Seasonal and annual variation in the diet of brown bears *Ursus arctos* in the boreal forest of southcentral Sweden

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Understanding a species' feeding ecology is essential for successful management and conservation, because food abundance can influence body mass, survival, reproductive success, movements, and habitat use. We describe annual and seasonal variations in the diet of brown bears *Ursus arctos* in southcentral Sweden, based on analysis of 527 fecal samples from 1994–1996 and 2000–2001. There was distinct seasonal variation in most of the 26 food items we documented. Ungulates, predominantly moose *Alces alces*, and insects comprised most of the estimated dietary energy content in spring and summer. Insects were represented almost entirely by ants, of which *Formica* spp. and *Camponotus herculeanus* were the most common. During autumn, berries dominated the diet. The most important berry species were bilberry *Vaccinium myrtillus*, crowberry *Empetrum hermaphoditum* and lingonberry *V. vitis-idaea*. We determined berry availability by inventorying 308 random plots three times for two consecutive years. These three berries occurred with great spatial, seasonal and annual variation in abundance. The bears showed the strongest positive preference for bilberries, a lesser positive preference for crowberries, but no preference for lingonberries. The proportion of berries in the autmn diet was stable between years, but the relative importance of the species changed, indicating that bears switched to crowberries when bilberries were less abundant. The effects of predicted future climatic change might have severe effects on the availability of the berries, which is the only important food available for fat acquisition prior to hibernation.

Knowledge about feeding ecology is essential for understanding the ecology of an animal species, as well as for successful management and conservation (Putman 1984). Ecologists often divide animals along a continuum from specialists to opportunists, with specialists using a narrow range of resources and generalists using a wide range of resources; when preferred food is scarce, generalists are better able to switch to alternative food items (Terraube et al. 2011). Thus, to successfully manage and conserve a species,

it is important to understand both a species' feeding ecology and how it is able to respond to changes in the availability of food resources. Changes in food availability can be a result of seasonal and annual variation in weather conditions, human-induced habitat changes, and climate change (Walther et al. 2002, Bojarska and Selva 2012).

Brown bears *Ursus arctos* are opportunistic omnivores with flexible ecological requirements (Krechmar 1995, Van Daele et al. 2012) and are able to change their diet in response to spatial and temporal variation in food resources (Mowat and Heard 2006, Bojarska and Selva 2012). Food abundance can influence their body mass, survival, and reproductive success, as well as movements, and habitat use

(Jonkel and Cowan 1971, Rogers 1976, Noyce and Garshelis 1997, 2011, Hilderbrand et al. 1999, Zedrosser et al. 2006, 2009, Van Daele et al. 2012). The period of predenning hyperphagia, during which bears must acquire fat reserves, is particularly important for survival and reproduction (Elowe and Dodge 1989), although the additional importance of protein is now being recognized (López-Alfaro et al. 2013, 2015). Poor autumn food availability has been found to increase movement and reduce reproductive success (Jonkel and Cowan 1971, Rogers 1976, Powell et al. 1997, Noyce and Garshelis 2011).

In spite of the importance of diet and its variation for wildlife populations, most studies of diet are descriptive and rarely assess the abundance and temporal variation of important food sources quantitatively. This is also true for bear populations, but see Hashimoto et al. (2003) for Asiatic black bears *Ursus thibetanus*.

The dietary habits of brown bears have been described for many populations in Europe and North America (Bojarska and Selva 2012). In the European boreal forest ecosystems, brown bears commonly consume vegetable matter, insects, and ungulates, with the importance of vertebrate meat increasing with latitude (Vulla et al. 2009). Studies of brown bear diet, based on scat studies or foraging sign, have been conducted in four areas of Scandinavia, (Haglund 1966, Elgmork and Kaasa 1992, Dahle et al. 1998, Swenson et al. 1999, Persson et al. 2001), but have not described the annual variation in diet or food resources.

Seasonally important food items in Scandinavia include carrion during spring, moose *Alces alces* and reindeer *Rangifer tarandus* calves in summer, free-ranging domestic sheep *Ovis aries* where present, and insects (mostly ants, *Componotus herculeanus*, *Formica* spp.) (Dahle et al. 1998, Swenson et al. 1999, Persson et al. 2001). In addition, brown bears frequently utilize bait and slaughter remains at dump sites (Steyaert et al. 2014). Berries of bilberry *Vaccinium myrtillus* and crowberry, *Empetrum nigrum* and *E. hermaphoditum,* are the most important food items during hyperphagia, with lingonberry *V. vitis-idaea* and a few other berry species being less important (Elgmork and Kaasa 1992, Dahle et al. 1998, Persson et al. 2001). All of these berry species show great annual variations in berry production in the Fennoscandian boreal forest (Wallenius 1999, Selås 2006). In addition, forest management can cause annual and spatial variation in brown bear foods, particularly ants and berries (Kardell 1979, Frank et al. 2015). Climate change is another factor that can affect the abundance and variation in food resources, especially because Scandinavia is one of the areas where climate warming has been greatest (Walther et al. 2002). The higher latitudes are also expected to experience an increase in late-winter thaws, which have been documented to cause major reductions in plant cover and berry production, especially bilberries (Bokhorst et al. 2008, 2011). In fact, warming during a 30-year period in northern Spain may have been an important factor in the reduction in *Vaccinium* berries in brown bear diet during that period (Rodríguez et al. 2007).

