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Authors: Persson, Inga-Lill, Wikan, Steinar, Swenson, Jon E., and Mysterud, Ivar

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The diet of the brown bear *Ursus arctos* in the Pasvik Valley, northeastern Norway

Inga-Lill Persson, Steinar Wikan, Jon E. Swenson & Ivar Mysterud

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The seasonal composition of and the annual variation in the diet of the brown bear *Ursus arctos* in the Pasvik Valley, northeastern Norway, were estimated based on the analysis of 137 bear scats. The importance of moose *Alces alces* and reindeer *Rangifer tarandus* in the diet was given special attention, because results from Russia suggest that brown bears are generally more carnivorous in the north. Ungulates, especially adult moose, comprised the most important food item for bears in the Pasvik Valley during spring and summer, contributing 85 and 70% of the Estimated Dietary Energy Content (EDEC), respectively. During autumn, when the bears have to build up fat reserves and increase lean body mass for hibernation, berries were the most important food item, contributing 49% of the EDEC, but ungulates were still important, contributing 30% of the EDEC. Insects and vegetation were of low importance in all seasons. The proportion of ungulates in the diet of brown bears in the Pasvik Valley was considerably higher than farther south in Scandinavia, and this regional difference is important concerning bear and moose management in northern areas.

Key words: brown bear, diet, management, moose, northern areas, Norway, ungulates

Inga-Lill Persson & Ivar Mysterud, Department of Biology, University of Oslo, P.O. Box 1066 Blindern, N-0316 Oslo, Norway*
Steinar Wikan, Svanhovd Environmental Center, N-9925 Svanvik, Norway
Jon E. Swenson, Department of Biology and Nature Conservation, Agricultural University of Norway, Box 5014, N-1432 Ås, Norway

**Present address: Department of Animal Ecology, Swedish University of Agricultural Sciences, SE-90183 Umeå, Sweden - e-mail: inga-lill.persson@szooek.slu.se*

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The population of brown bears *Ursus arctos* in Scandinavia is increasing (Sæther, Engen, Swenson, Bakke & Sandegren 1998), which implies an increase in bear numbers, density and distribution in Norway and Sweden in the future. Documenting the diet of Scandinavian brown bears is thus important to help predict the consequences of the return of this species to former habitats. Dietary estimates are an essential first step in understanding the productivity and density of current bear populations (Hilderbrand, Schwartz, Robbins, Jacoby, Hanley, Arthur & Servheen 1999, Jacoby, Hilderbrand, Servheen, Schwartz, Arthur, Hanley, Robbins & Michener 1999).

As a result of regional differences in the quality and availability of foods, brown bears have a broad diet range among regions (Krechmar 1995, Hilderbrand et al. 1999, Jacoby et al. 1999). Therefore, it is important for bear management in Scandinavia to document the variation in and the composition of the diet of several bear populations. Dietary studies of brown bears in Scandinavia have been conducted in central-south Norway (Elgmork & Kaasa 1992), south-central Sweden (Johansen 1997, Opseth 1998) and central Norway and Sweden (Dahle, Sørensen, Wedul, Swenson & Sandegren 1998), but no studies have been conducted in northern Scandinavia.

One aspect of the diet of brown bears that may vary geographically is the importance of meat. Studies from northern European Russia and northeastern Siberia suggest that brown bears are more carnivorous in northern than in southern areas (Kaleckaya 1973, Danilov 1983, Chernyavskii & Krechmar 1993, Krechmar 1995), and if the bear population is large enough, it has even been reported to bring about a decline in the number of moose *Alces alces* in the north (Kaleckaya 1973). Results from dietary studies of bears in southern and central Scandinavia indicate that bear-killed wild ungulates are not a major food item (Elgmork & Kaasa 1992, Opseth 1998, Dahle et al. 1998), except for calves in early summer (Opseth 1998). Many hunters are worried about what impact increasing populations of bears might have on the moose population and its hunting yield (Swenson, Sandegren, Bjärvall & Wabakken 1998). The results reported from Russia indicate that this concern might be most warranted in the north, and bears in the north may also kill more reindeer *Rangifer tarandus* than has been documented farther south.

The composition of the diet may also vary annually (Mattson, Blanchard & Knight 1991). Because of the relationship between diet and reproduction (Hilderbrand et al. 1999), annual variation in the diet might contribute to an annual variation in reproductive success.

