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BROWN BEAR FOOD HABITS AT THE BORDER OF ITS RANGE: A LONG-TERM STUDY

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Brown bear (*Ursus arctos*) food habits were examined from 1,500 fecal samples collected between 1974 and 2004 in the Cantabrian Mountains of northern Spain. The most important food items were graminoids and forbs in the spring, fleshy fruits (especially bilberries) in the summer, and hard mast in the autumn and winter (especially acorns). Animal matter also was consumed throughout the year. We found differences between 3 brown bear population nuclei within the Cantabrian population, which could be of enormous interest for habitat management. We also investigated how much interannual variation in different food items influenced our diet estimates. High fluctuations among years rather than values around a mean were inherent to some food items. However, for other items, the mean seems to be a reliable descriptor. We found that the additional years of data increased the coefficient of variation associated with some of our diet estimates and suggest the existence of directional changes in brown bear food habits that have been largely neglected. Although some studies suggest that diet is fixed and not changeable, our results show that long-term diet studies may reveal changes in habitat use patterns or habitat composition for brown bears and other wildlife species. Thus, incorporating diet studies into monitoring protocols can be helpful for designing and evaluating both current and future management actions.

Key words: Cantabrian Mountains, fecal analysis, interannual variation, long-term diet study, *Ursus arctos*

The brown bear is one of the few large-bodied monogastric animals that obtains most of its energetic requirements from plant matter. This forces bears to spend a high proportion of their daily activity in feeding (LeFranc et al. 1987; Stelmock and Dean 1986). In addition, because of winter hibernation, bears must accumulate sufficient fat layers to fuel metabolic and reproductive costs during denning. Thus, food habits are pivotal in brown bear ecology and behavior (Gende and Quinn 2004; Swenson et al. 1999; Welch et al. 1997). However, few studies have addressed the importance of diet composition for management and conservation (but see Clevenger et al. 1992; Craighead et al. 1995; Hilderbrand et al. 1999).

In the Cantabrian Mountains of northern Spain lives a remnant population of brown bears (Fig. 1). This population is considered threatened by the International Union for the Conservation of Nature and Natural Resources (Servheen et al. 1999) and is categorized as critically endangered in the Spanish Red List of Endangered Mammals (Naves and Fernández 2003). The distribution range is fragmented into 2 subpopulations with an estimated population size of 50–65 individuals in the west, and 20–25 in the east (Clevenger et al. 1992; Naves and Palomero 1993; Wiegand et al. 1998). The eastern subpopulation mainly occupies south-facing slopes of suboptimal natural habitat and relatively low human impact, whereas the western subpopulation occurs mainly on north-facing slopes with high human impact but otherwise good natural quality (Naves et al. 2003; Wiegand et al. 1998). In the western subpopulation, the reduction of human-induced mortality has been identified as the keystone for population recovery (Servheen et al. 1999; Wiegand et al. 1998), but some food items (beehives, livestock, and orchards) bring bears increasingly into conflicts with humans (Clevenger et al. 1992; Mattson et al. 1991; see also Huygens et al. 2003). Thus, the documentation of food habits is essential for effective management policies.

We studied brown bear food habits by analyzing 1,500 fecal samples collected in the Cantabrian Mountains of northern Spain between September 1974 and May 2004. Although Clevenger et al. (1992) discussed this topic, they mainly focused on the eastern subpopulation, whereas the larger

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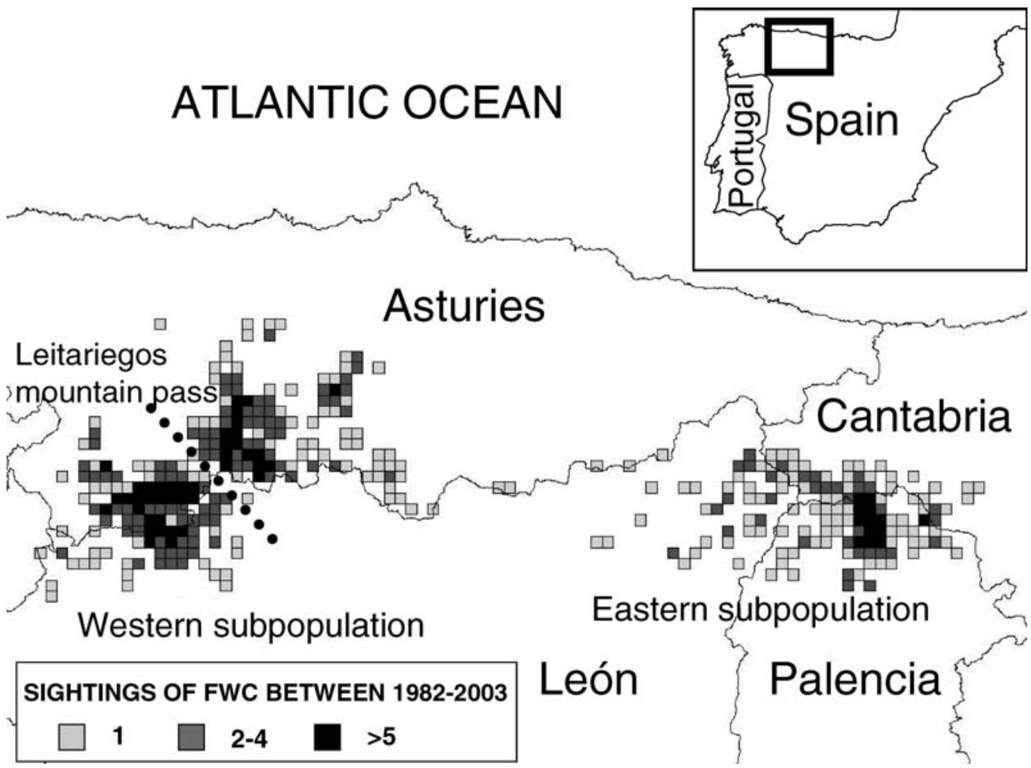

Fig. 1.—Distribution range of brown bears in the Cantabrian Mountains of northern Spain. The 3 study areas were delineated based on habitat features and sightings of females with cubs (FWC) on a grid of 2.5 × 2.5 km. The dotted line indicates the Leitariegos Mountain Pass.

western subpopulation remained almost unattended (but see Braña et al. 1977, 1988; Garzón and Palacios 1979). In addition, past analyses only covered short time periods (<5 years). To our knowledge, this is the 1st study to analyze long-term food habits in any Eurasian brown bear population. This long-term study not only allows us to detect sporadic use of rare food items (Craighead et al. 1995; Mattson et al. 1991), but also to include supra-annual schedules of mast producers that involve both high and low annual seed productions (Herrera et al. 1998).