Our aim was to document the diet of brown bears in southcentral Sweden, focusing on annual and seasonal variation. In addition, we hypothesized that this generalist forager would switch among berry species during hyperphagia in response to variation in their availability. To do this, we also aimed to document the availability of berries.

Study area

The study area was located in the boreal zone and comprised approximately 12 000 km² in Dalarna and Gävleborg counties, southcentral Sweden (centered at 61°N, 15°E). Mean daily temperatures are –7°C in January and 15°C in June, there is 350–450 mm precipitation during the vegetation period, and snow cover generally lasts from late November to April or May (Elfström et al. 2008). The topography is mostly hilly and undulating, with elevations ranging from 175 to 725 m above sea level and thus below the timberline (Dahle and Swenson 2003a, Martin et al. 2010).

The forest is intensively harvested, consisting of 80% managed coniferous forest (Linder and Östlund 1998). Clearcuts at various successional stages cover large proportions of the area and approximately 40% of the forest is younger than 35 years (Swenson et al. 1999). Predominant tree species are Scots pine *Pinus sylvestris* and Norway spruce *Picea abies* (Zedrosser et al. 2006). Deciduous trees, such as birch, *Betula pubescens* and *B. pendula*, aspen *Populus termula*, and gray alder *Alnus incana* are common on clearcuts and early successional stages. The shrub layer consists mainly of common juniper *Juniperus communis*, willows *Salix* spp. and rowan *Sorbus aucuparia*, and the ground layer is dominated by dwarf shrubs, such as heather *Calluna vulgaris* and berry-bearing species, including bilberry, lingonberry and crowberry (Elfström et al. 2008).

There is a dense network of logging roads (0.7 km per km²) and the area is sparsely populated, with 4 to 7 habitants per km² (Martin et al. 2010, Ordiz et al. 2013). Bear density has been estimated to be about 30 bears/1000 km² (Bellemain et al. 2005).

Methods

Scat samples

Scats were collected when encountered in the forest and along roads during general field activities in 1994–1996 and 2000–2001. We did not make an effort to search for scats where they might have been concentrated, such as at ungulate kill sites. Encountered scats were individually identified to collection date and location, placed in plastic bags, and frozen at –18°C until later analysis. We estimated the time from defecation to scat collection based on freshness in relation to recent weather conditions (rain, sunshine, etc.) in order to place the scat into one of three seasons. We defined the seasons according to threshold dates related to bear diet; spring was defined as den exit to the start of the moose calving season (late March to 20 May, Swenson et al. (1997)) and summer from 21 May until the mean day of first berry ripening, as determined from field observations during the 1994–2001 study period (31 July). Autumn lasted from 1 August until den entry, which usually occurs in October (Friebe et al. 2001, Manchi and Swenson 2005).

We collected and analyzed 527 scats (108 from 1994, 144 from 1995, 102 from 1996, 114 from 2000, 59 from 2001) that were assigned to spring (n = 139), summer (n = 83) or autumn (n = 305). In 2000 and 2001, we collected scats during autumn only. Scat volume averaged 425 ± 235.5 ml (10–1900 ml). We identified a total of 26 separate food items.

Fecal analysis followed the procedure described by Hamer and Herrero (1987) and Dahle et al. (1998). We determined weight and volume (by water displacement) before washing each fecal sample over a 0.6 mm mesh. We homogenized each scat and took five subsamples of 6 ml. We examined these using a 6.3–30 stereoscope and a 40–630 microscope. We identified all food items visually to the lowest taxonomic level possible and sorted them. We estimated the percent volume of each item visually and used the mean of the five subsamples in further analysis. Visual estimates of percent volume correspond well with those based on exact volumes (Mattson et al. 1991). Scat volume averaged 425 ± 235 ml (10–1900 ml). We indentified a total of 26 food items and found no differences in the volume of individual scats related to the dominating food item in scats that contained more than 50% of one item (F = 1.66, DF = 2, p = 0.20). Therefore, we did not consider individual scat volume in the analyses. We present the results as frequency of occurrence (FO) and percent of fecal volume (FV). Correction factors (CF_D) were used to calculate estimated dietary content (EDC), to avoid underestimation of easy digestible items and potential bias (Hewitt and Robbins 1996), using the formula:

$$EDC_i[\%] \frac{CF_{Di} \times FV_i}{\sum CF_D \times FV \ \ for \ all \ food \ items} \times 100$$

Correction factors were derived from Hewitt and Robbins (1996); *Vaccinium* spp. and *Empetrum* spp. 0.54, *Rubus* spp 0.87, ants and other insects 1.1, fungi, cryptograms, forbs and berry shrub materials 0.26, large mammals 2, and small mammals 4.

