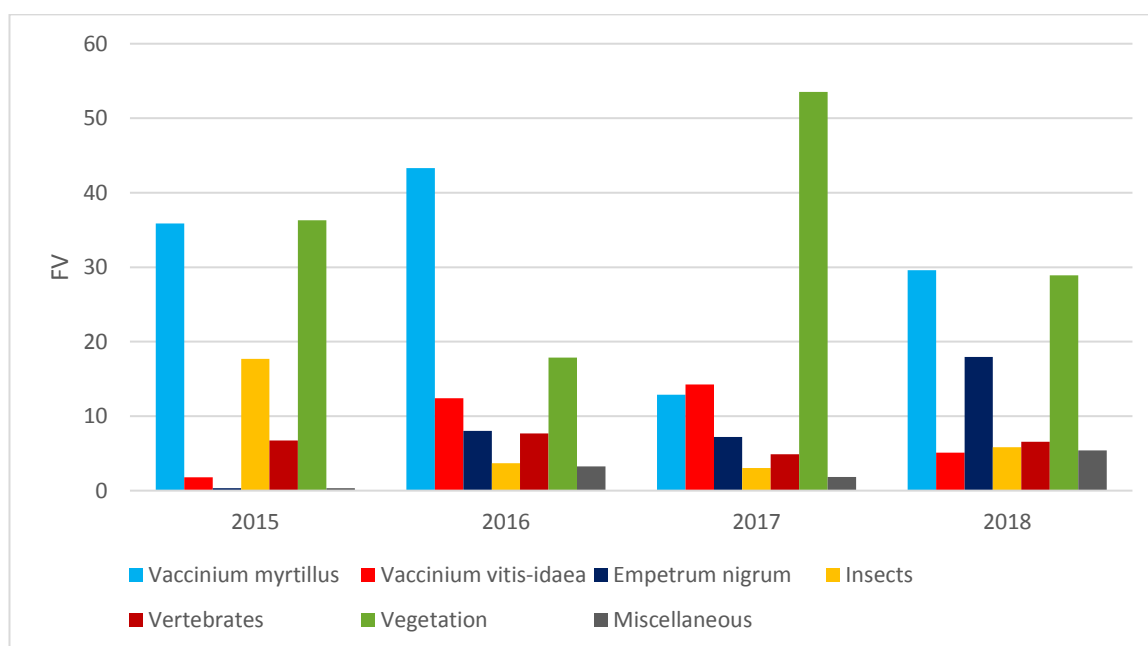


**Figure 2.** Differences in the Frequency of Occurrence (FO) of major food items in the scat of brown bears in Sweden, 2015-2018.

**Table 3.** Differences in the Frequency of Occurrence (FO) of food items in the scat of brown bears in Sweden, 2015-2018. Chi-square statistics were used to calculate p-values.

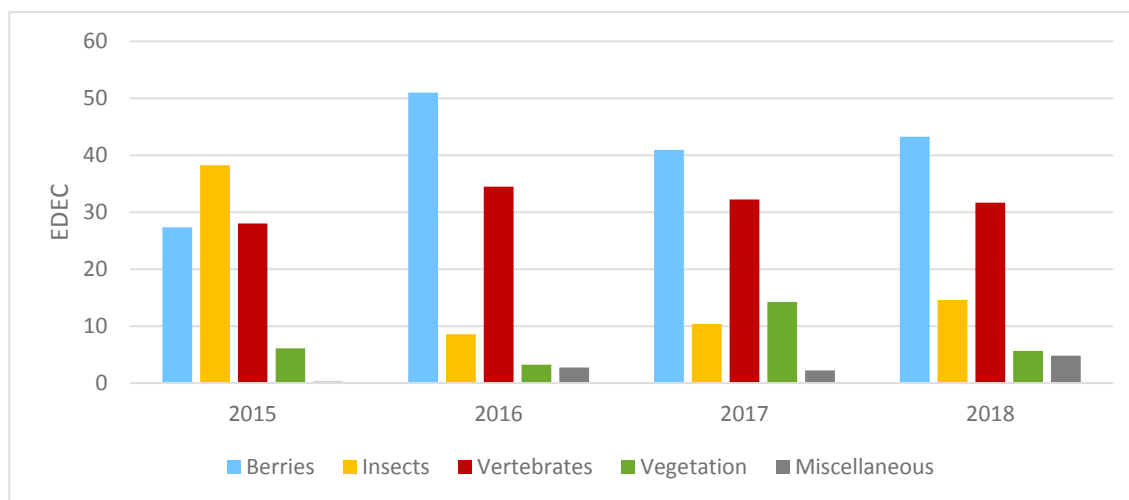
Food items	2015 (n=328)	2016 (n=164)	2017 (n=160)	2018 (n=306)	P-value
<i>V.myrtillus</i>	142	147	53	143	≤0.001
<i>V.vitis-idaea</i>	95	137	125	83	≤0.001
<i>E.nigrum</i>	16	108	40	126	≤0.001
Insects	183	122	104	111	≤0.001
Vertebrates	68	81	70	81	0.583
Veg.material	208	132	157	178	≤0.001
Miscellaneous	7	50	38	156	≤0.001

Results based on FV indicate that bilberry was the dietary item with the highest fecal volume in all years, except in 2017 (Table 1, Figure 3).



