Ann. Zool. Fennici 46: 395–415 ISSN 0003-455X (print), ISSN 1797-2450 (online)
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Carnivory is positively correlated with latitude among omnivorous mammals: evidence from brown bears, badgers and pine martens

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Received 17 Nov. 2008, revised version received 4 May 2009, accepted 16 Mar. 2009

Vulla, E., Hobson, K. A., Korsten, M., Leht, M., Martin, A.-J., Lind, A., Männil, P., Valdmann, H. & Saarma, U. 2009: Carnivory is positively correlated with latitude among omnivorous mammals: evidence from brown bears, badgers and pine martens. — *Ann. Zool. Fennici* 46: 395–415.

Omnivores exploit numerous sources of protein and other nutrients throughout the year, and meat is generally considered a high-quality resource. However, it is unknown if there is any general association between latitude and carnivorous behavior in omnivorous mammals. We examined the relative importance of meat and other dietary components, including anthropogenic food items, in the diet of brown bears (*Ursus arctos*) in Estonia using conventional scat- and stomach-content analyses as well as stable-isotope (δ^{15}N, δ^{13}C) analyses. When food habits of brown bears in Estonia were compared with those of other populations in central and northern Europe, the proportion of animal prey in the diet was positively correlated with latitude. Further comparison with the data on the diet of two other omnivorous mammals, the European badger (*Meles meles*) and the European pine marten (*Martes martes*), provides evidence that increased carnivory towards northern latitudes may be a general adaptation in omnivorous mammals.

Introduction

Geographic variation in the diet plays an important role in determining the abundance and distribution of mammal species, as well as shaping their evolutionary adaptations, life-history strategies and ecological roles. Compared with mammals exhibiting other feeding strategies, omnivores are more flexible and can select among numerous food items. However, omnivores are not as efficient as herbivores in digesting and assimilating plant food or as efficient as carnivores in feeding on animals (Chapman & Reiss 1999). Thus, omnivores must either obtain large quantities of food or select high-quality food items in order to satisfy their nutritional demands. For omnivorous animals, the consumption of different food items is influenced by spatio-temporal variation in the availability of potential food items. Omnivorous species occurring over large heterogeneous areas may therefore be predicted to exhibit geographic variation in their feeding habits, with locally-available, high-quality food items favored. However, information on geographic variation in the diet of omnivorous mammals living under natural conditions is scarce due to the difficulty of identifying the potentially large number of food items that are often efficiently digested and reduced to small fragments.

To date, relatively few studies carried out wide-scale comparisons of the food habits of widespread omnivorous mammals: two mustelids, the European badger (*Meles meles*) (Goszczynski *et al*. 2000) and the European pine marten (*Martes martes*) (Zalewski 2004), being the only examples. These studies found that animal-derived food items were consumed more frequently in northern as compared with southern latitudes (in the northern hemisphere). However, it is not known whether a similar trend would be observed in a large omnivorous mammal, such as the brown bear (*Ursus arctos*); nor did the previous studies investigate seasonal changes in the diet composition, which could help us to understand in greater detail the variables that influence the diet in regions with seasonally variable climate.

The diet of the European brown bear was well studied in recent decades (Appendix 1). The diet composition and the availability of suitable sources of food strongly affects brown bear population productivity (Hildebrand *et al*. 1999), habitat use (Nomura & Higashi 2000), and the spatial structure of populations (McLoughlin *et al*. 2000). In areas with high human population density, such as Europe, brown bear ranges often overlap with areas subject to human activity. These areas often provide aggregated and easily accessible food items for brown bears, such as livestock, grain and fruit. The consumption of anthropogenic food by bears may be a source of conflict in itself (Sagør *et al*. 1997), but may also increase the local density of bears (Fedriani *et al*. 2001) and reduce their wariness toward humans (Swenson 1999). The issue of so-called problem bears is likely to remain serious since much of the brown bear range world-wide coincides with areas of high human density. Therefore, detailed knowledge of the brown bear diet and consumption of anthropogenic food items is essential in order to minimize conflicts between bears and humans.

Conventional methods for evaluating the diet of mammals — based on the analysis of scat or stomach contents — are limited when studying omnivores, since these species consume a variety of food types that are digested to a differing degree. A valuable addition to these approaches is a stable-isotope analysis, which allows estimates of dietary inputs in cases where there are isotopically distinct dietary options available. Although the use of two stable isotopes allows for determination of inputs from only three isotopically distinct sources, the recent development of probabilistic models has made it possible to estimate the range of dietary inputs from more than three sources (Phillips & Gregg 2003). For omnivorous species like brown bears, which have access to a broad range of isotopically distinct foods, this approach may be particularly useful. There is currently a considerable interest in applying stable-isotope methods to deciphering the diets of extant and extinct bears and other wildlife in North America and Europe (Hildebrand *et al*. 1999, Hobson *et al*. 2000, Felicetti *et al*. 2003, Bocherens *et al*. 2004, Urton & Hobson 2005). Our study can provide important data regarding European bears in this context.

In this study, we analyzed the diet of the Estonian brown bear population during different seasons and compared it with that of other European populations, where dietary analyses have been conducted using the same methods (*see* Appendix 1). In particular, we considered whether there exists a latitudinal gradient of carnivory (with a larger proportion of animal food items in the diet at higher latitudes) in the brown bear and other omnivorous mammals for which the data were available. The specific aims of this study were: (i) to estimate the occurrence and energetic contribution of different food items

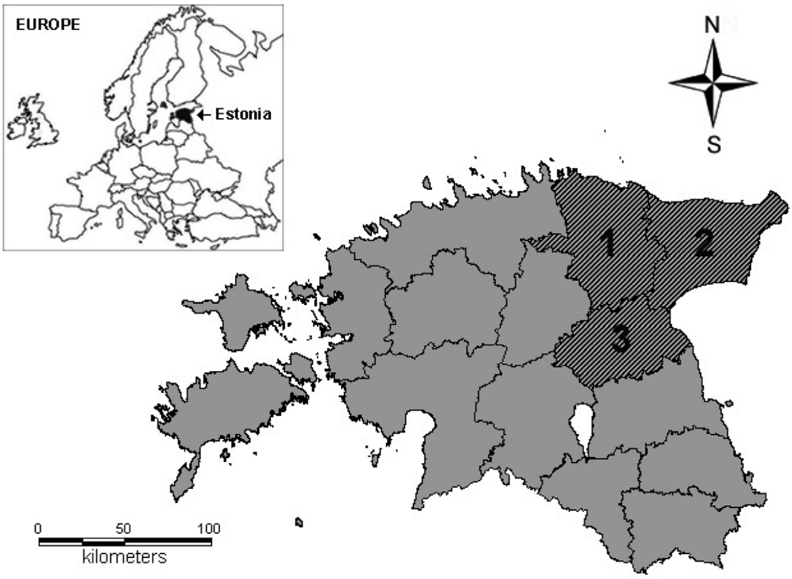

Fig. 1. Map of Estonia with marked study areas (1 = Lääne-Virumaa, 2 = Ida-Virumaa, 3 = Jõgevamaa), which together constitute the core area of brown bears in Estonia.

to the Estonian brown bear diet using analysis of fecal samples and stomach contents, with particular attention paid to items of anthropogenic origin; (ii) to compare the results of these conventional analyses with those derived from the stable-isotope analysis of brown bear hair samples; and (iii) to place our results in the context of previous work on other brown bear populations in Europe and of other omnivorous mammals.

Material and methods

Study area

Brown bear scat and stomach samples were collected from three counties in north-east Estonia: Lääne-Virumaa, Ida-Virumaa and Jõgevamaa (59°N, 26°E) (Fig. 1), which constitute the core area for the Estonian brown bear population (Valdmann *et al*. 2001). Bogs and coniferous forests are characteristic of the eastern part of the study area, while an agricultural landscape containing patches of both coniferous and deciduous forests dominates in the western part. Forest covers 57% of the study area, while 18.5% is used for agriculture (Estonian Ministry of the Environment 2005). The density of the human population is 8.6 individuals km^{-2}. During the study period, the number of brown bears in the study area was 297–332, giving a population density of 33.3 ± 4.7 (mean ± SD) bears per 1000 km^2 (Estonian Ministry of the Environment 2005). The densities of potential prey species for brown bear in the study area were the following (individuals per 1000 km^2): moose (*Alces alces*) 218.1, wild boar (*Sus scrofa*) 274.5, roe deer (*Capreolus capreolus*) 509.8 and red deer (*Cervus elaphus*) 4.1 (Estonian Ministry of the Environment 2005). Cereals, apples, and potatoes were available to foraging bears at wild-boar feeding sites. The density of feeding sites in the study area was 0.06 feeding sites km^{-2}. Carcasses of domestic animals (cows, pigs) were occasionally available at informal burial sites.