A second group of correction factors (CF_E) was used to convert dry matter to digestible energy, in order to calculate estimated dietary energy content (EDEC) (Hewitt and Robbins 1996):

$$EDEC_i[\%] \frac{CF_{Ei} \times EDC_i}{\sum CF_E \times EDC \ \ for \ all \ food \ items} \times 100$$

The CF_E values we used were: berries 11.7, *Diptera* spp. and *Coleoptera* spp. 11.3, *Formica* spp 17.7, *Camponutus* spp. 20.6, *Hymenoptera* spp., insect fragments, eggs and larvae 17.7, fungi, graminoids and cryptams 6.3, forbs 8.4, large mammals 19.3, small mammals 18.8, birds 18.8, and unspecified meat 19.3 (Mealey 1980, Harting 1987, Pritchard and Robbins 1990, Dahle et al. 1998, Swenson et al. 1999). We could not find CF_E values for *Myrmica* spp. and *Cerviformica* spp., but assumed that they were the same as for *Formica* spp. Berry shrub materials were assumed to be equal to graminoids.

We identified berries and ants to the lowest taxonomic level possible for all species having a FO higher than 1% in any season or year. We considered all items with values < 1% as a 'trace' and assigned them a value of 0.5 in the calculations

to avoid underestimation. Anthill material, twigs, wood fragments, needles from coniferous trees and other items assumed to contribute little to total energy assimilation, regardless of their FO, were lumped into a separate category ('other'). We did not calculate EDC or EDEC for this category.

Plot inventories

To determine the average temporal and spatial distribution of berries, we examined 308 randomly chosen plots in forest habitat within a quadratic 400 km^2 area in the center of the study area (61°27′N, 14°52′E) during 2000 and 2001. Due to flooding, only 304 plots were visited in 2000. To avoid a subjective bias when choosing the exact localization of a plot, we chose the plot center by walking 0–9 m from the computer-generated coordinate. The distance was determined by the last digit in the north–south coordinate, and the direction was determined by a random number between 0–359. At each plot, we inventoried berry occurrence three times, mid- to late July, last week of August – first week of September, and last week of September – first week of October, by placing a 1×1 m portable quadrate 5 m from the plot center in three directions. We sampled one quadrate per inventory. Plots lacking flowers or berries during the first visit were not revisited that year. Measurements in each quadrate included height and percent cover for the foliage of each berry species. We picked all the berries in the quadrate, sorted them to species and degree of ripeness, and counted and weighed them. This enabled us to calculate the number of berries m^{-2}, berries m^{-3} foliage, and yield of ripe berries per m^2 for each species, as these are important parameters for foraging bears (Welch et al. 1997).

Cranberries *Vaccinium oxycoccus* comprised 0.6% and 2.5% of the total number of berries in 2000 and 2001, respectively; corresponding values for bearberries *Vaccinium uliginosum* were 1.3% in 2000 and 0.95% in 2001. As these species also comprised a minor portion of diet composition, we did not consider them in further analyses. We report only the number of ripe berries m^{-3} foliage to describe the change in berry availability during the three collection periods in autumn, because we obtained the same results when using number of berries m^{-2} and mass of ripe berries per m^3 foliage.

Data analysis

We calculated mean FO, FV, and EDEC values for each season. Berry shrub material, eggs, larvae, and unidentified insect parts were not included in 1994–1997, due to differences in scat analyses.

We compared the frequency of occurrence (FO) of major food item categories in different seasons with a χ^2 test. Differences in FV between dietary items between years were tested using a Wilcoxon rank sum test with continuity correction. Differences between groups and years were compared with χ^2-tests.

