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Stomach contents of brown bears *Ursus arctos* in Hokkaido, Japan

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We determined the seasonal food habits of brown bears *Ursus arctos* in three regions of Hokkaido, Japan, over eight years (1991-1998) by analysing the stomach contents of 556 bears killed for nuisance control or sport hunting. Seasonally dominant food items changed from herbaceous plants (61-80% in volume) in spring, to herbaceous plants (53-97% in volume) and ants (0-18% in volume) in early summer, crops (32-46% in volume) and herbaceous plants (26-31% in volume) in late summer, and berries (25-39% in volume), acorns and nuts (8-16% in volume) in autumn. These diet shifts were consistent among the three investigated regions. Crop depredation by brown bears in late summer occurred extensively in Hokkaido and was probably driven by a shortage of alternative food sources during this season. The proportion of sika deer *Cervus nippon yesoensis* in the diet increased during the 1990s in eastern Hokkaido (25.2% in frequency), where bears consumed deer throughout the year. Bears probably acquired deer meat from carcasses left in the fields after the deer were shot for nuisance control and sport hunting. In the Oshima Peninsula of southern Hokkaido, bears consumed large amounts of anthropogenic waste (16% in frequency).

Key words: anthropogenic waste, carcass, Cervus nippon yesoensis, crop damage, diet, Japan, Ursus arctos

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The Japanese brown bear *Ursus arctos* only occurs on Hokkaido, the northern island of Japan. Brown bears were distributed throughout Hokkaido until the latter half of the 19th century. By 1991, however, their distribution had decreased by roughly 50% as a result of the development of major plains and riparian areas (Mano & Moll 1999), and five subpopulations are now recognised (Hokkaido Institute of Environmental Sciences (HIES) 2000). Because developers consider them to be agricultural pests and a threat to human life, bears are targeted for extermination (Mano & Moll 1999), and the bear population of Hokkaido is thought to be in steady decline over the long term (Hokkaido Government Nature Preservation Division 1986, Aoi 1990a, Mano 1993). Based on interviews with local hunters, the bear population was estimated to number 1,771-3,628 in the 1990s (HIES 2000). In the mid-1980s and early 1990s, the government of Hokkaido changed brown bear hunting regulations to reduce the overharvesting of bears (Mano 1998). Specifically, the use of box traps in sport hunting was prohibited in 1985, the spring cull was abolished in 1990, and the use of foot snares in sport hunting was prohibited in 1992.

Although there is little evidence for a rapid increase in brown bear populations during the last decade, many local people believe that the bear population is growing, based on increased crop damage and human-bear encounters (HIES 1995, 1996, 2000). This situation stimulates unnecessary killing of bears, because since 1918 it has been legal to kill nuisance bears throughout the year to protect life and property (Mano 1998). During 1991-1998, the average annual number of bears killed in Hokkaido, including those killed for nuisance control and sport hunting, was 236.1 bears per year (HIES 2000). Given the low reproductive rate of bears, it is unrealistic to assume that the population could have recovered rapidly under such heavy hunting pressure (Bunnel & Tait 1981). It is more probable that changes in bear behaviour have caused the increases in crop damage and human-bear encounters.

Brown bears are opportunistic omnivores that have a broad ecological plasticity to adapt to changes in ecological conditions (Stirling & Derocher 1990, Servheen et al. 1999). The habitat of brown bears in Hokkaido has certainly changed over the past decades. Exploitation of natural forests has increased markedly since the 1960s, and this has resulted in fragmentation of bear habitat and a decrease in herbaceous plants and fruit production in the forest (Aoi 1990a, b). Moreover, the forest habitat itself has become degraded (HIES 1995, 1996, 2000). In addition, the sika deer *Cervus nippon yesoensis* population has increased dramatically in the eastern part of Hokkaido, and was estimated to be about 200,000 in 1993, even though the species once faced extinction during the latter half of the 19th century (HIES 1997).

However, few data are available on the changes in bear behaviour. Because brown bears are opportunistic omnivores, their diets reflect naturalisation to their ecological conditions. Several studies investigated the food habits of brown bears in Hokkaido in the 1980s (Aoi 1985, Ohdachi & Aoi 1987, Abe et al. 1987, Yamanaka & Aoi 1988, Hokkaido Government Nature Preservation Division 1992); however, these studies covered only small areas or short periods. Moreover, no studies examined the food habits of bears in the 1990s, when human-bear conflict increased.

Since 1991, the government of Hokkaido has collected brown bear samples, including stomach contents from killed bears, from all over Hokkaido for purposes of scientific management (HIES 1994). The object of our study was therefore to document the seasonal composition of the diet of brown bears in three regions of Hokkaido by analysing and comparing the stomach contents of bears killed throughout the island during an eight-year period (1991-1998). Special attention was paid to any dependence on human-derived resources. The importance of crops, anthropogenic waste, and deer carcasses in the diet are discussed in connection with the recent increases in the human-bear conflict.