Fecal and stomach analysis

A total of 142 bear scats and 12 bear stomachs were collected by local hunters and project staff during 2003–2004. The scats were collected according to Dahle *et al*. (1998). The scats and stomachs were kept frozen until further analysis. To investigate seasonal differences in the diet composition, the activity period of brown bears during the year was divided — according to Dahle *et al*. (1998) — into three seasons based on the availability of major food items: spring (April–last week of May), summer (last week of May–July), autumn (August–October).

Laboratory analyses followed the methodology described by Hamer and Herrero (1987). Scats and stomach contents were washed through a 0.8 mm mesh. Five 6-ml wet subsamples were taken from homogeneous remains for content analyses. All food items were identified to the lowest taxonomic level possible using a microscope (magnification 9–80×), food items were separated from each other and their proportion (per volume) in the sample was visually estimated as described by Mattson *et al*. (1991). Food items with very low contribution to assimilated energy (twigs, pebble, wire, wood fragments, etc.) were defined as trash and were ignored in further analyses.

Frequency of occurrence (FO, %), and proportion (volumetric, FV, %) of each diet item in the scats were calculated for each season using the following equations of Dahle *et al*. (1998):

$$\mathrm{FO} = \frac{\begin{array}{c}\text{total number of scats containing}\\ \text{food item in a given season}\end{array}}{\text{total number of scats in that given season}} \times 100 \quad (1)$$

$$\mathrm{FV} = \frac{\begin{array}{c}\sum\text{\%volume of food item in each scat}\\ \text{in a given season}\end{array}}{\text{total number of scats in that given season}} \quad (2)$$

The parameters (FO and FV) were also calculated in the same manner for each food item found in the stomachs.

To estimate the dietary content (hereafter EDC, %), i.e. proportion of particular dietary items consumed, FVs of food items were multiplied by their correction factors given by Hewitt and Robbins (1996): graminoids = 0.24, forbs and mushrooms = 0.26, cereal and hard mast = 1.5, apples = 0.51, berries from genus *Vaccinium* = 0.54, berries from genus *Rubus* = 0.87, other berries = 1.2, potatoes = 0.93, insects = 1.1, small vertebrates = 4.0. Correction factor for the reamins of large vertebrates and carcasses of domestic animals was 1.5 (Johansen 1997).

To estimate the total dietary energy content (hereafter EDEC, %), i.e. proportion of energy provided by particular dietry items consumed, EDCs of food items were multiplied by their respective energy coefficients: 6.3 for graminoids, 8.4 for forbs, 11.7 for berries, potatoes and cereals, 18.8 for small vertebrates, 28.4 for large mammals (Dahle *et al*. 1998), 17.7 for insects (Swenson *et al*. 1999), 6.3 for mushrooms (Persson *et al*. 2001).

A Mann-Whitney *U*-test was used to test for differences in the proportion of food items found in stomachs and scats (FV). A Kruskal-Wallis ANOVA was used to test for differences in the frequency (FO) and proportion (FV) of food items between seasons. The data were standardized for the analyses of seasonal, annual and spatial variation in the use of different food items. All differences were considered statistically significant when $p < 0.05$. All statistical tests were performed using STATISTICA 8.0 (StatSoft, Inc.).

Stable isotope analyses

Most brown bear hair samples were collected from within the study area in 2000–2004 using a standard semi-invasive DNA hair-sampling method (Woods *et al*. 1996, Mowat & Strobeck 2000). A total of 37 hair-sampling sites were established in the study area between 25 March and 15 October. Each hair-sampling site consisted of an approximately 30-m perimeter fence of single-strand barbed wire placed 0.5 m above the ground and an elevated non-reward scent of liquid fish and cattle blood and/or rotten meat inside the perimeter (Woods *et al*. 1996). Sampling sites were visited 7 and 14 days after set up to remove hair samples. Samples from trophy furs collected within the study area in 1999–2004 were also included.

Reference samples for the stable-isotope analysis were taken from the main components of the brown bear diet: plants, ants, domestic and wild animals; these were the following: bilberry (*Vaccinium myrtillus*), cranberry (*Oxycoccus palustris*), cowberry (*Vaccinium vitis-idaea*), raspberry (*Rubus idaeus*), domestic apple (*Malus domestica*), stinging nettle (*Urtica dioica*), clover (*Trifolium* sp.), orchard grass (*Dactylis glomerata*), marsh hawksbeard (*Crepis paludosa*), meadowsweet (*Filipendula ulmaria*), wild angelica (*Angelica sylvestris*), fireweed (*Epilobium angustifolium*), oats (*Avena sativa*), barley (*Hordeum vulgare*), coltsfoot (*Tussilago farfara*), bishop's goutweed (*Aegopodium poda-

graria), hogweed (*Heracleum sibiricum*), aspen (*Populus tremula*), dandelion (*Taraxacum* sp.), moose, wild boar, domestic pig (*Sus scrofa* var. *domesticus*) and cattle (*Bos taurus*).

Bear hair samples were cleaned with 2:1 chloroform–methanol solution and dried under a fumehood. Plant material was cleaned using distilled water, dried at 60 °C and powdered with a mechanical grinder. Animal tissue samples were dried, and lipids removed using by rinsing in chloroform–methanol solution. Subsamples of approx. 1 mg were loaded into tin cups and analysed with a Europa 20:20 continuous flow mass spectrometer interfaced with a Robo-Prep elemental analyzer. Stable isotope measurements were expressed in standard delta notation relative to Vienna Pee Dee Belemnite (VPDB) and atmospheric air (AIR) for δ^{13}C and δ^{15}N, respectively. For hair and tissue samples, a working laboratory standard (egg albumen) was measured between every five samples in a sequence. This standard was replaced by a peagrain laboratory standard when analyzing plant material. Analytical error, based on the laboratory standards, was estimated to be ±0.1‰ for δ^{13}C and ±0.3‰ for δ^{15}N measurements.

We used the isosource mixing model (Phillips 2001) to gain insight into relative contributions of potential dietary items to bear during the period of hair growth. This iterative approach does not provide a unique solution to more than three dietary inputs using two stable isotopes. Rather, the model provides a range of possible solutions giving the consumer mean isotopic tissue values that fall within the solution space or mixing polygon of the model. The model requires knowledge of the isotopic discrimination factors between the diet and bear hair so that dietary endpoints in the model correspond to the values expected for a given consumer's tissue based on the consumption of that dietary material. We used equations relating bear plasma to diet derived by Felicetti *et al.* (2003) for bears raised in captivity on known diets ranging from fruits to meat:

$$\delta^{13}\mathrm{C} = -10.86 + 0.42x \tag{3}$$

and

$$\delta^{15}\mathrm{N} = 5.28 + 0.88x \tag{4}$$

where x is the stable isotope value of the diet. Hildebrand *et al.* (1996) showed that discrimination values calculated for bear plasma are the same as those for hair.

Latitudinal variation analyses

Analyses of latitudinal variation in the brown bear diet (animal *versus* plant items) was conducted using data from studies that applied similar analytical methods and seasonal subdivisions as here (*see* Appendix 1). If they were not given in the original sources, estimates of the total (year-round) consumption of plant and animal food were calculated as arithmetic means of seasonal estimates. Correlations between latitude and dietary composition (animal and plant items) were also calculated for badgers and pine martens. Badger and pine marten diets were compiled from studies listed in Appendix 2.

Results

Diet composition

We recorded 72 plant, 1 fungal and 31 animal taxa in bear scats and stomachs (*see* Appendix 3). Plants most frequently found in scats and stomachs were dandelion and umbelliferous plants such as bishop's weed and cow parsnip. The commonest vertebrate remains recorded were those of wild boar, domestic pig and cow, while the most frequently eaten invertebrates were ants, especially from groups *Formica* and *Lasius*.