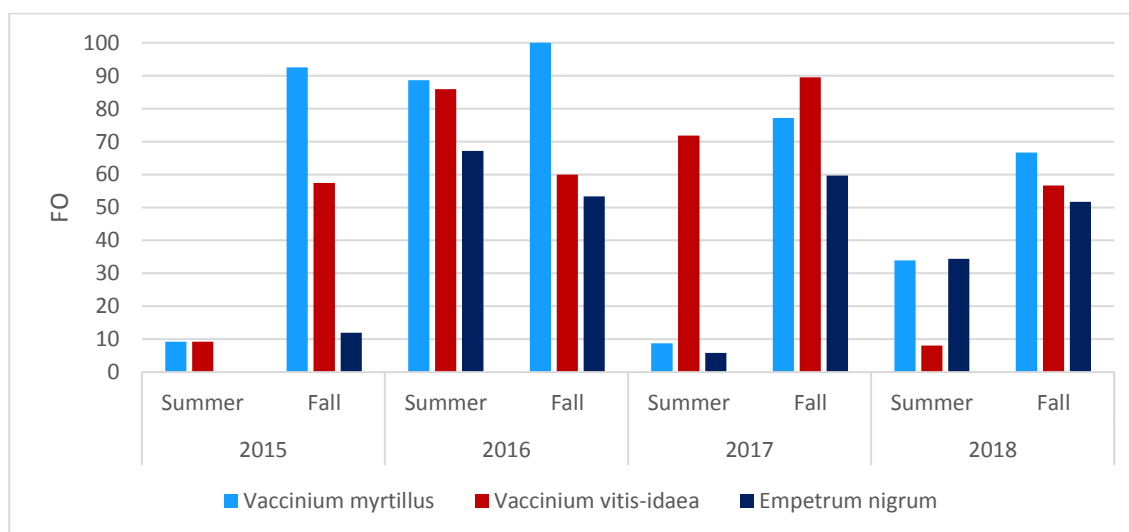
**Figure 3.** Differences in the Fecal Volume (FV) of major food items in the scat of brown bears in Sweden, 2015-2018.

The highest energy intake, based on EDEC from all years, was from bilberries (Table 1, Figure 4), except for 2015, when the highest energy intake was from insects. In general, the lowest energy intake for bears was from the category miscellaneous and from vegetative material (Figure 4).



**Figure 4.** Estimated dietary energy content (EDEC) of dietary items in the scats of brown bears in Sweden, 2015-2018.

Based on FO, the dominant dietary item during summer was vegetative material (79.11%) and insects (64.87%), during fall berries (93.56%) (Figure 5 and 6, Table 4). The EDEC was 1.54 % for vegetative material and 45.06 % for insects during summer. The main energy source for bears during the fall season was berries, with an EDEC > 98%; the most important berry species was bilberry, followed by lingonberry and then crowberry (Table 4).



**Figure 5.** Differences in the Frequency of Occurrence (FO) of berry species, between years and seasons (summer/fall), in the diet of brown bears in Sweden, 2015-2018.

