DIETS OF ASIATIC BLACK BEARS IN TAIWAN, WITH METHODOLOGICAL AND GEOGRAPHICAL COMPARISONS

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Abstract: Few studies have been conducted on the diet of bears in the tropics. During 1998–2000, we studied the diet of Asiatic black bears (*Ursus thibetanus formosanus*) in Yushan National Park, Taiwan, on the Tropic of Cancer. We used 3 methods to investigate their diet: scats, feeding sign, and interviews with indigenous hunters. Most scats (n = 654) were found during autumn and early winter, when bears congregated in an area of abundant oaks and foraged mainly on acorns. In 1999, when acorns were less abundant, bears preyed more frequently on ungulates. We found fewer scats (n = 37) during summer, when bears were more dispersed and foraged on soft mast, and only 2 scats during spring, both containing mainly green vegetation. These findings were corroborated by bear feeding sign that we found, including hundreds of oak and soft mast-producing trees with broken branches, some forming a structure resembling a nest. We also found evidence of bears feeding on carrion and insects. It was more difficult to determine seasonality of diet using sign, although this technique yielded a larger list of bear foods (n = 26) than scat analysis (n = 19). However, the largest tally of bear foods (n = 70) was obtained by interviewing indigenous people who hunted in or near the park. Data generated from these interviews were less quantitative but covered a much broader area and time span and provided better information on the diversity and seasonality of the diet than that obtained from scats and sign. The 3 methods, each somewhat biased and deficient, yielded complimentary views of bear diets. Our results were consistent with other studies of Asiatic black bears in broadleaf forests; these bears were omnivorous, opportunistic, and heavily dependent on hard mast. In our study, however, bears consumed medium-sized ungulates more frequently than in other areas.

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Whereas innumerable studies of food habits have been conducted on American black bears (*Ursus americanus*), much less data are available on the diet of its apparent ecological counterpart and close taxonomic relative (Talbot and Shields 1996), the Asiatic black bear. There have been several studies in Japan (Takada 1979, Nozaki et al. 1983, Torii 1989, Naganawa and Koyama 1994, Mizoguchi et al. 1996, Hashimoto and Takatsuki 1997, Horiuchi et al. 2000, Huygens and Hayashi 2001), plus some from Russia (Bromlei 1973), India (Schaller 1969, Manjrekar 1989, Saberwal 1989), and mainland China (Wu 1983, Wang 1988, Schaller et al. 1989, Chen 1991, Reid et al. 1991, Ma et al. 1994), but these represent a small portion of this species' total range. Moreover, results of many of these studies are not available in English. Here, we add new data on the diet of Formosan black bears, a subspecies inhabiting Taiwan. The only previous information on the diet and foraging behavior of Formosan black bears was obtained from feeding natural foods to a captive individual (Wang et al. 1992, Hwang and Wang 1993).

Other studies of bear diets have relied mainly on scat analyses. Some studies obtained ancillary dietary information from analyses of collected stomach contents, examination of feeding sign, or even observations of bears feeding. However, observations of forest-dwelling bears are generally rare, and there has been little effort to quantify feeding sign. Thus, feces have been the cornerstone for information on diets of black bears.

Feces may be found with relative ease and often in abundance, especially where bears exist at high density and routinely use trails (Matthews 1977). This, however, was not the case in Taiwan. The density of bears in Taiwan is unknown, but sighting information suggests it is low (Wang et al. 1993). Moreover, for that reason and possibly others discussed herein, scats are not commonly found on trails. Therefore, we could not rely on scat analysis alone to investigate the food habits of Formosan black bears. Consequently, we employed 2 additional methods: quantification of feeding sign and compilation of traditional ecological knowledge from interviews with indigenous hunters.

Our objectives were to: (1) describe seasonal and annual diets of Formosan black bears, (2) compare techniques for assessing bear diets, and (3) compare results of dietary studies of black bears from different geographic areas.

STUDY AREA

Taiwan is a 36,000-km^2 island located off the eastern coast of China. The island is characterized by a high diversity of fauna and flora, due to its location on the Tropic of Cancer (23°50' N) and rugged mountainous terrain, which dominates the interior.

Yushan National Park (YNP; 23°19' N, 121°10' E), es-

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tablished in 1985, comprises 1,055 km^2 of the Central Mountain Range and is the largest national park in Taiwan (Fig. 1). The elevation ranges from 300 m above sea level to the Yushan main peak at 3,952 m, the highest mountain in northeast Asia. Two-thirds of the park is above 2,000 m in elevation and there are >30 mountain peaks >3,000 m. Deep valleys and steep slopes (72% of terrain >55°) cause numerous landslides and waterfalls (S-J. Chen 1989). No hunting or human settlement is allowed within the park.

Y-F. Chen (1989) described 6 plant zones in YNP related to elevation: broadleaf forest (300–1,800 m, mainly consisting of *Lauraceae* spp. and *Fagaceae* spp.), *Chamaecyparis* (1,800–2,500 m), *Tsuga chinensis* (2,500–3,000 m), *Abies kawakamii* (3,000–3,500 m), subalpine shrub (>3,500 m), and an alpine herbaceous zone (>3,800 m). In southeastern YNP, Kou (1999) reported 527 species of vascular plants belonging to 360 genera and 125 families. He classified the vegetation zones in the area as subtropical evergreen broadleaf forest (*Cyclobalanopsis glauca–Machilus philippinenes* association), warm–temperate evergreen broadleaf forest (*Cyclobalanopsis glauca–Pheobe formosana* association), temperate evergreen broadleaf forest (*Pasania kawakamii–Machilus japonica* association), and temperate mixed forest (*Chamaecyparis formosensis–Pasania kawakamii* association). Besides black bears, 12 species of medium–large mammals inhabited the park, the most prevalent being muntjac (*Muntiacus reevesi*), Formosan serow (*Naemorhedus swinhoei*), Formosan wild boar (*Sus scrofa*), sambar deer (*Cervus unicolor*), and Formosan macaque (*Macaca cyclopis*) (Kou 1999).

