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The diet of brown bears *Ursus arctos* in central Scandinavia: effect of access to free-ranging domestic sheep *Ovis aries*

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The seasonal food habits of brown bears *Ursus arctos* were estimated based on the analysis of 266 scats in central Norway and Sweden. Free-ranging domestic sheep *Ovis aries* were common in the Norwegian part of the study area, but were not found in the Swedish part. Correction factors were used to correct for differences in digestibility and nutritional value of different foods. Because correction factors for ungulates are difficult to estimate, the results should be interpreted with some caution. In terms of digestible energy, ungulates, mostly carrion, were the most important food in both areas during spring. During summer, ants, forbs, and ungulates (reindeer *Rangifer tarandus* and moose *Alces alces*) were the most important food items in the Swedish area, and sheep were most important in the Norwegian area. The autumn diet was dominated by berries in the Swedish area and sheep and berries in the Norwegian area. Among berries, crowberry *Empetrum nigrum* was the most important species, followed by bilberry *Vaccinium myrtillus* in Sweden. The major difference between the Swedish and Norwegian areas was the large consumption of sheep in Norway, which provided protein and lipids, and was associated with a relatively reduced consumption of ants and forbs in summer and berries in the autumn. Based on different ingestion rates among the seasons, we estimated the relative contribution of major foods to total digestible energy. In the Swedish area, bears obtained 44-46 and 14-30% of their total annual energy from berries and ungulates, respectively. The remaining energy was obtained from insects (14-22%, mostly ants) and forbs and graminoids (12-18%, mostly blue sow thistle *Cicerbita alpina*). In Norway, bears obtained 65-87% of the energy from ungulates (mostly sheep), 6-17% from berries, 5-13% from insects, and 2-6% from forbs and graminoids. To gain weight prior to denning, brown bears in Norway selected lipid-rich and easily obtainable sheep in summer and autumn. In Sweden, they relied on carbohydrate-rich berries in autumn.

Key words: brown bear, correction factors, diet, domestic sheep, Norway, Sweden, Ursus arctos

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In Norway, the brown bear *Ursus arctos* is a predator of free-ranging domestic sheep *Ovis aries*, and sheep husbandry, where sheep are left free-ranging and unattended during the grazing season, is considered the most important threat to brown bear re-establishment and conservation in Norway (Sagør, Swenson & Røskaft 1997, Sørensen, Swenson & Kvam in press). Sheep farmers claimed that 3,175 sheep (of which 1,821 were compensated) were killed by brown bears in 1995, which represents 0.13% of the total number of grazing sheep (Aanes, Swenson & Linnell 1996). Although not important at a national level, many sheep farmers in local areas suffer high depredation losses (Knarrum 1996, Sørensen et al. in press). Based on the number of compensated sheep due to bear predation (Aanes et al. 1996) and the size of the bear population (Swenson, Wabakken, Sandegren, Bjärvall, Franzén & Söderberg 1995, Swenson & Wikan 1996) each brown bear in Norway killed on average 55 sheep in 1995, during the 3.5-month grazing season when sheep were available to bears. In Sweden, bears rarely take domestic sheep, even though the number of bears in Sweden is 20-30 times the number of bears in Norway. Annual reported losses due to bear predation in Sweden have averaged about 100 sheep (R. Franzén, unpubl. data). In both countries most sheep farming is restricted to areas where few or no bears are present, but in Sweden sheep do not graze freely in the forests, but in fenced pastures. The Scandinavian brown bear population is increasing in number and range, which results in increased conflicts between bears and sheep farmers as bears disperse into Norway from Sweden (Swenson, Sandegren, Bjärvall, Söderberg, Wabakken & Franzén 1994, Sørensen et al. in press).

Protein-rich food is important for structural growth in cubs and subadult bears. The importance of a calorie-rich diet during hyperphagy was stressed by Gilbert & Lanner (1994). They pointed out that populations with access to large amounts of spawning fish exhibit densities 20 times of those without access to this food. Even so, foods containing a large portion of digestible carbohydrates are more efficiently converted to fat than are proteinaceous foods (McDonald, Edwards & Greenhalgh 1981). In American black bears *U. americanus*, Brody & Pelton (1988) found an increase in assimilation of carbohydrates and lipids during autumn with a respective decrease in protein assimilation. This may also be true for brown bears, as on Kodiak Island where bears consumed more berries as they ripened, even though fish were still plentiful (Clark 1957). The lipid content of spawning salmon decreases during late summer and autumn (Brett 1980), whereas the fat content of sheep increases during the grazing season.

As other generalist predators, brown bears often switch to different foods dependent upon availability and vulnerability (e.g. Ustinov 1993, McLellan & Hovey 1995, Mattson 1997). We asked the question: what effect does the presence of vulnerable free-ranging domestic sheep have on the diet of brown bears in Scandinavia? The knowledge of the brown bear's diet in Scandinavia is based solely on the study of a minor, now-extinct, population in Norway during 1971-1979 (Elgmork & Kaasa 1992), and a qualitative study of spring food in Sweden (Haglund 1968).