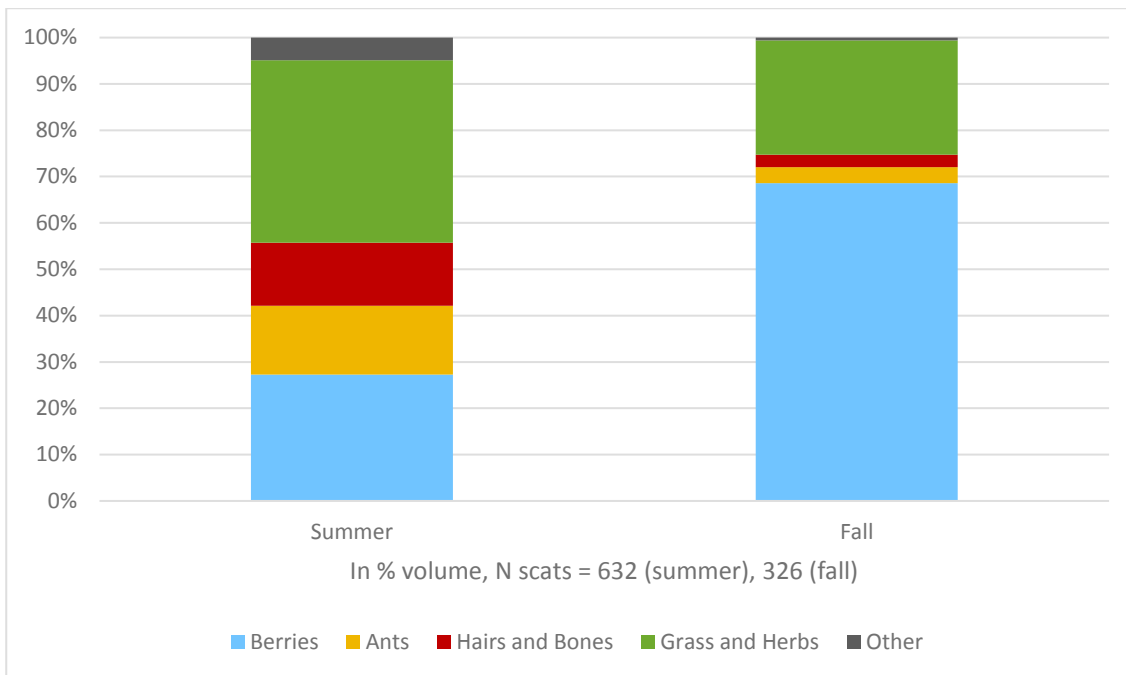


***Is there seasonal variation in the diet of bears?***

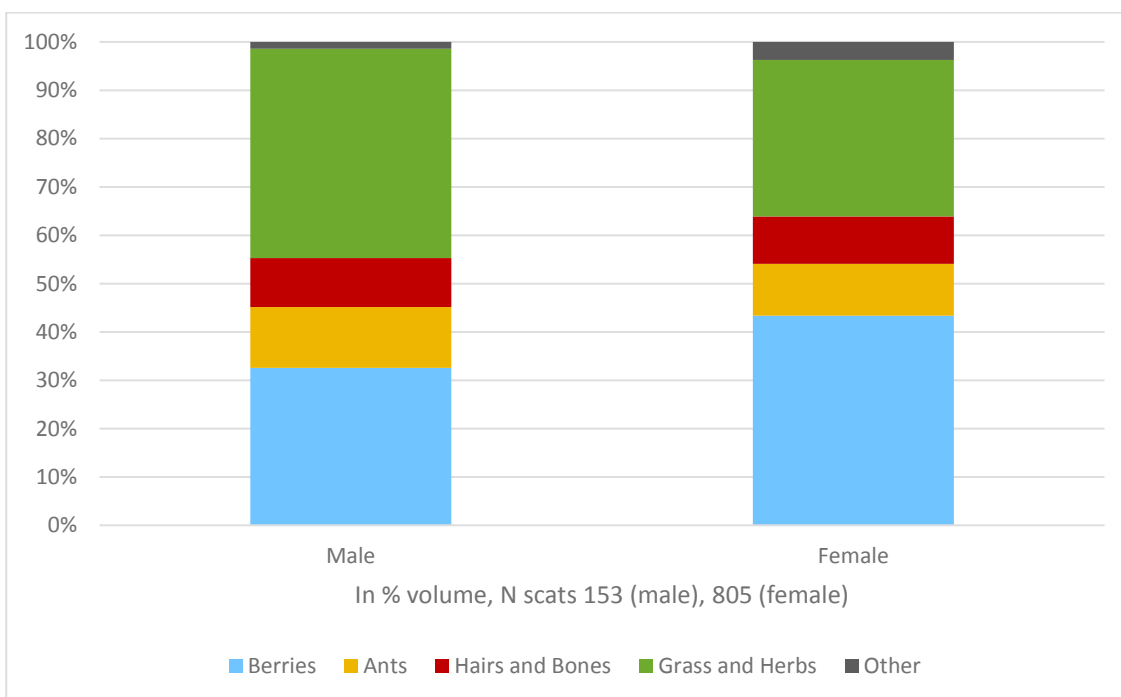
I found significant differences in the FO of food items in the scats of brown bears between summer and fall ( $\chi^2=109.13$ ,  $df=14$ ,  $p\text{-value}<0.001$ ). In general, the diet appeared more varied during summer compared to fall, when the main food item (~70%) were berries (Table 4, Figure 6).

**Table 4.** Seasonal diet of brown bears in Sweden, 2015-2018. The food items are presented as Frequency of Occurrence (FO), Fecal Volume (FV), Estimated Dietary Content (EDC), and Estimated Dietary Energy Content (EDEC).