For 2000 and 2001, we compared the autumn diet with the berry abundance data from the random plots. Differences in availability between years were tested using the middle inventory (August–September), as this was
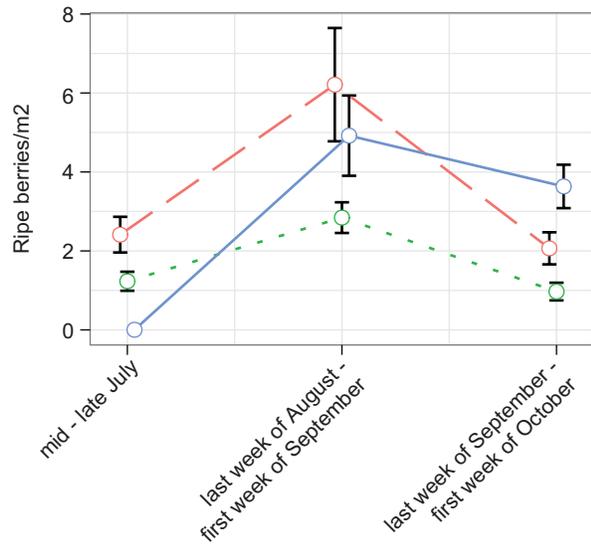
Figure 1. Mean number of ripe berries m^{-2} of billberry, lingonberry and crowberry on the random berry plots during the three inventory periods in 2000 and 2001 in southcentral Sweden. Error bars represent SD, dodged slightly horizontally for legibility. The dashed blue line is bilberry, continuous red line is lingonberry and dotted green line is crowberry.

the inventory with the greatest number of ripe berries for all species (Fig. 1) and most of the autumn scat samples were collected during August and September. Count data from plot inventories were log10 transformed prior to analysis to remove the skew in the data.

We used FV and the proportion of berries of each berry species from the inventories to calculate the Murdoch C preference index (Murdoch 1969);

$$C = \frac{U}{A}$$

where U = use of each berry species as defined as the overall FV of the berry species from all scats in relation to the sum of the FVs of all berry species from all scats, which was set to 100%, and A = availability, defined as the number of berries of a species collected in the random plots divided by the total number of berries collected. The logarithm of the index was used to produce symmetrical scales. χ^2-tests were used to test whether the index differed among the three main berry species.

We also compared berry abundance measurements between 2000 and 2001 on the second visit to the random plots (late August–early September) for each berry species with the Kruskal–Wallis one way analysis of variance. The level of significance of all tests was set at 0.05, but we comment on nonsignificant tendencies with a significance level < 0.10. All statistical tests were conducted in R 2.15.1 (< www.r-project.org >).

Results

Seasonal diets

Diet composition (FO) showed great variation among seasons and years (Table 1). When years were pooled, all major

Table 1. Frequency of occurrence of (FO) of major food item categories in brown bear fecal samples during the spring, summer, and autumn seasons in southcentral Sweden during the years of 1994–1996 and 2000–2001. Data were only available from the autumn in 2000 and 2001. Contributions below 1% are indicated by tr (trace).

Season	Category	1994	1995	1996	2000	2001
Spring	berries	66	14	54		
	insects	76	74	35		
	fungi	0	0	0		
	cryptograms	59	21	20		
	graminoids	83	66	50		
	forbs	24	tr	0		
	horsetails	tr	9	0		
	vertebrates	35	26	29		
Summer	berries	26	17	22		
	insects	80	77	78		
	fungi	0	0	11		
	cryptograms	26	20	0		
	graminoids	91	73	33		
	forbs	91	27	44		
	horsetails	tr	3	17		
	vertebrates	40	43	50		
Autumn	berries	98	98	100	99	97
	insects	39	26	30	79	93
	fungi	0	7	3	15	63
	cryptograms	tr	tr	tr	72	42
	graminoids	41	tr	23	47	85
	forbs	16	7	tr	13	73
	horsetails	5	0	tr	0	0
	vertebrates	9	14	27	13	3

food categories showed significant seasonal variation, except insects and horsetails *Equisetum* spp. (Table 2). The seasonal differences were evident for frequency, volume and estimated energy content for several dietary items (Table 3). In spring, the dominant food items were ants, plant material, and vertebrates (consisting exclusively of adult moose, because this season was before the calving season). Berries from previous autumn also were utilized. Vertebrates were the most important dietary item in terms of EDEC (Table 3).

In summer, EDEC was derived mostly from insects and vertebrates. The insect category was made up almost entirely of ants, as in other seasons. Species of the genera *Formica* and *Camponotus* were the most common (Table 3). Their relative proportion varied significantly among seasons ($\chi^2 = 18.076$, DF = 2, p < 0.001). Summer was the moose calving season and calf moose made the largest contribution to vertebrate EDEC (55%).

Table 2. Results of χ^2-tests comparing the mean frequency of occurrence (FO) of major food item categories in brown bear fecal samples during the spring, summer, and autumn seasons in southcentral Sweden, based on combined data from 1994–1996 and 2000–2001.

Category	χ^2	DF	p-value
Berries	56.0336	2	< 0.001
Insects	4.9135	2	0.086
Fungi	24.0745	2	< 0.001
Cryptograms	6.852	2	< 0.05
Graminoids	7.8636	2	< 0.05
Forbs	39.2463	2	< 0.001
Horsetails	4.4919	2	0.106
Vertebrates	16.9446	2	< 0.001

Table 3. Mean seasonal diet of brown bears in southcentral Sweden, based on combined data of fecal analyses from 1994–1996 and 2000–2001. Data are presented as frequency of occurrence (FO), percent fecal volume (FV) and estimated dietary energy content (EDEC). For summarizing categories, both identified and unidentified taxa were included. Contributions below 1% are indicated by t (trace) for clarity. Empty cells indicate that the item was not recorded in that season and dashes indicate that these categories were not recorded in all years in that season.