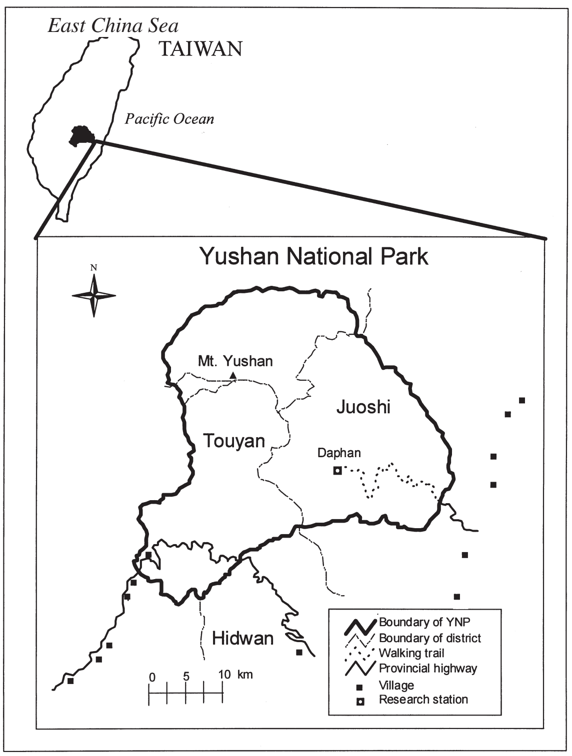

Fig. 1. Yushan National Park study area, Taiwan, showing the oak-rich area where Asiatic (Formosan) black bears congregated in autumn (Daphan) and 3 districts encompassing indigenous villages where we interviewed residents about bears.

Our primary study area was in southeastern YNP, within an elevation range of 300–2,800 m, in the watershed of the Lakulaku River. Except for routine trail maintenance and construction of bridges, this area had little human activity during our study because visitors were banned from most of the area. Crumbled stone walls, terraced slopes, small clearings, and overgrown trails existed as relicts of previous occupants of the area, including aboriginal people and Japanese. Our focus during the autumn and winter was within a once-settled hillside known as Daphan, where we conducted most of our bear trapping. This area, a 3-day hike from the park entrance (Fig. 1), was rich in oak trees (primarily *Cyclobalanopsis glauca*), which attracted bears during autumn.

Average annual rainfall during this study was 2,710 mm at 500 m elevation (lowest in Jan: 39 mm; highest in Oct: 816 mm). The monsoon rainy season occurred during May–October, with typhoons most prevalent during July–October. Snow occurred at elevations >3,000 m during December–March. Monthly mean daily temperatures were warmest in July (23.8°C) and coldest in January and February (13.8°C). Yearly average temperature was 10°C at 2,500–3,000 m and 5°C at 3,500 m.

METHODS

This study, part of a larger ecological study in which bears were captured and radiotracked, was conducted during July 1998–December 2000. We used 3 approaches for ascertaining bear diets: (1) scat analysis, (2) observations of feeding sign, and (3) interviews with indigenous people who lived near our study area and had an intimate association with the forest. During fieldwork we also observed and recorded annual and seasonal changes in availability of some fruits that were thought to be important bear foods. We subjectively rated fruit production as high, moderate, or low, based on the amount of fruit observed on trees and bushes.

Scat Analysis

We collected scats during August 1998–December 2000 in the course of trapping, radiotracking, and hiking in YNP. We also intensively searched for scats in areas where we located radiocollared bears or found bear sign. We recorded the location of scats and estimated how long they had been on the ground based on color, moisture content, and degradation.

For most scats, we identified food items by eye *in situ*, but also collected a small sample which was sun dried in the field. When we could not identify items in the field, we collected the whole scat and brought it to a laboratory for examination under a dissecting microscope. We identified individual food items to species or the lowest possible taxon. To aid in our identifications, we observed foraging sign around scat sites, relied on consulting botanists and indigenous field guides, and used a reference collection of plant specimens collected from the study site. We grouped food items into 5 general categories: hard mast, soft mast, mammal, vegetation (leaves, stems, or roots), and insect. We did not quantify bear hairs or debris such as soil, stones, and wood particles, which we assumed were ingested incidentally. We also excluded scats with human-related foods such as bait or items pilfered from our research station.

During 1998, we recorded only frequency of occurrence of different food items: FO_i (%) = (n_i/N) x 100, where N was the total number of fecal samples and n_i the number of samples containing food item i. During 1999 and 2000, we also estimated the relative volume of each item in each scat, and averaged these values among scats: RV_i (%) = $\sum V_i / N$, where N was the total number of scat samples and $\sum V_i$ was the sum of the volumetric percents for food item i among all scats.

We separated the data both seasonally and yearly. Seasons were determined by changes in climate and plant phenology and were defined as follows: spring (Mar–May), summer (Jun–Aug), autumn (Sep–Nov), and winter (Dec–Jan) (no scats were collected in February). We later combined autumn and winter and called this the oak season, the period when bears consumed mainly hard mast.

Observations of Feeding Sign

While foraging in trees, Asiatic black bears sometimes break branches to reach fruit on twigs. This behavior may lead to the formation of so-called tree platforms or nests, or more commonly, just obvious damage to the canopy. We recorded tree and shrub species with broken limbs caused by bears or with bear claw marks leading up to the canopy even if no branches were broken. Other feeding sign included remains of ungulates and beehives that we identified as having been consumed by a bear from tracks or other sign in the vicinity. We could not identify bear feeding sign on herbaceous species because many medium and large mammals consumed these. We found bear sign mainly during the course of other fieldwork. However, while radiotracking bears, we sometimes specifically searched for their sign after they left an area. For all bear feeding sign encountered, we recorded an estimate of freshness of the sign, location, elevation, and vegetation type.

Interviews of Indigenous People

During July 1998–May 2000, we conducted in-depth interviews with indigenous people living in villages neighboring YNP to gather information about their knowledge of bear diets. These were mainly Bunun tribal peoples who historically lived in mountainous regions where they practiced slash and burn agriculture, hunting, and gathering wild foods. Bears, locally called "Tumad" were killed, although they were seldom a primary target of their hunts. All bear hunting is now illegal, but nevertheless continues (Wang 1999; Wang and Hwang 1999, 2000).

We selected 3 Bunun districts for interviews. Interviews were conducted in 6 villages from each of the Touyan and Juoshi districts, located southwest and southeast of YNP, respectively (Fig. 1). Although only one village, Meishan of Touyan, was located within the boundary of YNP, the traditional hunting territory of these villagers covered most (>75%) of the park. In the third district, Hidwan, which was outside the southern border of YNP, we conducted interviews in only 1 village, Wulu.

The senior author conducted all interviews except one. The interviewer spent time living in the villages, which promoted more congenial and frank discussions. Several indigenous employees of YNP helped us identify experienced hunters who could provide information about bears. We also used a snowball sampling method (Biernacki and Waldorf 1981) of referrals from one interviewee to another. All interviewees were men because only men were involved in traditional hunting.