Study areas

The study area included eastern Nord-Trøndelag County in Norway and northwestern Jämtland County in Sweden (64°N, 14°E) (Fig. 1). The study area is intersected by large waterways that descend from about 350 m elevation in the west to about 300 m in the east. A large part of the area consists of mountains over the timberline (ca 650 m a.s.l.). Lakes and bogs cover large areas, but most of the area below the timberline is covered with coniferous forest and clearcuts of different ages. Timber harvest is intensive on both sides of the border, and results in large clearcuts of up to 300 ha and large even-aged stands. The human population is sparse, 0.6 persons/km^2 in the Norwegian part, and somewhat lower in the Swedish part.

Norway spruce *Picea abies* is the dominant tree species in the area, but Scots pine *Pinus sylvestris* is also common in Sweden. Of deciduous tree species, birches *Betula pubescens, B. pendula*, grey alder *Alnus incana*, willow *Salix* spp. and European mountain ash *Sorbus aucuparia* are the most common.

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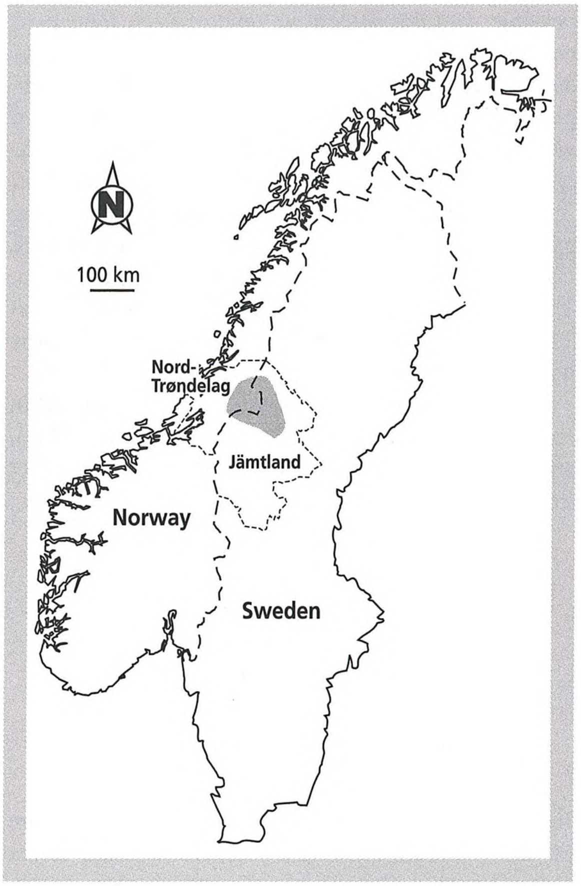

Figure 1. Location of the Norwegian and Swedish study areas (shaded).

Bilberry *Vaccinium myrtillus*, and to a lesser degree cowberry *V. vitis-idaea*, and crowberry *Empetrum nigrum* are common ground-layer species covering 13.1, 5.1 and 3.6% of the Swedish part of the study area, respectively (H. Jernelid, pers. comm.). Due to high precipitation and calcareous soils, parts of the study area have luxuriant undergrowths that includes tall forbs such as blue sow thistle *Cicerbita alpina*.

Unguarded free-ranging sheep at summer densities of about 2,800 sheep/1,000 km^2 (Knarrum 1996) were present in the Norwegian part of the study area (4,000 km^2), but were absent in the Swedish part (6,000 km^2). Sheep graze from June to the middle of September, when they are collected and kept in barns until the next spring. Potential wild prey for the bears include moose *Alces alces* (winter population: ca 650 moose/1,000 km^2) (E. Carlson, pers. comm.) and roe deer *Capreolus capreolus* at low densities. Besides the wild prey and sheep, large numbers of semidomestic reindeer *Rangifer tarandus* are potential prey for the bears (Knarrum 1996).

About 400-500 mm of precipitation falls during the growing season, during which about 650-750 degree-days of warmth accumulate. Snow usually covered the study area for a minimum of six months (mid November - mid May).

On average bears were active from mid-April to the end of October. Some bears entered their dens in the middle of October and emerged from them as early as the end of March whereas others emerged as late as the middle of May, depending on sex and reproductive status. Male home ranges in Scandinavia are about 1,400-1,500 km^2 in the population core area, but may be as large as 28,000 km^2 in areas where female density is low. Female home ranges are about 400-500 km^2 (Wabakken, Bjärvall, Franzén, Maartmann, Sandegren & Söderberg 1992).