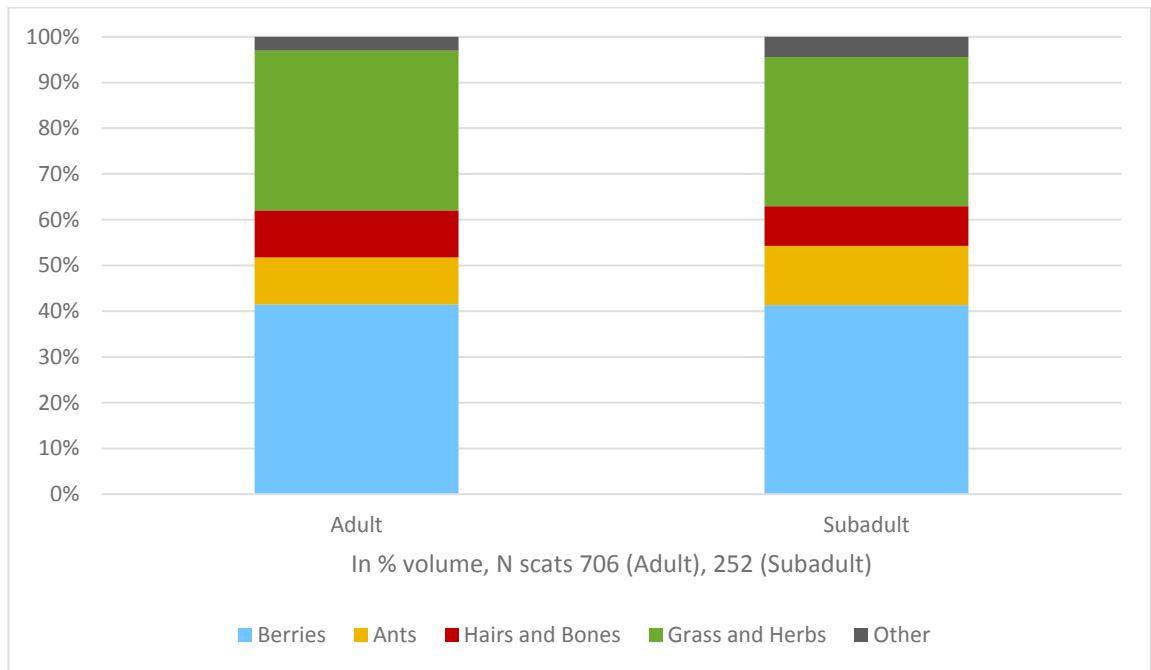
Food item	Summer (n=632)				Fall (n=326)			
	FO	FV	EDC	EDEC	FO	FV	EDC	EDEC
<i>Vaccinium myrtillus</i>	35.13	20.00	16.12	13.82	80.67	48.70	25.29	48.78
<i>Vaccinium vitis-idaea</i>	37.18	7.86	6.34	5.43	62.88	5.96	3.09	5.97
<i>Empetrum nigrum</i>	26.90	4.81	3.88	3.32	36.81	13.04	6.77	13.06
<b>Berries</b>	<b>53.96</b>	<b>61.93</b>	<b>48.05</b>	<b>39.21</b>	<b>93.56</b>	<b>91.50</b>	<b>88.36</b>	<b>98.22</b>
<i>Formica spp.</i>	40.66	5.52	9.07	11.76	16.87	1.47	1.55	4.53
<i>Camponotus spp.</i>	29.75	3.05	5.01	6.19	13.80	0.95	1.01	2.94
Ants unidentified	10.44	1.50	2.46	3.19	0.31	0.07	0.07	0.22
Eggs/Larvae	27.06	2.11	3.46	2.86	19.02	2.96	0.74	1.37
Other insects	40.66	3.86	6.33	5.24	24.85	2.96	3.13	5.84
<b>Insects</b>	<b>64.87</b>	<b>23.09</b>	<b>36.49</b>	<b>45.06</b>	<b>33.74</b>	<b>4.31</b>	<b>8.47</b>	<b>1.42</b>
Bones	20.09	1.51	4.49	6.19	8.28	0.29	0.56	1.72
Hair moose	30.06	6.63	19.79	27.25	7.36	0.60	1.15	3.56
Hair other	7.28	1.17	3.48	4.79	7.66	0.72	1.39	4.34
<b>Vertebrates</b>	<b>37.97</b>	<b>3.53</b>	<b>10.15</b>	<b>13.31</b>	<b>33.74</b>	<b>0.40</b>	<b>1.42</b>	<b>0.25</b>
Graminoids	57.91	20.29	7.27	3.35	27.61	4.73	1.40	1.13
Oats	9.65	5.41	2.10	1.29	17.48	13.51	3.38	4.68
Other vegetative material	47.31	12.39	4.44	2.05	24.85	5.90	1.36	1.41
<b>Vegetation</b>	<b>79.11</b>	<b>10.19</b>	<b>3.52</b>	<b>1.54</b>	<b>53.68</b>	<b>3.70</b>	<b>1.59</b>	<b>0.10</b>
<b>Miscellaneous</b>	<b>37.34</b>	<b>1.26</b>	<b>1.79</b>	<b>0.87</b>	<b>4.60</b>	<b>0.10</b>	<b>0.17</b>	<b>0.01</b>



**Figure 6.** Comparison of the average proportional volume of food items in scats of brown bears during summer and fall in Sweden, 2015-2018.