Food item	Spring (n = 141)			Summer (n = 93)			Autumn (n = 305)		
	FO	FV	EDEC	FO	FV	EDEC	FO	FV	EDEC
Berries	44.7	16.3	8.7	21.7	2.7	1.8	98.3	76.8	68
Vaccinium myrtillus	4.0	1.0	0.5	7.8	1.8	1.3	86.2	44.1	39.6
Vaccinium vitis-idaea	33.8	10.7	6.0	t	t	t	47.9	8.5	7.6
Empetrum hermaphroditum	22.3	5.3	2.3	6.8	t	t	74.3	23.1	20.9
Vaccinium uliginosum							3.3	t	t
Sorbus aucuparia				t	t	t	2	t	t
Rubus idaeus							1.6	t	t
Oxycoccus quadripetalus	t	t	t	t	t	t			
Insects	61.7	11.7	20.5	78.3	16.7	28.2	53.4	4.9	14.2
Hymenoptera	t	t	t	t	t	t	10.3	t	t
Coleoptera	t	t	t	t	t	t	1.5	t	t
Ants	60.3	11.7	20.3	78.3	16.7	28.2	32.5	4.1	11.1
Formica v.	56.0	10.7	16.8	55.7	5.0	8.3	27	1.6	4.3
Camponotusherculeanus	9.5	1.5	2.8	48.0	10.0	18.2	13.9	1.7	4
Myrmica spp.	3.7	t	t	14.8	t	t	6.6	t	t
Cerviformica spp.	3.5	t	t	t	t	t	12.7	t	1.1
Insect fragments*	—	—	—	—	—	—	52	t	t
Egg/larvaes*	—	—	—	—	—	—	60.3	1.7	3.9
Fungi				3.7	t	t	17.6	1.8	0.8
Cryptograms	33.3	t	t	15.3	1.0	t	23.1	1.2	0.5
Graminoids	66.3	21.7	3.0	65.7	25.0	3.7	39.2	2.7	0.9
Forbs	8.2	2.2	t	54.0	20.3	3.7	21.9	2.5	1.2
Horsetails	3.2	1.2	t	6.8	3.5	t	1.1	t	t
Shrub material*	—	—	—	—	—	—	98.2	7.2	1.6
Vertebrates	40.5	22.2	60.8	44.3	15.0	62.3	13.7	2.5	13.8
Other	73.7	16.7	—	77.3	16.0	—	56	5.6	—

*These items were not identified during 1994–1996, when the spring and summer samples were collected and analyzed.

The autumn diet consisted of berries, insects and vertebrates, of which berries were always the most important food item (FO > 96%, EDEC > 62%). Vertebrates and insects were of similar importance. Ranked by EDEC, the most important berry species were, in order of importance, bilberry, crowberry and lingonberry (Table 3).

Annual variation in diet

We found significant annual differences in FO for the following categories; insects ($\chi^2 = 70.5$, DF = 4, p < 0.001), fungi ($\chi^2 = 153.6$, DF = 4, p < 0.001), and vertebrates ($\chi^2 = 23.2$, DF = 4, p < 0.001) (Table). In terms of FV, fungi ($\chi^2 = 11$, DF = 4, p = 0.027) and plants ($\chi^2 = 11.9$, DF = 4, p = 0.018) differed significantly among years. Berry occurrence did not differ significantly among years when berries were considered as a group (Table 4). However, a significant annual difference was found in the FV for

bilberries ($\chi^2 = 24.6$, DF = 4, p < 0.001) and in both FO and FV for lingonberries (FO: $\chi^2 = 54.2$, DF = 4, p < 0.001, FV: $\chi^2 = 16.9$, DF = 4, p < 0.01) and crowberries (FO: $\chi^2 = 34.5$, DF = 4, p < 0.001, FV: $\chi^2 = 32.8$, DF = 4, p < 0.001). Based on FV in bear scats, the best years for bilberries were 1995 and 1996 and 2000 was a poor year, for crowberries, 2000 was the best year and 1996 was a very poor year. For lingonberries, 1994, 1996 and 2001 were good years and 1995 and 2000 were poor years (Table 4).

Spatial, seasonal and annual variation in berry abundance

All berry species occurred in a highly patchy distribution. The 10% of the plots with the highest number of berries by species contained 86% of the bilberries in 2000, and 80% in 2001. Corresponding results for lingonberries were 87% in 2000 and 86% in 2001 and for crowberries were 98% in

Table 4. Annual contribution of berry species to the autumn diet of brown bears in southcentral Sweden during 1994–1996 and 2000–2001, presented as frequency of occurrence (FO) and percent fecal volume (FV).