Methods

A sample of 266 scats from 200 locations was collected in 1987-1988 and 1993-1995. The scats were detected visually, except from a few that were found by a dog. The four scats first found at one site were collected and a fifth scat was collected if more than seven scats were present. On average 1.33 scats were collected at each site. In 1987-1988, 13% of the 141 scats were found incidentally when walking in the study area, e.g. for hunting or berry picking. The remaining scats from 1987-1988 were collected along transect lines. The 28 transect lines, 17 in Sweden and 11 in Norway, were used to document signs of bear activity. They had a length of about 15-20 km and were located to reflect the availability of different habitat types without following roads or trails. In practice this resulted in transect lines from the bottom of the valleys to well above the timberline in the mountain slopes, then returning to the bottom of the valley, or they went from the bottom of one valley, over a hill and down to the bottom of another valley. The transect lines were walked four times each year; once during late April - May, after most of the snow on the ground had melted, once in the middle of June, once at the end of July - beginning of August and once in September. In this way about 4,000 km were covered on foot, and each season was covered by the same sampling effort with the exception of October.

The year was divided into three seasons, spring (April - May), summer (June - July) and autumn

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(August - October) for analysis. These seasons were defined by shifts in the availability of major foods. The shift from spring to summer was the time when forbs and grass sprouted and became available to bears, and the shift from summer to autumn was the time when berries started to ripen. The age of scats was determined based on location of radio-marked bears, characteristics of the scats, and the vegetation under the scats. Each scat was classified into the presumed month of defecation. Scats decompose slowly in this cold-climate study area (pers. obs.), but scats older than two months were not collected.

In 1993-1995, 35% of the scats were collected at sites where radio-marked bears had been located. These bears were assumed to be representative for the population, as they were marked in the end of April - beginning of May when the sheep still were kept in barns. In 1993-1995, about 300 km were walked along four of the transect lines used in 1987-1988 (two in Norway and two in Sweden). They were walked once in June and once in August and 20 scats were collected. The remaining 44% of scats were collected incidentally in conjunction with walks to positions where radio-collared bears or radio-collared sheep had been located, or in conjunction with hunting and berry picking.

It was easier to detect scats in spring, when the ground was covered with snow and before the ground layer vegetation sprouted, than it was during summer and autumn, when the ground was covered with dense vegetation. To check for bias towards ungulates in the sampling methods used in 1993-1995, faecal volume of ungulates in 1987-1988 and 1993-1995 were compared with Mann-Whitney U-tests.

Analysis of scats collected in 1993-1995 followed procedures and techniques described by Hamer & Herrero (1987). Scats were frozen or air dried for later analysis in the laboratory. If different food items tend to occur in scats of different average sizes, the volume of each scat should be considered to avoid over or underestimating the relative consumption of different foods (Hewitt 1989). We therefore noted the weight and volume (measured by water displacement) of each scat for possible use in later calculations. Each scat was rehydrated and washed through a 0.8 mm mesh, the same size as used by Elgmork & Kaasa (1992). Five 6-ml subsamples were randomly selected from the homogeneous scat remains and analysed for content using a 7-30 power stereoscope and a 40-630 power microscope. All diet items were sorted, identified to the finest taxonomic resolution possible, and the percent volume of each food item was estimated visually. Hairs from moose and reindeer were pooled because they are difficult to distinguish. Visual estimates of percent correspond well with percent based on exact volumes (Mattson, Blanchard & Knight 1991a) and are thus more efficient. In 1987-1988 our analysis technique was the same, except that volumes of each food item in a scat were classified into one of seven categories: 0-1, 1-5, 5-25, 25-50, 50-75, 75-95 and 95-100% (Mace & Jonkel 1986). The midpoint of each volume category was used in calculations described below.

Scat analyses for each season were summarised in terms of percent of Frequency of Occurrence (FO), and percent of Faecal Volume (FV) for each diet item;

$$FOa = \frac{\text{total number of scats containing food item a in a given season}}{\text{total number of scats in that given season}} \quad (1),$$

$$FVa = \frac{\sum \text{the percent volume of food item a in each scat in a given season}}{\text{total number of scats in that given season}} \quad (2).$$

Faecal composition provides a highly biased measure of energy assimilated from different food items (Mealey 1980), given that foods differ in their digestibility and nutritional composition (Pritchard & Robbins 1990). Correction factors (CF_1) given by Hewitt & Robbins (1996) were used to estimate the original diet composition (Estimated Dietary Content, EDC in percent) from FV. The FV of each food item in a season was multiplied by its respective CF_1 (vegetation = 0.26; berries of *Rubus* = 0.87; berries of *Vaccinium* and *Empetrum* = 0.54; insects = 1.1; small mammals = 4). CF_1 for birds has not been estimated, but was set to 1.5 based on the relative amount of feathers to meat and because bears probably consume the entire carcass. CF_1 for adult ungulates depends on the amount of hide and bone consumed together with the meat and viscera (Hewitt & Robbins 1996). As the bears studied by Hewitt & Robbins (1996) were fed mule deer *Odocoileus hemionus*, and all the meat was consumed, their correction factors should apply to cervid prey or non-depleted cervid carcasses. Observations of cervids killed or scavenged by bears indicate that the amount of hide consumed normally varies between 20 and 80%. CF_1 for large cervids should therefore be set at 1-5 (assuming that bears consumed between 20 and 80% of skin and hair with