Interviews were done face-to-face with open-ended questions. We asked about foods that bears eat, how they obtain these foods, and how the person acquired this information. In some cases, indigenous park employees or other indigenous informants helped translate if the interviewee preferred using their Bunun language. Some interviews were tape recorded to later confirm the accuracy of translations. Many Bunun names for plants were initially unfamiliar to us. Thus, during interviews we asked for detailed descriptions of such plants, their fruiting phenology, distribution, and habitat. We then confirmed the plants while working with villagers in the field, or we collected plant specimens and verified them with villagers later. These were eventually identified using field guides and assistance from botanists.

RESULTS

Scat Analysis

We analyzed 693 bear scats: 268 in 1998, 95 in 1999, and 330 in 2000. We excluded 25 scats containing human-related food. We found only 2 scats during spring and 37 during summer; the remainder (654) were from the oak season. Scats were found at 1,000–2,100 m elevation, although most (>90%) were at 1,100–1,600 m. Individual scats contained 1–4 food items, but 77% had only 1 item and 19% had 2 items (mean = 1.3, SD = 0.5).

Plant material (hard mast, soft mast, and other plant parts) occurred in 99.3% of bear scats. Animal matter occurred in 12.3% of scats; 11.4% contained ungulate remains and 1.2% contained insects. In the volumetric analysis, plant and animal food composed 93.0% and 7.0% of scats, respectively. We identified 19 different food items: 3 species of ungulates, 3 species of insects, and 13 species of hard and soft fruits (Table 1). We did not try to identify vegetation, such as grass, leaves, stems, and roots, which occurred in 2.7% of scats.

The 2 scats found during spring consisted mainly of herbaceous plants (>95% relative volume). One of these also contained insects, and 1 contained muntjac remains.

Table 1. Diet of Asiatic black bears based on scat analysis (n = 693 scats), observations of feeding sign (n > 600 climbed fruit trees, eaten carcasses, etc.), and interviews (n = 70) with indigenous hunters (n > 440 reported items), Yushan National Park, Taiwan, 1998–2000.

			Methods[a]				
Category	Common name	Species name	Scats	Feeding sign	Interviews	Consumed part[b]	Season[c]
Hard mast	Ring-cupped oak	*Cyclobalanopsis glauca*	534	>300	44	f	a, w
	Devil tan oak	*Lithocarpus castanopsisifolius*		4	42	f	a, w
	Smoothleaf tan oak	*Pasania glabra*			24	f	a, w
	Long-leaf chinkapin	*Castanopsis carlesii*			20	f	a, w
	Arishan oak	*Quercus stenophylloides*	86	>200	13	f	a, w
	Mori oak	*Quercus morii*			12	f	a, w
	Tailuko oak	*Quercus tatakaensis*	1	2	6	f	a, w
	Taiwan walnut	*Juglans cathayensis*	33	1	6	f	a, w
	Long gland oak	*Cyclobalanopsis longinux*		20–30	4	f	a, w
	unknown oaks				2		
Soft mast	Nanmu	*Machilus* spp.	30	50–100	35	f	su
	Taiwan loquat	*Eriobotrya deflexa*	9	16	16	f	su, a
	Formosan apple	*Malus formosana*	5	20	11	f	a, w
	Indigenous cinnamon	*Cinnamomum osmophloeum*		18	11	f	su
	Giant taro	*Alocasia macrorrhizos*			10	f	su
	Taidon persimmon	*Diospyros oldhamii*		2	6	f	a, w
	Passion fruit	*Passiflora edulis*			6	f	su, a
	Taiwan cherry	*Prunus campanulata*		6	4	f, fl	sp
	Formosan kiwi	*Actinidia callosa*			4	f	su, a
	Luzon viburnum	*Viburnum luzonicum*	6	3	3	f	a
	Oldham persimmon	*Diospyros sasakii*			2	f	su, a
	Litsea	*Litsea* spp.		3	2	f	su
	Formosan sugarplum	*Arenga pinnata*			2	f, s	
	Shell ginger	*Alpinia speciosa*			1	f	
	Taiwan phoebe	*Phoebe formosana*		1	1	f	su, a
	Thunberg elaeagnus	*Elaeagnus thunbergii*			1	f	
	Autumn ample tree	*Bischofia trifoliata*			1	f	
	Wild mango	*Mangifera indica*			1	f	
	Cuming's wintergreen	*Gaultheria cumingiana*			1	f	su
	Raspberry	*Rubus* spp.			1	f	sp, su, a
	Rose	*Rosa* spp.			1	f	
	Konishi neolitsea	*Neolitsea konishii*			1	f	
	Jelly-fig	*Ficus pumila*			1	f	
	Taiwan mulberry	*Morus acidosa*			1	f	
	Blueberry	*Vaccinium donianum*		2		f	su, a
	Soap nut tree	*Sapindus mukorossi*		1			
	Rough-leaved tree	*Aphananthe aspera*	1			f	su
	Fetid securinega	*Securinega virosa*	1			f	a
	Mountain viburnum	*Viburnum propinqum*	1				su
	Pouteria	*Planchonella obovata*	1				
	unknown				20	f	
Vegetation	Dwarf bamboo	*Yushania niitakayamensis*			15	s	sp, su
	Japanese silver-grass	*Miscanthus floridulus*			4	l	
	Formosan taro	*Colocasia formosana*			3	l, f, fl	
	Taiwan kudzubean	*Pueraria lobata*			2	s	
	Sword fern	*Nephrolepis auriculata*			1	r	
	Orchid	Orchidaceae			1	l, s	

Table 1. (continued)

Category	Common name	Species name	Methods[a] Scats	Feeding sign	Interviews	Consumed part[b]	Season[c]
Vegetation	Taiwan dwarf banana	*Musa formosana*			1	l	
	Fern	*Pteridophyta* spp.			1	l	
	Nest fern	*Asplenium nidus*			1	l	
	Point-leaved maple	*Acer insulare*		5			
	Formosan alder	*Alnus formosana*		4			
	Taiwan cedar	*Taiwania cryptomerioides*		2			su, sp
	Indiacharcial trema	*Trema orientalis*		1			
	Taiwan red maple	*Acer morrisonense*		1			
	unknown			7	7	l	
Crop	Peach				5	f	
	Plum				5	f	
	Prune		1		3	f	su
	Pear				3	f	
	Papaya				3	f	
	Bamboo shoot				3	s	
	Corn				2	f	
	Banana				2	f	
	Italian millet				2	f	
	Sweet potato				1	r	
Insect	Common bee	Apidae		2	26		
	Hornet	Vespidae	5		2		sp, a, w
	Beetle larva	Coleoptera			4		
	Plant ball				1		
	Ant	Hymenoptera	1		1		su
	Termite	Hymenoptera		1			
	Beetle	Coleoptera	2				a, w
Mammal	Formosan muntjac	*Muntiacus reevesi*	79[d]	2	common		
	Formosan serow	*Naemorhedus swinhoei*	79[d]	1	common		
	Formosan wild boar	*Sus scrofa*	1		occasional		
	Sambar deer	*Cervus unicolor*			occasional		
	Chinese civet	*Viverricula indica*			1		
Bird	Bird				1		
	Chicken				1		
Fish	Fish				12		
Reptile	Snake				2		
Others	Stream crab				7		
	Stream shrimp				1		
	Earthworm				1		
	Mushroom				1		
Human- related food			11		common		sp, su, a, w