Study area

Hokkaido, the northernmost major island of Japan (Fig. 1), covers about 78,500 km^2. The mean annual temperature is around 8.5°C in the southwest and 6.0°C in the north, and the annual precipitation ranges within 800-1,200 mm. Forests cover ca 70% of the area. Most areas lie in the intermediate zone between the northern Asiatic temperate and the subarctic zones, and are dominated by mixed forests of conifers such as *Abies sachalinensis* and *Picea jezoensis*, and deciduous broad-leaved trees like *Acer mono* and *Tilia japonica* (Tatewaki

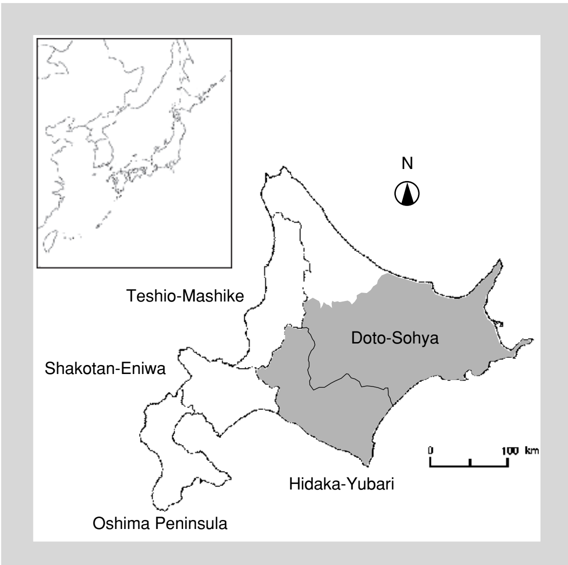

Figure 1. The five regions in the study area in Hokkaido, Japan, are divided by solid lines corresponding to the boundaries distinguishing five brown bear populations as described by the Hokkaido Institute of Environmental Sciences (1994). The shaded area is inhabited by a high-density sika deer population.

& Igarashi 1971). The Oshima Peninsula is located in southwest Hokkaido, entirely within the northern Asiatic temperate zone, which is characterised by *Fagus crenata*. The major land use is agricultural in the Oshima Peninsula and the Hidaka-Yubari region, whereas dry fields and pastures dominate the Doto-Sohya region.

About six million people live in Hokkaido. When bears cause damage, controlled killing of nuisance individuals is permitted, and the sport hunting season runs from 1 October to 31 January. The government of Hokkaido has divided the bear population into five regions to meet certain management objectives (HIES 1994). The numbers of legally killed bears in each region between 1991 and 1998 were: Oshima Peninsula: 512 (171 females, 338 males, three unknown); Shakotan-Eniwa: 21 (10 females, 11 males); Teshio-Mashike: 11 (one female, 10 males); Doto-Sohya; 696 (275 females, 415 males, six unknown); and Hidaka-Yubari: 640 (227 females, 403 males, 10 unknown; HIES 2000).

Material and methods

The Hokkaido Institute of Environmental Sciences (HIES) has been collecting the stomachs of bears killed for nuisance control and sport hunting since 1991. When hunters kill bears, they must report their kills to the government of Hokkaido, and they have been asked to collect and keep bear stomach contents and other organs. Occasionally, frozen specimens are couriered directly to the HIES by hunters, and in other cases they are sent via city, town or village offices, or via subprefectural offices of the government of Hokkaido. The samples are typically sent to the HIES about three days after a kill and are preserved in a freezer at -40°C before analysis. Because subprefectural government officials sometimes request hunters to kill nuisance bears under their hunting licenses during the sport hunting season, it is impossible to determine the correct numbers of the two categories with complete accuracy for statistical calculations. We therefore included all reported kills in our analyses.

After thawing, samples were washed with tap water on a 2.0-mm mesh sieve; material remaining on the sieve was spread onto an enamel tray (38 × 33 cm). We grouped the material into 11 categories: herbaceous plants, berries, acorns and nuts, fallen leaves and twigs, other plant material, mammals, insects, other animal material, crops, anthropogenic waste and 'other'. We recorded the frequency of occurrence of each diet category in each sample. Thereafter, we used two methods to determine the percent volume of each food item per sample. The samples collected from 1991 to 1993 were analysed by the graduated cylinder method (Sato et al. 2000). We first separated the contents into each category and then placed them in a graduated cylinder to determine the volume (ml). The samples collected from 1994 to 1998 were analysed by the point-frame method (Sato et al. 2000) to save time in the analysis. The tray across which the contents were spread was marked with a 1 x 1-cm grid at the bottom, and the points of intersection were regarded as point frames. We counted more than 400 points. Sato et al. (2000) confirmed statistically that these two estimates are directly related and provided an accurate method to evaluate the diet of brown bears. We also recorded the frequency of occurrence and the volume of smaller groups within the 11 categories, such as particular species or genera, to obtain a better picture of local and seasonal characteristics of the diet.

We analysed 758 stomach contents collected from March to January during 1991-1998. This included 40.3% of all bears killed (HIES 2000). Among the samples, 186 (19 of unknown origin, 102 box-trapped or baited and 65 with empty stomachs) were excluded from the analyses, and the remaining 572 samples were used. We divided them into five regions based on the sampling locations: Oshima Peninsula (223 samples), Shakotan-Eniwa (14), Teshio-Mashike (2), Doto-Sohya (218) and Hidaka-Yubari (115). These five regions corresponded to the distributions of the five subpopulations delineated by the Hokkaido Government Nature Preservation Division (1986). The Shakotan-Eniwa (14 samples) and Teshio-Mashike (two samples) regions were excluded from our study owing to their small sample sizes; so, we analysed food habits only from the remaining three regions, in a total of 556 stomachs.

We divided the samples into four seasons based on plant phenology: spring (March-May), early summer (June-July), late summer (August-September), and autumn (October-January) to reveal seasonal changes in the diet. We summed the frequency of occurrence of each diet item in each sample by season. The percent volume of each food item in a sample was categorised into seven grades: 0 for $x < 0.1\%$, 1 for $0.1\% \le x < 20\%$, 3 for $20\% \le x < 40\%$, 5 for $40\% \le x < 60\%$, 7 for $60\% \le x < 80\%$, 9 for $80\% \le x < 100\%$, and 10 for $x = 100\%$. We then totalled the score for each food item in each sample by season. Based on the values for the frequency of occurrence and the volume, we performed a Pearson chi-square test for equality (SPSS Base ver. 11.5J and SPSS Exact Test) to test for differences in the diet among seasons for the three regions, as well as for differences in the diet among the three regions for each season. Because of insufficient sample sizes, we excluded spring and early summer data from Hidaka-Yubari from the statistical analyses.

