Seasonal and annual variation in the food habits of Apennine brown bears, central Italy

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Only scanty and outdated knowledge is available on the food habits of the Apennine brown bear (*Ursus arctos marsicanus*) population, despite its critical conservation status. Based on 2,359 scats, collected from June 2006 through December 2009, we documented seasonal and annual variation in the diet of this bear population within its 1,294-km^2 core distribution in Abruzzo, Lazio, and Molise National Park and its external buffer area in central Italy. Using correction factors to estimate digestible energy, we revealed substantial consumption of plant matter by bears, including herbaceous vegetation in spring (mean $\pm$ *SD*; 31.7% $\pm$ 25%) and early summer (19.0% $\pm$ 7%), a variety of naturally occurring berries in summer (56.5% $\pm$ 14%), and hard mast (66.9% $\pm$ 21%), largely supplemented by fleshy fruits (26.3% $\pm$ 18%), in the fall. Bears also consumed insects, mostly ants, in early summer (38.3% $\pm$ 7%), and wild ungulates in spring (10.2% $\pm$ 11%). Hard mast production strongly influenced year-to-year variation in the diet. High-quality foods, such as berries and other fleshy fruits, were increasingly consumed by bears in years of low to null hard mast productivity, suggesting that habitat productivity is currently high and diversified enough to allow bears to avoid the risk of nutritional stress during occasional hard mast failures. Nevertheless, as exemplified by a negative trend in late-summer consumption of buckthorn (*Rhamnus* spp.) berries by bears, our findings demonstrate the need to implement management strategies that will ensure long-term habitat productivity and provide optimal foraging opportunities for Apennine brown bears.

Key words: Abruzzo National Park, Apennines, brown bear, diet, hard mast, *Rhamnus alpinus*, scat analysis, small populations, *Ursus arctos*

Brown bears (*Ursus arctos marsicanus*) in the central Apennines in Italy have been isolated from other northern bear populations for at least 400–700 years (Randi et al. 1994; Lorenzini et al. 2004). Recently estimated at about 50 bears (Gervasi et al. 2012), the Apennine bear population is considered critically endangered by the IUCN, both at the European (Kaczensky et al. 2013) and the national (Rondinini et al. 2013) scale. However, despite 90 years of protection within Abruzzo, Lazio, and Molise National Park (hereafter, Abruzzo National Park—Boscagli 1999), and the availability of suitable habitat across a much larger area (Posillico et al. 2004; Falcucci et al. 2008, 2009), the Apennine bear population failed to increase either in numbers or range (Boscagli 1999; Ciucci and Boitani 2008). In addition to persistently high rates of human-caused mortality, a lack of reliable knowledge on its basic ecology has impeded the design and implementation of science-based management and conservation efforts for this endangered bear population (Ciucci and

Boitani 2008). In particular, although supplemental feeding campaigns endorsed by the park are being criticized as unjustified and largely untested, neither management interventions to ensure habitat productivity in the long term, nor the prioritization of bear conservation over multiple uses, have been seriously contemplated (Ciucci and Boitani 2008).

Food-habit studies, though descriptive in nature, are an essential 1st step toward a deeper understanding of the linkages among habitat productivity, food accessibility to bears, and the performance of local bear populations that is needed to guide management interventions (Craighead et al. 1995; Persson et al. 2001; Naves et al. 2006; Baldwin and Bender 2009). In addition, because habitat productivity will change due to natural ecological processes or human activities (Robbins et al.

2004; Rodríguez et al. 2007), food-habit studies provide crucial information for maintaining or enhancing long-term habitat productivity for bears (Reynolds-Hogland et al. 2007), and offer a baseline for monitoring bear dietary responses to habitat changes (Naves et al. 2006; McLellan 2011). Food-habit studies are important for informing conservation planning, especially for small and isolated bear populations (Naves et al. 2006; Rodríguez et al. 2007; McLellan 2011).

Brown bear food habits have been investigated in many portions of the species' range (e.g., Cicnjak et al. 1987; Mattson et al. 1991; Elgmork and Kaasa 1992; Craighead et al. 1995; McLellan and Hovey 1995; MacHutchon and Wellwood 2003; Sato et al. 2004; Munro et al. 2006; Naves et al. 2006; Paralikidis et al. 2010), and depict brown bears as highly opportunistic omnivores with marked seasonal and geographical differences in diet (Bojarska and Selva 2012). Human activities may limit seasonal accessibility to key foods and restrict foraging opportunities for bears (Welch et al. 1997; White et al. 1999; Rode et al. 2001; Naves et al. 2006; Rodríguez et al. 2007), potentially exerting negative impacts on the condition and reproductive performance of local bear populations (Rode et al. 2006, 2007).

Food habits of brown bears in Europe vary according to latitude, season, and local conditions, all of which influence the availability of key foods for bears (Elgmork and Kaasa 1992; Vulla et al. 2009; Bojarska and Selva 2012). Whereas bears in northern regions are more carnivorous and consume less hard mast than southern populations (Elgmork and Kaasa 1992; Dahle et al. 1998; Persson et al. 2001; Swenson et al. 2007), due possibly to the simpler ecological structure of northern ecosystems, bears in southern Europe eat the highest percentages of fleshy fruits and hard mast and the lowest percentages of vertebrates (Cicnjak et al. 1987; Clevenger et al. 1992; Naves et al. 2006; Paralikidis et al. 2010). In southern Europe, bears consume a great diversity of plant material in accordance with seasonal plant phenologies, with hard mast and fleshy fruits predominating in the diet during fall (Cicnjak et al. 1987; Clevenger et al. 1992; Naves et al. 2006; Rodríguez et al. 2007; Paralikidis et al. 2010). Accordingly, because annual failures in hard mast production may expose hyperphagic bears to nutritional stress, a diversity of supplemental foods in the fall may be particularly important (Cicnjak et al. 1987; Clevenger et al. 1992; Naves et al. 2006; Paralikidis et al. 2010).

Unfortunately, little is known about the diet of Apennine brown bears. The only information available comes from a 1-year study conducted > 40 years ago (Zunino and Herrero 1972) and a few unpublished reports and undergraduate theses limited to short study periods and small portions of Abruzzo National Park (Zunino 1976; Fabbri 1988; Russo et al. 1996). We also have presented some preliminary data on the diet of Apennine bears in a recent methodological assessment (Di Domenico et al. 2012). In addition to impeding the timely adoption of science-based management for Apennine bears, this knowledge gap also prevents researchers from comprehensively comparing the ecology of brown bears across Europe

(e.g., Swenson et al. 2007; Vulla et al. 2009; Bojarska and Selva 2012).

In this paper, we report the results of a 4-year scat-analysis study that we conducted in the core of the Apennine brown bear's distribution. This is considered to be a sufficient time frame to understand the relative importance of various foods to bears (Mattson et al. 1991; Koike 2010). We describe the annual diet of Apennine brown bears, correcting for differential digestibility and energy content of various foods, and accounting for seasonal variability. In addition, we determine the onset and duration of seasonal dietary shifts toward high-quality foods by bears to provide a temporal reference for managing human activities that may negatively impact food accessibility and optimal foraging opportunities for Apennine brown bears (Clevenger et al. 1992; Rode et al. 2001, 2007; Naves et al. 2006; Rodríguez et al. 2007).

MATERIALS AND METHODS

Study area.—We conducted our study in the 1,294-km^2 core distribution of the Apennine brown bear (Ciucci and Boitani 2008), including Abruzzo National Park (507 km^2) and its external buffer zone (787 km^2) in the central Apennines, Italy (Fig. 1). The area is typically mountainous, with elevations ranging from 400 to 2,285 m, and is characterized by a Mediterranean montane climate, with dry summers and cold, snowy winters (Piovesan et al. 2003). Snow cover generally extends from mid-December to March, but with great
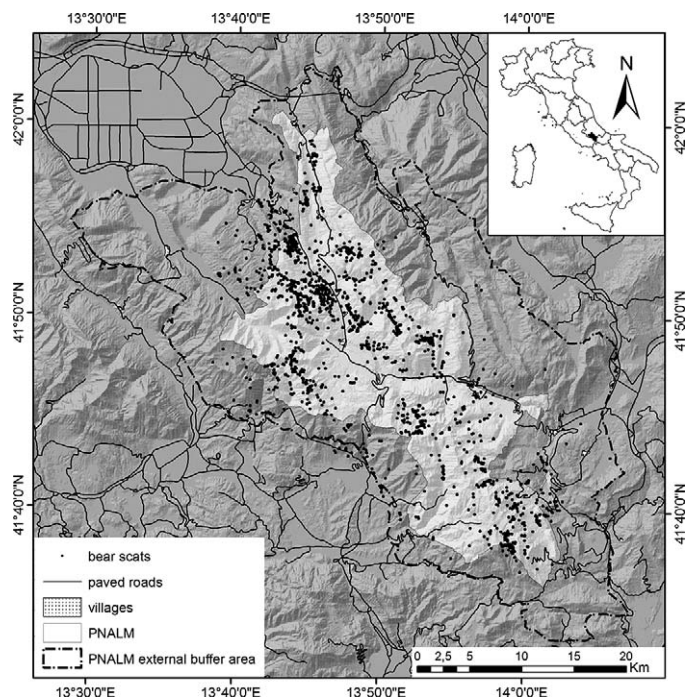
Fig. 1.—Location of the study area in Italy (inset) and spatial distribution of the 2,359 Apennine brown bear (*Ursus arctos marsicanus*) scats used to describe the diet of the Apennine brown bear in Abruzzo, Lazio, and Molise National Park, Italy, from June 2006 to December 2009.

orographic and annual variability. About 60% of the study area is covered by deciduous forests, followed by subalpine meadows and grasslands (21.8%) and intensive agricultural areas (3.5%—European Environment Agency [EEA] 2006). Forests are mostly composed of beech (*Fagus sylvatica*) but, at lower elevations, oaks (*Quercus cerris* and *Q. pubescens*), maples (*Acer* spp.), and fruit trees (e.g., *Pyrus pyraster*, *Malus sylvestris*, *Prunus* spp., and *Sorbus* spp.) prevail, the latter including domestic cultivars (e.g., cherries, pears, and apples) dispersed throughout the study area that were recently abandoned by humans (Zunino and Herrero 1972). Shrubs include numerous species of the *Berberidion vulgaris* alliance, including several fruiting plants (*Amelanchier ovalis*, *Crataegus* spp., *Rhamnus alpinus*, *Ribes* spp., *Rosa* spp., *Rubus idaeus*, and *Viburnum* spp.). Meadows in the montane and submontane zones are mainly represented by mesophilous, seminatural grasslands, whereas open grasslands above 1,800 m host communities of *Seslerion apenninae*, *Festuceto-Trifolietum thalii*, and *Festuco-Brometea* (Bazzichelli and Furnari 1979). Nitrophilous vegetation (*Chaerophyllum*, *Chenopodium*, *Rumex*, and *Urtica*) is common on deep soils related to pastoral activities, and primarily occurs near water sources.

Large ungulates in the study area included red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*), and Apennine chamois (*Rupicapra pyrenaica ornata*). Livestock also are present at high densities (Salvatori et al. 2012), with cattle and horses left free-ranging and unattended for most of the year (Galluzzi et al. 2010). Other large carnivores include wolves (*Canis lupus*), with at least 7 packs overlapping portions of the study area (Ciucci and Boitani 2010), and free-ranging dogs. Brown bears occupy the study area at a density of about 33 per 1,000 km^2 (Gervasi et al. 2012), and are generally active from mid-March to the end of November, with differences due to sex and reproductive status (Tosoni 2010).