The goal of our study was to document the seasonal composition of the diet of brown bears in northern Scandinavia, and to compare it with that of southern populations. Special attention was given to the importance of wild ungulates and semi-domestic reindeer in the diet. The importance of free-ranging domestic sheep *Ovis aries* in the bears' diet was not an objective of this study, because free-ranging sheep did not occur in the Pasvik Valley during the study period.

Study area

The study was conducted in the Pasvik Valley (1,330 km^2), in the municipality of Sør-Varanger, situated in the eastern part of the county of Finnmark (69°N, 28°E) at the border between Norway, Finland and Russia. The landscape is dominated by low moraine ridges ranging in elevation within 100-360 m a.s.l, and lakes and bogs cover large areas. The precipitation during the vegetation period ranges within 265-800 mm; the coastal areas are moister than the central parts of the valley. Snow covers the ground from mid-October to mid-May, sometimes to the end of May. The forest is dominated by Scots pine *Pinus sylvestris* and mountain birch *Betula pubescens*. Crowberry *Empetrum hermaphroditum*, bilberry *Vaccinium myrtillus* and cowberry *Vaccinium vitis-idaea* are common in the ground vegetation. Communities of tall forbs like meadow-sweet *Filipendula ulmaria* and wood cranesbill *Geranium sylvaticum* occur along rivers, brook courses and in richer sites in the birch forest. Hills higher than 250 m exhibit high mountain vegetation.

The bear population in the Pasvik Valley was estimated to be a minimum of 5-13 bears (4-10/1,000 km^2) during the study period 1976-1982 and is in the peripheral area of the Russian-Finnish-Norwegian bear population (Wikan, Mysterud & Haagenrud 1994, 1999a, 1999b). This area has been estimated to contain about 30% of the total number of 26-55 bears in Norway (Swenson & Wikan 1996). Moose at a density of about 300-400/1,000 km^2 in winter and semi-domestic reindeer were potential prey for the bears (Wikan et al. 1994). The number of reindeer in the study area was about 2,500 in autumn and early winter, and some hundred of these stayed in the area also during spring and summer.

Material and methods

The Pasvik Valley is the most important bear area in northern Norway, and an intensive study to estimate population size and bear activity in Pasvik was executed during 1978-1982. In spring, three loops of 120 km were driven by snowmobile twice a week until snow melt in late May. When bear tracks were observed, the bear was tracked backwards and all signs of bear activity were registered and collected when possible. After snow melt the field personnel systematically walked through the area with dogs for 1-2 days every week. The field workers moved on a straight line with a 100-m distance from each other. When a sign of bear activity was observed, the nearby surroundings were examined more carefully. After the snow fall in October, the same method as in spring was used. Registration and collection of bear scats were part of the study, and a sample of 220 bear scats was collected. Each scat was marked with the date and place it was found and then frozen to preserve for further analysis (Wikan et al.

1994). To analyse seasonal differences in foods consumed, the year was divided into three seasons: spring (April - mid-May), summer (mid-May - July) and autumn (August - October), based on changes in the availability of major foods. The beginning of the summer was defined by the start of the moose calving season, and the ripening of berries determined the transition between summer and autumn.

In some cases many scats were collected at the same feeding site. To avoid bias in the results caused by overrepresentation of certain food items eaten by individual bears, we corrected for this mainly by using the methods described by Dahle et al. (1998). All of the scats up to four (selected at random), collected at the same feeding site were used in the analysis. If six scats were present, five were used; if eight scats were present, six were used; and if more than 10 scats were present, seven were used. Only scats which could be dated to a specific season were used. After these corrections, 137 scats of the total sample remained for analysis.

Collection of scats at carcasses might bias the results, giving an overestimate of the real importance of meat in the diet. A total of 59 (43%) of the 137 scats were collected at or near carcasses of wild ungulates, mainly moose, and five (4%) were collected at a dead cow (classified as bait). Therefore, the contents of scats collected at carcasses were compared with the content of scats not collected at a carcass or bait (N = 73).

The scats were washed in warm water and transferred to 70% ethanol. Further analysis mainly followed the methods described by Hamer & Herrero (1987), which were also used by Johansen (1997), Opseth (1998) and Dahle et al. (1998). Each scat was washed through a mesh (0.8 mm). Five random 6-ml subsamples from the homogenous scat remains were analysed using a 7-30 power stereoscope and 40-630 power microscope. All diet items were sorted and identified to the finest taxonomic level possible. The percent volume of each food item was estimated visually by estimating the percentage of the different food items in each 6-ml subsample and by calculating the average percentage contribution of each food item for the five 6-ml subsamples. Visual estimates of percent volumes correspond well with percent based on exact volumes (Mattson et al. 1991), and our experience is that this is indeed true for as small samples as used in this analysis. The first part of the analysis was also conducted in co-operation with B. Dahle, T. Johansen and O. Opseth, who had used the same method to ensure that the results should be comparable to those executed by Johansen (1997), Opseth (1998) and Dahle et al. (1998).