[a] Each scat was a sample unit (values represent the number of scats containing the food item). The sample unit for sign was individual trees, carcasses, beehives, etc. The sample unit for interviews was the mention of a food item (values on table represent the number of times each item was mentioned).
[b] f = fruit, fl = flower, s = stem, l = leaf, r = root
[c] sp = spring, su = summer, a = autumn, w = winter
[d] Muntjac and serow hairs were not differentiated in scats (79 scats contained 1 or both species).

During summer, scats were comprised primarily of fruits (Fig. 2). Fruits of nanmu (*Machilus* spp.) were most prevalent (FO = 81%, RV = 77%) but these were found only in 2000, when they were noticeably more abundant in the forest than in the previous 2 years. We also found Taiwan loquats (*Eriobotrya deflexa*), Luzon viburnums (*Viburnum luzonicum*), mountain viburnums (*Viburnum propinqum*), rough-leaved trees (*Aphananthe aspera*), and wild plums (*Prunus* spp.). The next most frequently observed summer food category was mammals, followed by vegetation (Fig. 2). No hard mast was found in scats during spring and summer.

During the oak seasons of all 3 years, bears focused intensively on hard mast (Fig. 3). We identified 3 species of oaks consumed by bears (based mainly on the proximity of scats to a clump of oak trees): ring-cupped oak

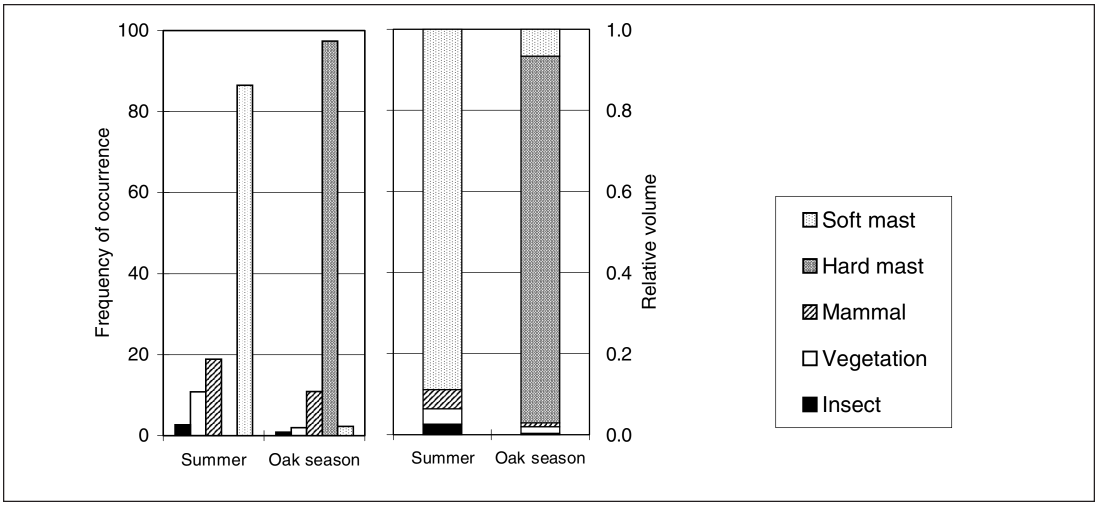

Fig. 2. Seasonal changes (summer: Jun–Aug; oak season: Sep–Jan) in the diet of Asiatic black bears based on frequency of occurrence and relative volume of items found in scats (*n* = 693), Yushan National Park, Taiwan, 1998–2000.

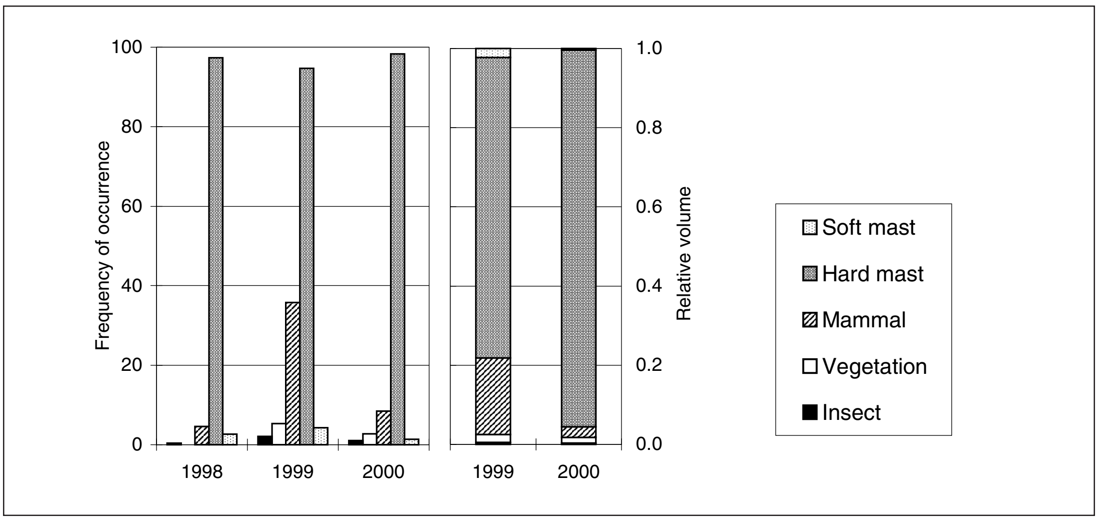

Fig. 3. Yearly variation in diets of Asiatic black bears based on frequency of occurrence and relative volume of items found in scats during the oak season (Sep–Jan) in Yushan National Park, Taiwan, 1998–2000. Only frequency of occurrence was measured in 1998.

(*Cyclobalanopsis glauca*), Arishan oak (*Quercus stenophylloides*), and Tailuko oak (*Q. tatakaensis*). Walnuts (*Juglans cathayensis*) also were observed in scats, although we did not recognize them until they were prevalent in 1999. Bears began consuming hard mast in mid-October and finished by mid-January, at which time they left the Daphan oak feeding area. Mammals, principally muntjacs and serows, were the second most common food item in scats during the oak season (FO = 10.9%, RV = 6.7%; Fig. 3). Soft fruits, vegetation, and insects each occurred in <3% of scats and comprised <3% of scat volume during the oak season.