Plants occurred in almost 97% of scats and constituted over a half of the brown bear EDC (59%), though they provided less than half (43.9%) of the yearly EDEC of brown bears, whereas animal remains constituted 37% of the bears' EDC (Table 1). Although insects were consumed three times more frequently than mammals, the latter constituted more than 70% of the EDEC derived from animal food items.

Annual and seasonal variation

The consumption of berries was significantly lower ($U = 700.5$, $p < 0.001$) in 2003 ($n = 64$) and consumption of apples was significantly higher ($U = 773$, $p < 0.001$) in 2003 as compared with those in 2004 ($n = 42$) in autumn. No additional significant inter-annual differences were found in the consumption of other food items either overall or for any season.

Season had a signifficant effect on the consumption of insects ($H = 6.2$, df = 2, $p = 0.04$), forbs ($H = 21.9$, df = 2, $p < 0.001$), cereals ($H = 13.2$, df = 2, $p = 0.001$) and berries ($H = 6.7$, df = 2, $p = 0.03$). In spring, the most important food items were mammals and forbs, with both constituting about 30% of EDC, followed by cereals and insects (Table 2). During summer, mammals were again the most important food item, contributing 37% to EDC, followed by insects, especially ants, which were consumed over four times more than in spring. Forbs contributed over 25% to EDC in summer, while graminoids and berries were of minor importance in summer. In autumn, carbohydrate-rich food items, such as cereals, berries and apples were the most important food items. Cereals contributed more than

Table 1. Average frequency of occurrence (FO, %), proportion (FV, %), estimated dietary content (EDC, %), and estimated dietary energy content (EDEC, %) of food items found in 142 brown bear scats, and FO and FV of food items found in 12 brown bear stomachs from the core area of the Estonian brown bear population in 2003–2004. Trace = items constituting < 0.5% of FV.

Food item	Scats				Stomachs	
	FO	FV	EDC	EDEC	FO	FV
Plants	96.5	82.8	59.1	43.9	91.7	74
Graminoids	48.3	8.6	3.5	1.3	25	1.1
Forbs	64.2	42.1	19.2	9.6	58.3	34.3
Berries	17.8	12.7	8	7.2	41.7	20.1
Apples	10.1	6.5	3.8	3.5	8.3	2
Cereals	21.3	12.9	24.6	22.3	41.7	16.5
Mushrooms	0	0	0	0	8.3	8.3
Animals	59.2	16.8	37.4	53.5	66.7	17.7
Insects	54.2	7.8	14	14.4	33.3	7.7
Mammals	16.9	9	23.4	39.1	41.7	10
Other	3.2	trace	0.9	0.9	0	0

Table 2. Average frequency of occurrence (FO, %), proportion (FV, %), estimated dietary content (EDC, %), and estimated dietary energy content (EDEC, %) of food items found in different seasons in 142 brown bear scats from the core area of the Estonian brown bear population in 2003–2004. Trace = items constituting < 0.5% of FV, EDC or EDEC.

Food item	Spring ($n = 16$)				Summer ($n = 20$)				Autumn ($n = 106$)			
	FO	FV	EDC	EDEC	FO	FV	EDC	EDEC	FO	FV	EDC	EDEC
Graminoids	68.8	13.4	6.1	2.4	50	10.9	4.4	1.5	26.4	1.4	trace	trace
Forbs	81.3	59.8	29.6	15.7	85	58.1	25.6	11.5	26.4	8.4	2.5	1.7
Berries	6.3	3.2	3.3	2.4	5	trace	trace	trace	47.2	31.8	20.8	19.3
Bilberries	0	0	0	0	5	trace	trace	trace	33	15.3	9.5	8.8
Cowberries	0	0	0	0	5	trace	trace	trace	12.3	5.1	3.1	2.9
Raspberries	0	0	0	0	0	0	0	0	2.8	2.8	2.8	2.6
Apples	0	0	0	0	0	0	0	0	30.2	19.6	11.5	10.6
Cereals	6.3	6.3	17.9	13.6	0	0	0	0	57.5	32.5	56	53.2
Oats	0	0	0	0	0	0	0	0	57.5	31.7	54.6	51.9
Insects	56.3	3.5	7.4	8.3	75	15.7	29.3	27.6	46.2	4.2	5.2	7.3
Formica sp.	38.9	2.6	5.6	6.2	57.7	6.4	11.9	11.2	32.3	2.1	2.6	3.7
Lasius sp.	16.7	0.9	1.8	2.1	63.5	8.3	15.5	14.6	28.6	1.5	1.9	2.7
Mammals	37.5	10.3	29.4	52.9	35	14.7	37.4	56.6	9.4	2	3.4	7.7
Other	trace	trace	trace	trace	5	trace	2.8	2.7	4.7	trace	trace	trace

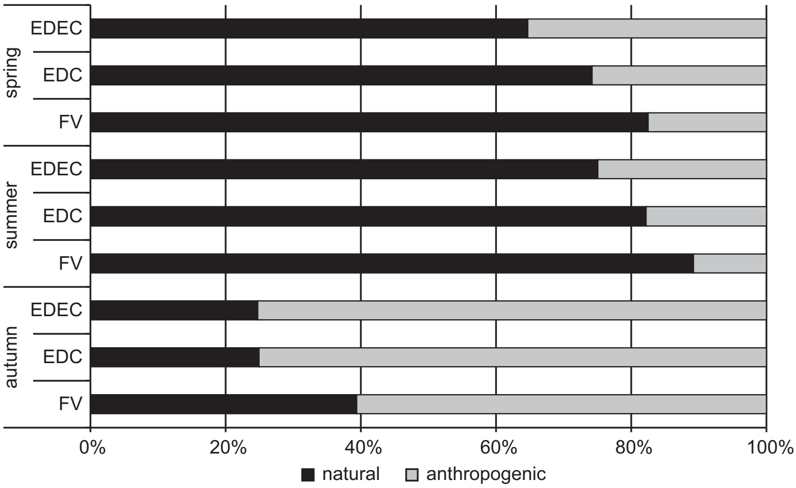

Fig. 2. Proportion (FV), estimated dietary content (EDC), and estimated dietary energy content (EDEC) of natural and anthropogenic food items found in different seasons in 142 brown bear scats collected from the core area of the Estonian brown bear population in 2003–2004.

half of EDC, followed by berries and apples, which constituted together about one-third of EDC. Mammals, insects and forbs, which were important food items in summer, were of lower importance in autumn, contributing a little more than 10% to EDC at that time of a year.

Use of anthropogenic food items

Anthropogenic food items occurred in scats in significantly lower volumes than natural food items in spring and summer ($U = 36$, $p = 0.002$, $n = 16$; and $U = 19$, $p < 0.001$, $n = 20$, respectively), but the situation was reversed in autumn ($U = 4359$, $p = 0.001$, $n = 106$) (Fig. 2). Seasonal patterns of frequency of occurrence for domestic and wild mammals differed significantly from each other ($\chi^2 = 27.13$, df = 2, $p < 0.001$): domestic animals occurred frequently in the bear diet in summer, while wild mammals were more common in spring and autumn. Cereals were the most important energy-rich anthropogenic food item in autumn, while the carcasses of domestic mammals were the most important anthropogenic food item by EDEC in spring and summer (Table 3).

Diet composition from stable isotope analyses

Twenty-nine hair samples were collected using the barbed-wire method and ten samples were obtained from trophy furs. We considered the broad dietary categories of mammals, insects, cereals, berries, graminoids and forbs (Table 4). Mean stable-isotope values for these categories were then converted into expected bear-hair isotope values and entered into Isosource using increment values of 1% and a tolerance of 0.1. Estonian bears had mean hair δ^{15}N of 5.4‰ ± 1.7‰ (range: 3.0‰ to 9.0‰) and mean hair δ^{13}C of –22.7‰ ± 0.6‰ (range: –24.6‰ to –21.3‰). The results of the Isosource mixing model for Estonian bears are shown in Fig. 3 and estimates of dietary inputs are summarized in Table 5.