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all the meat and viscera, Hewitt & Robbins 1996). During tracking of bears on snow in spring, we found that bears used depleted moose and reindeer carcasses with only a trace of available meat (pers. obs.). CF_1 for depleted cervid carcasses should probably be less than 1. As we do not know the proportion of scats having their origin from cervid prey and non-depleted carcasses, compared to old depleted carcasses, our CF_1 for cervids is a qualified guess ranging from 0.5-3. CF_1 for sheep is also difficult to set. All the scats containing sheep remains in spring (18% of the faecal volume in spring) in Norway came from carcasses of animals that died the previous summer and autumn. Due to decomposition and previous scavenging, these old carcasses predictably did not provide much if any meat. This was also indicated by the large amount of hide and bones found in scats with sheep remains in spring, as was the case for many of the spring scats containing moose and reindeer. As the presence of bone and hair may reduce the overall digestibility of protein in the diet (Johnson & Aldred 1982), as well as increase the excretion of endogenous protein, unstarved bears should avoid ingestion of these parts if they are to exercise an optimal nutritional 'strategy' (Best 1985). Sheep were readily available during summer and early autumn and were preyed upon by bears. Although sheep may not be directly comparable to the mule deer used by Hewitt & Robbins (1996) in their feeding trials, we use the regression of their Figure 1 for sheep in summer and autumn. Based on these considerations (only old sheep carcasses in spring and mostly bear-killed sheep during summer/early autumn), we chose a CF_1 interval for sheep with low values in spring (0.2-0.5) and higher values for summer and autumn (2-8, assuming consumption of 10-50% of hair and skin consumed with all meat and viscera). Although our CF_1's for cervids and sheep being qualified guesses rather than exact factors resulting from an experimental design, we feel that they improve our understanding of the importance of animal matter in the diet.

We used the following estimates of digestible energy (CF_2) to convert dry matter to digestible energy (percent of Estimated Dietary Energy Content, EDEC, Mealey 1980, Harting 1987, Pritchard & Robbins 1990, D.G. Hewitt, unpubl. data, Swenson, Jansson, Riig & Sandegren, submitted manuscript), i.e. the energy available for assimilation: 28.4 kJ/g for ungulates, 18.8 for small mammals and assumed to be the same for birds, 11.7 for berries, 17.7 for ants, 11.3 for other insects, 6.3 for horsetails *Equisetum* and graminoids (Poaceae and Cyperaceae), 8.4 for forbs, and 10.0 for mushrooms. The assimilation of digestible energy is generally high, about 90-95% (Best 1985, Pritchard & Robbins 1990) and the digestible energy is used in the presentation of the results. Anthill material, twigs, wood fragments, and small amounts of unidentified items were combined into the category 'other'. This category's contribution to the energy assimilation is considered to be very low, and was therefore ignored.

Brown bears have been reported to pass through three biochemical and physiological stages during their period of activity (Nelson, Folk, Feld & Ringens 1979), changing from low food intake (hypophagia) in spring to high food intake (hyperphagia) in autumn (Nelson et al. 1979, Nelson, Folk, Pfeiffer, Craighead, Jonkel & Steiger 1983). We used the scats found along the transect lines as an indicator of defecation rates and thereby ingestion rates. Because the transect lines were not walked in the end of October (the end of the bears' active period), we assumed that the mean number of scats/km in October was the same as in September. We used the data on scats collected per km to weight the seasonal contribution to total annual digestible energy.

The relative contribution of a food category a to total digestible energy (RC_a) was then calculated as

$$RC_a = \sum_{\text{spring}}^{\text{autumn}} EDEC_{ai} \cdot R_i \qquad (3),$$

where EDEC is percent of Estimated Dietary Energy Content (from Tables 2 and 3), $EDEC_{ai}$ is food category a's relative contribution to total digestible energy in season i, and R_i is the weighting factor of season i relative to the other seasons.

Kruskal-Wallis and Mann-Whitney U-tests were used to test whether scat size was related to scat composition. To compare the different scat collection methods used in 1987-1988 and 1993-1995, Mann-Whitney U-tests were used to test for differences in FV of ungulates in the different time periods. All tests were two-tailed, and differences were considered statistically significant when $P < 0.05$. Statistical tests were executed in SPSS.

Results

Scat collection along transect lines

Of the 143 scats found along the transect lines, 26

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were from spring, 54 from summer and 63 from autumn. This means a yield of 0.024, 0.05, and 0.088 scats/km in spring, summer and autumn, respectively. Based on these results, spring, summer, and autumn diet was weighted 0.15, 0.31 and 0.54, respectively.