The percentage of the frequency of occurrence for each diet item by season was calculated by dividing the frequency of occurrence by the total number of samples for each season. The percentage of the volume of each diet item by season was calculated by dividing the volume occurring in the samples in each season by the sum.

Results

Seasonal changes in the diet

Percent frequency of occurrence (F) and percent volume (V) of each diet category in the brown bear stomach contents from the three studied regions (Oshima Peninsula, Doto-Sohya and Hidaka-Yubari) are summarised in Tables 1-3. For all three regions, the diet composition based on 11 categories showed significant seasonal changes (Oshima Peninsula: $\chi^2 = 155.72$, df = 30, $P < 0.0001$ for F, $\chi^2 = 1121.09$, df = 30 , $P < 0.0001$ for V; Doto-Sohya: $\chi^2 = 114.51$, df = 30, $P < 0.0001$ for F, $\chi^2 = 1208.56$, df = 30, $P < 0.0001$ for V; Hidaka-Yubari: $\chi^2 = 40.88$, df = 10, $P < 0.0001$ for F, $\chi^2 = 362.28$, df = 10, $P < 0.0001$ for V).

We observed common trends in seasonal diet changes of bears among the three regions as follows. Herbaceous plants, including forbs, graminoids and *Symplocarpus renifolius*, were dominant in spring. They remained high in F and V throughout early summer, and consumption of insects, particularly ants, increased in early summer. In late summer, the amount of crops in the diet, particularly corn *Zea mays*, increased, consumption of herbaceous plants remained high, ants featured frequently, and berries appeared. In autumn, berries, particularly of *Actinidia arguta*, and acorns and nuts, particularly of *Quercus crispula*, were consumed, while the prevalence of herbaceous plants, ants and crops decreased. The fruits of *Vitis coignetiae* and *Actinidia polygama* were also important diet items in autumn in all three regions.

Comparisons among the three regions

We compared the frequencies of occurrence and the volume of the diet items among the three regions in each season. Significant differences were found in all cases, except for F in late summer (spring: $\chi^2 = 22.90$, df = 9, $P = 0.005$ for F, $\chi^2 = 149.67$, df = 9, $P < 0.0001$ for V; early summer: $\chi^2 = 23.42$, df = 9, $P = 0.003$ for F, $\chi^2 = 87.00$, df = 9, $P < 0.0001$ for V; late summer: $\chi^2 = 22.58$, df = 20, $P = 0.317$ for F, $\chi^2 = 110.14$, df = 20, $P < 0.0001$ for V; autumn: $\chi^2 = 71.23$, df = 20, $P < 0.0001$ for F, $\chi^2 = 441.40$, df = 20, $P < 0.0001$ for V).

The Oshima Peninsula region differed somewhat from the other regions in that in spring bears ate *Fagus crenata* nuts and *Quercus crispula* acorns that had matured the previous autumn, as well as the buds of *Fagus crenata*. Most of the graminoids that appeared in spring in the Oshima Peninsula region bore grains, indicating that bears consumed overwintering plants. A high frequency and great volume of ants in the diet in early summer were also characteristic. The second major crop consumed in late summer was rice *Oryza sativa*, but corn was the most important crop species. In autumn, consumption of crops remained high in the Oshima Peninsula. Anthropogenic waste, especially scraps and fishery waste, were consumed most frequently and in the largest proportions in the Oshima Peninsula (Fig. 2).

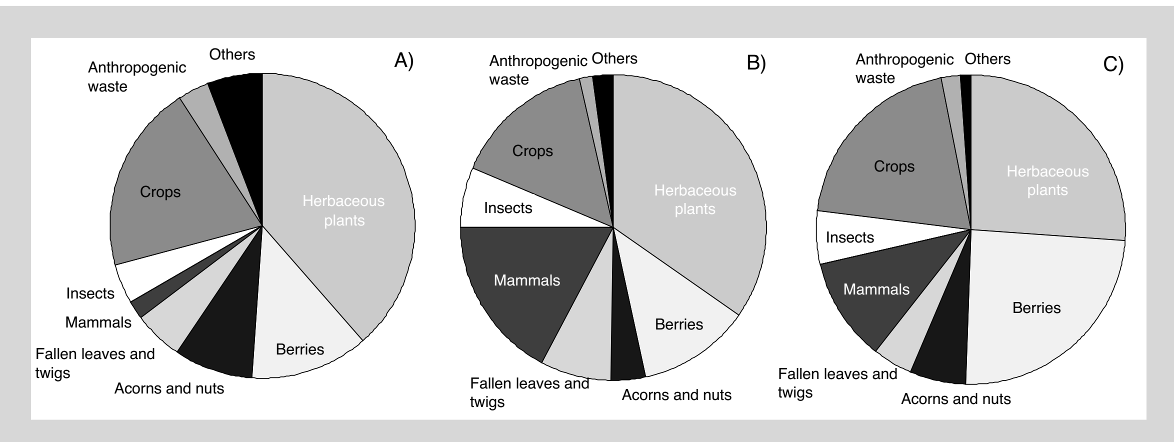

Figure 2. Percent volume for major diet categories in the brown bear stomach contents collected in the Oshima Peninsula (A; N = 209), Doto-Sohya (B; N = 212) and Hidaka-Yubari (C; N = 111) regions in Hokkaido, Japan, during 1991-1998.