Our goals were to describe brown bear food habits in the Cantabrian population on the basis of a long-term data series, to investigate whether food habits differ among different areas within the population, to assess the role played by the high trophic plasticity of brown bears in our estimates and diet descriptions, and to evaluate how additional years of diet data influence estimates of variation of single diet items.

Materials and Methods

Study area.—Our study area includes the entire range of the Cantabrian Mountains in the northwestern Iberian Peninsula (Fig. 1). These mountains run east–west along the Atlantic coast, with a maximum elevation of 2,648 m and average elevations of north- and south-facing slopes of 700 m and 1,300 m, respectively, and gradients of 34% and 21%. The chain's proximity to the ocean and the geographic orientation results in high rainfall on the north-facing slopes and a rain shadow on the southern slopes (average annual rainfall of 900–1,900 mm on the north-facing slopes and 400–700 mm on the south-facing slopes). This mountain range contains the largest portion of the remnant Atlantic deciduous forest on the Iberian Peninsula and constitutes the southernmost boundary of this system (García et al. 2005; Polunin and Walters 1985).

Woodland cover is more varied on north-facing slopes, with oaks (*Quercus petraea*, *Q. pyrenaica*, and *Q. rotundifolia*), beech (*Fagus sylvatica*), birch (*Betula alba*), and chestnut (*Castanea sativa*) trees, whereas south-facing forests are dominated by deciduous durmast oak (*Q. petraea* and *Q. pyrenaica*) and beech. Above 1,700–2,300 m, climatic conditions prevent forest growth, and subalpine shrubs (*Juniperus communis*, *Vaccinium myrtillus*, *V. uliginosum*, and *Arctostaphylos uva-ursi*) dominate. Stands of *Erica*, *Citysus*, *Genista*, and *Calluna vulgaris* also are common at this altitude. Human densities are 12.1 and 6.1 inhabitants/km^2 for the western and eastern bear subpopulations, respectively (Reques 1993). We distinguish between 3 local study areas: central, western, and eastern. We subdivided the western subpopulation into a central and a western area because the Leitariegos Mountain Pass (Asturies–León provinces) acts as a natural barrier (Fig. 1). There, roads, ski runs, and a concentration of villages largely inhibit bear movements between the 2 areas. In addition, west of the constriction, limestone almost disappears and forest cover is higher than east of the constriction (45% compared to 35%), as is the percentage of oak-forest cover (13% compared to 6%, respectively).

Feces collection and analyses.—We collected 1,500 fecal samples between 1974 and 2004, with varying intensity. Most of the collections (90%) were gathered in 1980–1987 and 1994–2002. In the 1st period, fecal samples were collected during randomly distributed treks within the brown bear Cantabrian range that aimed to allocate both daily beds and denning sites. In the 2nd period, fecal samples were mostly collected during systematic surveys by the Brown Bear Monitoring Program. This consisted of approximately 3-h-long transects across 2.5-km universal transverse mercator squares where bear signs were seasonally accounted as an index of presence or absence of the species in the study area. Fecal samples sporadically collected by other researchers and experienced rangers also were included. In both periods neither radiotracked bears nor places of reported bear activity were used, so sample biases due to these effects are irrelevant. Fecal samples were either air-dried or frozen before they were dissected over a tray and all diet items were identified (without mesh screening) to the finest taxonomic resolution possible. We avoid mesh screening because some foods (mainly forbs and some fleshy fruits) are easily identifiable if soft dissection was used, but modified and even destroyed by mesh screening. In addition, one of us (JN) has observed that some small food items such as ants tend to be misquantified with mesh screening. Food items were identified by using mammal hair keys (Dziurdzik 1973; Faliu et al. 1980; Teerink 1991) and botanical collections of fruits, seeds, and histological sections (Departamento de Biología de Organismos y Sistemas, University of Oviedo, Oviedo, Spain). After dissection, the percentage volume of each item in the scat was visually estimated. This estimation was standardized among different observers by the senior author to minimize potential effects on the results.

In our analyses, we relied on phenological periods rather than on calendar months. We assumed that foraging begins (and also vegetative growth) when bears leave their winter den in early spring. This period is characterized by low food intake (hypophagia) and coincides with estrus and the mating season (Fernández-Gil et al., in press; Mattson et al. 1991). As summer progresses, ambient conditions become drier and fleshy fruits start to ripen in late June–early July. The bears' food intake increases markedly, allowing them to gain weight until they enter a den for hibernation in November–December (Craighead and Mitchell 1982; LeFranc 1987). We refer to these 3 periods as mating season (April–June), hyperphagic season (July–November), and winter (December–March). We describe diet composition by summarizing the frequency of occurrence of each diet item and its percentage volume for each area and season.

To simplify both diet descriptions and analyses, and to allow for the comparison with other brown bear diet studies, we tallied food items into 4 major groups by 19 taxa (see Appendix I). For a general description of brown bear diet in the Cantabrian Range, and for statistical analyses where we were able to correct for different sample sizes, we used the entire sample. For season and area-specific descriptions, we only used data years with $\geq$20 scats for the hyperphagic season and $\geq$8 scats for the simpler diets of mating and winter seasons. To obtain these minimums for each season, we chose the year with the highest sample and calculated the contribution to the diet of each of the major food groups on the basis of 1 scat, 2, 3, and so on, chosen in random order, and we repeated this process 9 times. We calculated the coefficient of variation (*CV*) of the 10 runs for each simulated sample size and minimum sample sizes were set when the *CV* for all food groups were below 1. This area-specific description was not conducted for the eastern area because of the more scattered and opportunistic sampling scheme there.