Scat volumes

Individual scat volumes varied considerably (39-1,825 ml, x = 360 ± 291 ml (SD)) and scat size was related to scat composition (χ^2 = 8.1, df = 3, P = 0.045, Kruskal-Wallis). Scats containing more than 50% remains of ungulates (264 ± 163 ml) were smaller than scats containing more than 50% remains of berries (421 ± 308 ml; U = 1414, P = 0.005, Mann-Whitney U-test), and tended to be smaller than scats containing more than 50% remains of forbs and graminoids (384 ± 335 ml; U = 2014, P = 0.065). Scats containing more than 50% ants and anthill material (285 ± 164 ml) tended to be smaller than scats containing more than 50% remains of berries (U = 574, P = 0.069). However, because the scats containing more than 50% ants and anthill material were not different from the ungulate and forb/graminoids 'groups', the size of the scats were ignored in the further analyses.

The FVs of ungulates in scats collected in 1987-1988, when 87% were collected along transects, were

Table 1. Percent of faecal volumes (FV) of ungulates in independent scats, i.e. only one random scat used from each group from 1987-1988 when almost all were collected along transects and from 1993-1995. All between-periods are not statistically different (Mann-Whitney U-test, P > 0.05, sample size in parentheses).

	Norway		Sweden	
Years	1987-1988	1993-1995	1987-1988	1993-1995
Spring	68 (7)	46 (14)	32 (10)	39 (10)
Summer	58 (8)	24 (34)	6 (27)	2 (13)
Autumn	0 (3)	11 (20)	0 (49)	1 (5)

Table 2. Percent Frequency of Occurrence (FO), percent of Faecal Volume (FV), percent of Estimated Dietary Content (EDC), and percent of Estimated Dietary Energy Content (EDEC) of food items found in scats from the Swedish part of the study area. EDC and EDEC are not calculated for the last category 'other', but are considered to be very low. Items constituting less than 0.5% of FV, EDC, or EDEC are marked with tr (trace).

	SPRING (N = 25)				SUMMER (N = 52)				AUTUMN (N = 71)			
FOOD ITEM	FO	FV	EDC	EDEC	FO	FV	EDC	EDEC	FO	FV	EDC	EDEC
Mushrooms									13	2	1	1
Cryptogams	8	1	0-1		tr				tr			
Horsetails					tr							
Graminoids	36	26	5-18	1-6	13	1	1		tr			
Forbs (stems/leaves)	16	5	1-3	0-1	98	78	47-61	24-40	51	18	10	7
Cicerbita alpina	8	5	1-3	0-1	75	63	38-50	20-32	32	17	9	7
Unspecified forbs	tr				25	14	9-11	4-7	18	1	1	
Berries	16	5	2-7	1-4	15	1	1-2	1-2	92	74	82	80-81
Rubus idaeus									tr			
Vaccinium vitis-idaea	tr				tr				27		1	1
V. myrtillus					tr				45	20	23	22
Empetrum spp.	16	5	2-7	1-4	13	1	1-2	1-2	87	51	58	57
Insects	32	7	7-22	5-21	67	10	24-32	27-46	58	3	6	8
Diptera (maggots)					tr				tr			
Coleoptera	tr				tr				tr			
Bumblebees/wasps					tr				tr			
Ants	32	7	7-22	5-21	62	10	24-32	26-46	32	2	5	8
Formica spp.	8	4	3-11	2-10	12	1	3-4	3-5	tr			
Camponotus spp.					10	1	3-4	3-6	3	1	2	4
Camponotus/Formica	24	4	3-11	3-11	44	7	18-24	21-35	25	1	3	4
Lepidoptera					tr				tr			
Lizards					tr							
Birds					tr				8	1	3	4
Rodents					10		0-1	0-1				
Unspecified animals					2		0-1	0-1				
Ungulates	60	37	48-85	68-93	17	5	11-38	13-48	5		0-1	0-1
Alces alces (adults)	4	2	3-5	4-5					1		0-1	0-1
Rangifer tarandus	20	12	16-28	22-30	10	1	2-7	3-12	tr			
A. alces/R. tarandus	36	23	30-53	42-58	8	3	5-21	10-36	tr			
Other (anthill mat. etc.)	89	19	-	-	92	5	-	-	95	1		

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not different from those collected in 1993-1995 when few were collected along transects (Mann-Whitney U-test, Table 1). For this test independent scats were used, i. e. one random scat was chosen for the test if several were found together.

Scat analysis, Swedish area

In spring (April-May), ungulates composed most of the sampled faecal volume (Table 2). Most of the ungulates probably were animals that had died the previous autumn and winter, or remains from slaughtered hunter-killed moose from the previous autumn. Graminoids made up the second largest part of the faecal volume (FV). However, because of low digestibility and low energy content, only 1-6% of the energy came from this source (see Table 2). In terms of digestible energy, reindeer and moose dominated the diet, followed by ants, graminoids and berries from last autumn.

Forbs were common in this area and were consumed frequently by bears during summer (June-July). Forbs, especially blue sow thistle, were found in 98% of the scats collected, made up 78% of the faecal volume and contributed 24-40% of the digestible energy. Ants were eaten frequently, and contributed 26-46% of the digestible energy. Bears obtained *Formica* ants by excavating anthills and, in late spring, summer and early autumn, bears searched for *Camponotus* ants in coarse woody debris. The proportion of ant larvae ingested while eating ants increased from almost zero during spring to about 30-40% in summer. Even though low in FO and FV, bears obtained 13-48% of their digestible energy from ungulates (see Table 2).