The species and amount of hard mast consumed by bears varied by year (Table 2), and this matched the yearly fluctuations in productivity by these species. During 1998, 1999, and 2000, we rated the production of acorns by ring-cupped oak as high, low, and moderate, respectively; accordingly, this species was most common in scats during 1998, followed by 2000, and absent in 1999. Arishan oak acorns were rated as low–moderate, high, and low in these same 3 years, and were identified in scats only in 1999. However, Arishan oak is less common in the Daphen area than ring-cupped oak, so during 1999 the high production of Arishan oak did not make up for the low production of ring-cupped oak; hence, in that year bears fed more on walnuts and mammals (Table 2; Fig. 3).

Feeding Sign

Table 2. Frequency of occurrence (FO) and relative volume (RV) of hard mast food items identified in scats of Asiatic black bears during oak seasons (Sep–Jan), Yushan National Park, Taiwan, 1998–2000. Species of oak mast were identified mainly by trees in the vicinity of the scat.

	1998 (*n* = 263)	1999 (*n* = 95)		2000 (*n* = 296)	
Item	FO	FO	RV	FO	RV
All hard mast	97.3	94.7	75.9	98.3	95.2
Ringed-cup oak	97.3	0	0	94.3	94.2
Arishan oak	0	90.5	61.9	0	0
Tailuko oak	0	1.1	0	0	0
Walnut	Few[a]	28.4	14.0	1.6	1.0

[a] Walnuts were not identified in scats in 1998.

We found >600 occurrences of bear feeding sign on trees or shrubs, including 6 species that produce hard mast, 11 species that produce soft mast, 5 species of vegetation, and 4 unknown species (Table 1). Commensurate with our results from scat analysis, the most prevalent feeding sign was associated with ring-cupped and Arishan oaks (>300 and >200 trees, respectively). Our observations suggested that bears preferred some oak species to others. For example, we never found evidence of bears climbing large-leaf oaks (*Pasania ternaticupula*), even in good mast production years. Similarly, when both ring-cupped and long gland oaks (*Cyclobalanopsis longinux*) were productive in the same general area in 2000, bears used the former more frequently, based on numbers of trees with feeding sign (Table 1).

We frequently found sign of feeding in nanmu trees, particularly during the summer of 2000 when fruit production was especially good. We could not always identify the species of nanmu used by bears because field identification of the genus *Machilus* is quite difficult; however, of the trees we could identify, most bear sign occurred on narrow-leaved nanmus (*M. japonica*) and red nanmus (*M. thunbergii*). For some plant species, we could not identify which parts bears consumed or even whether bears climbed the trees for foraging. These included point-leaved maple (*Acer insulare*), Formosan alder (*Alnus formosana*), Taiwan cedar (*Taiwania cryptomerioides*), and Indiacharcial trema (*Trema orientalis*).

Numerous broken branches in the tops of trees was evidence of arboreal feeding behavior. Although we only observed bears feeding in trees twice, we ascertained how they fed from their sign. They often pulled fruit-bearing branches toward them with their forepaws or broke bigger limbs (e.g., >10-cm diameter) using their teeth. Sometimes, in oak and nanmu trees, these broken branches formed what looked like a platform or nest, especially when the accumulations of broken branches were stuffed into a fork and trampled by the bear. We occasionally observed several nest structures in a single tree. Repeated use by bears of some trees resulted in >80% of the canopy being damaged. One oak tree was used on at least 6 different occasions, although we do not know if these visits were by the same bear. Under trees with abundant fruit, we found up to 10 scats and many torn off branches, often with numerous uneaten fruits .

Non-vegetative items eaten by bears, as evidenced by their sign, included termites in rotten wood (*n* = 1), honeycombs in caves and underground (*n* = 2), and carcasses of mammals, including 2 muntjacs and 1 serow, plus a macaque and wild boar that had been caught in hunters' snares. We never observed bears pursuing ungulates, as reported by some hunters. They may have scavenged already dead mammals because carcasses (unrelated to human activities) were common; we found 28, including 18 muntjacs, 9 serows, and 1 young macaque.

Bears also sometimes took food from our research camps, generally when we were away. They usually carried this food to more secretive sites (e.g., under tall grass or behind big rocks or bushes). Their sign included scats, vomit, scraps of food and wrappers, and trampled resting sites.

Resting sites of bears (*n* = 46) often were associated with good food supplies or some form of protection, such as tall grass, tree roots, stone caves, or rock outcrops. Most were just depressions in the vegetation. However, in some cases (*n* = 18) bears constructed a bowl-shaped nest by intricately bending and twisting grasses (*Miscanthus floridulus*) or twigs (*Rhododendron rubropilosum*)(Fig. 4). The average size of these ground nests was about 110 cm in outside diameter, 60 cm inside diameter, and 30 cm in depth (*n* = 15 measured).

Fig. 4. Asiatic black bears in Yushan National Park, Taiwan, made bowl-shaped ground nests by twisting together blades of tall grass. These nests were not only a comfortable resting spot, but they provided protective cover, which bears sought especially when feeding near human-related food sources. These nests also may have served as a hiding place from which they could ambush ungulate prey. Measurements represent the range observed during this study (*n* = 15 of 18 were measured). Drawing by W-J. Yu.

Interviews with Indigenous People

We conducted 70 interviews with indigenous hunters, 27 from Juoshi, 38 from Touyan, and 5 from Hidwan district. Most of the interviewees (96%) were Bununs who historically lived in the mountainous regions of central Taiwan and were skilled in hunting. The average age of respondents was 57 (range = 30–80) years; 89% had experience hunting bears with guns or capturing them with wire snares or traps.

Most interviewees believed that bears were opportunistic foragers that ate anything edible, including plants, live animals, carcasses, and human-related foods. The most common food items first mentioned by interviewees were wild ungulates or their carcasses from hunter's traps. Many hunters also experienced bears taking food from their hunting huts. They believed bears had very short intestines and small stomachs, which caused them to vomit when they ate too much.

Aside from ungulates and human-related foods, individual interviewees mentioned 1–24 different food items (mean = 6.3, SD = 4.4; 43 of 70 listed 6 or less); 70 interviews generated a list of 440 foods (including repeated items). Plant foods included 9 species of hard mast, 24 soft mast, 9 non-fruiting plants, and 10 crops (Table 1), plus 26 items (not all different) that we could not identify from the descriptions or common names that the people used. Interviewees mentioned hard mast most frequently (45% of listed items), and reported that bears intensively used oaks in autumn and winter. Soft mast, they said, was more diverse and mainly used during the summer.