**Figure 7.** Comparison of the average proportional volume of food items in the scats of male and female brown bears in Sweden, 2015-2018.



**Figure 8.** Comparison of the average proportional volume of food items in the scats of adult (>4 years) and subadult ( $\leq 4$  years) brown bears in Sweden, 2015-2018.

### *Variation in the consumption of main food items*

#### *Bilberries*

There was a significant difference in the occurrence of bilberries between years. Bilberries also occurred significantly less often in bear scats in summer compared to fall, and there was a tendency for bilberries to occur more often in scats of female compared to male bears (Table 5). Age was removed as non-significant variable from the analysis.

**Table 5.** Results of a general linear model explaining the variation in the occurrence of bilberry in scats of brown bears in Sweden, 2015-2018.  $\beta$  denotes the parameter estimate, SE the standard error, t the t-value, and p is p-value.

<b>Variables</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>t</b>	<b>p</b>
Intercept	-0.052	0.231	-0.224	0.823
Sex (female)	0.418	0.242	1.729	0.084
Year 2016	1.134	0.243	4.672	$\leq 0.001$
Year 2017	-1.696	0.325	-5.217	$\leq 0.001$
Year 2018	-0.413	0.209	-1.988	0.047
Season (summer)	-2.196	0.191	-11.496	$\leq 0.001$

### *Lingonberries*

There was a significant difference in the occurrence of lingonberries between years (Table 6). Age, sex and season were removed as non-significant variables from the analysis.

**Table 6.** Results of a general linear model explaining the variation in the occurrence of lingonberry in scats of brown bears in Sweden, 2015-2018.  $\beta$  denotes the parameter estimate, SE the standard error, t the t-value, and p is p-value.

<b>Variables</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>t</b>	<b>p</b>
Intercept	-4.117	0.286	-14.421	$\leq 0.001$
Year (2016)	2.375	0.319	7.444	$\leq 0.001$
Year (2017)	2.421	0.319	7.594	$\leq 0.001$
Year (2018)	1.076	0.336	3.197	0.015

### *Crowberries*

There was a significant difference in the occurrence of crowberries between the years and seasons, when they occurred significantly less often during summer compared to fall. There was also a tendency for crowberries to occur more often in scats of female bears compared to males, and a tendency to occur more often in scats of adult compared to subadult bears (Table 7).

**Table 7.** Results of a general linear model explaining the variation in the occurrence of crowberry in scats of brown bears in Sweden, 2015-2018.  $\beta$  denotes the parameter estimate, SE the standard error, t the t-value, and p is p-value.

<b>Variables</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>t</b>	<b>p</b>
Intercept	-5.858	0.683	-8.581	$\leq 0.001$
Sex (female)	1.164	0.450	2.589	0.098
Year (2016)	3.448	0.594	5.806	$\leq 0.001$
Year (2017)	2.636	0.597	4.418	$\leq 0.001$
Year (2018)	3.789	0.565	6.707	$\leq 0.001$
Age (subadult)	-0.356	0.195	-1.844	0.065
Season (summer)	-1.604	0.182	-8.817	$\leq 0.001$

### *Insects*

There was a significant difference in the occurrence of insects between years and seasons (Table 8). Insects occurred significantly more often in bear scats during summer compared to fall. Age and sex were removed as non-significant variables from the analysis.

**Table 8.** Results of a general linear model explaining the variation in the occurrence of insects in scats of brown bears in Sweden, 2015-2018.  $\beta$  denotes the parameter estimate, SE the standard error, t the t-value, and p is p-value.

<b>Variables</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>t</b>	<b>p</b>
Intercept	-7.467	0.198	-37.706	$\leq 0.001$
Year (2016)	-2.038	0.280	-7.298	$\leq 0.001$
Year (2017)	-1.976	0.309	-6.395	$\leq 0.001$
Year (2018)	-0.883	0.151	-5.857	$\leq 0.001$
Season (summer)	1.636	0.206	7.960	$\leq 0.001$

### *Vertebrates*

There was a significant difference in the occurrence of vertebrates (ungulates) between the seasons (Table 9). Vertebrates occurred significantly more often in bear scats during summer compared to fall. Age, sex and year were removed as non-significant variables from the analysis.