Statistical analyses.—We used generalized linear models to investigate the differences in brown bear diet between our study areas. We used the presence or absence of major (above 3% of total volume in each season) food items in each scat as response (dependent) variables and area (western, central, or eastern) as explanatory variable. Because we focused on the presence or absence of food items, traces may potentially be analyzed equal to a food constituting a substantial portion of the scat. To avoid this, we only considered food items that occurred at a volume $> 9\%$. We built general linear models with S-Plus software (Professional, release 2 Mathsoft, Inc., Seattle, Washington) using a binomial function for errors and a logit link. For comparing levels within a factor, we selected the contrast treatment option, where the 1st level is assigned the value 0 (aliased with intercept) and then other levels measure the change from the 1st level. Because the relative importance of each food varied among seasons ($P < 0.001$ for all food items except for insects [$P = 0.03$] and vertebrates [$P = 0.01$]), separate models were derived for each season.

Because of the high number of food items present in the hyperphagic diet of the central area, we used principal component analysis (PCA) as a data reduction method. PCA was performed on the 10 most common food items (a higher number of items caused ill-conditioned results). The objective of PCA, other than reducing the number of independent variables, was to identify those items that tend to occur together and those that tend to occur separately.

Results

More than 100 taxa (25 species of berries and fleshy fruit, 7 species of hard mast, more than 60 species of green vegetation matter, and about 30 animal species) were identified as food items for brown bears in the Cantabrian Range (Table 1; Appendix I). Half of the sample showed monodiets, and in 79% of the fecal samples, a single food item represented more than 75% of the total volume.

Diet in the winter season.—Rough field conditions and lower bear activity because of winter dormancy caused a smaller sample size for this season. Hard mast was the most important food supply during winter for Cantabrian bears, together with graminoids and forbs (Tables 1 and 2). Consumption of almost all winter foods differed between areas (Table 3); chestnuts were absent in the eastern area, and hazelnuts (*Corylus avellana*) were only present in the west. Graminoids were the most important and constant winter food for bears in the central area, whereas graminoids are almost absent in the west (Table 2). There, bears mainly fed on acorns and beechnuts, although the latter showed a high interannual variation in its contribution to winter diet. The relative importance of both beechnuts and apples (*Malus*) in the central area also changed markedly from year to year (Table 2).

Diet of mating season.—In the mating season, Cantabrian bears mainly fed on forbs and graminoids, but also ate animal matter as well as acorn and beechnut crops from the previous autumn (Table 1). Occurrence of forbs, beechnuts, and acorns differed between areas (Table 4). Area-specific descriptions (Table 2) showed that forbs were the most important and constant food item for bears both in the central and western areas. Graminoids also were consumed with low interannual fluctuations in the western area, but more irregularly in the central area. Among overwintering hard mast, western bears fed on acorns, whereas central bears fed on beechnuts. Both showed a high interannual variation in their consumption. Vertebrates were consumed most frequently during this period; however, *CV* values for vertebrates suggest high interannual fluctuations.

Diet of hyperphagic season.—Berries, fleshy fruits, and hard mast constituted the bulk of the diet, although bears also consumed herbaceous plants (mainly forbs and graminoids) and animal matter (Table 1). Among fleshy fruits, only blackberries (*Rubus*), and *Sorbus* fruits were consumed in similar proportions in all 3 areas (Table 5). Bilberries (*Vaccinium*) were more frequently consumed in the western area, where

TABLE 1.—Seasonal frequency of occurrence and mean percentage volume of food items in diet of brown bears in the Cantabrian Mountains of Spain. *n* is number of species or taxa included in each food category (see Appendix I). Asterisks (*) identify food items included in the analyses. Digestibility (D) is included, where known, as percentage of dry matter (see Pritchard and Robbins 1990). Sample size is the number of fecal samples in each season.

			Winter		Mating		Hyperphagic	
Food items	*n*	D	Frequency	Volume (%)	Frequency	Volume (%)	Frequency	Volume (%)
Herbs								
*Forbs	34	45	12.2	5.2	58.7	45.4	14.1	6.7
*Graminoids	18		24.4	17.3	38.8	20.3	19.8	7
Total herbs	65		37	22.4	76	65.7	29.2	13.6
Fleshy fruits								
Arbutus	1		0.5	0.3			1.1	0.5
Arctostaphylos	1						0.1	0.0
Crataegus	1						1.9	0.8
Frangula	1		0.5	0.4			1.9	1.5
**Malus*	2		6.8	2.5	1.1	0.2	13.8	7.6
**Prunus*	4				1.4	1.1	10.9	6.8
**Rhamnus*	1						10	7.3
Rosa	1		2	1.6			1	0.5
**Rubus*	3				1.9	0.8	7.9	3.1
**Sorbus*	2						5.6	2.7
**Vaccinium*	2	65	0.5	0.2	0.6	0.1	16.4	11.3
Other	6				0.8	0.1	0.5	0.2
Total fleshy fruits	25		9.8	5	5.8	2.3	58	42.4
Hard mast								
**Castanea*	1		13.7	11.8	0.8	0.6	8.4	7
**Corylus*	1		3.4	2.9			11.9	6.4
**Fagus*	1		11.7	9.5	5.3	3.8	3	2.3
**Quercus*	3		49.3	42.6	16.3	13.4	21.6	16
Total hard mast	7		72.7	66.8	22.2	17.8	41.6	31.6
Animal								
*Insects	13		4.9	1.1	18.6	4.4	16.5	4.5
*Vertebrates	19	94	10.7	3	19.4	9.3	15.2	6.9
Total animal	32		15.6	4.2	36	13.7	29.8	11.4
Sample size			205		361		934	

Rhamnus fruits were absent. Apples (*Malus*) were more frequently consumed in the central and eastern areas (Table 5). Among hard mast, acorns were consumed less in the central area than in the other 2 areas. Chestnuts were rarely consumed in the west during this period. No differences among areas were found in the consumption of animal matter during the hyperphagic period (Table 5).