Interviewees considered muntjac and serow the most common ungulate prey of bears and mentioned wild boar and sambar deer less frequently. They suggested that bears sometimes pursued ungulates and preferred young or weak individuals. Additionally, bears purportedly ambushed ungulates by hiding near cliffs or in ground nests or even jumping on them as they passed under a tree. Bears also were reported to regularly use carrion, especially kills made by yellow-throated martens (*Martes flavigula*), which were reported to consume mainly the inner parts.

Other reported animal foods included 5 species of insects as well as fish, crabs, shrimp, civets, birds, chickens, snakes, earthworms, and mushrooms. Honey and beehives frequently were indicated as a preferred food. Interviewees reported seeing evidence of bears digging out hives of common bees (Apidae) and hornets (Vespidae) from trees or underground and mentioned that bears usually attacked these nests at dawn, when stinging insects were less active.

Hunters from the Juoshi and Touyan districts showed somewhat different responses, commensurate with their respective hunting areas. Predominate mast species at higher elevations (>1,500 m), such as Devil tan oaks (*Lithocarpus castanopsisifolius*) and long-leaf chinkapin (*Castanopsis carlesii*), were more frequently reported by hunters in Touyan, who hunted at a generally higher elevation than those from Joushi. Conversely, low elevation (<1,500 m) species, such as Taiwan loquat, were reported more frequently by Juoshi hunters. Nanmus, occurring in a broad elevational range, were reported as the most important summer soft mast in both districts.

DISCUSSION

Comparisons within and across Species

Most bears are omnivorous, opportunistic feeders, whose diets can vary seasonally, yearly, geographically, and by habitat. These variables, along with differences in investigative methodology, confound attempts to make generalizations and comparisons.

With these caveats in mind, we compared diets of Asiatic black bears inhabiting broadleaf forests similar to our study site. Our aim here was to view our results in the context of variation found among different populations of this species. We also compared our findings with American black bear diets in similar forest habitat types. Data on American black bears are often used as surrogates for Asiatic black bears for population and habitat assessments (Wang et al. 1994, Horino and Miura 2000, Park 2001) because the 2 species are considered to be genetically and ecologically similar, but data are often lacking for the latter. Our comparisons between the 2 species are thus meant to discern, at least on the level of diet, how ecologically similar they are.

Across the range of the Asiatic black bear, plant material comprised >80% of the overall diet and animals formed a small portion of the diet; however, the frequency of animal food in our study was higher than that in other areas (Takada 1979, Nozaki et al. 1983, Manjrekar 1989, Schaller et al. 1989, Torii 1989, Reid et al. 1991, Naganawa and Koyama 1994, Mizoguchi et al. 1996, Hashimoto and Takatsuki 1997, Horiuchi et al. 2000). The overall relative use of plant (~90%) and animal (~10%) foods appears to be similar for Asiatic and American black bears in broadleaf forests (summarized by Mattson [1998]).

Seasonal dietary shifts follow the same general pattern for both Asiatic (H. Lee et al. 1991, K. Lee et al. 1991, Reid et al. 1991, Hazumi 1994, Ma et al. 1994, Hashimoto and Takatsuki 1997, Horiuchi et al. 2000) and American black bears (reviewed by McDonald and Fuller [1993]). In spring, both species of black bears depend mainly on green, succulent vegetation. In summer, soft fruits become the main dietary component. In autumn, bears turn to hard mast, if available, and both black bear species prefer certain types of oak (Garshelis and Pelton 1981, Hashimoto and Takatsuki 1997, Huygens and Hayashi 2001, this study). Hard mast, mainly of the Fagaceae family, composed 50–90% of autumn diets of black bears in broadleaf forests throughout Asia (Table 3). In some areas, fallen hard mast from the previous autumn was consumed by both Asiatic and American black bears in spring and even summer (Nozaki et al. 1983; Ternent 1995; Huygens et al., 2000, Diet and ecological aspects of Asiatic black bear in the Northern Japanese Alps, Shinshu University, Matsumoto, Japan), although this did not occur in our study because acorns, without snow cover in winter, either rotted or were consumed rapidly by other animals.

Some forest types produce little hard mast. American black bears inhabiting such areas rely more on soft mast during autumn (Mattson 1998, Vaughan 2002). No studies of diet of Asiatic black bears have been conducted in places lacking hard mast, which may explain why this species appears (but may not necessarily be) the most hard-mast dependent of all the bears (Mattson 1998). Our study confirmed the importance of hard mast in bear diets in a forest where it is seasonally abundant. Hard mast is high in fat (Landers et al. 1979, Eagle and Pelton 1983, Kasbohm et al. 1995, Hashimoto and Takatsuki 1997, Kirkpatrick and Pekins 2002), and during autumn the digestive system of bears becomes more able to assimilate fat (Brody and Pelton 1988). Bears also undergo a period of pre-denning hyperphagia (Nelson et al. 1983) in which they substantially increase their intake of food. In combination, these factors result in rapid weight gain, an adaptation for hibernation. Our observations suggest that Asiatic black bears in Taiwan behaved similarly, even though these bears did not hibernate (Hwang et al. 2000).

One enigma is our observation of many fruit-laden branches beneath foraging trees, apparently neglected by bears. Schaller (1969) and Bromlei (1973) both observed Asiatic black bears descending from trees to eat fruits off branches that either fell or were intentionally dropped. We suggest that in their high-grading foraging strategy, which may be necessary to sustain a frugivore of this size (Welch et al. 1997), bears sometimes found it unprofitable to rummage through the fallen branches when trees with abundant mast were in the vicinity.

When key foods become scarce, both Asiatic and American black bears turn to less preferred, less accessible, or riskier (e.g., human-related) foods. When hard mast crops fail, they tend to rely more on green vegetation, soft mast, or agricultural crops (Hazumi and Maruyama 1986, 1987; Eiler et al. 1989; McDonald et al. 1994; Kasbohm et al. 1995; Hashimota and Takatsuki 1997; Vaughan 2002). In Japan, black bears resorted to tree cambium when natural broadleaf forests were converted to plantations with little available mast (Azuma and Torii 1980, Furubayashi et al. 1980, Hazumi 1994). Bears in our study faced with a poor acorn crop (1999) increased consumption of walnuts and ungulates.