Table 1. Percent frequency of occurrence (F) and percent volume (V) for each diet category in the brown bear stomach contents collected in the Oshima Peninsula region, Hokkaido, Japan, during 1991-1998.

	Spring		Early summer		Late summer		Autumn		Total	
	F (N = 50)	V (N = 46)	F (N = 20)	V (N = 19)	F (N = 65)	V (N = 61)	F (N = 88)	V (N = 83)	F (N = 223)	V (N = 209)
Plant material										
Herbaceous plants	*94.00*	*78.07*	*95.00*	*53.39*	*64.62*	*29.24*	*59.09*	*20.00*	*71.75*	*38.50*
Forbs	70.00	48.57	90.00	48.31	56.92	23.69	52.28	18.00	60.99	29.29
Graminoids	36.00	16.80	10.00	0.85	20.00	1.80	15.91	1.33	21.08	4.71
Symplocarpus renifolius	16.00	12.70	5.00	3.81	4.62	2.85	1.14	0.11	5.83	3.97
Equisetum spp.	2.00	-	5.00	0.42	6.15	0.90	5.68	0.56	4.93	0.52
Berries	*8.00*	-	*25.00*	*5.93*	*32.31*	*7.20*	*65.91*	*25.33*	*39.46*	*12.66*
Actinidia arguta	-	-	-	-	20.00	4.05	57.95	19.56	28.70	8.86
Actinidia polygama	-	-	-	-	4.62	0.30	3.41	1.22	2.69	0.57
Actinidia kolomikta	-	-	-	-	1.54	0.15	3.41	0.22	1.79	0.13
Vitis coignetiae	-	-	-	-	6.15	0.45	14.77	2.22	7.62	1.00
Aralia spp.	-	-	-	-	4.62	0.45	5.68	0.33	3.59	0.26
Prunus spp.	-	-	5.00	0.42	1.54	1.35	1.14	0.11	1.35	0.48
Swida controversa	-	-	-	-	-	-	4.55	1.44	1.79	0.57
Rubus spp.	-	-	10.00	0.42	-	-	-	-	0.90	0.04
Morus australis	-	-	5.00	2.97	-	-	-	-	0.45	0.31
Others	8.00	-	20.00	2.12	7.69	0.45	3.41	0.22	7.17	0.44
Acorns and nuts	*26.00*	*6.56*	-	-	*12.31*	*2.70*	*28.41*	*15.67*	*0.63*	*8.34*
Fagus crenata	12.00	2.87	-	-	-	-	3.41	2.78	4.04	1.70
Quercus crispula	10.00	3.48	-	-	7.69	1.50	14.77	8.89	20.45	4.67
Castanea crenata	-	-	-	-	-	-	3.41	1.56	1.35	0.61
Juglans mandshurica var. *sachalinensis*	-	-	-	-	4.62	1.20	1.14	0.11	1.79	0.39
Others	4.00	0.20	-	-	-	-	5.68	2.33	3.14	0.96
Fallen leaves and twigs	*58.00*	*5.74*	*55.00*	*8.90*	*36.92*	*5.55*	*44.32*	*3.67*	*46.19*	*5.19*
Others	*42.00*	*5.53*	*25.00*	*1.27*	*15.38*	*1.35*	*11.36*	*1.00*	*20.63*	*2.10*
Roots of forbs	4.00	2.05	-	-	3.08	-	1.14	-	2.24	0.44
Buds of *Fagus crenata*	22.00	1.84	10.00	0.42	-	-	-	-	5.83	0.44
Others	18.00	1.64	15.00	0.85	13.85	1.35	11.36	1.00	13.90	1.22
Animal material										
Mammals	*10.00*	*1.02*	-	-	*6.15*	*2.55*	*9.09*	*2.33*	*7.62*	*1.88*
Cervus nippon yezoensis	-	-	-	-	-	-	1.14	1.00	0.45	0.39
Unknown	10.00	1.02	-	-	6.15	2.55	7.95	1.33	7.17	1.49
Insects	*14.00*	*0.41*	*85.00*	*19.07*	*35.38*	*5.85*	*15.91*	*1.00*	*27.35*	*4.15*
Formicidae	4.00	0.41	85.00	17.80	24.62	4.35	9.09	0.33	19.28	3.32
Vespidae	2.00	-	5.00	0.42	10.77	1.35	2.27	0.22	4.93	0.52
Maggots	-	-	-	-	3.08	-	2.27	0.22	1.79	0.09
Others	12.00	-	15.00	0.85	7.69	0.15	6.82	0.22	8.97	0.22
Others	*6.00*	*0.41*	*10.00*	*0.42*	*10.77*	*1.95*	*15.91*	*1.89*	*11.66*	*1.44*
Cambaroides japonicus	4.00	0.41	5.00	0.42	9.23	0.60	10.23	0.78	8.07	0.61
Other invertebrates	2.00	-	-	-	-	-	2.27	-	1.35	-
Others	2.00	-	5.00	-	3.08	1.35	4.55	1.11	3.59	0.83
Crops										
Crops	-	-	-	-	*56.92*	*37.48*	*31.82*	*23.56*	*29.15*	*20.17*
Corn	-	-	-	-	33.85	23.69	23.86	17.67	19.28	13.84
Rice	-	-	-	-	18.46	13.19	2.27	2.11	6.28	4.67
Pear	-	-	-	-	1.54	-	3.41	1.56	1.79	0.61
Apples	-	-	-	-	-	-	1.14	1.11	0.45	0.44
Sugar beets	-	-	-	-	3.08	0.30	-	-	0.90	0.09
Grass	-	-	-	-	1.54	0.15	-	-	0.45	0.04
Carrots	-	-	-	-	1.54	0.15	1.14	1.11	0.90	0.48
Others										
Anthropogenic waste	*8.00*	*1.23*	*30.00*	*8.05*	*13.85*	*3.30*	*18.18*	*3.44*	*15.70*	*3.40*
Others	*8.00*	*1.02*	*40.00*	*2.97*	*10.77*	*2.85*	*29.55*	*2.11*	*20.18*	*2.18*
Soil and pebbles	8.00	0.61	40.00	2.97	10.77	0.45	13.64	1.67	13.90	1.22
Others	8.00	0.41	5.00	-	10.77	2.40	20.45	0.44	13.45	0.96