**Table 9.** Results of a general linear model explaining the variation in the occurrence of vertebrates in scats of brown bears in Sweden, 2015-2018.  $\beta$  denotes the parameter estimate, SE the standard error, t the t-value, and p is p-value.

<b>Variables</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>t</b>	<b>p</b>
Intercept	-8.277	0.259	-31.917	$\leq 0.001$
Season (summer)	1.629	0.272	5.984	$\leq 0.001$

### ***Vegetation***

There was a significant difference in the occurrence of vegetative material between sexes and seasons (Table 10). Vegetation occurred significantly less often in scats of females compared to males. Vegetation also occurred significantly more in summer scats compared to fall. Age and year were removed as non-significant variables from the analysis.

**Table 10.** Results of a general linear model explaining the variation in the occurrence of vegetative material in scats of brown bears in Sweden, 2015-2018.  $\beta$  denotes the parameter estimate, SE the standard error, t the t-value, and p is p-value.

<b>Variables</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>t</b>	<b>p</b>
Intercept	-5.757	0.103	-56.103	$\leq 0.001$
Sex (female)	-0.357	0.092	-3.895	$\leq 0.001$
Season (summer)	0.466	0.870	5.383	$\leq 0.001$

### ***Miscellaneous***

There was a significant difference in the occurrence of miscellaneous material between the seasons (Table 11). Miscellaneous material occurred significantly more often in bear scats in summer compared to fall. Age, sex and year were removed as non-significant variables from the analysis.

**Table 11.** Results of a general linear model explaining the variation in the occurrence of miscellaneous material in scats of brown bears in Sweden, 2015-2018.  $\beta$  denotes the parameter estimate, SE the standard error, t the t-value, and p is p-value

<b>Variables</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>t</b>	<b>p</b>
Intercept	-5.076	0.433	-11.736	$\leq 0.001$
Season (summer)	2.048	0.448	4.572	$\leq 0.001$

## 4. Discussion

In general, I found significant variation in the diet of brown bears in south-central Sweden in relation to year, season, and also sex of bears. Age (adult vs subadult) only had suggestive effects on the diet choice, which is similar to findings by Elfström *et al.* (2014) from the same study area. During summer, the diet of bears was relatively varied, which correspond well with changes in the accessibility of major food sources, such as insect and ungulates after snowmelt, seasonality of plants and ripening of berries. Based on FO, the dominant food items during the summer were: vegetative material (79.11%) and insects (64.87%), with *Formica* spp. (40.66%) as the most important group. The highest energy and protein intake during summer comes from insects (45.06%). In comparison, berries dominated in the diet during fall (FO: 93.56%) and are also the food item that results in the highest energy intake, necessary for winter hibernation and reproduction (Welch *et al.* 1997; Swenson *et al.* 1999; Lopez-Alfaro *et al.* 2013). Bilberry was the most important berry over the entire study period, except for one year, when bears switched to lingonberries. The amount of vertebrates consumed remained stable between years. Vegetative materials played an important role in diet of bears during the entire study period, but interestingly, I found that males consumed significantly more vegetation than females. My results generally confirm that the brown bear is an omnivorous species able to optimize its diet in relation to the food sources available (Bojarska and Selva 2012), which has also been found in earlier studies in Scandinavia (Dahle *et al.* 1998, Swenson *et al.* 1999, Stenset *et al.* 2016) and in other parts of the world (Cicnjak, *et al.* 1987, Welch *et al.* 1997, Rode and Robbins 2000, Naves *et al.* 2006).

Berries were the most important food item during the hyperphagia period in fall for all years. At this time of the year, foods that are high in carbohydrates and/or fats, necessary for building up fat reserves and body mass important for hibernation, dominate in the diet of bears (Elowe and Dodge 1989, Pasitschniak-Arts 1993, Welch *et al.* 1997, Rode and Robbins 2000, Persson *et al.* 2001, Robbins *et al.* 2004, Naves *et al.* 2006). In comparison to brown bear populations in other parts of the world, bears in Scandinavia have no access to spawning salmon (*Oncorhynchus* spp., Hamer and Herrero 1987, Ohdachi and Aoi 1987, Pasitschniak-Arts 1993, Hilderbrand *et al.* 1999, Ordiz *et al.* 2013) or hard mast, such as nuts or seeds (Beeman and Pelton 1980, Cicnjak, *et al.* 1987, Ohdachi and Aoi 1987, Clevenger *et al.* 1992, Naves *et al.* 2006). Berry shrubs are the most common ground layer species in the Swedish boreal forest (Kardell 1979) and important food source not only for brown bears. Bilberries were the most consumed berry

species in our study area during all years, except 2017, which has also been found in previous studies in Scandinavia (Dahle *et al.* 1998,1999, Swenson *et al.* 1999, Hertel *et al.* 2016, Stenset *et al.* 2016). We found that berries constituted 98% of the EDEC during the fall, which is 30% more than found by Stenset *et al.* (2016) in the same study area. Our results are closer to findings of Dahle *et al.* (1998) from Jämtland, Sweden, ca. 300 km northwest of our study area, where the authors detected 80-81% EDEC from berries, but higher than 49% EDEC reported by Persson *et al.* (2001) from northeastern Norway, ca 1,100 km north–northeast of our study area.