It was not possible to distinguish between calves of moose and reindeer. Remnants of adult ungulates were classified as moose or reindeer according to the methods described by Birkeland, Myhre & Myrberget (1972). Furthermore, it was often difficult to distinguish between adult moose and reindeer, and these remnants were classified as unspecified adult ungulates.

If certain food items tend to be found in smaller or larger scats more than other food items, the volume of each scat should be considered to avoid over- or underrepresentation of the importance of the food item (Hewitt & Robbins 1996). No measures of total volume per scat were available, but neither Johansen (1997), Opseth (1998) nor Dahle et al. (1998) found any relationship between content and size of the scats in other areas of Scandinavia. Therefore, it seems reasonable to assume that this was also the case in Pasvik.

The contents of scats for each season were summarised in terms of Frequency of Occurrence (FO) and percent Faecal Volume (FV). FO_a was:

$$\frac{\text{total number of scat items containing food item } a \text{ in a given season}}{\text{total number of scats in that given season}} \times 100\%.$$

FV_a was:

$$\frac{\text{volume of food item } a \text{ in a given season}}{\text{total faecal volume in that given season}} \times 100\%.$$

It is also important to estimate the contribution of a food item to the energy in the diet. The usefulness of faecal analysis is limited by the differential disappearance of food items during ingestion and passage (Hewitt & Robbins 1996). Highly digestible food items tend to be underestimated in scat-based studies, whereas poorly digestible food items tend to be overestimated. To resolve this problem, correction factors (CF_1) that relate faecal volume (FV) to original dietary content were developed by Hewitt & Robbins (1996) and discussed by Dahle et al. (1998). The use of correction factors is especially important when dealing with omnivorous animals like brown bears, because omnivores likely have the most substantial differences between faecal volume and original diet composition (Hewitt & Robbins 1996). The FV of each food item in a season was multiplied with its respective CF_1 to estimate the original diet composition in percent dry mass (Estimated Dietary Content, EDC). Correction factors used were for vegetation = 0.26, for berries of *Rubus* = 0.87, for berries of *Vaccinium* and *Empetrum* = 0.54, for insects = 1.1, for large mammals = 2.0 (assuming consumption of about 50% of skin and hair with all meat and viscera) or 1.0 (assuming consumption of old carcasses with only skin and hair and little meat or viscera; Hewitt & Robbins 1996), 1.75 for neonatal ungulates (in 50% of the cases of bear predation upon moose calves in south-central Sweden all of the meat but only about 50% of the hide and bones were consumed; Johansen 1997), 1.5 for birds (assumed to be consumed whole; Johansen 1997) and 1.5 for small mammals (we chose to use the same correction factor as for birds).

The estimated dietary content (EDC) was used with a second group of correction factors (CF_2) to convert dry matter to available energy and to obtain the percentage of Estimated Dietary Energy Content (EDEC) for each food item and season. Correction factors (CF_2) used were 6.3 kJ/g for graminoids and horsetails, 8.4 kJ/g for forbs, 11.7 kJ/g for berries, 18.8 kJ/g for small mammals (Dahle et al. 1998), 17.7 kJ/g for ants of the genus *Formica*, bumblebees and wasps, and 20.6 kJ/g for ants of the genus *Camponotus* (Swenson, Jansson, Riig & Sandegren 1999), 19.3 kJ/g for ungulates and bait (Mealey 1980) and 9.6 kJ/g for old ungulate carcasses (50% hair, 50% digestible; Johansen 1997). Digestible energy estimates for mushrooms and birds were set at 6.3 and 18.8 kJ/g (the same as for graminoids and small mammals, respectively). We chose to use the lower energy estimate from Mealey (1980) for ungulates and bait because in that study intake of hair and skin was taken into consideration. The estimates of EDEC were considered to be more important than the estimates of FO and FV in our study, because the energy contribution of a food item was assumed to best reflect the real importance of that food item for the bears.