Although the area has long been protected (Boscagli 1999), multiple uses are predominant in both the park and its external buffer area (Ciucci and Boitani 2008). In the park, livestock husbandry, forestry, and tourism are important economic activities, whereas agriculture is scarce and mostly occurs along valley bottoms near a few human settlements. Forest cutting must be approved by park authorities, who also rent privately owned forests to prevent bear habitat deterioration due to timber exploitation. Nevertheless, due to historical exploitation of the forests for timber and fuel, coppice, even-aged pole stands, and transitional structures are common and currently provide relatively little food for bears (Potena et al. 2009). Supplemental feeding of carrion to bears was discontinued by the park in the mid-1990s (Ciucci and Boitani 2008), although it still endorses the planting of apple trees and set-aside crops to enhance food availability for bears (Ciucci and Boitani 2008). Hunting is allowed in the external buffer area, including drive hunts of wild boars with dogs from October to January.

Field methods.—From June 2006 to December 2009, we used 3 complementary sampling methods to collect fresh, unweathered bear scats: systematically along established routes throughout the study area at 2- or 3-week intervals, incidentally to other field activities, and opportunistically during field inspection of global positioning system (GPS) clusters of 3–6 collared adult bears (Tosoni 2010). We subsampled the GPS clusters to account for different times of day and different portions of the bears' individual home ranges (Mattson 1997). Because multiple scats found at the same site may be autocorrelated and overrepresent certain food items (Mattson et al. 1991), we included ≤ 5 scats per collection site and occasion (Dahle et al. 1998). In addition, we combined scats of the same age collected at each GPS location into a single composite sample (Raine and Kansas 1990). To investigate seasonal variation in the diet, we classified scats into 4 dietary periods that are relevant to phases of brown bear biology and the availability of their primary foods (Nelson et al. 1983; Mattson et al. 1991; Craighead et al. 1995; McLellan and Hovey 1995): spring (March–May), corresponding to den emergence and hypophagia; early summer (June–July), corresponding to the peak of the mating season and an increased availability of insects; summer (August–September), corresponding to early hyperphagia, the ripening of wild berries, and the peak in livestock availability; and autumn (October–mid-December), corresponding to late hyperphagia and the availability of hard mast and fleshy fruits.

Laboratory processing.—Scats were stored at −20°C until processed. Following standard procedures, we rinsed each scat through a double sieve (0.8- and 0.1-mm mesh size) and thoroughly mixed its content. We then randomly selected two 10-ml subsamples for analysis (Di Domenico et al. 2012). For each subsample, we hand separated macrocategories (e.g., grasses, forbs, seeds, hair, and bones) and estimated their relative proportions using a reference grid and 11 volumetric classes, whose midpoints were averaged between the 2 subsamples (Mace and Jonkel 1986; Reynolds and Aebischer 1991; Dahle et al. 1998).

We used a 7–30× stereoscope and a 400–600× microscope to identify food items at the lowest taxonomic level possible. Based on leaf characteristics, we classified green vegetation into graminoids (including Gramineae, Cyperaceae, and Juncaceae) or forbs (all other herbaceous plants), because these categories include food items that have similar nutritional value to bears (Dahle et al. 1998; MacHutchon and Wellwood 2003). When present, we also used seeds to identify plant material (Marchi et al. 2002). A single experienced entomologist identified insects, and ants were assigned to the lowest taxonomic level possible based on their head capsules (Noyce et al. 1997; Swenson et al. 1999; Bull et al. 2001; Auger et al. 2004). Mammal remains in the scats were identified using microscopic hair characteristics by 2 trained technicians, whose accuracy (range: 99–100%) had been evaluated previously based on a blind test of 120 hair samples from local mammal species. Wild and domestic ungulates were further classified into 2 broad age classes: juveniles, from birth to 1st autumn

TABLE 1.—Seasonal and annual tallies of the 2,359 bear scats used to investigate food habits of the Apennine brown bears (*Ursus arctos marsicanus*) in Abruzzo, Lazio, and Molise National Park, Italy, from June 2006 to December 2009. Spring = March–May; early summer = June–July; late summer = August–September; autumn = October–mid-December. For scats collected at global positioning system (GPS) clusters, the number of collared bears is shown in parentheses.

		No. scats			
Year	Collection method	Spring	Early summer	Late summer	Autumn
2006	Systematic	—	67	89	126
	GPS cluster	—	—	—	46 (4)
	Total	—	67	89	172
2007	Systematic	60	93	238	172
	GPS cluster	15 (3)	53 (3)	96 (4)	59 (3)
	Total	75	146	334	231
2008	Systematic	28	102	87	83
	GPS cluster	—	9 (3)	5 (3)	27 (3)
	Total	28	111	92	110
2009	Systematic	68	137	247	131
	GPS cluster	52 (3)	53 (6)	134 (5)	82 (5)
	Total	120	190	381	213

molt, and adults, $\geq$ 4–5 months (Ciucci et al. 1996). A reference manual (Teerink 1991) and a hair collection from local species aided identification of mammal remains. We considered "nonfood" those items deemed to have been incidentally ingested by bears (e.g., ant nest material, moss, sticks, wood fragments, and debris), including bear hairs with mean volumetric proportions per scat $\leq$ 0.5%, that were presumably ingested during grooming.

Diet quantification.—We first quantified diet composition according to frequency of occurrence (FO; the number of scats containing a given item as a proportion of the total number of scats) and fecal volume (FV; the sum of the volumetric proportions of a given item divided by the total number of scats). We used a threshold FV value of 20% (Mattson et al. 2003) to estimate the onset and outset of dietary shifts for each key food item at 2-week intervals. Onset was determined as the 1st day of the 2-week period when consumption of a given food rose above the threshold, and outset as the 1st day of the following 2-week period when consumption fell below the threshold, with the interval in between representing the period of peak consumption.

Because of differential digestibility of the various foods consumed by bears, we also estimated their contribution to the diet in terms of ingested dry mass and energy content (Persson et al. 2001; Robbins et al. 2004). We estimated the dry matter ingested (estimated dietary content [EDC—Dahle et al. 1998]) by multiplying FV of each food category by the corresponding correction factor (CF$_1$; Appendix I), whereas digestible energy (estimated digestible energy content [EDEC—Dahle et al. 1998]) was estimated by multiplying the EDC of each food item by its energetic content (CF$_2$; Appendix I). Because of the large variability in CF$_2$ values used for ungulates in other studies, we conducted a sensitivity analysis to explore the risk of underestimating the relative importance of ungulates in the diet. We realize that application of correction factors that were not developed specifically for bears within the area of interest can be problematic (McDonald and Fuller 2005), and that absolute EDC and EDEC values are susceptible to the inherent

variability in the estimation of correction factors (Dahle et al. 1998; Persson et al. 2001). Nevertheless, we believe that these potential sources of bias outweigh the pitfalls of fecal analyses for omnivorous mammals that are based solely on frequency and volumetric data (Craighead et al. 1995; Hewitt and Robbins 1996; Robbins et al. 2004).

We used dietary rankings based on digestible energy to provide an overall annual description of the diet; we did not pool or average data across seasons because food intake and defecation rates in bears vary substantially on a seasonal basis (Dahle et al. 1998). To test for differences in diet composition among seasons within the same year and across years for the same season, we compared seasonal FV values accounting for null values (i.e., scats that did not contain a given food item—McLellan 2011). Because missing values limit the power of statistical tests (Lachenbruch 2001; Delucchi and Bostrom 2004), we conducted randomization tests (Manly 2007) based on 10,000 simulations using the Resampling and Monte Carlo routines in program POPTOOLS (version 3.2.5—Hood 2011) to account for sampling variability. Because randomization tests enabled simultaneous comparisons for each null hypothesis of no difference in dietary composition (i.e., 6 or 7 food categories by 3 [2006] to 4 [2007–2009] seasons for each year, and 4–7 food categories by 3 [spring] to 4 [all other seasons] years for each season), we used the Dunn–Šidák method to achieve an experimentwise error rate of $\alpha \leq 0.05$ (Sokal and Rohlf 1995).

RESULTS

We collected a total of 2,691 bear scats, including 1,749 (65%) from systematic and incidental sampling, and 942 (35%) at GPS clusters in an area that included the annual home ranges of at least 31 adult bears (Tosoni 2010; Gervasi et al. 2012). Forty-three percent of the GPS-collected scats ($n = 402$) were successively combined into 98 single composite samples to reduce overrepresentation and autocorrelation, whereas 28 scats collected during winter (mid-December through Febru-

TABLE 2.—Seasonal diet composition of Apennine brown bears (*Ursus arctos marsicanus*) based on mean annual values of estimated dietary content (EDC%) and estimated digestible energy content (EDEC%) based on analysis of 2,359 scats collected in Abruzzo, Lazio, and Molise National Park, Italy, from June 2006 to December 2009. Interannual coefficients of variation of EDEC% (*CV*) also are provided, excluding trace elements (tr ≤ 0.04%). With the exception of green vegetation and roots, items are ranked according to percentage EDEC in the fall (see Appendix II for frequency and volumetric dietary indexes and their interannual variability).