Some of the documented differences among areas are due to the sparser eastern area, where several food items (cherries [*Prunus*], hazelnuts, and chestnuts) that were common in the other areas were rare. Bears also consumed a higher proportion of graminoids and forbs (16% and 14% of total volume, respectively; $n = 98$ scats).

Area-specific description (Table 2) showed that the diet of the western area was characterized by 3 predominant food items that ripen sequentially: cherries are replaced by *Vaccinium* fruits at mid-summer, which are substituted by acorns at the end of this season. These 3 items comprised more than half of the diet during the hyperphagic season in the western area and showed a relatively low interannual variation. They were complemented with herbs, animal matter, and other hard mast and fleshy fruits, but all in volume proportions $< 10\%$.

As compared to the other 2 areas, the central area showed the most diverse, complex, and fluctuating diet. In fact, no single item (neither hard mast nor soft mast [berries and fleshy fruits]) comprised $>13\%$ of total volume in the hyperphagic period, and the majority of items showed high values of *CV* (Table 2). When PCA was performed on the 10 most common food items, they were grouped in 3 components that accounted for 34%, 21%, and 15% of the variance, respectively (Fig. 2). Principal component 1 grouped foods from lowlands (mainly apples, chestnuts, and cherries) at negative loadings, and foods from uplands (graminoids, *Vaccinium*, and *Rhamnus*) at positive loadings. Principal component 2 described groups in accordance with the use of forested areas. Hard mast from forests (acorns and hazelnuts) appeared at negative loadings; vertebrates, *Vaccinium*, and *Rhamnus* fruits appeared at positive loadings, and they mainly occur (at least the last 2) in open shrublands. Principal component 3 described the important contribution of herbs to brown bear diet, because both graminoids and forbs (negative loadings) were the main variables affecting this 3rd component (Fig. 2).

Profiting from our long-term data series, we calculated the accumulated value of the *CV* for each food item by including

Table 2.—Seasonal mean percentage volume and coefficient of variation (*CV*) of food items in diet of brown bears in 2 of the study areas (Cantabrian Mountains of Spain). Differences among years in the relative contribution of any item to diet (tested by running general linear models where the factor year was considered as explanatory variable) are noted by an asterisk (*). For more clarity, contributions below 3% are indicated by t (= trace). Sample indicates the number of fecal samples followed (in parentheses) by the number of data-years.

	Winter				Mating				Hyperphagia			
	Central		Western		Central		Western		Central		Western	
Item	$\bar{X}$	*CV*	$\bar{X}$	*CV*	$\bar{X}$	*CV*	$\bar{X}$	*CV*	$\bar{X}$	*CV*	$\bar{X}$	*CV*
Graminoids	40.17	0.7*			22.5	1.3*	20.04	0.55	10.03	0.8*	3.22	0.19
Forbs	9.25	0.97			53.16	0.5*	55.61	0.6*	6.47	0.8*	4.46	0.65
Rhamnus									12.83	0.9*	t	
Sorbus									t		t	
Rubus									3.27	1.2*	3.34	1.26
Prunus					3.19	1.38			6.23	1*	10.18	0.9*
Malus	10.06	2.1*	t		t				6.86	1.3*		
Vaccinium			t		t		t		9.73	1.5*	23.21	0.6*
Castanea	11.11	1.7*	17.61	1.4*	t		t		4.68	1.7*		
Quercus	12.20	1.5*	38.27	1*	t		7.47	1.66	11.11	1.6*	25.00	0.9*
Fagus	7.92	2.1*	33.44	1.7*	5.52	1.6*			3.49	2.9*		
Corylus			4.37	1.7*					7.18	1.5*	6.88	0.34
Vertebrates	t		t		10.63	1.3*	11.50	1.5*	8.78	0.54	6.73	0.58
Insects	t				3.14	1.25			3.83	0.80	8.00	1.4*
Sample	62 (5)		76 (3)		165 (7)		92 (5)		531 (10)		191 (5)	

data-years in a stepwise fashion. For apples, cherries, insects, and chestnuts, the *CV* decreased with additional years of data (Fig. 3). However, this was not a general pattern and for many food items (forbs, graminoids, *Quercus*, and vertebrates), the *CV* remained the same regardless of the number of data years used. For several food items (hazelnuts, *Vaccinium* and *Rhamnus* fruits, and beechnuts) the *CV* increased when additional data years were added (Fig. 3).

Discussion

Brown bears in the Cantabrian Mountains, as in the rest of Europe, showed omnivorous food habits with a high proportion of plant matter in their diet. Our results highlight the importance of both acorns and bilberries (*Vaccinium*) as essential food items for brown bears. Thus, oak forests and heathlike formations of clumped shrubs of *Vaccinium* should receive high conservation priorities as critical foraging habitats for this endangered species. Managers should restrict domestic ungulates (which feed on both the plant and their fruits—Fernández-Calvo and Obeso 2004) from accessing these *Vaccinium* formations. Additionally, mountain tourism, which negatively impacts bears (Naves et al. 2001; White et al. 1999), should be restricted during late summer and early autumn when bears are using these areas heavily. We also suggest a greater effort to limit hunting (especially during autumn and winter) and to avoid subcanopy clearings in old-growth oak forests. The opening of new tracks across the forest should be also avoided because they diminish the amount of suitable habitat for bears while increasing fragmentation.

The joint occurrence of acorns and fruits of *Vaccinium* in the brown bear diet is rarely documented. Those populations feeding on mast items from deciduous forests (mainly Eurasian populations below 50°N latitude, and extinct North American populations—Brown 1985 in Jacoby et al. 1999) seldom consumed fruits from *Vaccinium* (Berducou et al. 1983; Cicnjac et al. 1987; Fabbri 1987; Frackowiak and Gula 1992; Mertzanis 1992; Ohdachi and Aoi 1987; Vaisfeld and Chestin 1993). On the contrary, the notable proportion of more meridional (i.e., Mediterranean) food items (e.g., *Arbutus unedo*, *C. sativa*, and *Q. rotundifolia*) found in the Cantabrian bear's diet is similar to those found in other southern European populations,

Table 3.—Models that considered area as an explanatory variable for occurrence of major food items during winter in diet of brown bears in the Cantabrian Mountains of Spain. Contribution to diet of each item is shown as frequency of occurrence and percentage of total volume in the period. Values shown are parameter estimates ± *SE* and percentages of explained deviance (only provided for significant models).