Lingonberries were the second most important berry species in the diet of bears during our study period. Bears also switched to lingonberries in the fall of 2017, likely because the crop of bilberries was low. However, lingonberry was not only an important food item during fall, but also during early summer. Even though Stenset *et al.* (2016) detected that lingonberries were least preferred by bears in the same study area, we suggest (similar to findings by Hertel *et al.* (2016)), that lingonberries are often consumed by bears during both seasons, which is likely due to the fact that lingonberries overwinter on the bushes and are thus available for bears in early spring. In comparison, bilberries fall of the bushes in fall and are not available for bears in spring.

I detected consumption of crowberries during all years, mostly during fall, but not on the same scale as bilberries and lingonberries, which suggests that crowberries are the least used species among the three main berry species in our study area (Hertel *et al.* 2016). In comparison, Persson *et al.* (2001) detected that crowberries were the most common berry in the diet of brown bears in northeastern Norway, ca 1,100 km north–northeast of our study area. Based on the occurrence of crowberries shrubs in Scandinavia (which is lower than compared to bilberries and lingonberries), Dahle *et al.* (1998) found that the consumption of crowberries was higher than expected in the bear diet in south-central Sweden. Even though crowberries are one of the most important food sources for brown bears during fall (Persson *et al.* 2001, Stenset *et al.* 2016), our results are more similar to the findings of Johansen (1997), who showed that bilberries rather than lingonberries and crowberries dominate in the diet of brown bears in Sweden.

We detected a trend in the consumption of bilberries and crowberries, where males consumed these berries less often compared to females. This may be caused by the importance of high-energy foods for females, which have to put on comparatively more fat due to the needs of pregnancy and cub production (Blanchard *et al.* 1987).



In agreement with previous studies (Sweden: Dahle *et al.* 1998, Swenson *et al.* 1999, Stenset *et al.* 2016, Pyrenees: Elgmork and Kaasa 1992, Poland: Frąckowiak and Gula 1992), I found that insects were important food items in the diet of brown bears in Sweden, especially during the summer season. Ants are the most dominant insect food item during all years and occurred mostly during the summer season, where they constitute the highest energy intake (EDEC:45.06%). Similar results have also been found in other bear species, for example American black bears (*U. americanus*) (Landers *et al.* 1979, Eagle and Pelton 1983). Insects are a protein-rich food and add important macronutrient balance and essential amino acids to the bear's diet, which are unavailable in other spring foods (Swenson *et al.* 1999). In addition, protein-rich insects help to rebuild muscles after hibernation (Bojarska and Selva 2012), which may be especially important in northern areas where bears usually hibernate longer and lose more weight compared to more southern areas (Swenson *et al.* 2007). The consumption of ants and insects decreased during fall, when other energy-rich foods (i.e., berries) are available. Interannual variations in the consumption of ants are probably caused by seasonal and interannual variations in the availability of other food sources (Swenson *et al.* 1999). I did not find differences in the consumption of insects between sexes and age classes, in contrast with Johansen (1997), who found that male bears consumed less ants than females.

The most important group of ants in this study were *Formica* spp. (EDEC: 40.66%), which is similar to findings from Greece (Paralikiidis *et al.* 2010) and Slovenia (Große *et al.* 2003), but also in black bears in North America (Landers *et al.* 1979). However, this differs from findings of previous studies in my study area, where *Camponotus* spp. were the most important ant species (Swenson *et al.* 1999, Stenset *et al.* 2016). *Camponotus* spp. have a better digestibility for bears compared to *Formica* spp. (Große *et al.* 2003). The reasons for these differences in the consumption of ant species are not known, but could be related to differences in forestry techniques, that have resulted in less favorable habitat suitability for *Camponotus* species.