There are some limitations of faecal analysis which should be kept in mind. First of all, a scat simply reflects what was eaten in the bear's previous meal, and thus cannot be extrapolated across time. Second, our sample size is undoubtedly too small to make strict conclusions about the composition of the diet of bears in northern Scandinavia. The results might have been influenced by individual feeding behaviour of some bears that are overrepresented in the material. Third, considerable variation in correction factors exists for the same food item. The variation in correction factors is especially large concerning large mammals, depending upon the ratio of meat:hair-skin consumed (Hewitt & Robbins 1996). This ratio may vary considerably, also due to individual behaviour of bears. Observations of cervids killed or scavenged by bears indicate that the amount of hide consumed generally varies between 20 and 80%, and the CF_1 used for cervids is merely a qualified guess that varies within 0.5-3 (Dahle et al. 1998). However, in spite of these limitations, faecal analysis offers a coarse estimate of the diet of brown bears in northern Scandinavia, and thus is important as a first step in the management of bear populations living in these areas. We also estimated the variation in the content of the main food items among scats, and conducted sensitivity analyses with varying correction factors (CF_1) for wild ungulates to obtain an estimate of how this would affect the estimates of the Estimated Dietary Energy Content (EDEC). The CF_1 for old depleted carcasses might be <1 (Dahle et al. 1998) and was thus set at 0.5, and the CF_1 for non-depleted carcasses was varied within 1.0-3.0. The CF_1 for calves estimated at 1.75 was considered to be valid, and was not varied. Variation in the correction factors for other food items also exists (Hewitt & Robbins 1996), but we chose to focus on ungulates because their correction factors undoubtedly have the largest impact on the results of the analysis.

Statistical tests were executed in SPSS. The level of significance was set at $P < 0.05$. The Kruskal-Wallis test and Mann-Whitney U-test (when comparing two samples) were used to test for annual differences within seasons. When several statistical tests are executed, significant differences may be due to chance (Ims & Yoccoz 2000). To correct for this, levels of significance were adjusted using the Bonferroni method (Rice 1989).

Results

Annual variation

The proportion of scats containing the major food items (ungulates, insects, berries and vegetation) was tested for annual differences within seasons. The use of berries varied among years in the spring (Kruskal-Wallis test: $\chi^2 = 26.4$, df = 3, $P < 0.001$). Berries from the year before were utilised less in spring 1978 than in 1979 (Mann-Whitney U-test: U = 18.0, P = 0.007), 1980 (U = 153.0, P < 0.001) and 1982 (U = 18.0, P = 0.001). The use of ungulates (Kruskal-Wallis test: $\chi^2 = 9.5$, df = 2, P = 0.008) and berries (Kruskal-Wallis test: $\chi^2 = 6.3$, df = 2, P = 0.044) in summer also varied among years. Ungulates were used more in 1979 than in 1982 (U = 52.0, P = 0.003), but we were not able to identify which year differed in the use of berries during summer after using the Bonferroni method. The use of ungulates (Kruskal-Wallis test: $\chi^2 = 14.2$, df = 4, P = 0.007) and insects (Kruskal-Wallis test: $\chi^2 = 18.5$, df = 4, P = 0.001) varied among years in autumn. Ungulates were used more in 1981 than in 1980 (Mann-Whitney U-test: U = 9.0, P = 0.001), but we were not

Table 1. Percent Frequency of Occurrence (FO), percent Faecal Volume (FV), percent Estimated Dietary Content (EDC) and percent Estimated Dietary Energy Content (EDEC) of food items found in 35 brown bear scats from the Pasvik Valley in spring 1979-1982. EDC and EDEC were not calculated for the categories 'wood' and 'other', because they were considered to be very low. Items constituting <0.5% of FV, EDC or EDEC are marked with tr. (trace).

Food item	FO	FV	EDC	EDEC
Horsetails	8.6	4.9	1.2	tr.
Graminoids	17.1	2.6	0.6	tr.
Forbs	2.9	tr.	tr.	tr.
Berries	48.6	19.2	9.6	6.2
Empetrum hermaphroditum	48.6	18.9	9.5	6.1
Vaccinium myrtillus	11.4	tr.	tr.	tr.
Vaccinium vitis-idaea	5.7	tr.	tr.	tr.
Rubus chamaemorus	-	-	-	-
Vaccinium oxycoccus	-	-	-	-
Mushrooms	-	-	-	-
Ants	25.7	2.4	2.5	2.1
Formica spp.	25.7	2.4	2.5	2.1
Camponotus spp.	-	-	-	-
Bumblebees/wasps	-	-	-	-
Ungulates	77.1	47.9	79.7	84.5
Alces alces	54.3	32.7	58.0	61.5
Unspecified	22.9	12.5	17.4	18.4
Unspecified (calves)	2.9	2.7	4.4	4.6
Bait	-	-	-	-
Rodents	8.6	2.6	3.6	3.7
Birds	5.7	tr.	tr.	tr.
Unidentified mammals	8.6	1.8	2.5	2.6
Wood (including needles)	54.3	14.9	-	-
Other (e.g. anthill material)	15.1	3.4	-	-

able to identify which year differed in the use of insects in autumn with the Bonferroni method.