Food item[a]	Spring[b]			Early summer[b]			Late summer[b]			Autumn[b]		
		EDEC			EDEC			EDEC			EDEC	
	EDC%	%	CV	EDC%	%	CV	EDC%	%	CV	EDC%	%	CV
Hard mast	24	35.3	1.2	3.3	6.4	1.3	7.6	11.1	1.6	55.8	66.9	0.3
Fagus sylvatica	21.0	28.0	1.7	0.7	1.3	2.0	7.2	10.7	1.1	38.2	44.8	0.8
Quercus spp.	3.0	7.3	1.7	2.7	5.1	1.8	0.1	0.1	2.0	17.5	22.1	1.0
Corylus avellana	—	—		—	—		0.3	0.3	2.0	—	—	
Fleshy fruits	7.2	12.6	0.9	19.3	25.4	0.6	66.8	71.8	0.2	29.8	26.3	0.7
Malus spp.	—	—		0.4	0.6	1.5	2.2	2.4	0.8	8.7	8.0	1.1
Pyrus spp.	—	—		tr	tr		6.1	6.6	0.3	8.7	7.4	0.5
Ficus carica	—	—		0.1	0.2	1.6	1.0	1.1	1.8	2.3	2.1	0.9
Rosa canina	4.2	7.5	1.1	0.2	0.3	1.6	0.3	0.3	1.5	2.3	2.1	1.6
Sorbus domestica	—	—		—	—		0.4	0.4	1.5	2.1	1.8	2.0
Rhamnus spp.	—	—		1.8	2.4	1.2	42.2	45.1	0.4	1.9	1.5	0.3
Sorbus aria	—	—		—	—		0.4	0.4	1.7	0.7	0.6	1.7
Crataegus spp.	—	—		—	—		tr	tr		0.4	0.4	2.0
Rubus spp.	—	—		tr	tr		1.2	1.3	0.9	0.4	0.4	2.0
Viburnum spp.	—	—		0.4	0.5	0.9	2.7	2.9	1.2	0.4	0.3	1.8
Vitis vinifera	—	—		0.1	0.1	2.0	1.0	1.0	1.5	0	0.2	1.9
Prunus spinosa	—	—		—	—		0.2	0.2	1.8	0.3	0.2	2.0
Cornus mas	—	—		tr	tr		0.4	0.4	1.8	0.1	0.1	1.7
Olea europaea	0.6	1.2	1.7	—	—		—	—		0.1	0.1	2.0
Prunus avium	1.9	3.2	1.7	11.7	15.3	0.8	1.2	1.3	1.2	0.1	0.1	1.3
Prunus domestica	—	—		tr	tr		1.9	2.1	1.3	0.2	0.1	1.7
Prunus mahaleb	—	—		2.5	3.2	1.3	4.7	5.1	1.5	0.2	0.1	1.6
Prunus cerasifera	—	—		0.8	1.2	2.0	—	—		—	—	
Amelanchier ovalis	—	—		—	—		0.2	0.2	2.0	—	—	
Fragaria vesca	—	—		0.2	0.3	2.0	—	—		—	—	
Sorbus aucuparia	—	—		—	—		tr	tr		—	—	
Green vegetation	46.5	31.7	0.8	31.6	19.0	0.4	6.1	2.8	0.4	4.4	1.5	0.8
Graminoids	24.6	14.0	0.7	6.1	2.9	0.4	2.8	1.1	0.5	3.4	1.0	0.7
Forbs	18.5	15.0	1.0	22.9	14.5	0.4	3.3	1.6	0.5	1.0	0.4	1.2
Buds/leaves	2.7	2.2	0.9	2.4	1.5	1.2	tr	tr		—	—	
Roots[c]	1.7	2.6	1.0	1.0	1.2	1.2	2.4	2.4	0.6	1.0	0.8	1.1
Mammals	17.8	13.2	1.0	14.0	9.7	0.5	11.2	6.4	0.4	7.6	3.5	0.5
Wild ungulates	13.6	10.2	1.1	6.6	4.6	0.8	3.1	1.7	0.6	4.7	2.2	0.9
Cervus elaphus	9.4	7.1	1.1	3.9	2.7	1.2	2.4	1.4	0.7	2.4	1.1	1.3
Capreolus capreolus	0.1	tr		1.5	1.0	1.2	0.5	0.3	1.4	2.0	0.9	0.8
Sus scrofa	2.5	1.4	1.0	1.0	0.8	1.1	0.1	0.1	2.0	0.3	0.1	1.3
Rupicapra pyrenaica	—	—		—	—		—	—		tr	tr	
Domestic ungulates	1.4	1.1	1.3	6.3	4.4	0.3	7.7	4.3	0.3	2.2	1.0	0.8
Bos taurus	1.4	1.1	1.3	2.1	1.5	1.2	4.1	2.3	0.6	1.3	0.6	0.4
Ovis aries	—	—		2.6	1.8	0.8	0.7	0.4	0.9	0.1	tr	
Capra hircus	—	—		0.3	0.2	2.0	0.5	0.3	1.3	0.1	tr	
Equus caballus	tr	tr		1.1	0.8	1.3	1.9	1.1	0.8	0.5	0.3	2.0
Other mammals	2.0	1.0	1.7	0.6	0.4	1.9	0.3	0.2	0.8	0.3	0.1	1.1
Sciurus vulgaris	—	—		—	—		tr	tr		—	—	
Glis glis	—	—		—	—		0.1	0.1	1.5	—	—	
Lepus spp.	—	—		—	—		0.1	0.1	1.7	—	—	
Microtinae	—	—		—	—		tr	tr		0.1	0.1	2.0
Martes foina	—	—		—	—		—	—		tr	tr	
Ursus arctos[d]	2.0	1.0	1.7	0.6	0.4	1.9	0.1	0.1	0.9	0.2	0.1	1.9
Insects	2.8	4.7	1.5	30.8	38.3	0.2	5.8	5.4	0.5	1.3	1.0	1.0
Formicidae	2.4	4.3	1.4	27.6	35.7	0.1	4.0	4.2	0.6	0.9	0.8	1.0
Diptera (maggots)	—	—		2.5	2.1	1.6	0.9	0.6	1.2	tr	tr	

TABLE 2.—Continued.

Food item[a]	Spring[b]			Early summer[b]			Late summer[b]			Autumn[b]		
	EDC%	EDEC %	CV	EDC%	EDEC %	CV	EDC%	EDEC %	CV	EDC%	EDEC %	CV
Bombus spp.	—	—		0.3	0.2	2.0	tr	tr		—	—	
Coleoptera[e]	tr	tr		tr	tr		0.3	0.2	1.8	—	—	
Apis mellifera	0.4	0.4	1.7	0.3	0.2	1.6	0.4	0.3	1.6	0.3	0.2	1.0
Vespidae	—	—		—	—		tr	tr		0.1	tr	
Orthoptera	—	—		—	—		0.1	0.1	1.2	tr	tr	2.0

[a] Macro categories include unidentified items at higher taxonomic levels.

[b] See Table 1 for sample sizes.

[c] Including *Daucus carota* and unidentified roots.

[d] Excluding scats with volumetric proportions < 0.5% to minimize inclusion of hairs from grooming.

[e] Including Carabidae and Scarabaeidae.

ary) were excluded from the overall analysis. Thus, we used 2,359 bear scats for diet quantification (Fig. 1; Table 1).

Overall diet composition.—The diet of the Apennine brown bear was greatly diversified, including grasses, forbs, fruits, roots, invertebrates, and mammals (Table 2). Correcting FO and FV values (Appendix II) into EDC and EDEC values (Table 2) strongly influenced the relative contribution of green vegetation, and affected dietary rankings in the seasons when this food category was largely consumed by bears. The expected variation in the dietary energy contribution of large ungulates did not affect seasonal dietary rankings for this food item based on any of the 3 correction factors used (Table 3), because large ungulates ranked relatively low compared to other key foods (Table 2). In terms of annual energetic contributions, hard mast (beechnuts and acorns) and fleshy fruits ranked 1st, herbaceous vegetation and insects (mostly ants) ranked 2nd, wild ungulates and livestock ranked 3rd, and roots (mainly carrots) ranked 4th (Table 2). Bears also consumed some anthropogenic foods, including livestock, bees, some domestic fleshy fruits, and carrots.
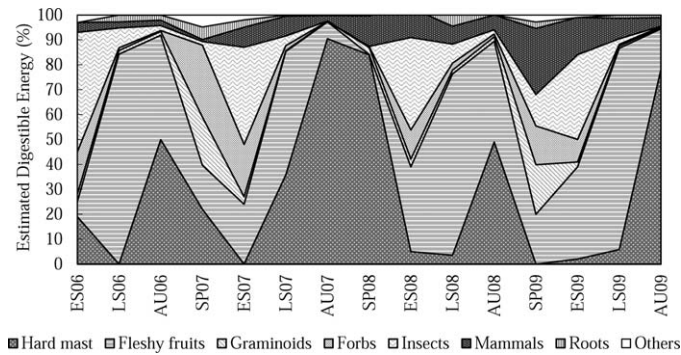
Seasonal and annual variation in the bear diet.—Green vegetation represented the bulk of the biomass ingested by bears in the spring; it also contributed an average of 31.7% digestible energy (Table 2) with substantial annual variation (3.7% and 53.0% in 2008 and 2007, respectively [Fig. 2]). Consumption of graminoids peaked in the spring ($P < 0.05$), although their digestible energy was similar to that provided by forbs. Consumption of overwintering hard mast in the spring was generally low, with the exception of 2008 when, following the mast year for beechnuts in 2007, it provided 84% of

digestible energy (Fig. 2). Correspondingly, spring consumption of forbs was lowest in 2008 ($P < 0.05$). Consumption of fleshy fruits (mostly dog rose [*Rosa canina*]) was at its lowest during the spring ($P < 0.05$), even though they represented a secondary food item in this season, with a contribution of digestible energy comparable to that of wild ungulates (Table 2). Consumption of wild ungulates (mostly red deer) peaked in this season ($P < 0.05$), when fawns and piglets cumulatively represented 65.1% of wild ungulate remains in bear scats.

Insects (primarily ants) predominated in the diet consistently ($CV = 0.2$) during early summer, when their seasonal consumption was highest ($P < 0.05$), and contributed 32.1–47.7% of digestible energy in this season. Bears consumed at least 14 genera and 40 species of ants, predominated by the genera *Lasius*, *Formica*, *Tetramorium*, and *Serviformica*. Fleshy fruits ranked 2nd in dietary energy during early summer. Although their use by bears was lower compared to late summer and fall ($P < 0.05$), consumption of cherries (*Prunus avium* and *P. cerasifera*) peaked in this season (Table 2). Green vegetation was by far the most frequently consumed food in early summer (Appendix II), with forbs consumed at higher rates compared to late summer and autumn ($P < 0.05$); it ranked 3rd in terms of digestible energy (Table 2). However, compared to fleshy fruits, green vegetation ranked higher in 2006 and provided a similar amount of digestible energy in 2007 (Fig. 2). Together, livestock and wild ungulates provided 9% of digestible energy in early summer (Table 2), with similar contributions by both categories.

TABLE 3.—Seasonal contribution of estimated digestible energy content (EDEC%) by large ungulates to the diet of Apennine brown bears (*Ursus arctos marsicanus*), and the corresponding dietary rank compared to all other primary food categories (cf. Table 2). Correction factors (CF_2) simulate variable conditions of carcasses available to bears, from most to least depleted (Johansen 1997; Persson et al. 2001).

CF_2	Spring		Early summer		Late summer		Fall	
	EDEC%	Rank	EDEC%	Rank	EDEC%	Rank	EDEC%	Rank
9.6	11.3	3	9.0	4	6.1	3	3.2	3
14.5	15.3	3	12.8	4	8.8	3	4.7	3
19.3	18.6	3	16.2	3.5	11.4	2.5	6.1	3

Fig. 2.—Seasonal and annual variation in dietary energy contribution (estimated digestible energy content percentage [EDEC%]) for the Apennine brown bear (*Ursus arctos marsicanus*) based on 2,359 scats collected in Abruzzo, Lazio, and Molise National Park, Italy, from June 2006 to December 2009. SP = spring (March–May); ES = early summer (June–July); LS = late summer (August–September); AU = autumn (October–mid-December). The category "Others" includes buds, leaves, and other unknown green vegetation.

Fig. 3.—Annual variation in the consumption (estimated dietary content percentage [EDC%]) of plant-derived food categories by Apennine brown bears (*Ursus arctos marsicanus*) based on analysis of 2,359 scats collected in Abruzzo, Lazio, and Molise National Park, Italy, from 2006 to 2009.

In late summer, fleshy fruits predominated in the bear diet, providing an average of 72% digestible energy. Fruit consumption by bears peaked in this season ($P < 0.05$), with the exception of 2006 and 2008, when we detected a similar level of consumption in the fall. A minimum of 19 fleshy fruit species were used by bears in late summer (Table 2), but were predominated by buckthorn (*Rhamnus* spp.) berries, that contributed up to 71.2% (2006) of digestible energy. Late-summer consumption of fleshy fruits by bears peaked in 2009 ($P < 0.05$) and corresponded to the lowest annual consumption of forbs in this season ($P < 0.05$; Fig. 2). Conversely, late-summer consumption of buckthorn berries was highest in 2006 ($P < 0.05$), and higher in 2007 compared to 2009 ($P < 0.05$), reflecting a negative trend from 2006 to 2009 (FV: $y = -8.68x + 55.45$; $R^2 = 0.92$; $F = 21.49$, $P < 0.05$). This trend was partly compensated by a corresponding increase in the consumption of other fleshy fruits, even though these trends were not statistically significant ($5.12 \leq F \leq 6.71$; $0.07 \leq P \leq 0.09$). On average, hard mast ranked 2nd in terms of dietary energy in late summer (Table 2), but this reflected abnormally high consumption ($P < 0.05$) during the mast year for beechnuts in 2007. Accordingly, late summer 2007 corresponded to the lowest annual consumption of fleshy fruits and graminoids by bears during this season ($P < 0.05$; Fig. 2). In the other years of the study, hard mast in late summer provided $\leq 6\%$ digestible energy, ranking lower than other secondary foods. These included insects, livestock, green vegetation, roots, and wild ungulates, each providing little digestible energy (2–8%) but together contributing an average of 17%.