Item	Frequency (%)	Volume	Intercept	Central area	Western area	Eastern area	χ^2	*P*	Deviance explained (%)
Quercus	49	43	−0.9 ± 0.2	0	1.3 ± 0.3	1.3 ± 0.4	19.56	<0.0001	7
Graminoids	24	17	−0.3 ± 0.2	0	−2.2 ± 0.5	−1.9 ± 0.6	34.63	<0.0001	16
Castanea	14	12	−2.7 ± 0.5	0	1.3 ± 0.5	0.1 ± 0.9	8.75	0.01	6
Fagus	12	10					2.19	0.33	
Forbs	12	5	−1.6 ± 0.3	0	−2.3 ± 0.8	−0.6 ± 0.7	13.47	0.001	11
Vertebrates	11	3					2.1	0.35	
Corylus	3	3		Absent	Present	Absent			

TABLE 4.—Models that considered area as an explanatory variable for occurrence of major food items during the mating period in diet of brown bears in the Cantabrian Mountains of Spain. The contribution to diet of each item is shown as frequency of occurrence and percentage of total volume in the period. Values shown are parameter estimates ± *SE* and percentages of explained deviance (only provided for significant models).

Item	Frequency (%)	Volume	Intercept	Central area	Western area	Eastern area	χ^2	*P*	Deviance explained (%)
Forbs	59	45	0.6 ± 0.2	0	−0.1 ± 0.2	−2.8 ± 0.5	60.81	<0.001	12
Graminoids	39	20					3.0	0.22	
Vertebrates	19	9					0.79	0.67	
Insects	19	4					3.1	0.21	
Quercus	16	13	−3.4 ± 0.4	0	1.0 ± 0.5	4.2 ± 0.5	115.2	<0.001	37
Fagus	5	4	−2.4 ± 0.3	0	−1.7 ±0.8	−7.8 ± 1.3	12.9	0.002	9

including Abruzzos (Italy), former Yugoslavia, and Greece (Cicnjac et al. 1987; Fabbri 1987; Mertzanis 1992). Interestingly, the Cantabrian population is the only known group to feed on both Mediterranean and boreal (e.g., *Vaccinium*) foods.

In summary, at the southwestern border of the brown bear's Eurasian range, its food habits are characterized by a high diversity of food items (with a substantial contribution of fruits of Rosaceae) that included Mediterranean (e.g., chestnuts), temperate (e.g., *Quercus petraea*), and relict-boreal species. Whether this high trophic diversity is the result of a low foraging efficiency (Pyke et al. 1984) or an optimized response to different availability of multiple food items constitutes an interesting question for further study.

Although these findings are applicable to the entire Cantabrian Range, each of the study areas showed significant differences. Acorns constituted the bulk of the winter diet for the Cantabrian brown bear population. However, bears in the central area also consumed a high proportion of low-energy items such as graminoids (although their apparent predominance is caused by the low digestibility of these foods—see Hewitt and Robbins 1996; Pritchard and Robbins 1990). Even taking this into account, the contribution of graminoids to the diet is high in this area. This observation was surprising because acorns provide much more energy than graminoids (Craighead et al. 1995; Grodzinski and Sawicka-Kapusta 1970) and foraging cost of acorns is probably lower. A possible explanation is a lower availability of acorns because of competition with other consumers, reflected in the high herbivore density in the central area (Obeso and Bañuelos 2003). Free-ranging livestock, and wild ungulates, especially wild boar (*Sus scrofa*) could cause a fast depletion of acorns during autumn and early winter, forcing bears to feed on graminoids when acorns become scarce.

Beechnuts (*Fagus*) also constitute an important food supply, especially because beech forest cover is higher than oak forest cover (ratio approximately 3:1—García et al. 2005). However, beech often fails to produce fruit, with periods of up to 4 consecutive years of mast failure (Clevenger et al. 1992). This could explain the low contribution of this item to the total diet and also why we were not able to find differences among areas for the winter season.

During the mating season, bears mostly fed on herbaceous plants, but also on overwintering acorns (*Quercus*). In fact, acorns constituted a high proportion of the diet of the eastern subpopulation (63% of volume; $n = 57$ scats). This could be explained by the deeper snow cover characteristic of several parts of this area. This prevents mast eaters—not only bears, but also wild boars, red deer (*Cervus elaphus*), free-ranging livestock, squirrels (*Sciurus vulgaris*), rodents (Rodentia), corvids (Corvidae: *Corvus*), and common wood-pigeons

TABLE 5.—Models that considered area as an explanatory variable for occurrence of major food items during the hyperphagic period in diet of brown bears in the Cantabrian Mountains of Spain. The contribution to diet of each item is shown as frequency of occurrence and percentage of total volume in the period. Values shown are parameter estimates ± *SE* and percentage of explained deviance (only provided for significant models).

Item	Frequency (%)	Volume	Intercept	Central area	Western area	Eastern area	χ^2	*P*	Deviance explained (%)
Quercus	22	16	−1.8 ± 0.1	0	0.9 ± 0.2	1.2 ± 0.2	36.25	<0.0001	4
Graminoids	20	7	−1.9 ± 0.1	0	−0.3 ± 0.2	0.7 ± 0.3	10.95	0.004	1.5
Vaccinium	16	11	−2.4 ± 0.1	0	1.6 ± 0.2	−0.2 ± 0.4	66.19	<0.0001	9
Insects	16	4					1.39	0.50	
Vertebrates	15	7					2.65	0.27	
Malus	14	7	−1.9 ± 0.1	0	−1.5 ± 0.4	0.3 ± 0.3	27.87	<0.0001	5
Forbs	14	7	−2.2 ± 0.1	0	−0.1 ± 0.3	1.0 ± 0.3	12.38	0.002	2
Corylus	12	6	−2.4 ± 0.1	0	0.5 ± 0.2	−2.2 ± 0.9	16.47	0.0003	3
Prunus	11	7	−2.4 ± 0.1	0	0.5 ± 0.2	−6.8 ± 6.1	24.76	<0.0001	4
Rhamnus	10	7	−1.9 ± 0.1	0	−3.6 ± 0.9	−0.2 ± 0.4	47.69	<0.0001	8
Castanea	8	7	−2.0 ± 0.1	0	−1.9 ± 0.5	−7.2 ± 6	45.17	<0.0001	9
Rubus	8	3					0.22	0.89	
Sorbus	6	3					3.2	0.2	