Table 3. Estimated proportion (%) of anthropogenic food items in the dietary energy content (EDEC) of the brown bear diet in different seasons. The analysis based on 142 scats collected in 2003–2004 from the core area of the Estonian brown bear population.

Season	Plants	Fruits/berries	Cereals	Mammals	Potatoes
Spring	1.4	0	14.4	19.5	0.05
Summer	0.8	0	0	24.2	0
Autumn	0	14.6	53.3	7.4	0

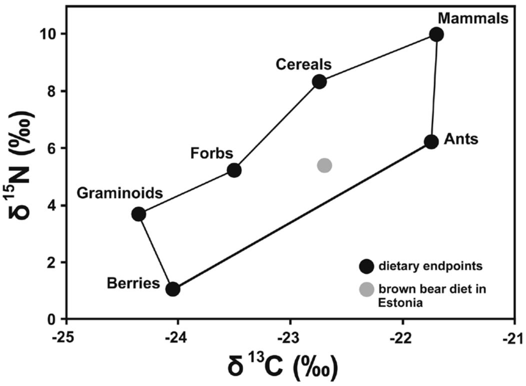

Fig. 3. A dual-isotope multisource-mixing polygon obtained by stable-isotope analysis of brown bear hairs and most important dietary items of brown bears in Estonia, representing the solution space for the Isosource model used to estimate the relative contributions of various categories of food items in Estonian brown bear diets.

Geographic variation in brown bear, badger and pine marten diet

Data from seven studies of the brown bear diet (this study included) revealed a latitudinal gradient in carnivory: in general, increasing latitude is accompanied by an increase in consumption of animal prey and a decrease in consumption of plant items (Fig. 4). Total proportion of animal food items in the brown bear diet was positively correlated with latitude ($r_s = 0.91$, $p = 0.004$) (Fig. 5), whereas a negative correlation was found between latitude and total consumption of plant food ($r_s = –0.89$, $p = 0.007$). However, taking each season separately, latitude was correlated positively only with consumption of animal food (Fig. 5), and negatively with consumption of plant food during spring (plant: $r_s = –0.82$,

Table 4. Summary of the mean isotopic values for dietary items of Estonian brown bears. Average values within each category were used in the Isosource model following conversion to hair-equivalent isotope values. Asterisk (*) indicates a combined sample of many (> 5) individual samples

Food item	*n*	δ^{15}N (‰)	δ^{13}C (‰)
Graminoids			
Orchard grass (*Dactylis glomerata*)	1*	–1.8	–32.1
Forbs			
Wild angelica (*Angelica sylvestris*)	1*	–1	–29.9
Stinging nettle (*Urtica dioica*)	1*	–4.1	–31.3
Hawksbeards (*Crepis* sp.)	1*	2.3	–33.1
Clover (*Trifolium sp*)	1*	–0.7	–31.7
Dandelion (*Taraxacum* sp.)	2	–0.1	–28.4
Bishop's weed (*Aegopodium podagraria*)	2	–0.2	–29.0
Colt's foot (*Tuissilago farfara*)	2	2.6	–29.0
Aspen (*Populus tremula*)	4	0.5	–28.0
Average		–0.09	–30.1
Berries			
Bilberry (*Vaccinum myrtillus*)	2*	–0.25	–33.5
Cranberry (*Oxycoccus palustris*)	1*	–6.7	–29.2
Cowberry (*Vaccinum vitis-idaea*)	1*	–7.4	–31.5
Average		–4.8	–31.4
Cereals			
Oats (*Avena sativa*)	1*	4.3	–28.5
Barley (*Hordeum vulgare*)	1*	2.6	–28.1
Average		3.5	–28.3
Insects			
Ants (*Formica* sp.)	1*	1.1	–25.9
Mammals			
Domestic cow (*Bos taurus*)	3	6.0	–26.6
Moose (*Alces alces*)	2	4.5	–26.5
Domestic pig (*Sus scrofa domesticus*)	1	5.2	–25.5
Wild boar (*Sus scrofa*)	2	6.0	–24.5
Average		5.4	–25.8

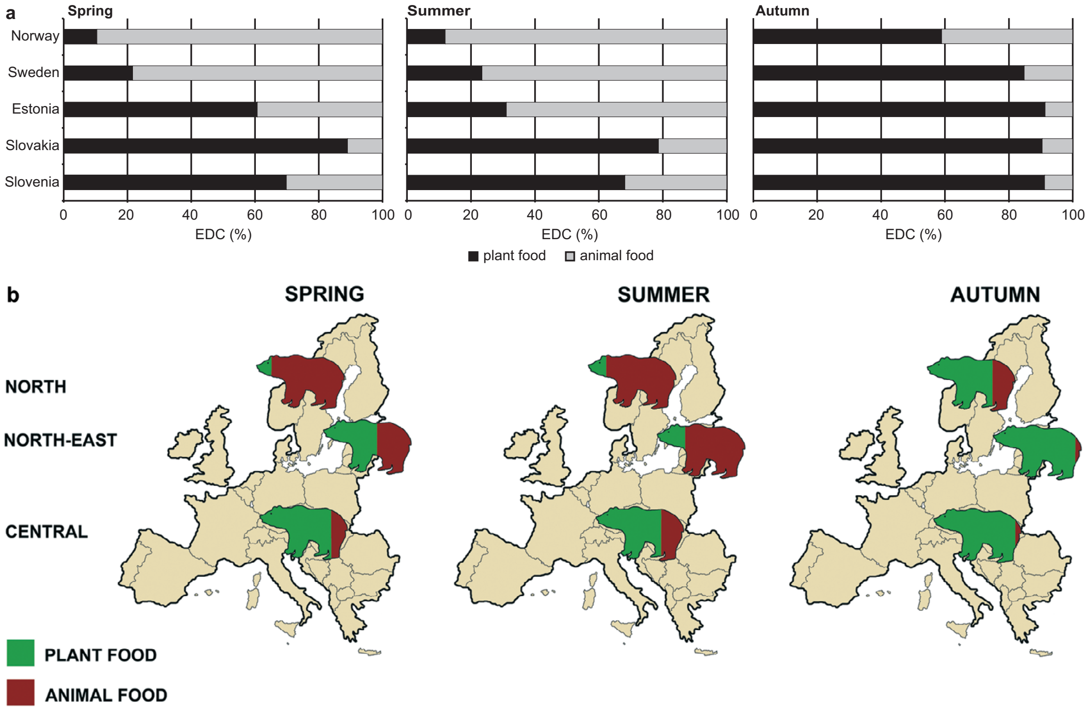

Fig. 4. (**a**) Seasonal variation in the relative proportions of animal and plant food in brown bear diet in central (Slovenia: Groβe (1999), Slovakia: Rigg & Gorman (2005)), north-eastern (this study), and northern (Sweden: Johansen (1997), Norway: Persson *et al.* (2001)) Europe. (**b**) Biogeographic variation in the diet of European brown bears: the proportion of animal and plant food in different European study areas.

$p = 0.02$) and summer (plant: $r_s = -0.8$, $p = 0.03$). By contrast, there were no significant correlations between latitude and either dietary class in autumn (Fig. 5). Badgers and pine martens also exhibited positive correlations between latitude and total annual consumption of animal food (badger: $r_s = 0.66$, $p = 0.005$; pine marten: $r_s = 0.50$, $p = 0.025$) (Fig. 5), and negative correlations between latitude and total consumption of plant food (badger: $r_s = -0.65$, $p = 0.006$; pine marten: $r_s = -0.58$, $p = 0.007$).

The diet composition of bears in Estonia during spring was very similar to that in Slovenia, containing fewer animals and more plant-food items than in more northerly countries, such as Sweden and Norway, but fewer berries and more mammals than in Slovakia (Fig. 6a). However, if food items with high energy content (berries, cereals, fruit, hard mast, insects and mammals) are summed, the proportion of high-energy *versus* low-energy items follows the latitudinal gradient (Fig. 6b). In summer, some general similarities existed in the diet composition of brown bears in Estonia and Sweden, though forbs were more commonly consumed in Estonia, while graminoids and mammals were more popular dietary items in Sweden (Fig. 6c). In summer, the proportion of high-energy food items in the bear diet was higher than in spring, with carbohydrate-rich food items in form of berries and cereals becoming available earlier in

Table 5. Contribution (%) of different food items to Estonian brown bear diet according to the Isosource mixing model (*see* Fig. 3).