Table 2. Percent frequency of occurrence (F) and percent volume (V) for each diet category in the brown bear stomach contents collected in the Doto-Sohya region, Hokkaido, Japan, during 1991-1998.

	Spring		Early summer		Late summer		Autumn		Total	
	F (N = 45)	V (N = 44)	F (N = 26)	V (N = 26)	F (N = 75)	V (N = 72)	F (N = 72)	V (N = 70)	F (N = 218)	V (N = 212)
Plant material										
Herbaceous plants	*82.22*	*60.79*	*92.31*	*63.57*	*72.00*	*31.89*	*52.78*	*11.27*	*70.18*	*34.65*
Forbs	62.22	31.95	88.46	58.21	68.00	28.04	44.44	6.96	61.47	25.36
Graminoids	33.33	6.02	19.23	5.00	28.00	3.85	26.39	4.18	27.52	4.54
Symplocarpus renifolius	28.89	22.82	3.85	0.36	-	-	1.39	0.13	6.88	4.75
Berries	2.22	0.21	11.54	3.57	26.67	6.82	66.67	27.72	33.03	12.09
Actinidia arguta	-	-	7.69	2.14	6.67	0.62	54.17	23.54	21.10	8.35
Actinidia polygama	-	-	-	-	1.33	-	-	-	0.46	-
Actinidia kolomikta	-	-	-	-	5.33	0.37	-	-	1.83	0.13
Vitis coignetiae	-	-	-	-	10.67	2.23	13.89	2.53	8.26	1.61
Aralia spp.	-	-	-	-	1.33	0.12	1.39	0.13	0.92	0.08
Prunus spp.	-	-	3.85	1.07	2.67	0.62	5.56	0.51	3.21	0.30
Swida controversa	-	-	-	-	-	-	1.39	-	0.46	-
Sorbus commixta	-	-	-	-	1.33	1.12	4.17	0.89	1.83	0.68
Rubus spp.	-	-	-	-	-	-	-	-	-	-
Others	2.22	0.21	3.85	0.36	5.33	1.74	4.17	0.13	4.13	0.93
Acorns and nuts	*13.33*	*2.49*	-	-	*2.67*	*0.62*	*22.22*	*8.23*	*11.01*	*3.48*
Quercus crispula	8.89	3.32	-	-	1.33	0.12	15.28	7.97	7.34	2.80
Juglans mandshurica var. *sachalinensis*	4.44	0.21	-	-	2.67	0.50	2.78	-	2.75	0.21
Others	4.44	0.41	-	-	-	-	4.17	0.25	2.29	0.47
Fallen leaves and twigs	*53.33*	*8.51*	*26.92*	*3.21*	*45.33*	*6.08*	*38.89*	*10.13*	*42.66*	*7.59*
Others	*8.89*	*0.41*	*7.69*	*3.21*	*8.00*	*0.62*	*12.50*	*0.25*	*9.63*	*0.76*
Roots of forbs	-	-	-	-	-	-	1.39	-	0.46	-
Others	8.89	0.41	7.69	3.21	8.00	0.62	12.50	0.25	9.63	0.76
Animal material										
Mammals	*42.22*	*23.86*	*23.08*	*4.29*	*18.67*	*6.20*	*56.94*	*28.86*	*36.70*	*17.18*
Cervus nippon yezoensis	33.33	18.26	15.38	3.57	9.33	4.59	55.56	28.73	30.28	15.35
Unknown	8.89	5.60	7.69	0.71	9.33	1.61	1.39	0.13	6.42	1.82
Insects	8.89	1.24	57.69	8.21	57.33	13.03	23.61	2.41	36.24	6.49
Formicidae	6.67	1.04	50.00	7.50	45.33	8.31	5.56	0.51	24.77	4.11
Vespidae	-	-	-	-	18.67	3.47	6.94	0.51	8.72	1.36
Maggots	2.22	0.21	3.85	0.36	1.33	0.87	6.94	0.89	3.67	0.68
Others	-	-	3.85	0.36	5.33	0.37	6.94	0.51	4.59	0.34
Others	*6.67*	*0.62*	*3.85*	*0.36*	*9.33*	*0.99*	*6.94*	*0.38*	*7.34*	*0.64*
Cambaroides japonicus	6.67	0.62	3.85	0.36	5.33	0.25	4.17	-	5.05	0.25
Other invertebrates	-	-	-	-	1.33	0.12	-	-	0.46	0.04
Others	-	-	-	-	2.67	0.62	2.78	0.38	1.83	0.34
Crops										
Crops	-	-	*19.23*	*12.50*	*48.00*	*32.26*	*11.11*	*7.34*	*22.48*	*14.97*
Corn	-	-	-	-	30.67	22.08	5.56	4.94	12.39	9.20
Wheat	-	-	3.85	0.36	-	-	-	-	0.46	0.04
Melons	-	-	3.85	0.36	1.33	0.12	-	-	0.92	0.08
Pear	-	-	-	-	-	-	1.39	0.13	0.46	0.04
Sugar beets	-	-	19.23	11.79	4.00	9.68	19.44	2.28	10.09	5.47
Grass	-	-	-	-	1.33	0.37	-	-	0.46	0.13
Others										
Anthropogenic waste	*6.67*	*0.62*	*11.54*	*1.07*	*8.00*	*0.62*	*11.11*	*2.91*	*9.17*	*1.44*
Others	*8.89*	*1.24*	-	-	*13.33*	*0.87*	*972.00*	*0.51*	*9.63*	*0.72*
Soil and pebbles	8.89	1.04	-	-	13.33	0.74	9.72	0.51	9.63	0.64
Others	8.89	0.21	-	-	1.33	0.12	5.56	-	4.13	0.08