Seasonal variation

Scats collected at or near carcasses or bait did not contain significantly more ungulate remnants than scats not collected at carcasses in any season (Mann-Whitney U-test: spring: U = 106.5, P = 0.28; summer: U = 254.0, P = 0.40; and autumn: U = 210.0, P = 0.23). These scats were therefore included in the analysed material, and were not considered separately.

The composition of the diet in the different seasons was estimated and the results from each season were summarised (Tables 1-3).

Table 2. Percent Frequency of Occurrence (FO), percent Faecal Volume (FV), percent Estimated Dietary Content (EDC) and percent Estimated Dietary Energy Content (EDEC) of food items found in 49 brown bear scats from the Pasvik Valley in summer 1979-1981. EDC and EDEC were not calculated for the categories 'wood' and 'other', because they were considered to be very low. Items constituting <0.5% of FV, EDC or EDEC are marked with tr. (trace).

Food item	FO	FV	EDC	EDEC
Horsetails	28.6	17.7	5.3	2.0
Graminoids	32.7	2.8	0.8	tr.
Forb	4.1	3.6	1.1	0.5
Berries	34.7	13.6	9.4	6.5
Empetrum hermaphroditum	32.7	10.0	6.3	4.3
Vaccinium myrtillus	4.1	1.0	0.6	tr.
Rubus chamaemorus	6.1	2.3	2.3	1.6
Vaccinium oxycoccus	-	-	-	-
Mushrooms	-	-	-	-
Ants	53.1	6.2	7.9	7.3
Formica spp.	53.1	6.2	7.9	7.2
Camponotus spp.	4.1	tr.	tr.	tr.
Bumblebees/wasps	4.1	tr.	tr.	tr.
Ungulates	57.1	32.5	64.0	70.4
Alces alces	38.8	20.4	41.7	45.1
Unspecified	14.3	7.8	13.5	15.4
Unspecified (calves)	6.1	4.3	8.7	9.9
Bait	10.2	6.4	11.1	12.6
Rodents	-	-	-	-
Birds	4.1	-	-	-
Unidentified mammals	-	-	-	-
Wood (including needles)	22.4	4.0	-	-
Other (e.g. anthill material)	61.2	12.9	-	-

Table 3. Percent Frequency of Occurrence (FO), percent Faecal Volume (FV), percent Estimated Dietary Content (EDC) and percent Estimated Dietary Energy Content (EDEC) of food items found in 53 brown bear scats from the Pasvik Valley in autumn 1978-1982. EDC and EDEC were not calculated for the categories 'wood' and 'other', because they were considered to be very low. Items constituting <0.5% of FV, EDC or EDEC are marked with tr. (trace).

Food item	FO	FV	EDC	EDEC
Horsetails	9.4	6.4	2.7	1.3
Graminoids	18.9	4.0	1.7	0.8
Forbs	3.8	0.8	tr.	tr.
Berries	83.0	62.8	55.5	49.4
Empetrum hermaphroditum	83.0	50.8	44.5	39.6
Vaccinium myrtillus	30.2	9.4	8.2	7.3
Vaccinium vitis-idaea	5.7	tr.	tr.	tr.
Rubus chamaemorus	13.2	0.9	1.3	1.1
Vaccinium oxycoccus	3.8	1.3	1.1	1.0
Mushrooms	9.4	tr.	tr.	tr.
Ants	34.0	2.1	3.8	4.4
Formica spp.	34.0	2.1	3.8	4.4
Camponotus spp.	-	-	-	-
Bumblebees/wasps	20.8	2.9	5.2	6.1
Ungulates	35.8	12.6	25.7	30.4
Alces alces	26.4	7.5	13.3	12.2
Unspecified	9.4	2.0	10.7	15.7
Unspecified (calves)	1.9	0.7	1.7	2.5
Bait	-	-	-	-
Rodents	7.5	tr.	1.0	1.4
Birds	1.9	-	-	-
Unidentified mammals	3.8	1.7	4.1	5.9
Wood (including needles)	9.4	2.7	-	-
Other (e.g. anthill material)	30.2	3.5	-	-

In spring, ungulates were the most important food item making up 85% of the estimated dietary energy content, EDEC (see Table 1). The second most important food item, based on EDEC, was berries from the year before, mostly crowberries, followed by rodents, other small mammals and red forest ants *Formica* spp. Wood made up 15% of the FV, but was ignored when calculating EDC and EDEC, because the energy content was assumed to be negligible.