Consumption of hard mast by bears peaked in the fall ($P < 0.05$), when it predominated the diet, and provided more than two-thirds of the digestible energy (Table 2), ranging from 49% in 2006 to 90.4% in 2007 (Fig. 2). Fleshy fruits, mostly pears and apples, ranked 2nd in terms of digestible energy in the fall. Bears consumed more fleshy fruits in the fall than in
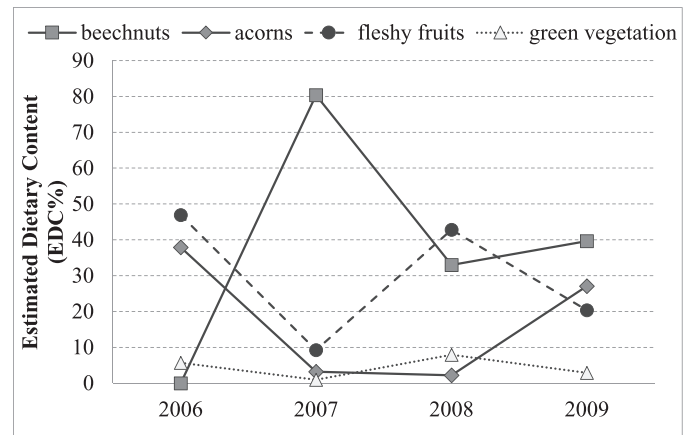
spring and early summer ($P < 0.05$), but less than in late summer ($P < 0.05$), in only 2 of the 4 years of the study (Fig. 2). Other foods (wild ungulates, green vegetation, livestock, insects, and roots) were consumed at their annual minimum in this season, cumulatively providing an average of 6.5% of digestible energy. We detected complementary year-to-year fluctuations in key foods consumed by bears in the fall (Fig. 3). In this season, consumption of hard mast peaked in 2007 ($P < 0.05$), and was higher in 2009 than in 2006 and 2008 ($P < 0.05$; Fig. 2). In particular, beechnut consumption ranged from null in 2006 (mast failure year) to 80% in 2007 (mast year), and was related to their annual productivity ($R^2 = 0.92$). We detected more moderate annual fluctuations in the consumption of acorns in the fall (Fig. 3), with acorns providing 49.7% of dietary energy in the fall of 2006 (i.e., the year of beechnut failure) and 22% in the next spring. Accordingly, fall consumption of fleshy fruits, graminoids, and forbs was lowest in 2007 ($P < 0.05$), and lower in 2009 compared to 2006 and 2008 ($P < 0.05$). In years of lower hard mast consumption, bears consumed a higher diversity of fleshy fruits in the fall ($e^H_{2006,2008} = 0.6 \pm 0.1$ versus $e^H_{2007,2009} = 0.4 \pm 0.1$). Based on the few scats we collected during winter ($n = 28$), hard mast contributed most of the digestible energy (81%) during that season, supplemented by apples and dog rose.

Onset of dietary shifts in key foods.—During our 4-year study, interannual variability in the onset of dietary shifts (Table 4) was relatively modest for fleshy fruits, including buckthorn berries ($\pm$ 1 week); larger for graminoids, insects, and hard mast ($\pm$ 2 weeks); and largest for forbs ($\pm$ 4–5 weeks [Fig. 4]). On average, peak consumption of selected key foods ranged from about 3.5 weeks for insects to 4.2 months for fleshy fruits (Table 4). Some foods, such as herbaceous vegetation, insects, and beechnuts during mast years, were consumed at lower proportions by bears during the rest of the active period.

TABLE 4.—Onset and outset of dietary shifts in key foods consumed by Apennine brown bears (*Ursus arctos marsicanus*) in Abruzzo, Lazio, and Molise National Park, Italy, from June 2006 to December 2009. For each food category, dates represent the 1st day of the 2-week period corresponding to fecal volume (FV) $\geq$ 20% (onset), and the 1st day of the following 2-week period corresponding to FV $<$ 20% (outset), averaged across the years of the study.

| Food category	Onset		Outset		Peak consumption (days)	
	$\bar{X}$	Range	$\bar{X}$	Range	$\bar{X}$	Range
Graminoids	16 March	(1 March–1 April)	15 June	(15–16 June)	91	76–106
Forbs	12 May	(1 April–16 June)	8 August	(1–16 August)	88	61–137
Insects	21 June	(1 June–1 July)	16 July	(1 July–1 August)	25	15–31
Fleshy fruits	28 July	(16 July–1 August)	30 November	(16 October–denning[a])	126	76–153
Rhamnus	4 August	(1–16 August)	19 September	(1 September–1 October)	46	31–61
Hard mast[b]	4 October	(16 September–16 October)	Denning[a]	—	71	60–90

[a] Mean date of den entrance set at 15 December.

[b] Acorns: from 16 October through denning (2006 only); beechnuts: from 1 October (range: 16 September–16 October) through denning. Consumption of overwintering hard mast in the spring is excluded.

DISCUSSION

Our findings confirm the essentially herbivorous food habits of Apennine brown bears (Zunino and Herrero 1972), and are comparable to the food habits of bears in other southern European populations (Berducou et al. 1983; Cicnjak et al. 1987; Clevenger et al. 1992; Naves et al. 2006; Vulla et al. 2009; Paralikidis et al. 2010). However, we revealed a stronger dependency of Apennine bears on beechnuts and animal matter than was previously reported for this population (Zunino and
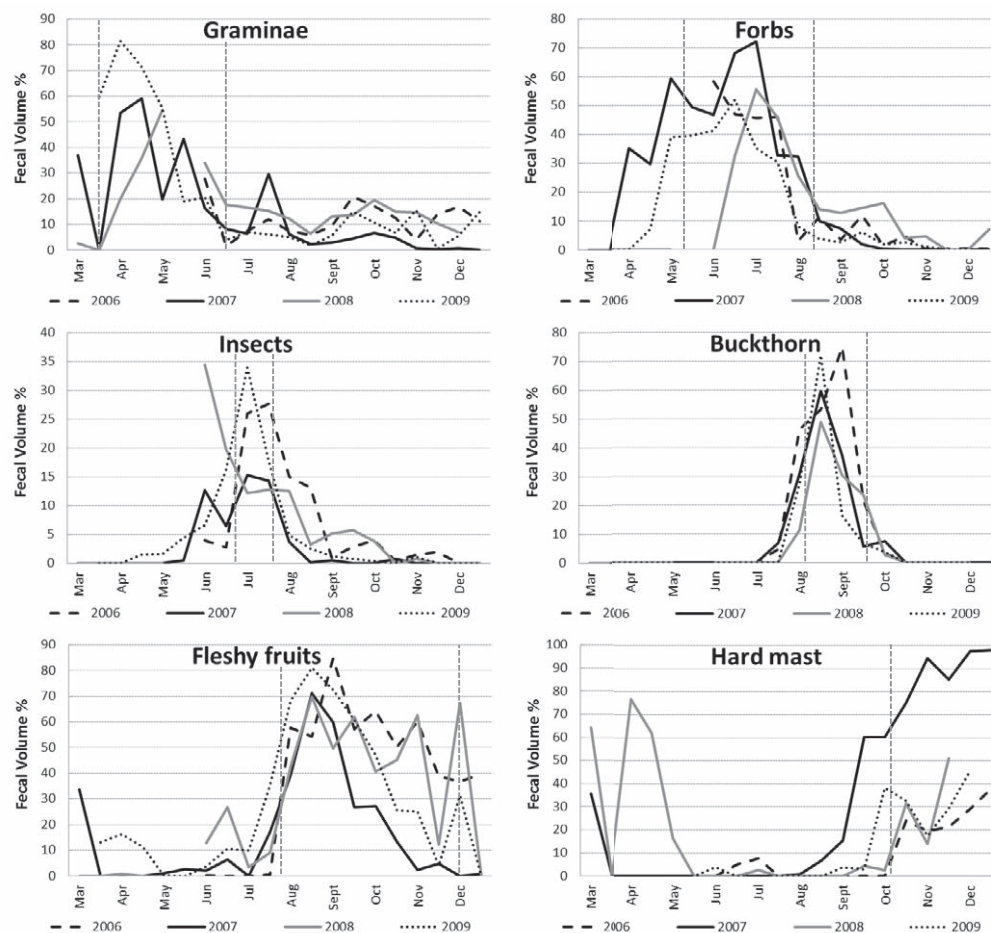
FIG. 4.—Onset (fecal volume [FV] $\geq$ 20%) and outset (FV $<$ 20%) of major dietary shifts by Apennine brown bears (*Ursus arctos marsicanus*) based on analysis of 2,359 scats in Abruzzo, Lazio, and Molise National Park, Italy, from June 2006 to December 2009. In each panel, vertical dashed lines indicate average onset (left) and outset (right) dates, unless peak consumption extended through denning. Note that the scale on the y-axis differs among the panels.

Herrero 1972; Fabbri 1988), possibly reflecting changes in hard mast productivity and the increased availability of wild ungulates in our study area since the late 1970s. As described for other bear populations living in human-dominated landscapes (e.g., Naves et al. 2006; Sidorovich 2006; Vulla et al. 2009; Paralikidis et al. 2010), we also documented some consumption of anthropogenic foods, but their contribution to the diet could be only grossly estimated through scat analysis. For example, we did not distinguish between cultivated and wild herbaceous plants, or between wild and domestic cultivars for some fleshy fruits (apples, pears, figs, and cherries), the latter including trees that have been abandoned and are accessible to bears throughout the study area, as are noncultivated fruit trees. The relative importance of wild versus domestic cultivars, including apple trees planted during past supplemental feeding campaigns, needs to be addressed in future studies. Conversely, we did not detect corn seeds in bear scats, even though corn plantations were used in the past as a supplemental food, whereas carrots contributed only marginally to the bear diet.

Key foods.—Hard mast, especially beechnuts, was the most important food for Apennine bears, especially (but not exclusively) during hyperphagy. Its high caloric content makes hard mast an ideal food for accumulating fat for winter denning (Watts and Jonkel 1988), and beechnuts are relatively rich in crude protein (14.6%) and lipids (18.4%) compared to fleshy fruits (Cicnjak et al. 1987). A fall diet based primarily on beechnuts rather than fleshy fruits may correspond to a higher efficiency of both fat and lean body mass accumulation in hyperphagic bears (Persson et al. 2001). The latter is particularly important for reproducing females as a source of proteins and minerals for cub production and lactation (Atkinson and Ramsay 1995; Persson et al. 2001). Accordingly, we believe that hard mast productivity acts as one of the major predictors of reproductive rates in the Apennine bear population, as others have reported in other bear populations (Rogers 1987; Clevenger et al. 1992; Costello et al. 2003; Hashimoto et al. 2003; Reynolds-Hogland et al. 2007). Because hard mast is subject to marked annual fluctuations and occasional mast failures (Koenig and Knops 2000; Piovesan and Adams 2001), bears may be at risk of nutritional stress unless high-quality supplemental foods are locally available (Cicnjak et al. 1987; Mattson et al. 1991; Craighead et al. 1995). In our 4-year study, we might have missed the greater supra-annual fluctuations that have been detected in longer term (> 10 years) studies (Mattson et al. 1991; Craighead et al. 1995; Naves et al. 2006). Nevertheless, we did capture years of low and high hard mast production and revealed the complementary contribution to the bear diet of beechnuts versus acorns in the fall (Fig. 3), indicating that production from one hard mast species may compensate for the small crop from another and vice versa (Reynolds-Hogland et al. 2007). Most importantly, in years of low to moderate hard mast availability, Apennine bears consumed a larger amount and diversity of carbohydrate-rich fleshy fruits in the fall (Fig. 3), further suggesting that habitat productivity in our study area

currently allows hyperphagic bears to prevent nutritional deficiencies in years of hard mast failure. Although large ungulates occur at high densities in our study area, hard mast was consumed by bears up to the denning period (Fig. 4), persisted in many forest stands after the onset of denning, and was an important component of the spring diet of bears following mast years. Therefore, we found no evidence of competition for hard mast between Apennine bears and other herbivorous and omnivorous ungulates (see Naves et al. 2006).