Food item	Min.	Max.	Mean
Graminoids	0	42	10.9
Forbs	0	57	12.3
Berries	0	45	18.0
Cereals	0	37	7.9
Total plants			49.1
Insects	29	65	41.9
Mammals	0	42	9.1
Total animals			51.0

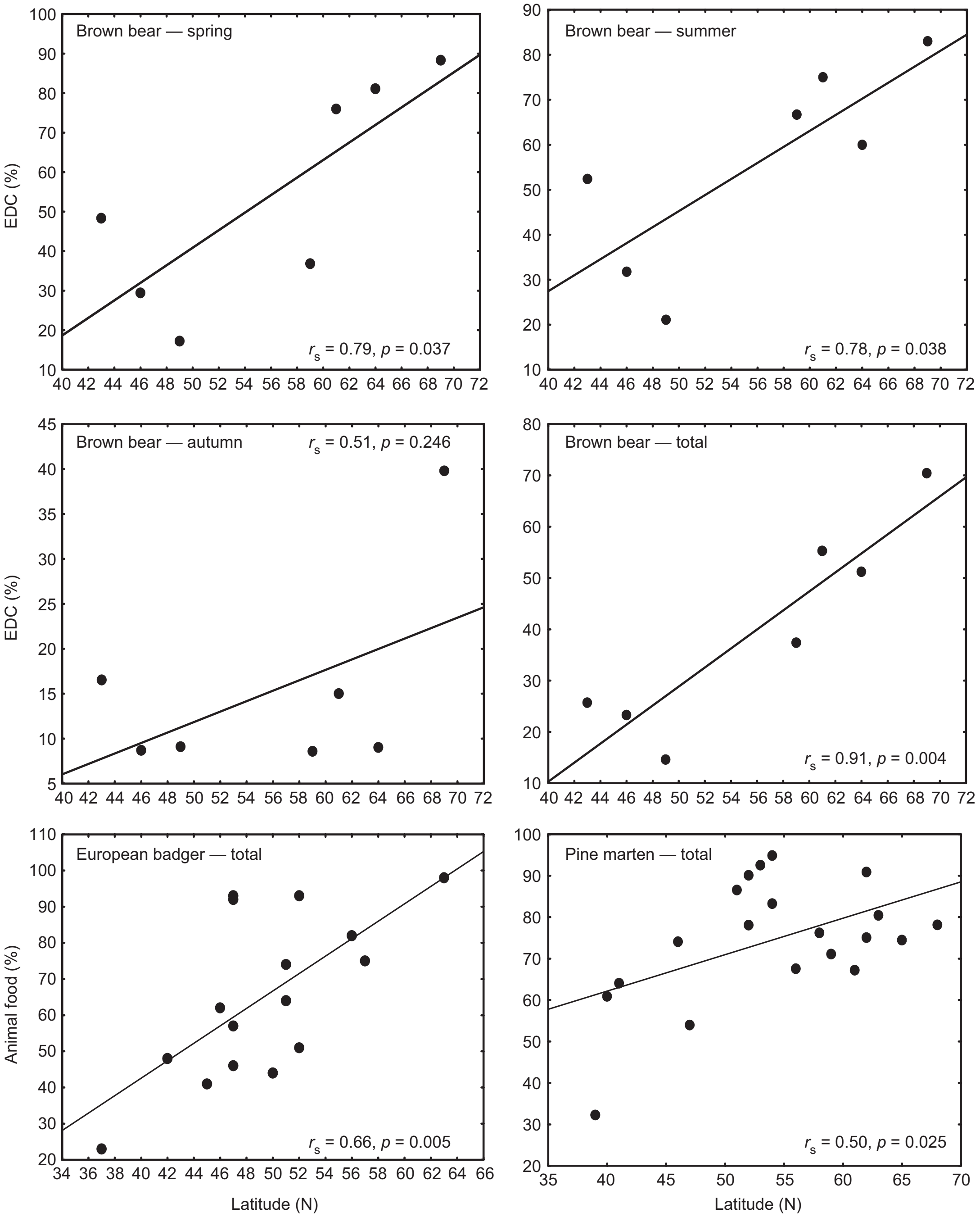

Fig. 5. Correlation between latitude and the percentage of animal food in the diet of brown bears, European badgers and pine martens, based on the data from this study and from the literature (*see* Appendices 1 and 2 for details and references).

southern regions (Fig. 6d). In autumn, the diet composition of bears in Estonia was surprisingly similar to that in Slovakia and to a lesser extent also to that in Slovenia (Fig. 6e). The percentage of carbohydrate-rich food items (berries, fruits, and cereals) in the autumn diet was greater than 75% in all populations (with the exception of Norway) (Fig. 6f).

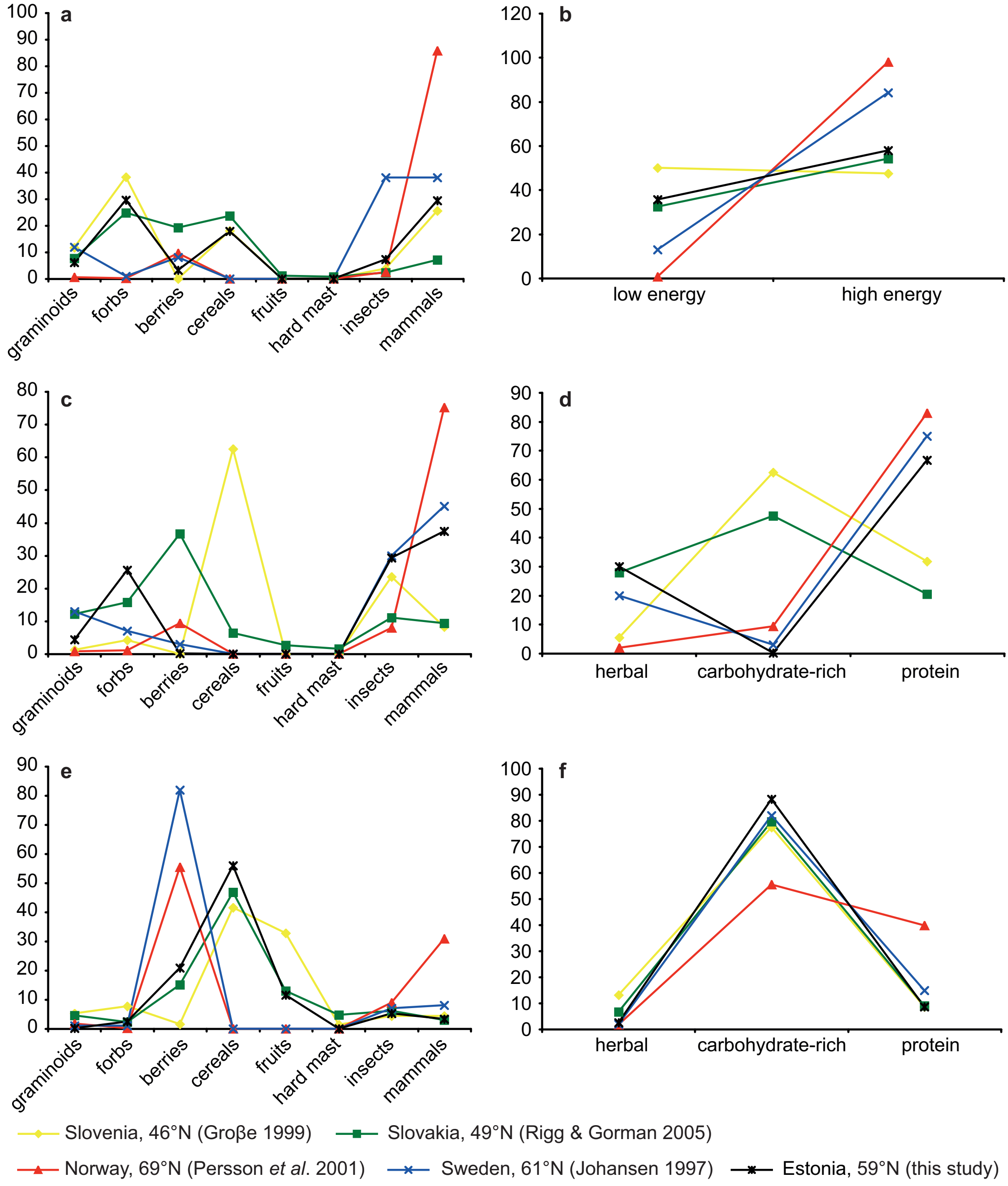

Fig. 6. Estimated dietary content (EDC, %) of brown bear in (**a**, **b**) spring, (**c**, **d**) summer and (**e**, **f**) autumn in different European study areas. Summed food-classes in **b**, **d** and **f** comprise: "low energy" & "herbal" = graminoids and forbs; "high energy" = berries, cereals, fruits, hard mast, insects and mammals; "carbohydrate rich" = berries, cereals, fruits and hard mast; "protein" = insects and mammals.