The digestive system of bears is better adapted for meat than more structurally-complex plant material (Bunnell and Hamilton 1983, Pritchard and Robbins 1990, Hewitt and Robbins 1996). However, mammals compose a small portion of black bear diets, and insects seem an especially variable component of the diet (Landers et al. 1979, Takada 1979, Beeman and Pelton 1980, Graber and White 1983, Grenfell and Brody 1983, Torii 1989, Raine and Kansas 1990, Holcroft and Herrero 1991, Hashimoto and Takatsuki 1997, Khramtsov 1997). In our study, insects were a very small portion of the diet, but mammals seemed generally more important than in other studies of Asiatic or American black bears (Table 3; Mattson 1998). Similar to our study, Wu (1983) found that Asiatic black bears in China preyed on ungulates when plant food was less available. Most studies of American black bears indicated that they preyed mainly on young or weak prey animals (Wilton 1983, Mathews and Porter 1988, Schwartz and Franzmann 1991, Ballard 1992, Kunkel and Mech 1994, DeBruyn 1997). We suggest that the relatively small

Table 3. Autumn diets, based on scat analysis, of Asiatic black bears in broadleaf forests of different geographic regions[a], ordered from south to north. Bears in Taiwan (this study) were more reliant on vertebrate (ungulate) prey than in other areas.

				Diet composition (%)				
Site	Location	Method[b]	Sample size	Vegetation	Soft mast	Hard mast	Vertebrate	Invertebrate
Taiwan	23°N, 121°E	FO/RV	654	1.8/1.6	2/0.8	85.8/90.5	9.6/6.7	0.8/0.4
China	31–33°N, 103–105°E	RV	46	5	5	90	Few	0
India	34°N, 75°E	RV	45	0	17.2	80.4	0	0.7
Gifu, Japan	36°N, 137°E	RV	80	<0.1	14.2	84.1	<0.1	0.2
Nagano, Japan	37°N, 138°E	RV	86	<0.1	34.9	63.1	0.1	1.8
Russia	42–50°N, 130–140°E	FO	70	10.5	33	52.1	0.4	4

[a] Values obtained only from published studies in which >40 scats were collected over a period of >1 month during autumn–early winter. Where data were grouped by weeks, months, or years, we recalculated an overall average for this season, weighting time periods by sample size.
Sources — China: Schaller et al. (1989); India: Manjrekar (1989); Gifu, Japan: Mizoguchi et al. (1996); Nagano, Japan: Takada (1979); Russia: Bromlei (1973).
[b] FO — frequency of occurrence standardized to 100%; RV — relative volume.

size (10–20 kg) and apparent high density of ungulates (muntjacs and serows) in our study area may have prompted bears to be more carnivorous than reported elsewhere. Bears may encounter these ungulates especially frequently in oak areas, where bears and ungulates both congregate. With varying availability of fruits, it may be that abundant populations of small-bodied ungulates are important for sustaining black bear populations in Taiwan and other parts of Asia.

Arboreal feeding seems to be common among Asiatic black bears in broadleaf forests (Schaller 1969, Bromlei 1973, Wang 1988, Saberwal 1989, Schaller et al. 1989, Reid et al. 1991, Ma et al. 1994). The large number of reports of this behavior suggests that Asiatic black bears are more arboreal than American black bears; this may be partly explained by differences in the structure of their feet (Pocock 1932; Huygens et al. 2000, unpublished report) as well as a greater prevalence of tree-borne instead of a bush-borne fruits in Asian forests. Although American black bears build tree nests in some areas (D. Garshelis, personal observation), such nest building seems much more common among Asiatic black bears (Bromlei 1973, Schaller 1969, Nozaki et al. 1983, Schaller et al. 1989, Reid et al. 1991, Ma et al. 1994, Huygens et al. 2000, unpublished report). It is also common among sun bears (*Helarctos malayanus*; Erdbrink 1953, McConkey and Galetti 1999, Meijaard 1999), which inhabit many of the same areas as Asiatic black bears.

It is not entirely clear whether tree nests serve a specific purpose or merely arise as a result of feeding activity. Whereas these platforms may be a comfortable and secure place for a bear to sit, our observations suggest that in Taiwan they are mainly the result of bears pulling food-laden branches toward the relatively stable center of the tree. Most of the platforms we saw consisted of a jumbled array of branches, rather than a carefully formed structure. Indigenous hunters indicated that they rarely saw bears resting in these platforms. Observations by others, however, suggest that Asiatic black bears may sometimes construct platforms for rest and protection, especially when the ground is water-logged (Yin 1954, Steinmetz et al. 1999). Andean bears (*Tremarctos ornatus*) may use tree nests for resting or to guard feeding sites, especially human-related foods (Goldstein 1991, 2002); similarly, sun bear tree nests seem most common in human-disturbed areas (Meijaard 1999).

Ground nests of black bears have been remarked upon much less frequently than tree nests. Asiatic black bears have been observed to rake leaves into a bed for resting during cold or rainy weather (Bromlei 1973, Wu 1983). Large beds (130 cm diameter, 3–30 cm deep) constructed of piled up broken bamboo, shrubs, or vines have been reported for Asiatic black bears in China (Wu 1983, Wang 1988, Schaller et al. 1989). Often, several scats occurred nearby, suggesting that they were sites of extended rest periods. Ground nests of Asiatic black bears in China appeared similar to nests that we observed in Taiwan made by wild boar. In contrast, bears in Taiwan tended to bend and twist tall grass or shrubs and form them into a distinctive bowl, rather than bite off and pile up pieces of grass or broken branches. Similar bowl-shaped ground nests made of bamboo were apparently constructed by bears in South Korea (W.M. Kim, National Institute of Environmental Research, Incheon, South Korea, personal communication, 2001). Some hunters that we surveyed thought that ground nests were made for security or prey surveillance. Because these hunters had experiences with bears consuming their trap-captured prey, it is perhaps expected that they would suggest a predatory explanation for the nests.

From the information at hand, it is difficult to ascribe a reason for these ground nests. We posit 3 different, but non-mutually exclusive explanations. (1) Because we found several such nests near our field camp after being raided by bears, we presumed that bears used these nests while they remained in the area. Possibly the function, in this case, was to provide protective cover when near human threats, similar to what appears to be the case for some tree nests built by sun bears and Andean bears (Goldstein 1991, 2002; Meijaard 1999). (2) Ground nests also tended to be built along rocky ridges, near cliffs, or beside trails, where terrain was uneven, and so may have functioned mainly to enhance resting comfort. (3) Ridges, cliffs, and trails also tend to funnel the movements of ungulates, which in this population served as a food source for bears. Hence, it may be that the nests were, as the hunters presumed, used by bears to ambush prey, especially where other ground cover was lacking. It may not have been coincidental that the most elaborate ground nest-building so far observed for this (or any other bear) species was in an area where ungulate prey was an important dietary component.