Fleshy fruits were an important high-quality food for Apennine bears primarily during late summer and fall, similar to many other bear populations (e.g., Cicnjak et al. 1987; Elgmork and Kaasa 1992; McLellan and Hovey 1995; Welch et al. 1997; Dahle et al. 1998; Munro et al. 2006; Naves et al. 2006). Although fleshy fruits are low in protein (Welch et al. 1997; Rode and Robbins 2000; Felicetti et al. 2003; Robbins et al. 2007), they are rich in digestible carbohydrates that are converted to fat efficiently (Dahle et al. 1998), thus providing an important source of energy for fat accumulation prior to denning. In late summer, including years of anticipated beechnut availability, bears in our study area depended heavily on buckthorn berries (e.g., 44.2% of dietary energy in late summer of 2007). Buckthorn berries (about 0.26 g/berry) appeared to be ingested efficiently by bears (see Welch et al. 1997), because many scats contained 100% buckthorn berry residue, excluding leaves or twigs. Buckthorn shrubs are patchily distributed, and the berries on each shrub are readily apparent to bears, occurring in clusters of 3–8 or more along the underside of the main branches; these are actively manipulated by bears with 1 or both paws, often in a sitting position. Reduced search time and feeding efficiency should correspond to high intake rates (Welch et al. 1997), making buckthorn berries an ideal fleshy fruit for hyperphagic bears that consumed them in large numbers for about 7 weeks each year. Accordingly, the negative trend we detected in the consumption of buckthorn berries from 2006 to 2009, although compensated by an increased use of alternative fleshy fruits, should elicit urgent management concern. Pears and apples also were critical foods to hyperphagic bears and, along with other fleshy fruits, provided a supplemental, high-quality, and more dependable food, offsetting occasional hard mast failures (Fig. 3). Although Apennine bears, because of their lower absolute energy requirements, are expected to be less constrained by an essentially frugivorous diet than larger bears (Welch et al. 1997; Rode and Robbins 2000; McLellan 2011), a mixed diet comprising both beechnuts and fleshy fruits during hyperphagy would allow them to reduce their energy metabolism, facilitating fat accumulation and gain of lean body mass (Rode and Robbins 2000; Robbins et al. 2007).

Apennine bears also consumed insects (mostly ants) in early summer and mammals, including wild ungulates in spring and early summer, and livestock in early and late summer. Such protein- and lipid-rich foods in spring and summer are important for bears to build up lean body mass and to enhance structural growth in cubs and subadults (Hilderbrand et al. 1999a). Ants contain up to 50% protein (Southwood 1973) and

can be a source of essential amino acids (Eagle and Pelton 1983; Redford and Dorea 1984; Noyce et al. 1997). Adult females, cubs, and subadults, because of their lower absolute energy requirements compared to larger males, would be expected to more efficiently exploit ants (Hilderbrand et al. 1999a, 1999b; Bull et al. 2001), and ant consumption by females with cubs also may reduce the risk of infanticide (Ben-David et al. 2004; Mowat and Heard 2006).

With the exception of chamois, which were detected at very low frequency in bear scats, Apennine bears consumed all other wild ungulate species present in the study area, with red deer predominating, likely due to its wider distribution, higher density, and greater accessibility (e.g., rut-weakened bulls in the fall) relative to other species. Both the vulnerability of fawns and piglets and the availability of winter-killed carcasses (including wolf kills) could have enhanced the accessibility of wild ungulates to bears in the spring. Although we did not detect predation on ungulates by Apennine bears, red and roe fawns and wild boar piglets were commonly consumed in spring and early summer (65.1% and 46.4% of wild ungulate occurrence in the diet, respectively), suggesting that bears in the Apennines may kill vulnerable neonates, as was reported in the Cantabrian mountain range (Blanco et al. 2010). Livestock compensated for the decreased consumption of wild ungulates in early and late summer. Because the local health authority often exempts farmers from having to remove dead livestock in mountainous terrain (L. Gentile, Abruzzo National Park, pers. comm.), bears often scavenged livestock carcasses. However, depredations by bears on sheep and free-ranging calves do occasionally occur in our study area (Latini et al. 2005; Galluzzi et al. 2010). Apennine bears fed less on large ungulates (FV = 4.3% in the spring) than did bears in northern Europe (range: 25–48% [Dahle et al. 1998; Opseth 1998; Persson et al. 2001]). This is expected because the smaller size of Apennine bears should enable them to meet their mass-gain requirements with a more frugivorous diet than larger bears (Welch et al. 1997; Rode et al. 2001; Robbins et al. 2007). The lower feeding rate on large ungulates by Apennine bears may also indicate the need to reevaluate the dietary meat hypothesis to explain the relationship between body size and diet composition of European bears (Swenson et al. 2007) across a wider latitudinal and ecological gradient.

Apennine bears consumed large amounts of graminoids and forbs, which contributed an average of 29% and 17.4% of dietary energy in spring and summer, respectively (Table 2). Herbaceous vegetation is an important source of protein and energy to bears in the weeks following den emergence (Cicnjak et al. 1987; McLellan and Hovey 1995), when newly sprouted plants are rich in soluble nutrients and poor in structural components (Hamer and Herrero 1987). Forbs predominated over graminoids in the early summer diet of the Apennine bear, likely due to their larger leaves (i.e., larger bite size) and higher protein content relative to graminoids (Cicnjak et al. 1987; Rode et al. 2001), and because forbs retain higher nutritional values with advancing phenology (McLellan and Hovey 1995).

Apennine brown bears also consumed herbaceous vegetation in late summer and fall (but at much lower rates) especially in years of lower than average beechnut consumption (2006 and 2008 [Fig. 3]), possibly to ensure access to protein-rich foods when the diet includes mostly fruits (Rode and Robbins 2000). However, herbaceous vegetation contributed only marginally to the dietary energy of Apennine bears during hyperphagy (Table 2), providing no indication of either depletion of other more nutritious foods (Clevenger et al. 1992) or low habitat productivity (Naves et al. 2006).

The scarcity of roots and other storage organs of plants in the diet of Apennine bears confirms a tendency revealed previously in other European bear populations (Elgmork and Kaasa 1992), which contrasts with findings for brown bears in North America (e.g., Hamer and Herrero 1987; Mattson et al. 1991; Craighead et al. 1995). Carrots were an exception but in our study area they were not available to bears from cultivations but, rather, by being dumped by farmers for free-ranging cattle and horses. Nonetheless, their contribution in digestible energy was marginal relative to other seasonally available foods (Table 2).

Management implications.—Apennine brown bears consumed a diversity of high-quality foods, and we found no evidence of nutritional stress or marked dependency on anthropogenic foods. Thus, a primary management goal for the conservation of this endangered bear population should be to maintain the current diversity and accessibility of foods to bears in the long term. Habitat management should aim to maintain abundant mature stands of beech and oak, while ensuring the sustained availability of other key foods (Clevenger et al. 1992; Reynolds-Hogland et al. 2007; Baldwin and Bender 2009). The timing of major dietary shifts among Apennine bears (Table 4) provides a useful temporal reference for managers and administrators to directly control human activities that may affect the amount and accessibility of key foods to bears (Rode et al. 2001; Naves et al. 2006; Rodríguez et al. 2007). We recommend that critical foraging areas be mapped and given high conservation priority over multiple uses (Naves et al. 2006). Because intake rates would be inadequate if foraging were limited to periods of lowest human activity (Rode et al. 2001), we also recommend facilitating access by bears to lowland drainages that contain abundant grasses and forbs in spring and early summer.

Finally, additional studies should be conducted on other aspects of the nutritional ecology of Apennine bears, including investigating sex and age effects on diet composition, relating habitat productivity to population performance, and assessing the effects of sustained use of anthropogenic foods. Diet studies should be routinely incorporated into broader, long-term monitoring programs of this endangered bear population to help inform conservation planning (cf. Naves et al. 2006).

LITERATURE CITED

ATKINSON, S. N., AND M. A. RAMSAY. 1995. The effects of prolonged fasting of the body composition and reproductive success of female polar bears (*Ursus maritimus*). Functional Ecology 9:559–567.

AUGER, J., G. L. OGBORN, C. L. PRITCHETT, AND H. L. BLACK. 2004. Selection of ants by the American black bear (*Ursus americanus*). Western North American Naturalist 64:166–174.

BALDWIN, R. A., AND L. C. BENDER. 2009. Foods and nutritional components of diets of black bear in Rocky Mountain National Park, Colorado. Canadian Journal of Zoology 87:1000–1008.

BAZZICHELLI, G., AND F. FURNARI. 1979. Ricerche sulla flora e sulla vegetazione d'altitudine nel Parco Nazionale d'Abruzzo. Pubblicazioni Istituto di Botanica della Università di Catania 2:43–87 (in Italian).

BEN-DAVID, M., K. TITUS, AND L. R. BEIER. 2004. Consumption of salmon by Alaskan brown bears: a trade-off between nutritional requirements and the risk of infanticide? Oecologia 138:465–474.

BERDUCOU, C., L. FALIU, AND J. BARRAT. 1983. The food habits of the brown bear in the national park of the western Pyrenees (France) as revealed by faeces analysis. Acta Zoologica Fennica 174:153–156.

BLANCO, J. C., F. BALLESTEROS, A. GARCÍA-SERRANO, J. HERRERO, C. NORES, AND G. PALOMERO. 2010. Behaviour of brown bears killing wild ungulates in the Cantabrian Mountains, southwestern Europe. European Journal of Wildlife Research 1:669–673.

BOJARSKA, K., AND N. SELVA. 2012. Spatial patterns in brown bear *Ursus arctos* diet: the role of geographical and environmental factors. Mammal Review 42:120–143.

BOJARSKA, K., AND N. SELVA. 2013. Correction factors for important brown bear foods in Europe. Ursus 24:13–15.

BOSCAGLI, G. 1999. Status and management of the brown bear in central Italy (Abruzzo). Pp. 81–84 in Bears: status survey and conservation action plan (C. Servheen, S. Herrero, and B. Peyton, eds.). IUCN/SSC Bear and Polar Bear Specialist Groups, IUCN, Gland, Switzerland.

BULL, E. L., T. R. TORGERSEN, AND T. L. WERTZ. 2001. The importance of vegetation, insects, and neonate ungulates in black bear diet in northeastern Oregon. Northwest Science 75:244–253.