In summer, ungulates were once again the most important food item making up 70% of the EDEC (see Table 2). The second and third most important food items were bait (carcasses left by humans) and ants, comprising 13% and 7% of the EDEC, respectively. Horsetails *Equisetum* spp. were relatively common in FV, but lost most of their importance concerning EDC and EDEC, due to low correction factors. Graminoids and forbs were of minor importance both for FV, EDC and EDEC.

In autumn, berries were the most important food item making up 49% of the EDEC (see Table 3), and crowberries constituted 80% of the total contribution from berries. The second most important food item was ungulates making up 30% of the EDEC, followed by insects, among which red forest ants contributed 4% and wasps of the order *Hymenoptera* 6%.

Variation among scats

The content of the main food items (ungulates, insects, berries and vegetation) estimated as FV varied considerably among scats. The results (mean and standard deviation) are presented in Table 4.

Sensitivity analysis

Varying the correction factors (CF_1) used for wild ungulates (undepleted carcasses) from 1.0 to 3.0 had a moderate effect on the estimates of EDEC. The contribution from wild ungulates varied within 76-90% in spring, within 60-79% in summer and within 22-41% in autumn (Table 5).

Table 4. Mean and standard deviation (SD) of the content of the four main food items estimated as Faecal Volume (FV) in spring, summer and autumn 1978-1982.

	Ungulates		Insects		Berries		Vegetation	
Season	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Spring	45.4	38.2	10.6	2.5	31.9	20.1	19.9	8.0
Summer	32.2	37.6	6.5	11.5	13.5	30.6	23.9	37.1
Autumn	10.5	24.7	5.2	11.9	64.7	41.8	11.5	25.7

Table 5. Percent Estimated Dietary Energy Content (EDEC) with varying correction factors (CF_1) for non-depleted carcasses of adult wild ungulates in spring, summer and autumn 1978-1982.

CF_1	Spring	Summer	Autumn
1.0	76	60	22
1.5	82	67	28
2.0	86	72	33
2.5	88	76	37
3.0	90	79	41

Discussion

We found relatively little year-to-year variation in the use of different food items. The variation in use of berries in spring may have been due to variation in the snow cover from year to year, and the variation in use of ungulates in summer may have been due to variation in the availability of ungulate carcasses from early spring. Some harsh winters around 1980 removed weaker individuals from the moose population, and these were probably scavenged by bears. Weakened moose may also have been easier prey for the bears in spring and early summer. Thus, it seems that the food supply for brown bears in northern Scandinavia is relatively stable from year to year, which agrees with results from dietary analyses from southern areas (Johansen 1997, Opseth 1998, Dahle et al. 1998), but contrasts with those from interior North America where considerable annual variation is often found (Mattson et al. 1991).

Ungulates, especially adult moose, were the most important food item contributing to the total energy assimilation for the brown bears in the Pasvik Valley. No reindeer were observed to have been killed by bears during snow tracking (Wikan 1996), and low predation rates on reindeer also have been reported from other studies (Haglund 1968, Danilov 1983, 1990). Moose has been reported to be the preferred prey among wild ungulates for brown bears both in European Russia (Semenov-Tyan-Shanskii 1972a, 1972b, Danilov 1983) and in the Yellowstone National Park, USA, probably because of their solitary habits and because they inhabit forested surroundings that favours the stalking of moose (Mattson 1997). Carcasses of reindeer that have died from causes other than bear predation are undoubtedly important for the bears in the Pasvik Valley, however, and contribute to the large proportion of ungulates in their diet. Intensive scavenging on reindeer carcasses has also been observed in the nearby Lapland Reserve in Russia (Semenov-Tyan-Shanskii 1972b).