Comparisons of Methodologies

We used 3 methods to investigate bear diets. Each of the methods indicated a strong reliance on certain species of hard mast in autumn and soft mast in summer (Table 1), but each also yielded some unique items that were not identified by the other methods (Table 4).

Putnam (1984:79) observed that scats are "the most readily-available and easily-collected source of information" for assessing diets. The principal difficulty in interpreting scats is that they reflect only proportional amounts of undigested material, not foods consumed (Hewitt and Robbins 1996, Litvaitis 2000). We faced an additional problem, notwithstanding Putman's (1984) statement, in

Table 4. Attributes of 3 methods used to obtain dietary information on Asiatic black bears in Yushan National Park, Taiwan, 1998–2000. Our subjective scoring was based on the following scale: – virtually no information; + little; ++ moderate; +++ high.

	Scats	Feeding sign	Interviews
Foods eaten (identified items; unique items)[a]	+ (19; 5)	++ (26; 8)	+++ (70; 48)
Plant parts consumed	+++	+	++
Volume consumed	++	+	+
Foraging behavior	–	+	++
Seasonality of diet	+	+	++
Reliability of data	++	+	+
Efficiency of data collection	+	++	+++

[a] Total number of food items identified using particular method; number of items uniquely identified using that method (n = 84 items identified among all 3 methods).

the mere collection of scats. Our sample in the spring was so small that we could not reliably ascertain the spring diet from scats. A relatively small sample size of scats in spring or summer also was reported in other studies (Bromlei 1973, Takada 1979, Manjrekar 1989, Schaller et al. 1989, Hashimoto and Takatsuki 1997). A paucity of scats in spring may be due to low ingestion rates (Roth 1980, Mattson et al. 1991) and high rates of decomposition of scats composed of green vegetation, particularly in humid environments such as Taiwan. Additionally, in spring and summer, black bears in Yushan were highly dispersed (Wang and Hwang 1999, 2000), making scats difficult to find. Conversely, in autumn, scats composed of acorns were found in abundance because bears congregated in a feeding area and likely consumed large quantities of abundant food and thus defecated frequently. Moreover, acorn scats persisted for 1–2 months in dry oak forests. The disproportionate numbers of scats found during the 3 seasons is thus a substantial source of bias.

Another source of bias relates to where scats were found. In spring and summer we collected scats while hiking on trails and radiotracking; thus we were more apt to find scats within the elevational range that was most accessible to us. We spent most of the fall trapping in an oak-rich area that attracted bears, so we found many scats composed largely of oak mast. We sometimes found a large group of scats in the same general area, or even under the same tree. Although it is likely that these did not represent independent sample units, we had no way of distinguishing true sample units (scats from different bears).

Feeding sign had some of the same biases as scats, namely non-independence of individual trees that occur in clumps and a possibly non-representative sampling reflective of our activities. Additionally, bears leave evident sign when feeding on some types of foods but not others. Herbaceous plants are absent in our data on feeding sign, as would be some shrub-borne fruits and certain types of insects. Some trees show clear evidence of bear feeding, especially species in which bears break branches, whereas others may be more difficult to detect. Hence, we made no attempt to quantitatively compare feeding sign by season, or even with other methods, but used the data instead to increase our knowledge of what and how bears ate.

We identified more individual food items from sign than from scats (Table 4) with roughly the same overall sample size (i.e., total $n > 600$, Table 1); hence, sign seemed a more efficient means of data collection (Table 4). Additionally, more behavioral information was gained from sign (e.g., tree and ground nests) than scats. Sign also persisted longer, so gave a better record of past feeding events (i.e., 1–2 years before), although that made it more difficult to determine the season of the feeding event. Furthermore, in some cases we could not identify from feeding sign the actual food that was eaten.

Interviews with indigenous hunters yielded a long list of bear foods and information about when and how bears ate them (Table 4). Other studies have similarly documented the striking breadth and depth of "what people untutored in science, know about plants and animals" (Ellen 1998:89). Ellen (1993) found that the Nuaula people in southeast Asia knew an enormous amount about foods and behaviors of wild pigs, an animal that they hunted. Hunters' knowledge about bears in Taiwan came from personal observations and experiences conveyed through generations; thus, it covered a much longer period and broader area than we observed first hand, and so was less prone to spatial or temporal biases. These data were clearly more inclusive of spring and summer foods than data obtained from scats and feeding sign. However, food items listed by interviewees were difficult to quantify in terms of relative importance to bears. As an approximate index to this, we used the number of interviewees reporting each food item (Table 1).

The principal problem with collecting ethnobiological information in our study was the interpretation and reliability of the data (Table 4). Interpretations may be confounded by language difficulties, as some ethnobiologists have indicated (Posey 1992, Ellen 1998, Berkes 1999). We attempted to avoid this problem by living in the villages, going into the field with interviewees, and collecting samples of food items that were discussed. However, informants sometimes used local names that we could not translate or described plants that they could not name. The larger potential problem was misinformation relayed to us because of misconceptions by the local hunters. These hunters had a vested interest in being astute observers of nature because they had to rely upon their knowledge to obtain food for themselves and their family (Ellen 1998, 1999; Berkes 1999; Berlin 1999; Diamond and Bishop 1999). However, most hunters did not specifically seek bears, and the circumstances in which they most often encountered bears or their sign, namely around their ungulate traps or sometimes in their crop fields, may have prejudiced their impressions. Hunters seemed well aware that bear diets were basically vegetarian, yet they invariably listed ungulates as a common food item even though few hunters ever saw bears attacking ungulates. We do not know how many based their opinions of bear carnivory on scats or natural sign (carcasses) versus just bear sign at their traps. We also wondered at times whether their descriptions of bear diets were based only on direct observations or included some degree of supposition, imagination, and enhancement (Peyton 1980, Berkes 1999, Huntington 2000). We were aware of one case where information was evidently obtained from television because it concerned another species of bear.

None of the 3 methods that we used to ascertain the diet of black bears was unbiased or error-free. They had differing attributes (Table 4), however, which made them complimentary rather than redundant. We recognize that in most other studies, scats are sufficient to describe bear diets. More attention to feeding sign, however, might improve interpretations of feeding behaviors. Finally, in situations such as ours, where bears are at low density and wet conditions cause scats to rapidly disintegrate, traditional ecological knowledge may greatly enhance the biological data set. To biologists wary of second-hand information, we suggest that time spent with local, knowledgeable people may be more productive than time spent wandering about the forest looking for scats and sign of rare animals.

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