Dietary item	1994 (n = 44)		1995 (n = 58)		1996 (n = 30)		2000 (n = 109)		2001 (n = 59)	
	FO	FV	FO	FV	FO	FV	FO	FV	FO	FV
Vaccinium myrtillus	80	43	85	60	83	61	88	20	95	36
Vaccinium vitis-idaea	41	11	29	4	67	16	21	1	81	11
Empetrum hermaphroditium	82	26	81	23	30	2	94	46	85	19
Berries	98	82	98	90	100	79	99	67	97	66

Table 5. Comparison of the standing crops of ripe berries (measured as mean values of berries m^{-2}, berries m^{-3} foliage and yield in kg ha^{-1}) of the three main species of berries in the brown bear diet in southcentral Sweden between 2000 and 2001 using Mann–Whitney rank sum test with continuity correction. The values were calculated based on the random plot inventory during late August-early September, recognizing that some berries had fallen by that time and others were not yet ripe.

		Year		Statistics	
Standing crop	Berry species	2000	2001	W	p
Berries m^{-2}	Vaccinium myrtillus	2.3	4.2	123395.5	< 0.001
	Vaccinium vitis-idaea	13.0	6.6	144974.5	0.312
	Empetrum hermaphroditium	11.1	3.4	146559.5	0.074
Berries m^{-3} foliage	Vaccinium myrtillus	57	106	120870.5	< 0.001
	Vaccinium vitis-idaea	260	149	145617	0.180
	Empetrum hermaphroditium	1304	458	145892.5	0.055
kg ha^{-1}	Vaccinium myrtillus	5.3	12.5	111118	< 0.001
	Vaccinium vitis-idaea	9.9	13.4	130120.5	0.025
	Empetrum hermaphroditium	28.9	7.7	142163.5	0.151

2000 and 96% in 2001. When considering both years, 54% of the plots did not have berries of any species present.

The number of bilberries m^{-3} foliage differed significantly among the three inventories in both years (2000: H = 18.9, DF = 2, p < 0.001; 2001: H = 17.8, DF = 2, p < 0.001), as it did for lingonberries (2000: H = 86.4, DF = 2, p < 0.001; 2001: H = 89.9, DF = 2, p < 0.001). For crowberries, the three inventories did not differ significantly (2000: H = 1.1, DF = 2, p = 0.583, 2001: H = 2.8, DF = 2, p = 0.241).

Bilberries were significantly more abundant in 2001 than in 2000, both in terms of berries m^{-2}, berries m^{-3} foliage and yield (kg ha^{-1}) (Table 5). For lingonberries, however, only the yield was significantly different between years, and was higher in 2001. The lower yield of lingonberries in 2000, despite higher berry densities, was due to a low proportion of ripe berries in the second sampling period. No significant annual variation was found for crowberries, although there was a tendency towards more berries in 2000, especially regarding berries m^{-2} (p = 0.07) and berries m^{-3} foliage (p = 0.055) (Table 5).

Use of berries according to their occurrence during hyperphagia

We could only evaluate the effect of berry abundance on the annual differences in diet composition for 2000 and 2001. There were significant differences in the FV of the berry species in both years (2000: H = 177.8, DF = 2, p < 0.0001; 2001: H = 26.0, DF = 2, p < 0.0001). The FV of bilberries was significantly greater in 2001 than in 2000 (two-sample t test, t = 5836, p = 0.005), as it was for lingonberries (t = 7184.0, p < 0.0001). Crowberries, however, showed the opposite pattern (t = 3594.0, p < 0.001).

The Murdoch C preference index indicated significant differences in preferences among berry species both in 2000 (χ^2 = 83.2, DF = 2, p < 0.001) and in 2001 (χ^2 = 26.9, DF = 2, p < 0.001), with similar orders and magnitudes of preference in both years. The strongest positive preference was found for bilberries and a weaker positive preference was found for crowberries. Lingonberries were not preferred in either year (Fig. 2).

Discussion

We found that the diet of brown bears varied significantly among seasons and that the seasonal diet varied among years for most food items. As we hypothesized, we found that brown bears switched their foraging in relation to to the availability of bilberry, the most selected berry species during hyperphagia.