Table 3. Percent frequency of occurrence (F) and percent volume (V) for each diet category in the brown bear stomach contents collected in the Hidaka-Yubari region, Hokkaido, Japan, during 1991-1998.

	Spring		Early summer		Late summer		Autumn		Total	
	F (N = 11)	V (N = 10)	F (N = 3)	V (N = 3)	F (N = 32)	V (N = 32)	F (N = 69)	V (N = 66)	F (N = 115)	V (N = 111)
Plant material										
Herbaceous plants	*100.00*	*79.63*	*100.00*	*96.77*	*78.13*	*26.03*	*52.17*	*14.77*	*65.22*	*26.08*
Forbs	100.00	74.07	100.00	77.42	75.00	20.82	37.68	8.66	55.65	19.95
Graminoids	27.27	1.85	66.67	19.35	28.13	2.19	18.84	1.14	23.48	1.99
Symplocarpus renifolius	18.18	3.70	-	-	12.50	3.01	7.25	4.97	9.56	4.14
Berries	*9.09*	-	-	-	*25.00*	*5.21*	*72.46*	*39.20*	*51.30*	*24.42*
Actinidia arguta	-	-	-	-	9.38	0.82	56.52	28.69	36.52	16.97
Actinidia polygama	-	-	-	-	3.13	0.82	8.70	2.13	6.09	1.49
Actinidia kolomikta	-	-	-	-	3.13	-	-	-	0.87	-
Vitis coignetiae	-	-	-	-	3.13	0.27	26.09	5.11	16.52	3.06
Aralia spp.	-	-	-	-	12.50	1.92	1.45	-	4.35	0.58
Sorbus commixta	-	-	-	-	-	-	1.45	0.14	0.87	0.08
Rubus spp.	-	-	-	-	3.13	1.37	-	-	0.87	0.41
Others	9.09	-	-	-	3.13	-	5.80	3.13	5.22	1.82
Acorns and nuts	-	-	-	-	*3.13*	*0.27*	*14.49*	*9.80*	*9.57*	*5.79*
Quercus crispula	-	-	33.33	-	-	0.27	13.04	9.09	8.70	5.38
Castanea crenata	-	-	-	-	-	-	1.45	0.71	0.87	0.41
Fallen leaves and twigs	*36.36*	*4.63*	*33.33*	*3.23*	*43.75*	*4.66*	*46.38*	*3.98*	*44.35*	*4.22*
Others	*9.09*	-	-	-	*9.38*	*0.55*	*10.14*	*0.85*	*9.57*	*0.66*
Animal material										
Mammals	-	-	-	-	*12.50*	*3.56*	*33.33*	*16.76*	*23.48*	*10.84*
Cervus nippon yezoensis	-	-	-	-	3.13	1.92	21.74	16.34	13.91	10.10
Unknown	-	-	-	-	9.38	1.64	14.49	0.43	11.30	0.75
Insects	*36.36*	*2.78*	*33.33*	-	*50.00*	*12.33*	*23.19*	*2.70*	*32.17*	*5.55*
Formicidae	36.36	2.78	33.33	-	34.38	4.66	4.35	0.14	16.52	1.74
Vespidae	9.09	-	-	-	18.75	5.75	4.35	-	8.70	1.74
Maggots	-	-	-	-	3.13	0.82	5.80	0.28	4.35	0.41
Others	-	-	-	-	15.63	1.10	10.14	2.27	10.43	1.66
Others	-	-	-	-	*6.25*	-	*10.14*	*0.14*	*7.83*	*0.08*
Cambaroides japonicus	-	-	-	-	-	-	4.35	0.14	2.61	0.08
Other invertebrates	-	-	-	-	-	-	2.90	-	1.74	-
Others	-	-	-	-	6.25	-	2.90	-	4.35	-
Crops										
Crops	-	-	-	-	*68.75*	*46.30*	*18.84*	*10.37*	*30.43*	*20.03*
Corn	-	-	-	-	21.88	14.79	11.59	8.24	13.04	9.27
Rice	-	-	-	-	9.38	3.01	2.90	0.57	4.35	1.24
Wheat	-	-	-	-	3.13	1.92	1.45	-	1.74	0.58
Watermelons	-	-	-	-	6.25	5.21	-	-	1.74	1.57
Melons	-	-	-	-	28.13	14.25	1.45	0.71	8.70	4.72
Pear	-	-	-	-	-	-	2.90	0.85	1.74	0.50
Apples	-	-	-	-	3.13	1.37	-	-	0.87	0.41
Grapes	-	-	-	-	3.13	2.47	-	-	0.87	0.75
Sugar beets	-	-	-	-	6.25	3.29	-	-	1.74	0.99
Others										
Anthropogenic waste	*9.09*	*12.96*	-	-	*3.13*	*0.27*	*10.14*	*0.99*	*7.83*	*1.82*
Others	-	-	-	-	*9.38*	*0.82*	*18.84*	*0.43*	*13.91*	*0.50*
Soil and pebbles	-	-	-	-	9.38	0.55	18.84	0.28	13.91	0.33
Others	-	-	-	-	9.38	0.27	4.35	0.14	6.09	0.17