Discussion

Diet composition

Despite the large number of animal and plant taxa found in brown bear scats and stomachs, some expected food items such as fireweed and moose, which are important constituents of the brown bear diet in other countries (Pažetnov 1990, Elgmork & Kaasa 1992, Swenson *et al.*

2007b) were not recorded in this study. Moreover, it is known from personal reports that Estonian bears do occasionally feed on moose carcasses. Thus, the absences of some food items in this study may simply indicate that these items are used infrequently by bears in Estonia and may have resulted from smaller sample sizes collected in spring and summer, as dense undergrowth made it extremely hard to find bear scats during these seasons. The absence of moose in bear samples may also be partly explained by the significantly lower density of moose in the study area as compared with densities in other countries where moose is an important component in the bear diet. For example, the density of moose in our study area was more than four-times lower (218.1 individuals per 1000 km^2) than in Sweden (920 individuals per 1000 km^2), whereas bear densities were comparable (33 individuals per 1000 km^2 in Estonia and 30 individuals per 1000 km^2 in Sweden (Swenson *et al.* 2007b)). The true role of moose, and particularly moose calves, in the brown bear diet in Estonia requires additional investigation.

Results of fecal analysis showed that brown bears were not highly carnivorous in Estonia, with only a 23.4% contribution to the total EDC made by vertebrates. The frequent consumption of wild boar might be explained by the high density of this species in our study area. Wild boars have also been shown to play an important role in the brown bear diet in north-west Russia (Pažetnov 1990) and in Ukraine (Slobodjan 1993).

Remains of yellow beard truffle (*Rhizopogon luteolus*) were found from feces and stomachs in autumn 2003. According to Couturier (1954), the beard truffle is an accidental food item in the brown bear diet due to its narrow distribution and low abundance. Dahle *et al.* (1998) and Mattson *et al.* (2002) also considered fungi to be an occasional food item in the brown bear diet.

Annual and seasonal variation

Protein-rich food items such as mammals and insects were most frequently consumed in spring and summer. Among plants, forbs were favored in these seasons, because of their higher protein content as compared with that of graminoids (Rode *et al.* 2001). In autumn, bears largely consumed carbohydrate-rich plants, such as cereals (mainly oats), berries and apples, but few animal-food items, in order to effectively accumulate fat reserves before hibernation (Rode & Robbins 2000). It is known that bears forage on apples both in orchards of abandoned and in active farms. A poor apple crop in 2004 was probably the reason for the significantly lower consumption of apples in that year as compared with 2003. There was a compensatory effect observed in the consumption of berries, which was by contrast higher in 2004. Thus, in years when the apple crop is low, the availability of wild berries in autumn is particularly important in allowing bears to meet their nutritional demands. On the other hand, in years with a poor crop of wild berries, or in areas where berries are scarce, apples may represent a very important food item in autumn when bears prepare for hibernation (Welch *et al.* 1997).

Use of anthropogenic food items

Anthropogenic food items are often aggregated, and their consumption may therefore be expected to result in a decrease in energy spent on foraging. Our results demonstrated that anthropogenic food items were especially important in autumn when large quantities of food are required to build up fat reserves prior to hibernation. Use of anthropogenic food was lower in spring and summer, a trend that has also been observed in Slovakia (Rigg & Gorman 2005). Unlike other anthropogenic food, carcasses of domestic mammals were mainly taken in spring and summer. Thus, the consumption of different anthropogenic food items seemed to reflect the annual pattern of consumption of comparable natural food items by the brown bear. The most commonly consumed anthropogenic food item was cereals, which were also found to be dominant in the autumn diet of Slovakian bears (Rigg & Gorman 2005). The proportion of cereals and potatoes demonstrates the importance of feeding sites for bears in seasons when many natural food items are scarce or unavailable. Consumption of cereals might also explain the relatively high levels of predation upon wild boar compared with moose, as brown bear are known to visit feeding places set up for wild boar. A similar phenomenon has also been documented in Slovenia (Adamič & Jerina 2005).

Stable isotope model

The stable isotope model was based on hair samples that represented a period of dietary integration between late summer and autumn. Thus, we can only compare results of the isotope model with those using conventional approaches from the same period. According to the model, insects were among the most important dietary categories with an input of 29% to 65%. Unfortunately, the other dietary categories produced largely overlapping inputs-ranges (0% to 57%) (Table 5). This suggests roughly equivalent importance of the various dietary inputs (*see* Fig. 3). Further interpretation is difficult because the solution space defined by the mixing model actually represents thousands of possible solutions with the proviso that the sum of all inputs is 100% of the diet. In future, careful grouping of dietary options might be appropriate if just the proportion of for example, mammals, insects and plant materials are required. That would represent a two-isotope three-endpoint model which would provide a unique solution. However, due to the isotopic breadth of these combined endpoints, the error in the resulting discrete proportions would be magnified. Another possible solution may be to add other stable isotopes such as ^{34}S. The use of a three-isotope model would allow for a unique solution to a four dietary input model (Felicetti *et al*. 2003).

While we are faced with a complex isotopic challenge for delineating bear diets in Europe, our study has demonstrated how, in cases where long-term field collection of scats or stomachs is not feasible, important dietary information can be obtained from the analysis of hairs or other tissues. Whereas scats and stomach analyses represents only one or few meals, the isotope approach can be used to give a longer-term dietary average (covering the whole period when hair is growing), depending on the tissue chosen. The greater or lesser incorporation of mammals in the diet through time will tend to enrich or deplete hair ^{15}N and so even the measurement of this single isotope could prove of use in long-term monitoring studies.

By combining conventional and stable-isotope approaches, we were able to limit the range of isotopic analyses of wild foods to a manageable degree. While the algorithm of Felicetti *et al*. (2003) relating bear-hair stable-isotope values to those of the diet spanned the range of plant through meat diets, one weakness in our isotope approach was that we did not modify the model to account for differential assimilation of carbon and nitrogen from various food sources (e.g. Gauthier *et al*. 2003). That requires detailed knowledge of the digestive physiology of bears for each of the dietary types considered. Future refinements of the isotope approach to omnivorous bears should include this approach when such information is available. Should researchers be interested in reducing the model to only three dietary inputs, then the C:N ratios for each of the dietary items could be used in a concentration dependent mixing model (Phillips & Koch 2002).

Despite these limitations, we encourage the use of the stable-isotope approach for other bear populations in Europe, especially in conjunction with non- or semi-invasive sample collection. This would allow long-term monitoring of the use of anthropogenic foods in various populations and would be particularly useful as many of these populations are faced with habitat alterations as well as global climate change.

Correlation between carnivory and latitude

The level of biogeographic variation that exist in the diet of different brown bear populations in Europe is relatively little is known. Variation has been demonstrated at the genetic level, with the brown bear population in Europe divided into two major maternal lineages: the eastern and western. Of the populations compared in this study, bears from Estonia and Slovakia belong to the eastern, whereas those in Norway, southern Sweden, Slovenia and Spain belong to the western lineage. Although the eastern and western lineages have different historic background, that is they originate from different ice-age refugia (Taberlet & Bouvet 1994, Kohn *et al*. 1995, Saarma *et al*. 2007, Saarma & Kojola 2007, Korsten *et al*. 2009), the contemporary brown bear diet does not vary according to genetic background, but it does vary along a latitudinal gradient.