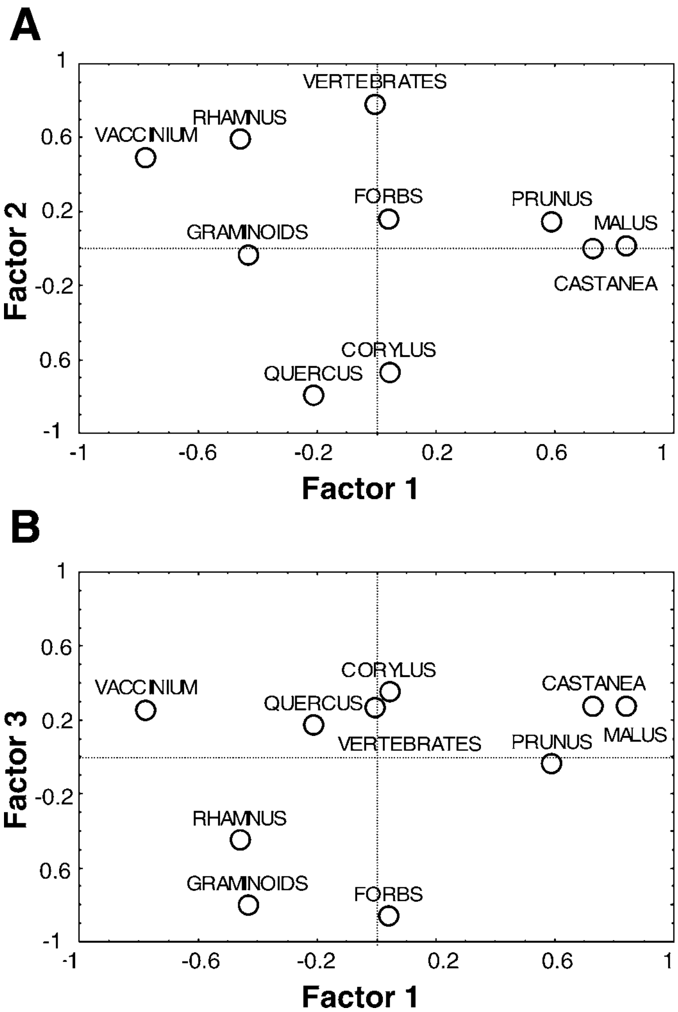

FIG. 2.—Relationships between factors in principal component analysis of diet of brown bears in the central area (Cantabrian Mountains of Spain). A) Factor 1 relative to factor 2. B) Factor 1 relative to factor 3. Factor 1 grouped foods from uplands (*Vaccinium*, *Rhamnus*, and graminoids) at negative loadings and foods from lowlands (*Prunus*, *Malus*, and *Castanea*) at positive loadings. Factor 2 grouped foods from forested areas (*Corylus* and *Quercus*) at negative loadings and foods from open areas (*Vaccinium* and *Rhamnus*) at positive loadings. Factor 3 accounted for the important contribution of graminoids and forbs (as negative loadings) to brown bear diet.

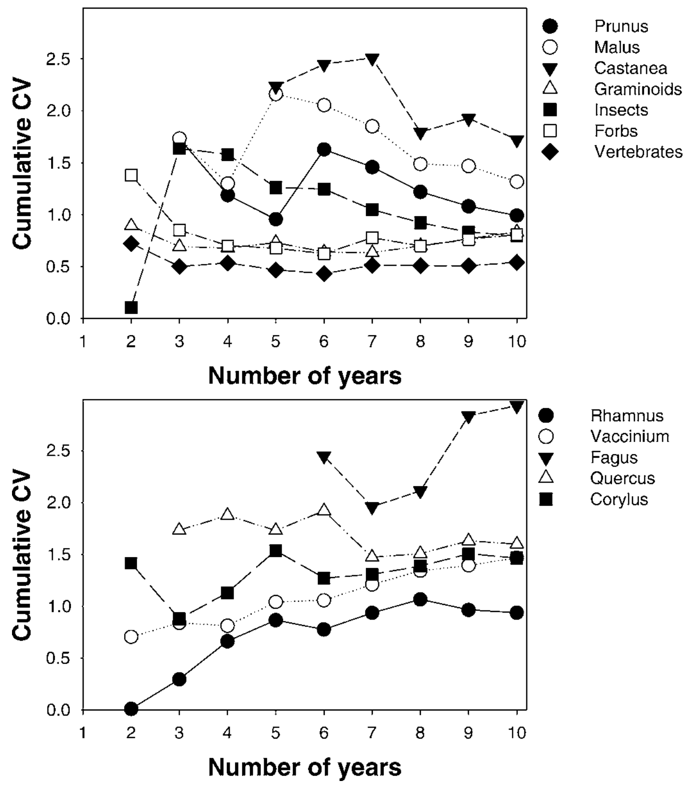

FIG. 3.—Cumulative value of coefficient of variation (*CV*) for each food item in diet of brown bears over a 10-year period for the central study area (Cantabrian Mountains of Spain) during the hyperphagic season (shown in 2 graphs to display results for 10 plant types and 2 animal groups without crowding). Some foods were not consumed at the beginning, but they were incorporated into the graph upon appearance.

(*Columba palumbus*)—from accessing acorns during winter. When snow melts in spring, acorns become available for brown bears in the eastern area. However, in the western and central areas, winter cover may have been sufficiently less to allow other mast eaters (which are especially abundant in the central area, see above) access to the acorns during winter (see Shimano and Masuzawa [1995] for similar effects of snow cover on seed preservation).