A characteristic of the bears in the Doto-Sohya region was that they fed on sika deer meat throughout the year (see Fig. 2). A high proportion of sika deer meat was observed in spring and autumn (F = 33.3%, V = 18.3% in spring, and F = 55.6%, V = 28.7% in autumn). In early spring, *Symplocarpus renifolius* appeared in the northern part of the Doto-Sohya region. Consumption of crops in early summer, particularly sugar beets *Beta vulgaris*, was observed only in this region (F = 19.2%, V = 11.8% for sugar beets). Sugar beets were the second major crop consumed in late summer, whereas the most important species was corn. Berries of *Actinidia arguta* and sika deer meat made up the largest volume in autumn (23.5% for *Actinidia arguta* and 28.7% for sika deer).

The percent volume of crops eaten in late summer was highest in the Hidaka-Yubari region (46.3%), and the major crops consumed were corn and melons. In autumn, the percent volume of berries was the highest, with *Actinidia arguta* berries being the most important (V = 28.7%). Sika deer meat was also a major contributor to the diet in autumn (V = 16.3%). Percent volume of berries is the largest in the Hidaka-Yubari region in total (see Fig. 2).

Consumption of sika deer in eastern Hokkaido

Sika deer meat represented as much as 89% of the stomach contents containing mammals in the Doto-Sohya region and 93% in the Hidaka-Yubari region. Samples containing sika deer were collected primarily from the central and eastern parts of Hokkaido, which correspond to the sika deer distribution (HIES 2000, Kaji et al. 2000). Sika deer occurred more frequently in samples from areas with dense deer populations (HIES 1994; see Fig. 1) than in those from areas with fewer deer (25.2 vs 1.3%, $\chi^2 = 61.71$, df = 1, $P < 0.0001$). During 1991-1993, deer meat appeared in the diet only in late summer and autumn, while after 1994 it was also part of the spring and early summer diet (Fig. 3). Maggots comprised a greater proportion of the diet in the Doto-Sohya and the Hidaka-Yubari regions than in the Oshima Peninsula (see Tables 1-3), as they were highly associated with deer meat, which was consumed mainly in the former regions.

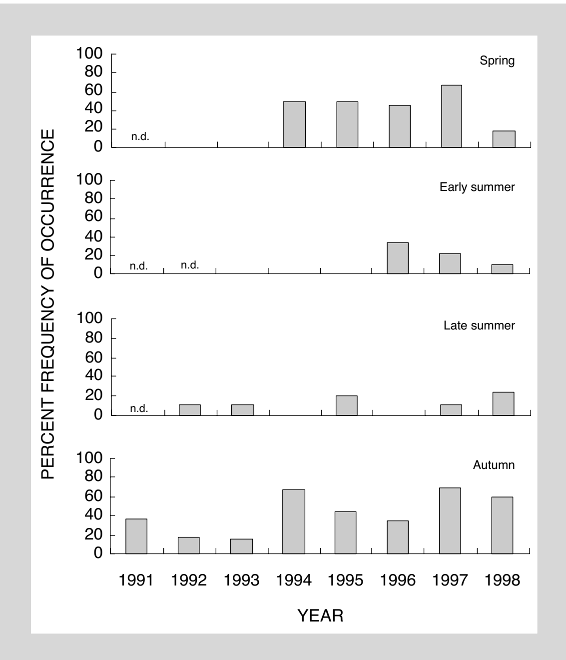

Figure 3. Seasonal changes in frequency of occurrence of sika deer meat in the stomach contents of brown bears killed in Hokkaido, Japan, during 1991-1998. n.d. indicates that no data were available.

Discussion

Seasonal changes in the diet of Hokkaido brown bears

All three regions showed similar seasonal changes in the foods eaten by brown bears, i.e., the dominant food items were herbaceous plants in spring and summer and fruits in summer and autumn. This pattern corresponds with those reported for other brown bear populations around the world (Yugoslavia: Cicnjak et al. 1987; USA: Mattson et al. 1991; Spain: Clevenger et al. 1992; Norway: Elgmork & Kaasa 1992; Canada: McLellan & Hovey 1995). However, it is difficult to conclude the same for the Hidaka-Yubari region because of the small sample sizes in spring and early summer.

In early spring when herbaceous plants were dormant, overwintering fruits were used in the Oshima Peninsula and the Doto-Sohya region. A similar phenomenon has been reported in southern Siberia, USSR (Bromlei 1965), Montana, USA (Mace & Jonkel 1986) and Alaska, USA (Stelmock & Dean 1986). In our study, deer meat appeared in the Doto-Sohya region during spring. Spring use of ungulates by brown bears has been reported from Spain (Slobodyan 1976), France (Berducou et al. 1983), Norway (Persson et al. 2001), Russia (Danilov 1983), the USA (Mattson et al. 1991) and Canada (McLellan & Hovey 1995).

In late summer, crops were important in all three regions. Since late summer is an intermediate season, when the nutritional values of herbaceous plants decrease (Cicnjak et al. 1987) and berries are still immature, brown bears eat various items. Bears living in habitats where different berries are available eat berries (e.g.