The wide dietary range with distinct seasonal variation in the food habits of brown bears that we documented has also been found in earlier studies in other areas in Scandinavia
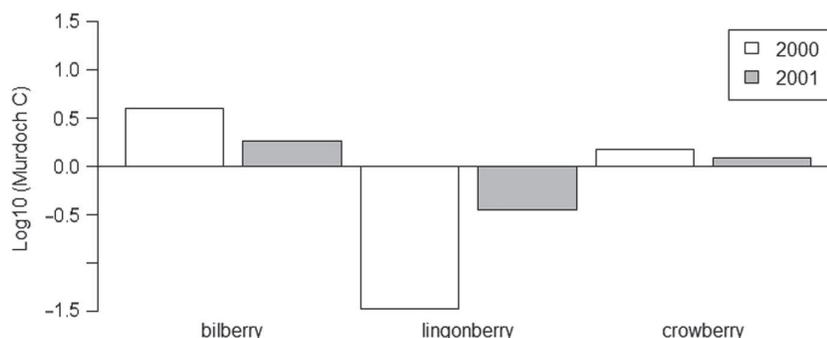

Figure 2. Murdoch C preference index for *Vaccinium myrtillus*, *Vaccinium vitis-idaea* and *Empetrum hermaphroditum* shown by brown bears in southcentral Sweden, calculated as the relationship between use (proportion of fecal volume, when total fecal volume was set to 100%) and availability (absolute number of picked berries divided by the total amount of all species). The logarithm of the index was used to produce symmetrical scales.

(Elgmork and Kaasa 1992, Dahle et al. 1998, Persson et al. 2001). The seasonal shifts coincided with changes in resource availability, most notably the seasonality of plants, birth of moose calves, and ripening of berries. Berries was the most important food item during the predenning hyperphagia period in all of these studies.

The importance of vertebrates in our study was less than in other studies from Scandinavia (Elgmork and Kaasa 1992, Dahle et al. 1998, Persson et al. 2001). This could be explained by differences in species availability, because free-ranging domestic sheep *Ovis aries* and domestic reindeer *Rangifer tarandus* were absent in our study area. Elgmork and Kaasa (1992) did not report moose in the scats they analyzed. It was difficult to compare the use of moose in our study and those of Dahle et al. (1998) and Persson et al. (2001), because they reported difficulties in distinguishing between hairs of moose and reindeer. The high proportion of ungulate prey in the bears' diet during summer coincided with the period when they prey on moose calves (Swenson et al. 2007, Rauset et al. 2012). The predation rate on adult moose by bears on our study area is low (Dahle et al. 2013), which suggests that much of the ungulate EDEC in spring likely came from scavenging, rather than predation.

In agreement with earlier studies in Europe, we found that myrmecophagy was important (Swenson et al. 1999, Große et al. 2003). The ant genera *Formica* and *Camponotus* dominated the insect category and were the second largest contributors to EDEC during spring and summer. Coogan et al. (2014) found that ants can be an important food item for brown bears, because of their favorable macronutrient balance for bears. We found that myrmecophagy showed no interseasonal variation, but the FO of ant genera varied significantly by season. The use of *Formica* was most seasonally stable and *Componotus* were used most during the summer. *Componotus* ants became available to bears later in the year than *Formica* ants (Swenson et al. 1999). Compared to berry yields, ant populations are likely to be relatively stable in their annual abundance. Both vertebrates and ants yield protein necessary for mass gain (Robbins et al. 2007, López-Alfaro et al. 2013).

As expected, berries constituted the most important food item during hyperphagia in autumn. This supports previous findings that the majority of autumn fat reserves come from carbohydrates from berries (Welch et al. 1997). We found that berries constituted 68% of the estimated dietary energy content in autumn, which was intermediate between the 49% reported from northeastern Norway, ca 1100 km north–northeast of our study area (Persson et al. 2001) and the 80–81% documented from Jämtland, Sweden, ca 300 km northwest of our study area (Dahle et al. 1998).

Previous studies conducted farther north in Scandinavia have found that crowberry was the most important berry species during hyperphagia, based on EDEC in autumn, followed by bilberry (Dahle et al. 1998, Persson et al. 2001). Elgmork and Kaasa (1992) found that the two species were of approximately equal importance in southeastern Norway, ca 350 km southwest of our study area. In our study, we found that bilberry was the most important in terms of FO, FV and EDEC, followed by crowberry and then lingonberry.

Dahle et al. (1998) suggested that crowberry appeared to be selected over bilberry, based on the percent cover of foliage on their study area. In our study, we found that bilberry was most strongly preferred and that lingonberry was least preferred, based on occurrence of berries, which is a better parameter to measure to evaluate selection.