CICNJAK, L., D. HUBER, H. U. ROTH, R. L. RUFF, AND Z. VINOVRSKI. 1987. Food habits of brown bears in Plitvice Lakes National Park, Yugoslavia. International Conference on Bear Research and Management 7:221–226.

CIUCCI, P., AND L. BOITANI. 2008. The Apennine brown bear; a critical review of its status and conservation problems. Ursus 19:130–145.

CIUCCI, P., AND L. BOITANI. 2010. Conservation of large carnivores in Abruzzo. A research project integrating species, habitat and human dimension: 2008 annual report. Wildlife Conservation Society, New York.

CIUCCI, P., L. BOITANI, E. R. PELLICCIONI, M. ROCCO, AND I. GUJ. 1996. A comparison of scat-analysis methods to assess the diet of the wolf *Canis lupus*. Wildlife Biology 2:37–48.

CLEVENGER, A. P., F. J. PURROY, AND M. R. PELTON. 1992. Food habits of brown bears (*Ursus arctos*) in the Cantabrian Mountains, Spain. Journal of Mammalogy 73:415–421.

COSTELLO, C. M., D. E. JONES, R. M. INMAN, K. H. INMAN, B. C. THOMPSON, AND H. B. QUIGLEY. 2003. Relationship of variable mast production to American black bear reproductive parameters in New Mexico. Ursus 14:1–16.

CRAIGHEAD, J. J., J. S. SUMNER, AND J. A. MITCHELL. 1995. The grizzly bears of Yellowstone. Island Press, Washington, D.C.

DAHLE, B., O. J. SRENSEN, E. H. WEDUL, J. E. SWENSON, AND F. SANDEGREN. 1998. The diet of brown bears *Ursus arctos* in central Scandinavia: effect of access to free-ranging domestic sheep *Ovis aries*. Wildlife Biology 4:147–158.

DELUCCHI, K. L., AND A. BOSTROM. 2004. Methods for analysis of skewed data distributions in psychiatric clinical studies: working with many zero values. American Journal of Psychiatry 161:1159–1168.

DI DOMENICO, G., E. TOSONI, L. BOITANI, AND P. CIUCCI. 2012. Efficiency of scat-analysis lab procedures for bear dietary studies: the case of the Apennine brown bear. Mammalian Biology 77:190–195.

EAGLE, T. C., AND M. R. PELTON. 1983. Seasonal nutrition of black bears in the Great Smoky Mountains National Park. International Conference on Bear Research and Management 5:94–101.

ELGMORK, K., AND J. KAASA. 1992. Food habits and foraging of the brown bear *Ursus arctos* in central south Norway. Ecography 15:101–110.

EUROPEAN ENVIRONMENT AGENCY (EEA). 2006. Corine land cover raster data 2006. http://www.eea.europa.eu/data-and-maps/data/corine-land-cover-2006-raster-3#tab-gis-data. Accessed 3 April 2014.

FABBRI, M. 1988. Le abitudini alimentari dell'orso bruno nel Parco Nazionale d'Abruzzo. M.S. thesis, Università di Parma, Parma, Italy (in Italian).

FALCUCCI, A., P. CIUCCI, L. MAIORANO, L. GENTILE, AND L. BOITANI. 2009. Assessing habitat quality for conservation using an integrated occurrence–mortality model. Journal of Applied Ecology 46:600–609.

FALCUCCI, A., L. MAIORANO, P. CIUCCI, E. O. GARTON, AND L. BOITANI. 2008. Land-cover change and the future of the Abruzzo brown bear: a perspective from the past. Journal of Mammalogy 89:1502–1511.

FELICETTI, L. A., C. T. ROBBINS, AND L. A. SHIPLEY 2003. Dietary protein content alters energy expenditure of the mass gain in grizzly bears (*Ursus arctos horribilis*). Physiological and Biochemical Zoology 76:256–261.

GALLUZZI, A., V. DI PIRRO, L. SAMMARONE, AND P. CIUCCI. 2010. Indagine conoscitiva del comparto zootecnico. Pp. 93–104 in Riqualificazione del comparto zootecnico nell'areale interregionale di presenza stabile dell'orso bruno marsicano (P. Ciucci and L. Boitani, eds.). Regione Abruzzo, Ufficio Conservazione della Natura, Technical Report DN8-56:1–134 (in Italian).

GERVASI, V., P. CIUCCI, J. BOULANGER, E. RANDI, AND L. BOITANI. 2012. A multiple data source approach to improve abundance estimates of small populations: the brown bear in the Apennines, Italy. Biological Conservation 152:10–20.

HAMER, D., AND S. HERRERO. 1987. Grizzly bear food and habitat in the front ranges of Banff National Park, Alberta. International Conference on Bear Research and Management 7:199–213.

HASHIMOTO, Y., M. KAJI, H. SAWADA, AND S. TAKATSUKI. 2003. Five-year study on the autumn food habits of the Asiatic black bear in relation to nut production. Ecological Research 18:485–492.

HEWITT, D. G., AND C. T. ROBBINS. 1996. Estimating grizzly bear food habits from faecal analysis. Wildlife Society Bulletin 24:547–550.

HILDERBRAND, G. V., S. G. JENKINS, C. C. SCHWARTZ, T. A. HANLEY, AND C. T. ROBBINS. 1999a. Effect of seasonal differences in dietary meat intake on changes in body mass and composition in wild and captive brown bears. Canadian Journal of Zoology 77:1623–1630.

HILDERBRAND, G. V., ET AL. 1999b. The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. Canadian Journal of Zoology 77:132–138.

HOOD, G. M. 2011. POPTOOLS. Version 3.2.5. www.poptools.org. Accessed 4 April 2014.

JOHANSEN, T. 1997. The diet of the brown bear (Ursus arctos) in central Sweden. M.S. thesis, Norwegian University of Science and Technology, Trndheim, Norway.

KACZENSKY, P., G. CHAPRON, M. VON ARX, D. HUBER, H. ANDRÉN, AND J. LINNELL (eds.).2013. Status, management and distribution of large carnivores—bear, lynx, wolf & wolverine—in Europe. IUCN/SSC Large Carnivore Initiative for Europe. www.lcie.org/Publications.aspx. Accessed 4 April 2014.

KOENIG, W., AND J. KNOPS. 2000. Patterns of annual seed production by Northern Hemisphere trees: a global perspective. American Naturalist 155:59–69.

KOIKE, S. 2010. Long-term trends in food habits of Asiatic black bears in the Misaka Mountains on the Pacific coast of central Japan. Mammalian Biology 75:17–28.

LACHENBRUCH, P. A. 2001. Comparisons of two-part models with competitors. Statistics in Medicine 20:1215–1234.

LATINI, R., C. SULLI, L. GENTILE, AND A. DI BENEDETTO. 2005. The conflict between humans and large carnivores in the Abruzzo, Lazio and Molise National Park (central Italy): assessment, experiences and management perspectives. Biologia e Conservazione della Fauna 115:151–159 (in Italian with English summary).

LORENZINI, R., M. POSILLICO, S. LOVARI, AND A. PETRELLA. 2004. Noninvasive genotyping of the endangered Apennine brown bear: a case study not to let one's hair down. Animal Conservation 7:199–209.

MACE, R. D., AND C. J. JONKEL. 1986. Local food habits of the grizzly bear in Montana. International Conference on Bear Research and Management 6:105–110.

MACHUTCHON, A. G., AND D. W. WELLWOOD. 2003. Grizzly bear food habits in the northern Yukon, Canada. Ursus 14:225–235.

MANLY, B. F. J. 2007. Randomization, bootstrap, and Monte Carlo methods in biology. 2nd ed. Chapman & Hall, London, United Kingdom.

MARCHI, P., E. PEPE D'AMATO, AND G. BIANCHI. 2002. Famiglie di piante vascolari: 31–60. Università La Sapienza Edition, Roma, Italy (in Italian).

MATTSON, D. J. 1997. Use of lodgepole pine cover types by Yellowstone grizzly bears. Journal of Wildlife Management 61:480–496.

MATTSON, D. J., K. BARBER, R. MAW, AND R. RENKIN. 2003. Coefficients of productivity for Yellowstone's grizzly bear habitat.

United States Geological Survey, Biological Resources Division, Biological Science Report USGS/BRD/BSR-2002-0007:1–99.

MATTSON, D. J., B. M. BLANCHARD, AND R. R. KNIGHT. 1991. Food habits of Yellowstone grizzly bears, 1977–1987. Canadian Journal of Zoology 69:1619–1629.

MCDONALD, J. E., JR., AND T. K. FULLER. 2005. Effects of spring acorn availability on black bear diet, milk composition, and cub survival. Journal of Mammalogy 86:1022–1028.

MCLELLAN, B. 2011. Implications of a high-energy and low-protein diet on the body composition, fitness, and competitive abilities of black (Ursus americanus) and grizzly (Ursus arctos) bears. Canadian Journal of Zoology 89:546–558.

MCLELLAN, B. N., AND F. W. HOVEY. 1995. The diet of grizzly bears in the Flathead River drainage of southeastern British Columbia. Canadian Journal of Zoology 73:704–712.

MOWAT, G., AND D. C. HEARD. 2006. Major components of grizzly bear diet across North America. Canadian Journal of Zoology 84:473–489.

MUNRO, R. H. M., S. E. NIELSEN, M. H. PRICE, G. B. STENHOUSE, AND M. S. BOYCE. 2006. Seasonal and diel patterns of grizzly bear diet and activity in west-central Alberta. Journal of Mammalogy 87:1112–1121.

NAVES, J., A. FERNÁNDEZ-GIL, C. RODRÍGUEZ, AND M. DELIBES. 2006. Brown bear food habits at the border of its range: a long-term study. Journal of Mammalogy 87:899–908.

NELSON, R. A., ET AL. 1983. Behavior, biochemistry, and hibernation in black, grizzly, and polar bears. International Conference on Bear Research and Management 5:284–290.

NOYCE, K. V., P. B. KANNOWSKI, AND M. R. RIGGS. 1997. Black bears as ant-eaters: seasonal associations between bear myrmecophagy and ant ecology in north-central Minnesota. Canadian Journal of Zoology 75:1671–1686.

OPSETH, O. 1998. Brown bear (Ursus arctos) diet and predation on moose (Alces alces) calves in the southern taiga zone in Sweden. M.S. thesis, Norwegian University of Science and Technology, Trndheim, Norway.

PARALIKIDIS, N. P., N. K. PAPAGEORGIOU, V. J. KONTSIOTIS, AND A. C. TSIOMPANOUDIS. 2010. The dietary habits of the brown bear (Ursus arctos) in western Greece. Mammalian Biology 75:29–35.

PERSSON, I. L., S. WIKAN, J. E. SWENSON, AND I. MYSTERUD. 2001. The diet of the brown bear Ursus arctos in the Pasvik Valley, northeastern Norway. Wildlife Biology 7:27–37.

PIOVESAN, G., AND J. M. ADAMS. 2001. Masting behaviour in beech: linking reproduction and climatic variation. Canadian Journal of Botany 79:1039–1047.

PIOVESAN, G., M. BERNABEI, A. DI FILIPPO, M. ROMAGNOLI, AND B. SCHIRONE. 2003. A long-term tree ring beech chronology from a high-elevation old-growth forest of central Italy. Dendrochronologia 21:1–10.

POSILLICO, M., A. MERIGGI, E. PAGNIN, S. LOVARI, AND L. RUSSO. 2004. A habitat model for brown bear conservation and land use planning in the central Apennines. Biological Conservation 118:141–150.