British Columbia, Canada: McLellan & Hovey 1995). In some populations, bears move to a variety of habitats to forage on premature herbaceous plants, e.g. northern slopes (Spain: Clevenger et al. 1992), creek bottoms (Yellowstone Park, USA: Mealey 1980) or alpine habitats (Alberta, Canada: Hamer & Herrero 1987). In other populations, bears eat alternative foods such as roots of Leguminosae (Alaska, USA: Stelmock & Dean 1986; Alberta, Canada: Hamer & Herrero 1987), ants (southern Siberia: Bromlei 1965; Pyrenees, France: Berducou et al. 1983), livestock (Pyrenees, France: Berducou et al. 1983) and fish (Yellowstone Park, USA: Mattson et al. 1991). We therefore assume that Hokkaido brown bears forage on crops during this season to compensate for a shortage of alternative natural foods.

Use of sika deer

It is noteworthy that the amount of sika deer meat in the diet increased during the 1990s. Although there were some observations of Hokkaido brown bears consuming deer before then (HIES 2000), food habit studies conducted in the 1980s found little or no use of sika deer (Aoi 1985, Ohdachi & Aoi 1987, Yamanaka & Aoi 1988). The extinction of wolves *Canis lupus*, replacement of native mixed hardwood forests with conifer plantations, and increased areas of pastureland all contributed to the expansion of sika deer in the late 1900s (Kaji et al. 2000). It is therefore quite probable that the increase in deer meat in the diet of bears has been caused by the marked increase in the sika deer population.

Exploitation of human-derived resources

Crops

Bears consumed crops most intensively in late summer and continued to eat them until autumn. In North America and Eurasia, brown bears invade crop fields and villages in the autumn (Yellowstone Park, USA: Blanchard & Knight 1991, Mattson et al. 1992; Spain: Slobodyan 1976; Baikal, Russia: Ustinov 1976). Consumption of crops often increases in years when other food resources are less available (Blanchard & Knight 1991); this seems to be the case in Hokkaido. When natural food production is low in autumn, the bears are forced to invade agricultural fields, causing damage to crops and resulting in nuisance control killing. Crop use in late summer is more habitual across Hokkaido.

In all of the regions studied, bears did not eat various species of crops, but rather limited themselves to just one or two species, particularly corn. Corn is nutritious and also provides cover for bears. In the Hidaka-Yubari region, melons were the second crop most commonly exploited by bears. Melons are economically highly valuable, particularly in the Yubari district, and bear damage is therefore serious. In the Doto-Sohya region, sugar beets contributed 12.5% of the bears' diet in early summer, as sugar beet roots are available for a long time, from early summer until autumn.

Anthropogenic waste

Since most of the samples were collected from 'nuisance controlled' bears, we had expected to find significant amounts of anthropogenic waste in the stomachs. Bears ate a lot of garbage, including scraps and fishery waste, particularly in the Oshima Peninsula. Anthropogenic waste strongly attracts bears (Herrero 1985, Craighead et al. 1995), and food-conditioned bears tend to be accustomed to people and invade human residential areas (Herrero 1985, Craighead et al. 1995). These bears are then regarded as 'nuisance bears' and are typically killed. To avoid this, it is necessary to control garbage disposal. Unnecessary kills can be reduced by providing proper garbage disposal facilities, as was done at camp sites in Yellowstone National Park (Herrero 1985).

Deer carcasses

In the early 1990s, bears in eastern Hokkaido consumed sika deer meat only during late summer and autumn (see Fig. 3). After 1994, however, deer meat appeared in the diet in spring and early summer. Year-round use of deer by Hokkaido brown bears is unique; bears in other areas eat ungulate meat mostly in spring (Boertje et al. 1988, Green et al. 1997, Mattson 1997), except in northern Europe (Danilov 1983, Persson et al. 2001). In northern Europe, ungulates are frequently attacked by bears and comprise the most important food for bears during summer (Persson et al. 2001), suggesting that brown bears are generally more carnivorous in northern areas (Danilov 1983, Persson et al. 2001). The range of Hokkaido brown bears, however, is located at the southern limit of Asian brown bears (Servheen 1990).

We consider it probable that Hokkaido brown bears consume deer meat more by scavenging on carcasses than by aggressive predation, for the following reasons. About 30,000 deer were hunted between 1994 and 1999 (during November-January) and more than 20,000 deer were shot for nuisance control throughout the year, outside the hunting season (Hokkaido Government 2000). After shooting the deer, hunters in eastern Hokkaido often leave the carcasses in the fields (HIES 2000, Lead Poisoned Eagles Network 1999, 2000, 2001); these would then be consumed by bears. The high incidence of maggots in the stomachs that contained deer meat suggests that bears scavenge on deer. Since deer-control measures are often applied near crop fields, and consequently deer carcasses are often left there, encounters between people and bears become more frequent in such areas. This problem is more serious in Hokkaido, where people live in close proximity to bear habitat.

Management implications

Because generalist omnivores are capable of adapting to a changing environment, bears will consume human-derived resources such as crops, anthropogenic waste and deer carcasses when they are available. Therefore, over 200 bears are killed for nuisance control purposes in Hokkaido each year. The most important and urgent measure of management for Hokkaido brown bears is to prevent them from using human-derived resources. We have demonstrated that the heaviest conflict between humans and bears occurs over crop damage, and that damage occurs most frequently in late summer because of the shortage of alternative foods during the season, when herbaceous plants used in the early summer have passed and berries, acorns and nuts used in autumn are not yet available. We must prevent bears from invading crop fields. Once bears become habituated to foraging on crops in agricultural fields, they will not refrain from invading crop fields. It is essential to promote non-lethal methods of prevention, such as clear-cutting bushes around crop fields and erecting electric fences. Appropriate disposal of anthropogenic waste and deer carcasses near crop fields must be carried out rapidly throughout Hokkaido under the direction of the administration.

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