In this study, we used the estimated dietary content (EDC) to assess the proportion of animal and plant food items in the brown bear diet. Although an attempt to compare brown bear diets between different geographic regions has already been made by Elgmork and Kaasa (1992) that comparison is limited since the analysis combined the results of studies obtained using different methods. Nevertheless, their analysis gave an indication that consumption of animal *versus* plant food items may increase towards northern latitudes. However, while these were the parameters primarily used in the literature reviewed by Elgmork and Kaasa (1992), neither the volume nor frequency of occurrence of food items are adequate for comparing the proportion of animal *versus* plant food in the brown bear diet. This is because they do not take into account the fact that foods differ significantly in their digestibility, which can lead to highly biased results (Hewitt & Robbins 1996). The measure of the EDC used in this study provides a more appropriate basis for such an analysis as it takes into account differences in digestibility. Similarly, the isotope approach is based entirely on assimilated and not just ingested food items. Another earlier study of the brown bear diet in northwestern Russia showed that bears consumed more moose in northern than in southern areas. However when those data were divided into seasons, this was found to be valid only for spring, and the opposite trend was shown for summer and autumn (Danilov *et al*. 1993). Moreover, although moose can be an important food item in some regions, it is not possible to assess the proportion of animals in the brown bear diet using solely moose data, since the brown bear diet consists of many other animal items.

It is notable that brown bears consume more animal food items in northern areas in Europe during spring and summer, but not in autumn. It seems likely that this pattern reflects seasonal variation in the availability of different food items, but also differences in the energy demands of bears living at different latitudes. Since it is known that the vegetation period is shorter and plant species richness is lower at higher latitudes (Rosenzweig 1995, Cox & Moore 2005), it is clear that the availability of plants varies latitudinally. However, it is likely that a similar pattern also exists for animals; mammal prey-species biomass decreases at northern latitudes (Jędrzejewski *et al*. 2007), though more ants are available in northern areas (Groβe *et al*. 2003). Nonetheless, as brown bears are known to feed extensively on carcasses, a higher abundance of other top predators, such as wolves and lynx in northern latitudes may increase the availability of carcasses and thereby the proportion of mammals in the brown bear diet. The abundance of easily accessible domestic animals such as sheep in Norway, can also significantly increase the contribution of mammals in the brown bear diet (Dahle *et al*. 1998).

It has been shown that bears from southern Europe lose weight in spring while northern bears gain weight during this time (Swenson *et al*. 2007a). In southern areas, bears seem to meet their energy requirements by consuming energy-rich plant food in spring, while in northern areas animal food is essential for meeting energy demands after hibernation. This study has also shown that there exists latitudinal gradient in the consumption of food items with high energy value (both plants and animals) in spring (Fig. 6b). Because muscle protein concentration declines 10%–20% during winter sleep (Hissa *et al*. 1998), this trend might result from a difference in the duration of hibernation; thus, bears need more high-quality food to recover quickly from hibernation in northern areas. Moreover, bears in northern latitudes may have adapted to use more animal food in spring as there is shortage of energy-rich plant items. While the larger proportion plant items consumed by brown bears in southern areas in spring likely reflects the earlier onset of the vegetation period, the same preference for plants in summer is likely to reflect the earlier onset of fruiting, producing high energy berries and cereals (Hewitt & Robbins 1996). The proportion of insects (predominantly ants), increases significantly both in northern and southern latitudes in summer, since their biomass is then high and larvae are in abundance.

The high proportion of plant food items consumed in autumn is a result of the requirement for carbohydrate-rich food items for building up fat reserves prior to hibernation, which is vital for successful hibernation and fecundity. This requirement for carbohydrates in autumn seems to apply equally to bears throughout Europe such that the variation in plant/animal food ratio in the bear diet along latitudinal gradient disappears at this time of year.

Although significant trends can be observed in the diet, brown bears are true omnivores and exploit a wide range of resources. In each season, even if some food items are preferred, they continue to use other items to a lesser extent. This may help not only to balance their energy demands, but also to balance their diet with respect of other important nutrients such as vitamins, minerals and microelements, which in turn can strengthen their immune system to fight against parasites and other pathogens. For example brown bears in Estonia are known to have significantly fewer endoparasites as compared with carnivores such as lynx and wolf (E. Moks pers. comm.).

A latitudinal gradient of animal *versus* plant food items in brown bear, badger and pine marten diet

The conclusion from this study, that brown bears in northern areas are more carnivorous than their southern counterparts, has been drawn to certain extent also for other omnivorous mammals such as the European badger and the European pine marten (Goszczynski *et al.* 2000, Zalewski 2004). While it has been demonstrated that the consumption of earthworms by badgers is positively correlated with latitude, and conversely that the consumption of plant food is negatively correlated with latitude (Goszczynski *et al.* 2000), it had not previously been demonstrated that a positive correlation also exists between latitude and total annual animal food in the badger diet. For pine martens, although proportions of different animal and plant food items were presented by Zalewski (2004), no correlation analysis between latitude and animal/plant items was performed. Here, we demonstrate, using data from 14 badger and 20 pine-marten studies that, as is the case for brown bears, increasing latitude is accompanied by an increase in the consumption of animal prey and a decrease in the consumption of plant items in these species (Fig. 5). Although these three mammal species constitute a small number of examples, they indicate a general trend of increased consumption of animal food items towards northern latitudes for omnivorous mammals. As in the case of the brown bear, the diets of these other omnivores are adapted to cope with the harsh climate and lower availability of plant items in northern latitudes. Whereas studies on the diet of badgers and pine martens analysed overall food habits, the brown bear example in this study has clearly shown the necessity to investigate the seasonal variability of omnivore diets, as consumption of different food items is likely to vary importantly between seasons.

Acknowledgements

We thank Bellis Kullmann, Marge Sarv, Vallo Tilgar, Jüri Saealle, Sulev Kaivapalu, Aare Aalja, Erin Urton, John Davison and Jon Swenson for their generous help. B.X. Mora-Alvarez assisted with sample preparation for stable isotope analyses that were performed by M. Stocki at the Department of Soil Sciences, University of Saskatchewan. The study was supported by the Environmental Investment Centre at the Estonian Ministry of Finance, the European Union through the European Regional Development Fund (Center of Excellence FIBIR), target financing grants SF0180122 and SF0170057 from the Estonian Ministry of Education and Sciences and by operating funds provided to KAH from Environment Canada.

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Appendix 1. Description and results of various brown bear diet studies from Europe. The method to estimate proportion of animal (A) and plant (P) diet items is shown in the column "Method" (*V* = percentage of fecal volume, *F* = frequency of occurrence (%), IRC = index of relative contribution, *W* = percentage of dry weight, EDC = estimated dietary content (%). Studies marked with asterisk were used in the correlation analysis of latitudinal variation of brown bear diet.

Country	Lat. (°N)	Method	*n*	Spring		Summer		Autumn		Winter		Total		References
				A	P	A	P	A	P	A	P	A	P	
Spain	42	V	1500	4.2	94.2	13.7	85.8	11.4	87.6	–	–	9.8	89.2	Naves *et al.* 2006
France	43	IRC	482	–	–	–	–	–	–	–	–	24.9	74.5	Berducou *et al.* 1983
Spain*	43	V	929	14.2	86.5	32.8	67	12.8	89.7	5.8	94.6	13.9	86.2	Clevenger *et al.* 1992
Croatia	44	F	95	3.6	96.4	25	75	20.4	79.6	5.5	94.5	13.6	86.4	Cicnjak *et al.* 1987
Slovenia*	46	EDC	288	31.8	68.1	31.8	68.1	8.7	90.7	71.9	28.2	36.1	63.8	Groβe 1999
Poland	49	W	46	5.8	91.5	–	–	8.4	83.6	–	–	–	–	Frackowiak & Gula 1992
Slovakia*	49	EDC	373	17.2	77.7	21.1	76.4	9.1	90.3	–	–	14.6	83.4	Rigg & Gorman 2005
Belarus	54	EDC	732	–	–	–	–	–	–	–	–	44.6	48	Sidorovich 2006
Estonia*	59	EDC	142	36.8	56.9	66.7	30	8.6	90.8	–	–	53.5	43.9	This study
Sweden*	61	EDC	234	76	25	75	24	15	85	–	–	55.3	44.7	Johansen 1997
Sweden*	64	EDC	148	81	18.5	53.5	56.5	9.5	93	–	–	48	56	Dahle *et al.* 1998
Norway	64	EDC	118	90.5	12.5	85.5	10	65.5	53.5	–	–	80.5	25.3	Dahle *et al.* 1998
Norway*	69	EDC	137	88.3	11.4	83	16.6	39.8	59.9	–	–	70.4	29.3	Persson *et al.* 2001

Appendix 2. Mean percentage of animal and plant items in diet of the European badger and the European pine marten at different latitudes in Europe (data from various studies).