Diet during the hyperphagic season was the most complex and diverse, and has major implications on bear ecology and behavior (Craighead et al. 1995; LeFranc et al. 1987). As many as 13 food items contributed to hyperphagic diet of bears in the central area, but their relative importance changed from year to year. PCA indicated that these interannual differences may be due to different habitat selection, which is probably driven by food availability. Bears can mostly feed on cherries, apples, and chestnuts in lowlands, but they also can feed on *Vaccinium* as well as *Rhamnus* fruits in uplands. At middle altitudes, bears were able to obtain a 3rd feeding option (acorns and hazelnuts) from forests (Fig. 3).

Clevenger et al. (1992) documented that the brown bear's diet in the eastern subpopulation was less diverse than in other parts of the Cantabrian Range. Despite the importance of diet composition during the hyperphagic season when bears are storing fat before denning, bears in this subpopulation consume a high proportion of low-energy items such as graminoids and forbs. This probably constrains the amount of fat bears can accumulate and thus limits the time they can spend denning and the number of cubs females can produce and rear (see Bunnell and Tait 1981; Rogers 1987). This abundance of low-quality food items in the bear's diet supports previous work that characterized this area by its lower natural suitability for the brown bear (Naves et al. 2003). Other authors also have suggested the potential influence of feeding conditions during the hyperphagic period in denning, documenting a higher number of nonhibernating bears during years of low food availability (Vaisfeld and Chestin 1993). Conversely, there is a constant presence of high-quality food items in the diet of the western area almost annually, supporting the higher natural quality of the habitat, which also was stressed by Naves et al. (2003).

The differences in diet composition among the study areas (Tables 2–5) highlighted the importance of considering local scales (brown bear population nuclei) when studying diets at wide geographical ranges. In addition to their implications for diet description (see Tables 1 and 2), these differences have enormous interest for brown bear management, because each of the studied areas belongs to a different protected area (within the regional and national reserve network). Managers of each area are then responsible for proposing, designing, and implementing their own management actions. For instance, our results suggest that improving feeding conditions for bears should constitute a priority for managers of the central and eastern areas, whereas such management seems not to be necessary in the western area.

Many diet studies have assumed (explicitly or implicitly) that diet is an unchanging component of animal ecology. In fact, some efforts exist to calculate the number of years necessary to determine interannual fluctuations in the diet. However, this only makes sense if the annual contributions of a food item fluctuate around a mean, and thus the more data-years available, the more robust the estimate becomes (low *CV*). However, long-term studies have suggested that environmental fluctuations and land-use changes could result in long-term oscillations in diet composition (Mattson et al. 1991). Examination of our data set suggests long-term trends in the availability or use of some diet items, particularly for fleshy fruits and hard mast, except those items involved in supra-annual schedules of highly fluctuating seed production (mainly acorns and beechnuts—Herrera et al. 1998), which would require additional study. Because conclusions drawn from many studies of brown bear food habits are often relevant for management (see Craighead et al. 1995), the results of this study indicate that assessing local differences in food habits could be of enormous interest when populations are spatially structured, and each of the subpopulations (or nuclei) could be managed following different criteria, mainly because of their peculiarities, but also because of administrative reasons; and that it is necessary to incorporate diet studies in monitoring protocols for some endangered populations. Diet studies constitute a valuable tool to detect changes in habitat at a scale that may not be apparent solely with habitat monitoring. Directional changes in food habits during a certain time period may provide important cues to design and implement management actions, to evaluate actions already in progress, or both. Our results suggest that these changes are occurring in the Cantabrian Range, probably as the brown bears respond to changing food availability or as a consequence of changes in foraging habitat selection (perhaps due to anthropogenic factors). It remains a challenge to investigate which environmental changes have occurred during the last decades in this range that could explain these changes in diet, as well as to assess their potential effects on the brown bear population from both the nutritional and the conservation point of view.

Resumen

Se estudian los hábitos alimenticios del oso pardo cantábrico a partir de 1,500 excrementos recogidos entre septiembre de 1974 y mayo de 2004. Los osos pardos consumieron una gran proporción de gramíneas y megaforbias durante la primavera, frutos carnosos durante el verano y frutos secos durante el otoño e invierno. De hecho encontramos una gran diversidad de frutos de especies mediterráneas, templadas y boreales relictas. También consumieron materia animal durante todo el año, aunque con menor frecuencia en la estación invernal. En términos de composición de la dieta, nuestros resultados subrayan la importancia de las bellotas y los arándanos como alimentos fundamentales para el oso pardo. También encontramos diferencias significativas entre las 3 áreas de estudio, que pueden ser de enorme interés para la gestión del hábitat en cada una de ellas. Por último, investigamos el papel que juega la variación interanual característica de la dieta del oso pardo en nuestras estimas acerca de la contribución relativa de los diferentes alimentos, y por tanto en la descripción de la dieta. Usando el coeficiente de variación (*CV*) como medida de dispersión encontramos que algunos alimentos contribuyen de forma más o menos constante a la dieta, mientras que otros lo hacen de forma sustancial, pero esporádica, lo que hace más difícil caracterizar su importancia. También comprobamos que al aumentar el número de años considerados para caracterizar la dieta, el *CV* asociado a algunos alimentos aumentó, lo que apunta a la existencia de tendencias temporales en su consumo que deberán ser considerada por estudios posteriores a éste. Asimismo, dichas tendencias sugieren la incorporación de estudios de dieta a los programas de seguimiento de especies amenazadas, ya que lejos de ser inmutable, la dieta puede sufrir cambios sustanciales que sirvan como indicadores que ayuden a mejorar las medidas de gestión diseñadas para dichas especies.

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APPENDIX I

Results of scat analyses at the highest taxonomic resolution for brown bears in the Cantabrian Mountains of Spain. After each food item, we show its absolute frequency of occurrence. For summarizing categories, this frequency accounts for both identified and unidentified taxa. Brown bear also appeared as a food item because we found substantial contribution of bear's hair to scat composition, although we cannot ascertain the origin of such hairs (i.e., whether they correspond to real consumption or not). Asterisks indicate food items determined at the species level from field observations when collected (*Quercus*), or based on the presence of characteristic leaves in the scat (*V. uliginosum*); however, these were made sporadically, and thus all acorns were considered as *Quercus* species, and all bilberries were conferred to be *V. myrtillus* (the main species in the study area).