Berries, such as bilberry and crowberry, started ripening in the beginning of August and dominated the diet throughout the autumn. Berries were found in 92% of the scats, made up 74% of the faecal volume,

Table 3. Percent Frequency of Occurrence (FO), percent of Faecal Volume (FV), percent of Estimated Dietary Content (EDC), and percent of Estimated Dietary Energy Content (EDEC) of food items found in scats from the Norwegian part of the study area. EDC and EDEC are not calculated for the last category 'other', but are considered to be very low. Items constituting less than 0.5% of FV, EDC, or EDEC are marked with tr (trace).

	SPRING (N = 28)				SUMMER (N = 58)				AUTUMN (N = 32)			
FOOD ITEM	FO	FV	EDC	EDEC	FO	FV	EDC	EDEC	FO	FV	EDC	EDEC
Mushrooms	tr				tr				28	5	1-3	1
Cryptogams	11	2	0-1		tr				tr			
Horsetails					tr				tr			
Graminoids	43	8	2-6	0-2	29	2	0-1		41	1	0-1	
Forbs (stems/leaves)	36	8	2-6	1-2	91	49	4-14	1-5	66	25	6-16	2-6
Cicerbita alpina					53	40	4-12	1-4	25	15	4-10	1-3
Angelica sp.									3	3	1-2	0-1
Unspecified forbs	36	8	2-6	1-2	47	9	1-3	0-1	43	7	2-4	1-2
Berries	18	4	2-6	1-3	16	2	0-1	0-1	84	42	22-58	11-29
Rubus chamaemorus									tr			
R. idaeus									9	3	2-6	1-3
Vaccinium myrtillus	tr				tr				47	6	3-8	2-4
Empetrum spp.	14	4	2-6	1-3	12	2	0-1	0-1	78	33	17-44	11-29
Insects	56	10	9-30	6-25	59	6	2-7	1-6	71	7	7-18	6-14
Diptera (maggots)	7	1	1-3	0-2	17		0-1	0-1	22		0-1	0-1
Coleoptera	tr				tr							
Bumblebees/wasps					tr				22		0-1	0-1
Ants	46	9	8-27	6-23	44	5	1-6	1-5	53	6	6-16	5-12
Formica spp.	18	2	2-6	1-5	19	1	0-1	0-1	31	4	4-11	3-8
Camponotus spp.					21	3	1-4	1-3	12	1	1-3	1-2
Myrmica spp.					tr				tr			
Camponotus/Formica	29	7	6-20	5-18	9	1	0-1	0-1	9	1	1-3	1-2
Lepidoptera					tr				tr			
Birds	tr				tr							
Rodents	7		1-2	1-2								
Ungulates	75	52	53-86	68-92	67	37	68-94	89-97	31	10	41-65	51-81
Alces alces (adults)	4	2	3-5	3-5	tr				3	2	2-6	3-7
Rangifer tarandus	21	14	19-34	24-36								
A. alces/R. tarandus	29	16	21-39	27-42	9	3	2-3	2-3	tr			
Ovis aries	21	20	8-11	9-14	57	34	68-81	88-94	25	8	39-59	48-74
Other (anthill mat. etc.)	79	16	-	-	64	4	-	-	53	10	-	-

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82% of the dry matter ingested, and 80-81% of the digestible energy (see Table 2). Crowberry was the most important berry, followed by bilberry. Blue sow thistle and ants were eaten during autumn, mostly in August. Birds, probably grouse, accounted for 4% of the assimilated energy. However, this figure seems high because of the rather low grouse population and because bears probably are not effective hunters on these birds. The result may be due to sampling error because of the small sample of faeces.

Scat analysis, Norwegian area

Moose, reindeer, sheep (available as carcasses from the previous year), and to a lesser degree ants were the most important food items in spring. Although graminoids, forbs and berries were eaten frequently, they were, like rodents, of minor importance in providing energy (Table 3).

In summer, forbs (mostly blue sow thistle) were eaten in considerable amounts and made up most of the faecal volume. However, as the correction factors for ungulates (CF_1 and CF_2) are much higher than for forbs, sheep contributed 88-94% of the digestible energy (see Table 3).

Ungulates (mostly sheep) and berries were also the most important foods in autumn. As in the Swedish area, forbs and ants were eaten in August. Mushrooms and bumblebees/wasps were found in 28 and 22% of the scats, respectively, but were not energetically important (see Table 3).

Comparison between areas

Relative contributions by the major foods to the total annual digestible energy were estimated according to equation (3). Protein and lipid-rich food such as ungulates (mostly sheep in Norway) and insects (mostly ants) combined contributed 36-43 and 78-92% of the digestible energy, in the Swedish and Norwegian areas, respectively (Fig. 2). Berries, which are high in carbohydrates, contributed 44-46 and 6-17% of the digestible energy in the same areas, respectively. Graminoids and forbs contributed about 2-6% of the digestible energy in the Norwegian area, whereas the corresponding figure in the Swedish area was 12-18%.