Brown bears kill ungulates when they are most vulnerable and will typically eat meat whenever available (Chatelain 1950, Mattson 1997). The use of ungulates peaked in spring, as has also been reported by others (Kaleckaya 1973, Haglund 1974, Zavatskii 1978, Semenov-Tyan-Shanskii 1982, Boertje, Gasaway, Grangaard & Kelleyhouse 1988). Some bears in the study area apparently specialised in killing moose in conditions of deep snow in spring, and yearling moose in bad condition and pregnant moose cows in normal condition seemed to be most vulnerable (Wikan et al. 1996). However, ungulates were also the most important food item contributing to the energy in the diet in summer, and summer predation upon moose was observed in the study area (Wikan et al. 1999). To our knowledge, our study has documented the most extensive use of ungulates both in spring and (especially) in summer yet reported for brown bears.

We are aware that our results should be interpreted with caution. The sample size is rather small, several scats were collected at the same feeding site and were probably deposited by the same individual bear, and there was considerable variation in the content of the main food items among scats. Thus, the results of the analysis might be biased due to small sample size, individual feeding habits among bears, and overrepresentation of scats from some individual bears. However, the fact that there were no significant differences in the content of ungulates in scats collected at or near a carcass or bait and scats not collected at a carcass or bait in any season undoubtedly indicates that a high content of ungulates in the diet of bears in the Pasvik Valley was real and not only due to sampling bias. The results of the sensitivity analysis with varying correction factors for ungulates also confirm the importance of ungulates for the bears in the Pasvik Valley; the contribution to the EDEC was estimated to be as high as 90% in spring and no lower than 22% in autumn.

There might be several explanations for the high utilisation of ungulates in the Pasvik Valley, including more carnivorous behaviour of bears in the north (Danilov 1983, Kaleckaya 1973, Krechmar 1995) and a simpler ecological structure of northern ecosystems (Wikan et al. 1994). Total ungulate use is likely to vary with the availability of alternative food sources (Mattson 1997). Access to meat in the diet is probably more important to brown bears at northern latitudes (Wikan 1996), especially in early spring when a thick cover of snow prevents utilisation of alternative food sources. The moose population in the Pasvik Valley was large during the study period, and the moose were in rather bad physical condition and therefore easy prey for the bears in spring (Wikan 1996). Favourable snow conditions for bears that hunt moose in early spring are also more pronounced at northern latitudes (Semenov-Tyan-Shanskii 1982, Danilov 1983).

An additional explanation for the high utilisation of ungulates might be that the bear population was recolonising the Pasvik Valley during the study period. Higher predation rates in areas recolonised by carnivores have been documented both for lynx *Lynx lynx* predation on wild ungulates in the Swiss Alps (Breitenmoser & Haller 1989) and for brown bear predation upon adult moose in south-central Sweden (Persson 1998), and has been suggested to be a general and temporary phenomenon (Breitenmoser & Haller 1989). Moose populations probably lose some of their anti-predator behaviour when their natural predators are removed, and therefore temporarily are easier prey when these predators return (Berger 1998). Compared with the Pasvik Valley, the use of ungulates was considerably lower in the Lapland Reserve, which is situated 200 km southeast of Pasvik and which holds an established bear population (Semenov-Tyan-Shanskii 1972a, 1972b). In the Lapland Reserve, ungulates constituted only about 16% of the diet on an annual basis (Semenov-Tyan-Shanskii 1972a, 1972b). Unfortunately, he did not describe the methods he used in his study. The moose population in Pasvik was larger than the moose population in the Lapland Reserve (Wikan 1996), so the results from there should be interpreted with caution. Nevertheless, if an expanding bear population has a higher *per capita* impact on the moose population along the expanding front, one should expect the utilisation of ungulates to decline after the bear population has become established in the area. Today, bear reproduction occurs almost annually in Pasvik (Swenson & Wikan 1996), and it would be important to reexamine the extent of predation upon moose in Pasvik now that the bear population has become well established.

Ants were a relatively less important part of the protein-rich diet, contributing 2-7% of the EDEC. Carpenter ants *Camponotus* spp. have been documented to be preferred to red forest ants among bears in south-central Sweden (Swenson et al. 1999). Surprisingly, carpenter ants were only found as a trace in two scats, although destroyed stumps were common signs of bear activity in the Pasvik Valley (Wikan et al. 1999a). The low utilisation of ants might also be explained by sex differences in feeding behaviour. Female bears use ants more than males (Johansen 1997), and the results from snow-tracking indicated a predominance of male bears in Pasvik during the study period, which is to be expected in peripheral bear populations (Swenson, Sandegren & Söderberg 1998). In addition, ants appear to be used as a buffer food source when few other nutritious food items are available (Mattson et al. 1991, Swenson et al. 1999), and ungulates were apparently abundant during this study. Bears are reported to use ants if they do not have access to meat (Semenov-Tyan-Shanskii 1982, Makarova & Yermolayev 1986), and ants might thus have been of low importance to the bears in the Pasvik Valley because of satisfactory access to ungulate meat.