POTENA, G., ET AL. 2009. Monitoring brown bear (Ursus arctos) critical food resources in beech (Fagus sylvatica) forest: beechnut production in the central Apennines, Italy. Proceedings of the 13th World Forestry Congress, Buenos Aires, Argentina.

PRITCHARD, G. T., AND C. T. ROBBINS. 1990. Digestive and metabolic efficiencies of grizzly and black bears. Canadian Journal of Zoology 68:1645–1651.

RAINE, R. M., AND J. L. KANSAS. 1990. Black bear seasonal food habits and distribution by elevation in Banff National Park, Alberta. International Conference on Bear Research and Management 8:297–304.

RANDI, E., L. GENTILE, G. BOSCAGLI, D. HUBER, AND H. U. ROTH. 1994. Mitochondrial DNA sequence divergence among some west European brown bear (*Ursus arctos* L.) populations. Lessons for conservation. Heredity 73:480–489.

REDFORD, K. H., AND J. G. DOREA. 1984. The nutritional value of invertebrates with emphasis on ants and termites as food for mammals. Journal of Zoology (London) 203:385–395.

REYNOLDS, J. C., AND N. J. AEBISCHER. 1991. Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations, based on a study of the fox *Vulpes vulpes*. Mammal Review 21:97–122.

REYNOLDS-HOGLAND, M. J., L. B. PACIFICI, AND M. S. MITCHELL. 2007. Linking resources with demography to understand resource limitation for bears. Journal of Applied Ecology 44:1166–1175.

ROBBINS, C. T., J. K. FORTIN, K. D. RODE, S. D. FARLEY, L. A. SHIPLEY, AND L. A. FELICETTI. 2007. Optimizing protein intake as a foraging strategy to maximize mass gain in an omnivore. Oikos 116:1675–1682.

ROBBINS, C. T., C. C. SCHWARTZ, AND L. A. FELICETTI. 2004. Nutritional ecology of ursids: a review of newer methods and management implications. Ursus 15:161–171.

RODE, K. D., S. D. FARLEY, J. T. FORTIN, AND C. T. ROBBINS. 2007. Nutritional consequences of experimentally introduced tourism in brown bears. Journal of Wildlife Management 71:929–939.

RODE, K. D., S. D. FARLEY, AND C. T. ROBBINS. 2006. Sexual dimorphism, reproductive strategy, and human activities determine resource use by brown bears. Ecology 87:2636–2646.

RODE, K. D., AND C. T. ROBBINS. 2000. Why bears consume mixed diets during fruit abundance. Canadian Journal of Zoology 78:1640–1645.

RODE K. D., C. T. ROBBINS, AND L. A. SHIPLEY. 2001. Constraints on herbivory by grizzly bears. Oecologia 128:62–71.

RODRÍGUEZ, C., J. NAVES, A. FERNÁNDEZ-GIL, J. R. OBESO, AND M. DELIBES. 2007. Long-term trends in food habits of a relict brown bear population in northern Spain: the influence of climate and local factors. Environmental Conservation 34:36–44.

ROGERS, L. 1987. Effects of food supply and kinship on social behavior, movements, and population growth of black bears in northeastern Minnesota. Wildlife Monographs 97:1–72.

RONDININI, C., A. BATTISTONI, V. PERONACE, AND C. TEOFILI (eds.). 2013. Lista Rossa IUCN dei vertebrati Italiani. Comitato Italiano IUCN e Ministero dell'Ambiente e della Tutela del Territorio e del Mare, Roma, Italy. http://iucn/it. Accessed 10 August 2013 (in Italian).

RUSSO, L., R. SGAMMOTTA, AND G. DI CLEMENTE. 1996. Primi risultati dello studio dell'alimentazione dell'orso bruno marsicano mediante l'analisi degli escrementi. Atti III Simposio Italiano sui Carnivori. Associazione Italiana di Teriologia, Perugia, Italy (in Italian).

SALVATORI, V., A. GALLUZZI, F. QUATTROCIOCCHI, AND P. CIUCCI. 2012. Analisi della pratica zootecnica e sviluppo di indirizzi di gestione per la convivenza con i predatori. European Commission, Environment, Life Programme, Technical Report Life09NAT/IT/000160—Action A1:1–68 (in Italian).

SATO, Y., T. AOI, K. KAJI, AND S. TAKATSUKI. 2004. Temporal changes in the population density and diet of brown bears in eastern Hokkaido, Japan. Mammal Study 29:47–53.

SIDOROVICH, V. E. 2006. Ecological studies on brown bear (*Ursus arctos*) in Belarus: distribution, population trends and dietary structure. Acta Zoologica Lituanica 16:185–190.

SOKAL, R., AND F. J. ROHLF. 1995. Biometry. 2nd ed. W. H. Freeman and Company, New York.

SOUTHWOOD, T. R. E. 1973. The insect/plant relationship—an evolutionary perspective. Pp. 3–30 in Insect/plant relationships (H. F. van Emden, ed.). Royal Entomological Society, London, United Kingdom.

SWENSON, J. E., M. ADAMIC, D. HUBER, AND S. STOKKE. 2007. Brown bear body mass and growth in northern and southern Europe. Oecologia 153:37–47.

SWENSON, J. E., A. JANSSON, S. RIIG, AND F. SANDEGREN. 1999. Bears and ants: myrmecophagy by brown bears in central Scandinavia. Canadian Journal of Zoology 77:551–561.

TEERINK, B. J. 1991. Hair of west-European mammals: atlas and identification key. Cambridge University Press, Cambridge, United Kingdom.

TOSONI, E. 2010. Indagini ecologiche relative alla popolazione di orso bruno marsicano (*Ursus arctos marsicanus*) nel territorio del Parco Nazionale d' Abruzzo, Lazio e Molise. Ph.D. dissertation, University of Rome "La Sapienza," Rome, Italy (in Italian).

VULLA, E., ET AL. 2009. Carnivory is positively correlated with latitude among omnivorous mammals: evidence from brown bears, badgers and pine martens. Annales Zoologici Fennici 46:395–415.

WATTS, P. D., AND C. JONKEL. 1988. Energetic cost of winter dormancy in grizzly bear. Journal of Wildlife Management 52:654–656.

WELCH, C., J. KEAY, K. KENDALL, AND C. T. ROBBINS. 1997. Constraints on frugivory by bears. Ecology 78:1105–1119.

WHITE, D., JR., K. C. KENDALL, AND H. D. PICTON. 1999. Potential energetic effects of mountain climbers on foraging grizzly bears. Wildlife Society Bulletin 27:146–151.

ZUNINO F. 1976. Orso bruno marsicano: risultati di una ricerca sull'ecologia della specie. Pp. 603–710 in SOS fauna in pericolo in Italia (WWF Italia, ed.). WWF Italia, Roma, Italy (in Italian).

ZUNINO, F., AND S. HERRERO. 1972. The status of the brown bear in Abruzzo National Park, Italy, 1971. Biological Conservation 4:263–272.

APPENDIX I

Correction factors (CF_1) used to estimate dry matter ingested from volumetric proportions (Dahle et al. 1998). CF_1 for ungulates varies considerably, depending on the proportion of hide and skin consumed along with meat and viscera (Hewitt and Robbins 1996). Following Dahle et al. (1998) and Persson et al. (2001), we used anecdotal observations of carcasses used by bears to conservatively estimate about 30% hair and skin consumption on carcasses of large adult ungulates (red deer, cattle, horses), whereas a higher proportion of indigestible components (i.e., lower CF_1 value) was assumed for juveniles and all other ungulates.

Item	CF_1	Reference	CF_2 (kJ/g)	Reference
Green vegetation	0.26	Hewitt and Robbins 1996; Dahle et al. 1998; Persson et al. 2001		
Graminoids			6.3	Dahle et al. 1998; Persson et al. 2001
Forbs			8.4	Dahle et al. 1998; Persson et al. 2001
Fleshy fruits			18.1	Pritchard and Robbins 1990
Apples and pear	0.51	Hewitt and Robbins 1996		
Prunus spp.	1.93	Bojarska and Selva 2013		
Rhamnus spp. and *Viburnum* spp.[a]	1.08	Hewitt and Robbins 1996		
Rubus spp. and *Fragaria vesca*	0.87	Hewitt and Robbins 1996		
Other fleshy fruits[b]	0.93	Hewitt and Robbins 1996		
Roots	0.80	Hewitt and Robbins 1996	16.5	Pritchard and Robbins 1990
Hard mast			26.7	Pritchard and Robbins 1990
Fagus sylvatica	1.18	Bojarska and Selva 2013		
Corylus avellana	1.58	Bojarska and Selva 2013		
Quercus spp.	1.5	Hewitt and Robbins 1996		
Large ungulates			9.6[c]	Johansen 1997; Persson et al. 2001
Cattle, horse, and red deer[d]	3.0	Johansen 1997; Dahle et al. 1998; Persson et al. 2001		
Other ungulates[e]	1.5	Johansen 1997; Dahle et al. 1998; Persson et al. 2001		
Small mammals	4.0	Hewitt and Robbins 1996	18.8	Dahle et al. 1998; Persson et al. 2001
Insects	1.1	Hewitt and Robbins 1996; Dahle et al. 1998; Persson et al. 2001		
Ants			17.7	Dahle et al. 1998; Persson et al. 2001
Other insects			11.3	Dahle et al. 1998

[a] Average value for berries of *Rubus* spp., *Shepherdia canadensis*, and *Vaccinium* spp. are from Hewitt and Robbins (1996).

[b] Including grapes, figs, plums, olives, *Sorbus* spp., and other berries (*Amelanchier ovalis*, *Crataegus* spp., *Cornus mas*, and *Rosa canina*).

[c] Conservatively assuming equal consumption of skin and meat (Persson et al. 2001).

[d] Only adults, accounting for an estimated 30% consumption of skin and hair on carcasses of adult ungulates.

[e] Including juveniles of all ungulate species.

APPENDIX II

Mean ($\pm$ *SD*) annual values of percent frequency of occurrence (FO) and percent fecal volume (FV) of food items detected in 2,359 Apennine brown bear (*Ursus arctos marsicanus*) scats collected in Abruzzo, Lazio, and Molise National Park, Italy, from June 2006 to December 2009. With the exception of green vegetation and roots, items are ranked according to percentage estimated digestible energy content in the fall (see Table 2; tr = trace elements with FO or FV $\leq$ 0.04).