The consumption of ungulates did not vary from year to year, however, showed a significant variation between seasons. This supports the findings of many other studies that have shown that bears are highly omnivorous species and consume meat whenever possible (Mattson *et al.* 1991, Persson *et al.* 2001, Niedzialkowska *et al.* 2019); thus I agree, bears are good predators, especially on moose calves (Dahle *et al.* 1998, Stenset *et al.* 2016), sometimes also on domestic animals in Greece: Paralikiidis *et al.* (2010), in

Poland Frąckowiak and Gula (1992), in Norway Dahle *et al.* (1998), and are also often scavengers (Clevenger *et al.* 1992). My results are also similar to results by Swenson *et al.* (1999) and Dahle *et al.* (1998) from the same area, who showed that ungulates, especially moose, dominate in the bear diet mostly during summer. This timing in the use of ungulates coincides well with the period when moose calves are born (Swenson *et al.* 2007, Rauset *et al.* 2012) and are easily preyed upon by bears, but also with the availability of carcasses in early spring (Frąckowiak and Gula 1992, Persson *et al.* 2001). In other parts of Europe (Poland: Frąckowiak and Gula 1992; Spain: Clevenger *et al.* 1992), only small amounts of ungulates have been documented in the diet of bears, however, during all seasons. This suggests that brown bears in the North of Europe are more carnivorous than in the South (Pasitschniak-Arts 1993, Persson *et al.* 2001), potentially due to a lower variability in the food items available in spring and early summer.

Vegetative material occurred in the diet of bears during all years and seasons. During summer, bears consumed significantly more vegetation (mainly graminoids) compared to fall, when bears consumed less vegetation. However, the dominant vegetation in fall were oats (*Avena* spp.). High seasonal variation in the consumption of vegetation are common in bear diets across the world (Yugoslavia: Cicnjak, *et al.* (1987); Spain: Clevenger *et al.* (1992); Poland: Frąckowiak and Gula (1992)). Even though the energy intake via vegetation is relatively low, vegetation is a dominant dietary item during summer, which may be caused by the low concentration of undigestible parts, such as lignin and cellulose, and high concentrations of soluble proteins and nutrients important for bears (Hamer and Herrero 1987, Mealey 1980, Clevenger *et al.* 1992). I found a significant difference in the consumption of vegetation between the sexes, where males consumed more vegetative material than females. This may be potentially explained by different dietary preferences between the sexes, where females choosing rather energy-rich foods (berries), which help them produce comparatively more fat due to the needs of pregnancy and cub production (Blanchard *et al.* 1987); on the other hand, males may choose a more varied diet to optimize the intake of macronutrients and proteins, which helps them to maximize their mass gain and size, important for male-male competition (Rode and Robbins 2000, Costello *et al.* 2016).

It is difficult to collect scat samples in an unbiased manner, because differences in the detectability of scats in different habitats and/or differences in search effort may cause biases, the age and sex of the producing individuals are unknown, as is the date of

deposition (Dahle *et al.* 1998). However, due to the use of bed sites of GPS-collared bears as efficient way to collect samples, I am confident that such biases have been avoided, as information on the age and sex of the individual was known, bed site habitats are relatively similar among bears (Ordiz *et al.* 2011), and the time of deposition could be estimated relative accurately based on the time stamp of the GPS locations (Rauset *et al.* 2012). Some authors consider fecal analysis as a biased method for estimating diet composition (Frąckowiak and Gula 1992). However, this method is still a commonly used, accepted, inexpensive and low-tech method for coarse but reliable determination of diet composition in mammals, including bears (Robbins *et al.* 2004, Stenset *et al.* 2016). Because not all food items are digested the same, I used correction factors to give the best estimation of the true diet composition (Hewitt and Robbins 1996, Bojarska and Selva 2012, Stenset *et al.* 2016).

## 5. Conclusion

In conclusion, the diet of brown bears varies significantly among the seasons and shows variance among the years. Berries (in order of importance: bilberries, lingonberries, crowberries) represent the most important food item for brown bears in our study area during the pre-denning period in fall. Ants and vegetative materials are important food items during spring season.

Scandinavia is one of the areas where recent climate warming has been greatest (Walther *et al.* 2002, Stenset *et al.* 2016) and future climate change may affect the abundance and variation in food resources for bears (Bojarska and Selva 2012). Unlike in other populations in Europe (e.g., Rodríguez *et al.* 2007) or North America (Hewitt and Robbins 1996, Hilderbrand *et al.* 1999) that have access to several different food resources in fall, bears in northern Europe rely almost exclusively on berries during hyperphagia. The bears in this study were able to adapt to annual changes in the availability berry species by switching between to another berry species, for example, in years of failure of the bilberry crop, bears heavily rely on lingonberries instead. However, brown bears in Scandinavia depend almost exclusively on berries to gain body mass prior to hibernation and have few other abundant and carbohydrate-rich foods available (Stenset *et al.* 2016). In my study area, food availability has been shown to affect yearling offspring size (Dahle and Swenson 2003) and reproductive success (Zedrosser *et al.* 2007). Therefore, changes in climatic conditions that affect the abundance of berry species may be especially problematic for bears in Scandinavia (Stenset *et al.* 2016).

The present study is important for the documentation and understanding of feeding habits of brown bears, to understand the potential responses and adaptations of bears to climatic changes, and ultimately, for the effective management and conservation of the species.

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