Berries are rich in carbohydrates (Källman 1991) and comprised the most important energy source in the autumn diet of bears. The importance of berries in the diet is reinforced by the fact that in autumn the bears have to build up fat reserves and increase lean body mass before hibernation (Atkinson & Ramsay 1995, Atkinson, Nelson & Ramsay 1996, Hilderbrand, Schwartz, Robbins & Hanley 2000). The magnitude of the fat stores in autumn is an important factor influencing the relative magnitude of catabolic losses of lean body mass during the denning period (Atkinson et al. 1996, Hilderbrand et al. 2000). Free-ranging bears, especially lactating females, are documented to use some muscle protein in concert with fat as a metabolic substrate and a source of water during hibernation (Atkinson et al. 1996, Tinker, Harlow & Beck 1998, Hilderbrand et al. 2000). The accumulation of lean body mass may be necessary to provide musculature to support the large fat stores, and to provide protein and minerals for cub production and lactation in reproducing females (Atkinson & Ramsay 1995). These reserves can likely not be built up entirely on berries, because berries are low in protein and fat (Källman 1991). A certain amount of animal material in the diet might thus be essential also in autumn. Crowberry is the most common berry species in the ground vegetation in the Pasvik Valley, and was also the most commonly occurring berry in the diet of the bears. Opseth (1998) and Dahle et al. (1998) found that bears used crowberries more than expected, based on the occurrence of crowberry plants, both in south-central Sweden and in central Scandinavia. Cloudberries *Rubus chamaemorus* have been reported to be a preferred food source for brown bears (Semenov-Tyan-Shanskii 1972a, 1982), but seemed to be of low to moderate importance in Pasvik. The scats were collected during years with a normal crop of cloudberries. Cloudberries are also documented to be even less utilised by bears in other areas in Scandinavia than in Pasvik (Elgmork & Kaasa 1992, Johansen 1997, Opseth 1998, Dahle et al. 1998).

Graminoids and forbs were of minor importance both concerning the faecal volume (FV) and the estimated dietary energy content (EDEC). This might be due to the carnivorous behaviour of the bears in Pasvik, making vegetation less important as a food resource. Low utilisation of vegetation might also partly be due to habitat selection. Although luxuriant undergrowth occurs along courses of brooks, rivers and on richer patches in the birch forest in the Pasvik Valley, the bears seemed to prefer the drier ridges. Horsetails had a high FV and seemed to be a preferred food item, although contributing little to the energy assimilation. Horsetails also had a high FV in south-central Sweden (Johansen 1997), and are reported to be common in the diet of brown bears both in Alberta (Hamer & Herrero 1987) and Siberia (Krechmar 1995 and references therein).

The cambium and phloem layers of trees contain some carbohydrates and protein (Källman 1991). However, wood was assumed to contribute little to the total energy of the bears' diet, and as far as we know no correction factors have been developed for wood. Energy demands is thus probably not the explanation for the surprisingly high FV of wood in the spring diet. Intake of wood was not associated with intake of ants either. Carpenter ants were not found in spring, and red forest ants were only found as traces in three of the scats containing wood. Rather the intake of wood was associated with intake of meat. An explanation for the consumption of wood could be that wood fibres might be important for an adequate gastrointestinal function during periods of more or less pure meat consumption, as proposed by Mysterud (1975). The amount of wood in the diet was considerably lower in summer and autumn (4 and 3% of FV, respectively) than in spring (15% of FV), when meat consumption peaked. Intake of wood in association with intake of meat has also been documented at moose carcasses (Mysterud 1973, Sørensen & Kvam 1984) and sheep carcasses (Mysterud 1975).

Management implications

The large proportion of wild ungulates in the diet of brown bears in the Pasvik Valley supports the hypothesis that brown bears generally are more carnivorous in the north (Kaleckaya 1973, Danilov 1983) and in areas they are recolonising (Persson 1998). It is therefore important to take local and regional differences in bear foraging behaviour into account in moose management in Scandinavia. The moose and bear populations should be carefully monitored and the hunting quotas of moose should be more conservative in bear areas in the north than farther south, especially during periods when bear populations are expanding. We recommend that a follow-up study be conducted in the Pasvik Valley, so that the predation on moose can be documented now, with an established and more dense bear population.

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