Food item[a]	Spring[b] FO	Spring[b] FV	Early summer[b] FO	Early summer[b] FV	Late summer[b] FO	Late summer[b] FV	Autumn[b] FO	Autumn[b] FV
Hard mast	19.9 ($\pm$ 32.0)	16.4 ($\pm$ 26.9)	1.7 ($\pm$ 1.4)	1.2 ($\pm$ 1.3)	9.9 ($\pm$ 11.1)	5.0 ($\pm$ 7.4)	54.4 ($\pm$ 28.2)	41.6 ($\pm$ 27.6)
Fagus sylvatica	19.0 ($\pm$ 33.0)	15.8 ($\pm$ 27.4)	0.8 ($\pm$ 1.3)	0.4 ($\pm$ 0.7)	8.3 ($\pm$ 11.0)	4.8 ($\pm$ 7.4)	39.4 ($\pm$ 36.0)	31.9 ($\pm$ 31.3)
Quercus spp.	0.9 ($\pm$ 1.5)	0.6 ($\pm$ 1.1)	0.9 ($\pm$ 1.4)	0.9 ($\pm$ 1.4)	1.1 ($\pm$ 0.9)	tr	15.3 ($\pm$ 14.6)	9.6 ($\pm$ 9.2)
Corylus avellana	—	—	—	—	0.5 ($\pm$ 1.0)	0.2 ($\pm$ 0.4)	—	—
Fleshy fruits	8.1 ($\pm$ 5)	2.5 ($\pm$ 2.3)	15.0 ($\pm$ 8.6)	7.5 ($\pm$ 4.9)	78.8 ($\pm$ 11.7)	63.1 ($\pm$ 14)	66.1 ($\pm$ 27.5)	37.0 ($\pm$ 17.3)
Pyrus spp.	—	—	0.2 ($\pm$ 0.4)	tr	17.4 ($\pm$ 2.5)	10.5 ($\pm$ 2.6)	23.3 ($\pm$ 9.0)	14.5 ($\pm$ 7.2)
Malus spp.	—	—	0.8 ($\pm$ 1.1)	0.4 ($\pm$ 0.5)	7.3 ($\pm$ 4.6)	3.6 ($\pm$ 2.6)	22.4 ($\pm$ 19.9)	12.5 ($\pm$ 12.6)
Ficus carica	—	—	0.4 ($\pm$ 0.5)	0.1 ($\pm$ 0.1)	2.8 ($\pm$ 4.2)	1.0 ($\pm$ 1.9)	2.9 ($\pm$ 2.7)	1.9 ($\pm$ 1.6)
Rosa canina	6.1 ($\pm$ 6.4)	1.7 ($\pm$ 1.9)	0.4 ($\pm$ 0.4)	0.1 ($\pm$ 0.3)	0.3 ($\pm$ 0.5)	0.3 ($\pm$ 0.4)	3.3 ($\pm$ 5.1)	1.8 ($\pm$ 2.9)
Rhamnus spp.	—	—	1.1 ($\pm$ 1.5)	0.8 ($\pm$ 0.9)	43.1 ($\pm$ 13.3)	33.7 ($\pm$ 11.7)	3.0 ($\pm$ 1.7)	1.6 ($\pm$ 1.0)
Sorbus domestica	—	—	—	—	0.5 ($\pm$ 0.6)	0.4 ($\pm$ 0.5)	3.1 ($\pm$ 5.3)	1.5 ($\pm$ 3.0)
Sorbus aria	—	—	—	—	1.4 ($\pm$ 2.4)	0.4 ($\pm$ 0.7)	1.0 ($\pm$ 1.2)	0.6 ($\pm$ 0.8)
Crataegus spp.	—	—	—	—	0.1 ($\pm$ 0.1)	tr	0.7 ($\pm$ 1.4)	0.3 ($\pm$ 0.7)
Prunus spinosa	—	—	—	—	0.6 ($\pm$ 0.7)	0.2 ($\pm$ 0.4)	0.5 ($\pm$ 0.9)	0.3 ($\pm$ 0.5)
Rubus spp.	—	—	0.7 ($\pm$ 0.1)	tr	7.0 ($\pm$ 4.0)	1.3 ($\pm$ 1.2)	1.5 ($\pm$ 2.1)	0.3 ($\pm$ 0.6)
Prunus domestica	—	—	0.2 ($\pm$ 0.3)	tr	2.9 ($\pm$ 3.2)	2.0 ($\pm$ 2.5)	0.6 ($\pm$ 0.7)	0.2 ($\pm$ 0.3)

APPENDIX II Continued.

Food item[a]	Spring[b]		Early summer[b]		Late summer[b]		Autumn[b]	
	FO	FV	FO	FV	FO	FV	FO	FV
Viburnum spp.	—	—	0.5 (± 0.4)	0.2 (± 0.2)	3.4 (± 3.6)	2.2 (± 2.8)	0.3 (± 0.4)	0.2 (± 0.4)
Cornus mas	—	—	0.2 (± 0.5)	tr	2.2 (± 2.0)	0.4 (± 0.8)	0.7 (± 0.8)	0.1 (± 0.1)
Olea europaea	0.3 (± 0.5)	0.3 (± 0.5)	—	—	—	—	0.1 (± 0.2)	0.1 (± 0.2)
Prunus avium	0.9 (± 1.5)	0.3 (± 0.5)	6.1 (± 4.7)	3.9 (± 3.4)	1.0 (± 1.2)	0.5 (± 0.6)	0.5 (± 0.4)	0.1 (± 0.1)
Prunus mahaleb	—	—	1.6 (± 1.9)	0.9 (± 1.2)	3.9 (± 5.0)	2.3 (± 3.5)	0.3 (± 0.4)	0.1 (± 0.2)
Vitis vinifera	—	—	0.4 (± 0.7)	tr	2.7 (± 3.4)	0.9 (± 1.4)	1.0 (± 1.4)	0.1 (± 0.3)
Amelanchier ovalis	—	—	—	—	0.6 (± 1.1)	0.2 (± 0.4)		
Fragaria vesca	—	—	0.3 (± 0.5)	0.2 (± 0.4)	—	—	—	—
Prunus cerasifera	—	—	0.5 (± 1.0)	0.2 (± 0.4)	—	—	—	—
Sorbus aucuparia	—	—	—	—	0.1 (± 0.2)	tr	—	—
Green vegetation	85.0 (± 18)	70.5 (± 28.4)	83.5 (± 4.9)	65.9 (± 8.2)	50.5 (± 7.7)	20.4 (± 5.6)	45.8 (± 17.4)	13.1 (± 7.9)
Graminoids	66.4 (± 18.4)	39.8 (± 8.2)	46.4 (± 15.5)	12.9 (± 3.5)	40.5 (± 6.3)	9.2 (± 3.7)	42.3 (± 17.7)	10.3 (± 5.1)
Forbs	34.9 (± 23.3)	25.2 (± 20.7)	61.1 (± 8.1)	47.7 (± 6.2)	21.9 (± 8.6)	10.8 (± 5.5)	10.2 (± 9.5)	2.8 (± 3.1)
Buds/leaves	8.4 (± 8.0)	3.6 (± 3.3)	5.9 (± 5.6)	4.7 (± 5.1)	0.1 (± 0.1)	tr	—	—
Roots[c]	1.9 (± 2.1)	0.7 (± 0.7)	2.9 (± 2.6)	0.6 (± 0.7)	5.0 (± 2.9)	2.5 (± 1.9)	2.8 (± 2.1)	1.1 (± 1.0)
Mammals	15.3 (± 12.4)	5.5 (± 5.6)	15.7 (± 8.3)	4.3 (± 2.6)	23.8 (± 9.4)	4.2 (± 2.3)	15.0 (± 8.4)	3.0 (± 0.9)
Wild ungulates	8.8 (± 6.7)	4.0 (± 3.6)	6.9 (± 4.9)	2.0 (± 1.5)	5.0 (± 1.8)	1.1 (± 0.8)	7.7 (± 4.0)	1.9 (± 1.1)
Cervus elaphus	4.4 (± 3.6)	2.3 (± 1.9)	3.6 (± 5.0)	1.0 (± 1.2)	3.1 (± 1.7)	0.7 (± 0.6)	3.4 (± 2.3)	0.6 (± 0.7)
Sus scrofa	2.7 (± 3.9)	1.3 (± 2.0)	1.4 (± 1.6)	0.4 (± 0.4)	0.6 (± 1.1)	0.1 (± 0.1)	0.6 (± 0.8)	0.2 (± 0.3)
Capreolus capreolus	1.2 (± 2.1)	tr	1.8 (± 2.2)	0.6 (± 0.8)	1.1 (± 1.4)	0.3 (± 0.4)	3.6 (± 2.9)	1.1 (± 0.8)
Rupicapra pyrenaica	—	—	—	—	—	—	0.2 (± 0.5)	tr
Domestic ungulates	1.7 (± 1.8)	0.3 (± 0.2)	6.1 (± 0.8)	1.9 (± 0.9)	13.9 (± 4.0)	2.9 (± 1.4)	4.6 (± 3.2)	0.8 (± 0.7)
Bos taurus	1.5 (± 1.9)	0.2 (± 0.2)	2.1 (± 2.0)	0.4 (± 0.4)	6.6 (± 3.8)	1.3 (± 1.0)	2.7 (± 2.8)	0.4 (± 0.3)
Ovis aries	—	—	1.9 (± 1.1)	1.0 (± 0.8)	1.8 (± 1.3)	0.4 (± 0.4)	0.7 (± 0.2)	tr
Capra hircus	—	—	0.9 (± 1.8)	0.1 (± 0.2)	1.3 (± 0.4)	0.3 (± 0.4)	0.1 (± 0.2)	tr
Equus caballus	0.3 (± 0.5)	tr	1.3 (± 1.1)	0.2 (± 0.3)	3.1 (± 1.1)	0.5 (± 0.4)	0.5 (± 0.9)	0.2 (± 0.5)
Other mammals	3.1 (± 3.5)	1.2 (± 2.1)	1.4 (± 1.4)	0.3 (± 0.6)	3.6 (± 4)	0.1 (± 0.1)	1.7 (± 2.7)	0.2 (± 0.3)
Glis glis	—	—	—	—	0.1 (± 0.2)	tr	—	—
Lepus spp.	—	—	—	—	0.4 (± 0.5)	tr	—	—
Martes foina	—	—	—	—	—	—	0.1 (± 0.2)	tr
Microtinae	—	—	—	—	0.3 (± 0.5)	tr	0.1 (± 0.3)	tr
Sciurus vulgaris	—	—	—	—	0.1 (± 0.1)	tr	—	—
Ursus arctos[d]	3.1 (± 3.5)	1.2 (± 2.1)	1.4 (± 1.4)	0.3 (± 0.6)	2.6 (± 3.2)	0.1 (± 0.1)	1.4 (± 2.5)	0.1 (± 0.3)
Insects	10.2 (± 10.0)	1.0 (± 1.5)	43.4 (± 5.7)	15.7 (± 2.8)	28.2 (± 8.3)	4.5 (± 1.9)	5.9 (± 4.0)	0.9 (± 0.8)
Formicidae	9.7 (± 9.2)	0.8 (± 1.3)	41.2 (± 6.3)	14.3 (± 2.7)	19.8 (± 4.9)	3.1 (± 1.6)	2.5 (± 1.7)	0.6 (± 0.5)
Diptera (maggots)	—	—	3.3 (± 2.5)	1.1 (± 1.6)	4.9 (± 2.6)	0.7 (± 0.7)	0.3 (± 0.4)	—
Bombus spp.	—	—	0.2 (± 0.3)	0.1 (± 0.2)	0.4 (± 0.8)	—	—	—
Coleoptera[e]	0.3 (± 0.5)	tr	1.4 (± 1.7)	tr	1.3 (± 0.9)	0.2 (± 0.4)	—	—
Apis mellifera	0.3 (± 0.5)	0.1 (± 0.2)	2.3 (± 4.0)	0.2 (± 0.3)	1.0 (± 0.8)	0.3 (± 0.4)	1.6 (± 1.2)	0.2 (± 0.2)
Vespidae	—	—	—	—	0.6 (± 0.8)	tr	0.6 (± 0.9)	tr
Orthoptera	—	—	—	—	0.3 (± 1.0)	0.1 (± 0.1)	0.1 (± 0.2)	tr

[a] Macro categories include unidentified items at higher taxonomic levels.

[b] See Table 1 for sample sizes.

[c] Including *Daucus carota* and unidentified roots.

[d] Excluding scats with volumetric proportions < 0.5% to minimize inclusion of hairs from grooming.

[e] Including Carabidae and Scarabaeidae.