Domestic ungulates (85).—Equus caballus, 9; *Bos taurus*, 26; *Capra hircus*, 13; *Ovis aries*, 1; *Sus domesticus*, 1.

Wild artiodactyls (61).—Capreolus capreolus, 45; *Cervus elaphus*, 2; *Rupicapra pyrenaica*, 5; *Sus scrofa*, 1.

Small mammals (14).—Rodentia, 4; *Apodemus*, 1; Arvicolinae, 2; *Arvicola terrestris*, 3; *Microtus lusitanicus*, 1; Soricidae, 1; *Crocidura*, 1; *Erinaceus europaeus*, 1.

Carnivora (5).—Canis lupus, 2; *Meles meles*, 1; *Ursus arctos*, 2.

Birds (8).—Passeriformes, 2; Phasianidae, 2; *Gallus domestica*, 1.

Hymenoptera, Formicidae (138).—Campoctus, 1; *Dendrolasius*, 1; *Formica*, 8; *Formica pratensis*, 3; *Formica rufa*, 3; *Lasius*, 1; *Myrmica*, 1.

Hymenoptera, non-Formicidae (19).—Apis mellifera, 17.

Coleoptera (18).—Carabidae, 8; unidentified (larvae), 10.

Orthoptera (2).—Ensifera, 1; Acrididae, 1.

Lepidoptera (1).—Unidentified (larvae), 1.

Opistophora (1).—Lumbricus, 1.

Forbs (369).—Achillea millefolium, 1; *Actaea spicata*, 1; *Anchusa officinalis*, 1; Apiaceae, 1; Asteraceae, 1; *Cardamine pratensis*, 1; *Cardus*, 1; Cariofilaceae, 1; *Centaurea*, 1; *Centranthus*, 1; *Chaerophyllum hirsutum*, 36; *Chrysosplenium oppositifolium*, 2; *Echium*, 1; *Euphorbia hyberna*, 1; *Galium*, 1; *Helianthemum canun*, 1; *Helianthemum nummularium*, 1; *Heracleum spondylium*, 81; *Lithodora difusa*, 3; *Meum athamanticum*, 27; *Pimpinella*, 2; *Plantago*, 2; *Plantago lanceolata*, 1; *Polystichum*, 1; *Potentilla montana*, 2; *Sanguisorba minor*, 4; *Scrophularia*, 1; *Sedum anglicum*, 2; *Stachys officinalis*, 2; *Stellaria uliginosa*, 1; *Teucrium chamaedris*, 1; *Teucrium scorodonia*, 1; *Thymus*, 1; *Trifolium*, 5; *Typha*, 2; *Vicia sepium*, 1.

Graminoids (375).—Anthoxantum odoratum, 1; *Avenula*, 2; *Avenula pubescens*, 2; *Avenula sulcata*, 6; *Avenula vasconica*, 3; *Brachipodium sylvaticum*, 1; *Bromus racemosus*, 4; *Carex sylvatica*, 1; *Cynosurus crystatus*, 1; *Dactylis glomerata*, 11; *Deschampsia flexuosa*, 11; *Festuca*, 10; *Festuca ovina*, 1; *Festuca rubra*, 15; *Holcus lanatus*, 2; *Holcus mollis*, 3; *Juncus*, 2; *Luzula*, 4; *Luzula sylvatica*, 13; *Poa*, 1; *Poa nemoralis*, 1; *Poa pratensis*, 3.

Berries and fleshy fruits (704).—Arbutus unedo, 11; *Arctostaphylos uva-ursi*, 1; *Crataegus monogyna*, 18; *Ficus carica*, 1; *Frangula alnus*, 19; *Hedera helix*, 1; *Ilex aquifolium*, 1; *Malus*, 139; *Malus sylvestris*, 5; *Malus domestica*, 1; *Pyrus communis*, 2; *Prunus*, 64; *Prunus avium*, 29; *Prunus domestica*, 2; *Prunus persica*, 6; *Prunus spinosa*, 6; *Rhamnus alpina*, 93; *Ribes*, 1; *Rosa*, 12; *Rosa canina*, 1; *Rubus*, 70, *Rubus fructicosus*, 3; *Rubus idaeus*, 1; *Rubus ulmifolius*, 7; *Sorbus*, 23; *Sorbus aria*, 12; *Sorbus aucuparia*, 17; *Vaccinium myrtillus*, 156; *Vaccinium uliginosum**; *Viburnum lantana*, 2.

Hard mast (662).—Castanea sativa, 109; *Corylus avellana*, 118; *Fagus sylvatica*, 71; *Quercus*, 362; *Quercus petraea**; *Quercus pyrenaica**; *Quercus rotundifolia**; *Ulmus*, 2.

Sprouts and stems (19).—Crataegus monogina, 2; *Daboecia cantabrica*, 1; *Fagus sylvatica* (buds), 6; *Frangula alnus*, 2; *Genista hispanica*, 1; *Quercus petraea* (buds)*, 1; Rosaceae, 1; *Salix* (flowers), 3; *Sorbus torminalis* (leaves), 1; *Ulex europaeus*, 1.

Cryptogams (24).—Mushrooms, 7. Lichens (3): *Cladonia*, 1; *Nephroma laevigatum*, 1. Mosses, 7; Ferns (2): *Pteridium aquilinum*, 2.

Tubers and roots (7).—Bromus, 2; *Cardamine pratensis*, 1; *Chaerophyllum hirsutum*, 1; *Luzula sylvatica*, 1; *Solanum tuberosum*, 2.

Legumes (7).—Cytisus multiflorus, 1; *Cytisus scoparius*, 1; *Genista*, 2; *Genista florida*, 1; *Genista hispanica*, 2.

Grain (9).—Zea mays, 7; *Hordeum vulgare*, 2.

Others (2).—Bark or wood, 2.