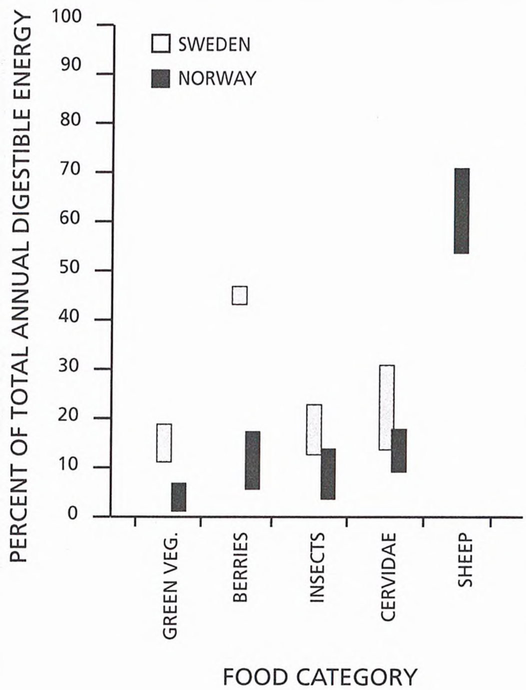

Figure. 2. Relative contribution from major food categories to total annual digestible energy of brown bears in the Norwegian and the Swedish parts of the study area. The data from spring, summer and autumn are pooled according to equation (3), p. 151.

Discussion

Sampling bias

It may be difficult to sample food use based on faecal collections in an unbiased manner, especially when all individuals (in this case scats) in a population are not equally obtainable (Ims & Yoccoz 1996). Surprisingly few authors have discussed this problem. An estimated 18,000 scats/1,000 km^2/year are defecated in the core of the Swedish study area (based on defecation rates of captive brown bears, Roth (1980), and an estimated density of 24 bears/1000 km^2), but only 266 scats were collected. Thus the sample comprised a very small fraction of the available scats. A significant bias might thus be introduced by gathering a disproportionate number of faecal samples from near ungulate carcasses, for example, or during a time of year when a particular food was selectively used (Craighead, Sumner & Mitchell 1995).

The FVs of ungulates in 1993-1995 were not different from FVs of ungulates in 1987-1988 when almost all scats were collected along transect lines (see Table 1), so the sampling techniques used in 1993-1995 did not seem to introduce a bias towards ungulates in the scats. Most scats in the autumn sam-

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ple, especially from the Norwegian part, were collected in August, when sheep were still available in Norway. If scats had been collected throughout the autumn season, the importance of berries would probably have increased and the importance of sheep and forbs in the diet would have decreased.

Defecation rates

Some authors have reported a negative or small weight gain from spring until late summer, (Jonkel & Cowan 1971, Pearson 1975, Beeman & Pelton 1980), indicating low food intake during spring. However, Noyce & Garshelis (in press) showed that American black bears in north-central Minnesota increased their weight also in spring, and they proposed that the negative foraging concept has been used uncritically. With constant defecation rates, we should in fact expect more scats to be found in spring, as scats are easier to detect in spring when the ground is covered with snow, and the ground layer vegetation has not yet sprouted. In spite of this bias, our results showed that the defecation rate nearly doubled from spring to autumn. Increased defecation rates were also found by Mattson et al. (1991a), but the increase in defecation rates was not quite as pronounced as for brown bears fed ad libitum in a zoo (Roth 1980). We have very limited data on weight changes during the season in Scandinavian brown bears.

Correction factors

Correction factors for most food items in this study could be employed without additional interpretation or judgements. The exception is CF's for large ungulates. CF_1 for adult ungulates depends on the amount of hide and bone consumed together with the meat and viscera (Hewitt & Robbins 1996), and should therefore be set to reflect the consumption of skin and hair as well as the use of old carcasses (see Methods).

Compared with Elgmork & Kaasa (1992), we used a lower CF_1 for bilberry, cowberry and crowberry (0.54 compared with 0.93) as recommended by Hewitt & Robbins (1996, see Table 1). The CF_1's for ungulates are presented as ranges of possibilities rather than single values.

Only a few authors (Mattson, Gillin, Benson & Knight 1991b, Elgmork & Kaasa 1992, Craighead et al. 1995, Mattson & Reinhart 1995) have adopted correction factors in their analyses of bear scats. Due to higher digestibility and energy content of animal matter compared to plant material, most other studies (e.g. Clevenger, Purroy & Pelton 1992, Mace & Jonkel 1986) that interpreted results based on percent of faecal volume or importance value, have underestimated the importance to bears of animal matter in the diet. The effect of applying CFs in the interpretation of food habits based on scat analysis was considerable. For example, in the Swedish and the Norwegian parts of the study area, forbs constituted 78 and 49% of faecal volume in summer, respectively, but due to the Norwegian bears' access to sheep, forbs comprised no more than 1-5% of the assimilated energy in this season. In the Swedish area, forbs made up 24-40% of the assimilated energy (see Tables 2 and 3). On the other hand, because remains of ungulates occur in smaller scats than remains of berries or forbs/graminoids, the contribution of ungulates to digestible energy was slightly overestimated in relation to berries and forbs/graminoids.