Species	Country	Lat. (°N)	Animal	Plant	References
Badger	Spain	37	23	77	Rodriguez & Delibes 1992
	Italy	42	48	52	Ciampalini & Lovari 1985
	Italy	45	41	63	Kruuk & de Kock 1981
	France	46	62	38	Mouches 1981
	France	47	57	43	Lambert 1990
	France	47	93	7	Henry 1983
	Switzerland	47	92	8	Weber & Aubry 1994
	Switzerland	47	46	43	Lüps *et al.* 1987
	England	50	44	56	Sheperdson *et al.* 1990
	Poland	51	74	26	Goszczynski *et al.* 2000
	England	51	64	31	Hofer 1988
	Poland	52	93	7	Goszczynski *et al.* 2000
	England	52	51	49	Skinner & Skinner 1988
	Denmark	56	82	23	Andresen 1954
	Scotland	57	75	25	Kruuk & Parish 1981
	Norway	63	98	2	Brøseth *et al.* 1997
Pine marten	Spain	39	32	52	Clevenger 1995
	Spain	40	61	34	Clevenger 1993
	Russia, Caucasus Mts.	41	64	36	Donaurov *et al.* 1938
	Hungary	46	74	26	Lanszki *et al.* 2007
	German	47	54	46	Russell & Storch 2004
	Poland	51	87	13	Posłuszny *et al.* 2007
	Poland	52	78	9	Jędrzejewski *et al.* 1993
	Belarus	52	90	6	Datskevich 1979
	Russia, Zhiguli Mts.	53	93	5	Yurgenson 1951
	Belarus	54	83	4	Serzhanin 1973
	Russia, Bashirskii Reserve	54	95	4	Mozgovoi 1971
	Belarus	56	68	25	Sidorovich 1997
	Russia, Perm region	58	76	20	Grakov 1981
	Sweden	59	71	11	Helldin 1999, 2000
	Norway	61	67	28	Selas 1992
	Russia, Pechora river	62	91	8	Yurgenson 1951
	Russia, Pechora river	62	75	22	Yazan 1962
	Russia, N Dvina river	63	80	13	Grakov 1981
	Russia, Karelia	65	75	13	Danilov & Ivanov 1967
	Russia, Laplandskii Reserve	68	78	15	Nasimovich 1948

Appendix 3. List of taxa recorded in the diet of Estonian brown bears during analysis of 142 feces and 12 stomach contents in 2003–2004.

Fungi
Yellow beard truffle (*Rhizopogon luteolus*)
Plants
Meadow horsetail (*Equisetum pratense*)
European aspen (*Populus tremula*)
Comon hazel (*Corylus avellana*)
Stinging nettle (*Urtica dioica*)
Common sorrel (*Rumex acetosa*)
Creeping buttercup (*Ranunculus repens*)
Polish buttercup (*Ranunculus cassubicus*)
Oilseed rape (*Brassica napus* subsp. *napus*)
Hedge mustard (*Sisymbrium officinale*)
Aven (*Geum* sp.)
Raspberry (*Rubus idaeus*)
Stone bramble (*Rubus saxatilis*)
Strawberry (*Fragaria* sp.)
Lady's mantle (*Alchemilla* sp.)
Domestic apple (*Malus domestica*)
European rowan (*Sorbus aucuparia*)
European fly honeysuckle (*Lonicera xylosteum*)
Norway maple (*Acer platanoides*)
Glossy buckthorn (*Frangula alnus*)
Purple chokeberry (*Aronia x prunifolia)*
White clover (*Trifolium repens*)
Bishop's weed (*Aegopodium podagraria*)
Cow parsley (*Anthriscus sylvestris*)
Burnet saxifrage (*Pimpinella saxifraga*)
Wild angelica (*Angelica sylvestris*)
Hogweed (*Heracleum sibiricum*)
Heather (*Calluna vulgaris*)
Wild rosemary (*Ledum palustre*)
Cranberry (*Oxycoccus palustris*)
Bog blueberry (*Vaccinium uliginosum*)
Bilberry (*Vaccinum myrtillus*)
Cowberry (*Vaccinium vitis-idaea*)
Yellow archangel (*Galeobdolon luteum*)
Cut-leaf deadnettle (*Lamium hybridum*)
Ground ivy (*Glechoma hederacea*)
Black mullein (*Verbascum nigrum*)
Potato (*Solanum tuberosum*)
Germander speedwell (*Veronica chamaedrys*)
Common plantain (*Plantago major*)
Narrowleaf plantain (*Plantago lanceolata*)
European cranberrybush (*Viburnum opulus*)
Spreading bellflower (*Campanula patula*)
Common nipplewort (*Lapsana communis*)
Wall lettuce (*Mycelis muralis*)
Burdock (*Arctium* sp.)
Cabbage thistle (*Cirsium oleraceum*)
Melancholy thistle (*Cirsium heterophyllum*)
Dandelion (*Taraxacum* sp.)
Marsh hawksbeard (*Crepis paludosa*)
Coltsfoot (*Tussilago farfara*)
Rush (*Juncus* sp.)
Woodrush (*Luzula* sp.)
Timothy (*Phleum pratense*)
Meadow foxtail (*Alopecurus pratensis*)
Velvet bentgrass (*Agrostis canina*)
Creeping bentgrass (*Agrostis stolonifera*)
Reed grass (*Calamagrostis* sp.)
Tufted hairgrass (*Deschampsia caespitosa*)
Oats (*Avena sativa*)
Mountain melick (*Melica nutans*)
Purple moorgrass (*Molinia caerulea*)
Orchard grass (*Dactylis glomerata*)
Narrow-leaved meadow-grass (*Poa angustifolia*)
Smooth meadow-grass (*Poa pratensis*)
Meadow fescue (*Festuca pratensis*)
Red fescue (*Festuca rubra*)
Common wheat (*Triticum aestivum*)
Quackgrass (*Elymus repens*)
Common barley (*Hordeum vulgare*)
Tule (*Scirpus* sp.)
Sedge (*Carex* sp.)
Orchid (*Orchidaceae*)
Animals
Invertebrates
Black garden ant (*Lasius niger*)
Yellow meadow ant (*Lasius flavus*)
Cornfield ant (*Lasius alienus*)
Lasius umbratus
Jet ant (*Lasius fuliginosus*)
European red wood ant (*Formica polyctena*)
Scottish wood ant (*Formica aquilonia*)
Formica cinerea
Black-backed meadow ant (*Formica pratensis*)
Formica cunicularia
Southern wood ant (*Formica rufa*)
Slave-making ant (*Formica sanguinea*)
Common black ant (*Formica fusca*)
Narrow-headed ant (*Formica exsecta*)
Hairy wood ant (*Formica lugubris*)
Japanese ant (*Formica truncorum*)
Red ant (*Myrmica ruginodis*)
Common red ant (*Myrmica rubra*)
Camponotus ligniperda
Camponotus herculeanus
Camponotus fallax
Flies (*Diptera*)
Butterfly (*Lepidoptera*)
Gastropod (*Gastropoda*)
Vertebrates
Domestic cow (*Bos taurus*)
Roe deer (*Capreolus capreolus*)
Domestic pig (*Sus scrofa domestica*)
Wild boar (*Sus scrofa*)
Raccoon dog (*Nyctereutes procyonoides*)
Bird (*Aves*)
Lizard (*Lacerta* sp.)
Bony fish (*Osteichythes*)

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