Bears should select berry species that maximize energy and provide a balanced nutrient intake (Coogan et al. 2014) in addition to growing in a clustered manner, allowing the bears to reduce search time, take larger bites, and thus forage more efficiently (Welch et al. 1997). Eriksson and Ehrlén (1991) reported that both the carbohydrate content and mean fresh berry weight were much higher in bilberries (31.1% of dry weight and 0.48 g, respectively) than in lingonberries (15.4%, 0.25 g) or crowberries (14.4%, 0.14 g). During the two years of berry inventory, crowberry showed the greatest concentration of berries (annual means of 458 and 1304 berries m^{-3} foliage), lingonberry was intermediate (149 and 260), and bilberries showed the lowest concentration (57 and 106). Welch et al. (1997) showed experimentally that maximum bite rates of brown bears were depressed when initial fruit density fell to $<$ 50 berries m^{-3}. They conluded that tall, leafy shrubs, such as bilberry in our study, produce fewer, singly spaced berries that are obscured by relatively large leaves, causing bears to search more for and to select individual berries, resulting in lower bite rates and smaller bite sizes. In contrast, they concluded that compact, low-growing berries, which produces a carpet of closely spaced berries, such as crowberry and lingonberry in our study, allow higher bite rates, allowing bears to increase daily mass gain. Based on this, we explain the selection for bilberry that we observed to be due to the species' large and nutritious berries, even if they were the least concentrated. We explain the lesser degree of selection for crowberries on the very high concentration of berries, which provided high foraging efficiency. However, we acknowledge that other factors may be important.

Total berry yields can fluctuate greatly between years in the boreal forest, although yields of crowberry are generally more stable (Wallenius 1999). Nevertheless, we found that the occurrence and volume of combined berries in the bears' diet was constant across years, suggesting that bears compensated for changes in the abundance of one species by switching to other species. In 2000 and 2001 we had data on both use and availability of berries. Bilberries were about twice as available in 2001 as in 2000 and their FV in scats was 1.6 times higher in 2001. Based on FV in bear scats, 2000 was the poorest bilberry year during our study. During 2000, the FV of crowberries in bear scats was the highest we documented, and was 1.4 times higher than in 2001. Although there was no statistical difference in crowberry abundance between the years, there was a tendency towards higher abundance in 2000 (p $<$ 0.10). Thus, we conclude that the bears compensated for low bilberry availability in 2000 by switching to crowberries. Lingonberries had a higher yield in 2001 than in 2000 and had a higher FV in bear scats in 2001, but this species was not selected by bears during 2000 or 2001. Nevertheless, Elfström et al. (2014) reported that lingonberry occurred more often in

bear feces (FO) than both bilberry and crowberry, based on DNA metabarcoding of feces collected on our study area during 1 May–1 October 2010. Unfortunately, we do not have data on berry availability in 2010 and do not know if it had been a poor year for both bilberries and crowberries. We found that lingonberries were more available to bears later in the autumn than the other two species, providing the possibility that bears used lingonberry more late in the autumn and that we had underestimated its use then. We do not consider this to be a major bias, however. Nilsen (2002) did not find a significant trend in the FV of lingonberry in bear scats on our study area during the period from late July to early October 2001.

Feces analysis is a generally accepted and commonly used methods to determine diet in mammals, including bears (Kohn and Wayne 1997, Robbins et al. 2004, Klare et al. 2011). As items vary in their susceptibility to digestion, we used correction factors (CF) to give the best approximation of the true diet (Hewitt and Robbins 1996, Klare et al. 2011, Bojarska and Selva 2012). Of particular interest is the CF for meat, which depends on the amount of bone, skin and hair consumed. Grade of depletion of the carcass therefore affects CF. However, Persson et al. (2001) found, using a sensitivity analysis, that varying CF from 1.0 to 3.0 only had a moderate effect on EDEC. Nevertheless, the results regarding vertebrates reflect one's choice of CF (López-Alfaro et al. 2015).

Scandinavia is one of the areas where recent climate warming has been greatest (Walther et al. 2002) and future climate change may affect the abundance and variation in food resources. Experimental studies have shown that multiple late winter thaws, which are expected to increase at higher latitudes, caused major reductions in berry production, especially bilberries (52–95%) and crowberries (11–75%), and high shoot mortality for all species (bilberry 80%, crowberry up to 52%, lingonberry 51%) (Bokhorst et al. 2011). These results suggest that late winter thaws could have a major affect on the availability of berries, which is the main food source for the bears in our study area during the hyperphagia period prior to hibernation. Rodríguez et al. (2207) suggested that warming over 30 years was an important reason why brown bears in northern Spain switched from *Vaccinium* berries to other foods during hyperphagia. However, we found that 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. In addition, brown bears can optimize their micronutrient diet in the autumn when foraging primarily on berries (Coogan et al. 2014). On our study area, food availability has been shown to affect yearling offspring size (Dahle and Swenson 2003b) and reproductive success (Zedrosser et al. 2007). Other studies also have shown a relationship between berry abundance and reproductive success in bears (Jonkel and Cowan 1971, Rogers 1976, Young and Ruff 1982, Powell et al. 1997). Therefore, a major decline in berry availability may greatly reduce the carrying capacity of the Scandinavian boreal forest for brown bears. Our results from 1994–2001 can serve as a reference point for future studies of the diet of brown bears in the area.

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