Diet selection

Bears fattened during autumn in the Swedish area by consuming large quantities of berries rich in carbohydrates. In the Norwegian area bears fattened on both sheep and berries, but the former was considerably more important. In both areas, the diet in spring was dominated by protein-rich foods, such as ungulates and ants. In summer, bears in the Norwegian part switched to the protein and lipid-rich sheep as they became available. The blue sow thistle has a high protein content, especially early in the growing season (Ohlson & Högbom 1993), and in Sweden blue sow thistle and ants constituted the most protein-rich foods readily available to bears, although blue sow thistle was less common in the Swedish area than in the Norwegian area (pers. obs.).

Sheep husbandry did not exist in the Swedish part of the study area, so sheep were only available to bears in Norway. Sheep seemed to be highly selected by bears there, based on the difference in diet between bears in the Norwegian and Swedish parts of the study area, and by the fact that each year compensation is paid, on average, for about 55 sheep for each bear in Norway. The fat content of animals generally increases with maturity (Robbins 1983) and bears may consequently increase their energy intake by selecting adult individuals within a prey species. Bear selected adult sheep, and bear predation resulted in the loss of 22% of the ewes and 4% of the lambs in the Norwegian area (Knarrum 1996). Only fat from the udder and sternum regions was eaten from 69% of the ewes killed. Even so, bears are effective

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scavengers and often returned to many of these ewes and consumed most of the meat (Knarrum 1996, pers. obs.). Polar bears *U. maritimus* have been reported to strip the skin from seals prior to eating them (Smith 1980) and often ingest only the blubber (Lønø 1970). Despite longer gastrointestinal transit time for blubber than for meat, polar bears consuming a blubber diet would assimilate energy at twice the rate of polar bears feeding a meat diet (Best 1985). Thus selection of the most lipid-rich part of the prey is expected when there is a surplus of prey lacking effective antipredator strategies. In Norway, sheep graze unattended, in contrast to the protection they receive in most parts of Europe (Kaczensky 1996). Although hard to quantify, we consider reindeer to be more important than, or at least as important as, moose in both areas.

Forbs were apparently preferred by bears over graminoids during summer and autumn in both the Norwegian and Swedish parts of the study area. Forbs, but not graminoids were eaten in August, probably because forbs retain higher nutritional quality compared to graminoids later in the growing season (Cook 1972, McLellan & Hovey 1995). According to the percent cover of the plants, crowberry appeared to be selected over bilberry and cowberry. The availability of berries was not estimated during this study.

Comparison with other studies

Elgmork & Kaasa's (1992) study in central south Norway and Johansen (1997) are the only other quantitative studies of the diet of brown bears in Scandinavia. Bears in south-central Sweden preferred bilberry over crowberry and cowberry (Johansen 1997), whose study otherwise revealed results similar to ours. Elgmork & Kassa's study differed from ours in that bears in central south Norway used catkins of *Salix* and *Betula* in spring, used ants less during summer, and consumed no wild ungulates. Domestic sheep were eaten only during late summer (July-August), in contrast to more prolonged use in the Norwegian part of our study area. During Elgmork & Kaasa's (1992) study, the study 'population' may have consisted of only one female bear (Bækken, Elgmork & Wabakken 1994), which certainly could have had an effect on the results. In the Cantabrian Mountains, Spain, less than 0.10% of the sheep within bear range were killed by bears, but a substantial amount of sheep material occurred during summer indicating that bears in this area were efficient scavengers (Clevenger et al. 1992). A high proportion of energy obtained from ungulates is also documented from the Yellowstone National Park, an area with several ungulate species (Mattson et al. 1991b, Mattson 1997).

Conclusions

Our results showed that the presence of free-ranging domestic sheep had a great impact on the diet of brown bears. As expected, bears in Norway with access to unguarded sheep consumed large quantities of this vulnerable protein and lipid-rich prey when it was available during summer and most of the autumn. As a result, bears decreased their relative use of ants and forbs in summer and berries in August and September where sheep were available. Lipid accumulation is important for bears for survival while hibernating during winter. Fat may be accumulated by the conversion of protein or carbohydrates to fat or by the physiologically less expensive direct conversion of lipid from lipid, and bears often selected adult sheep with higher lipid content and the lipid-rich parts of these sheep (sternum fat and mammary glands) (Knarrum 1996). However, the welfare of bears in Norway is not dependent upon sheep, as bears in Sweden survive well without them and are the most productive brown bears yet studied (Sæther, Engen, Swenson, Bakke & Sandegren in press).

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