SIZE AND GROWTH PATTERNS OF THE YELLOWSTONE GRIZZLY BEAR

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Abstract: Weights and/or measurements of 151 grizzly bears (*Ursus arctos*) captured 261 times were recorded from 1975 to 1985. Males were consistently heavier than females within all age classes beginning at age 2. Mean weight for 65 adult males (5+ years old) was 192 kg and 135 kg for 63 adult females (5+ years old). Mean monthly weights by sex and age class indicated adults lost weight from den emergence through July, generally regaining emergence weight by August. Weaned yearlings lost weight July–September, whereas unweaned yearlings gained weight during the same period. Sexual dimorphism in body measurements within age classes was apparent in cubs and became significant in all body measurements by age 3. Girth was the measurement most closely correlated with weight for both males and females. Adults feeding at garbage dumps weighed more than bears relying on natural food sources. Bears were smaller and weighed less in this study than during the period 1959–70, when major dumps were available as a food source. Mean annual weights of nondump females were highly correlated with annual habitat productivity indices for Yellowstone Park. Correlations between mean adult female weight and cub litter size ($r = 0.92$) and mean age at 1st cub production ($r = -0.52$) were apparent. In general, females with reliable high-energy foods tended to attain larger body sizes, mature at an earlier age, and have larger cub litters than females using relatively low-energy foods.

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Differences in size, weight, and growth patterns have been reported for several populations of grizzly bears in North America (Pearson 1975; Reynolds 1976, 1981; Ballard 1980; Glenn 1980; Spraker et al. 1981; Craighead and Mitchell 1982; Nagy et al. 1984). Nutrition has been suspected to be the major factor producing these differences in grizzly bears (Rausch 1963) and black bears (*U. americanus*) (Rogers et al. 1976, Beecham 1980).

The Yellowstone grizzly bear population was intensively studied from 1959 to 1970 by Frank and John Craighead (Craighead et al. 1974). During that period, major dumps were available to grizzly bears and provided a stable seasonal food source. Closure of those dumps in 1970 and 1971 eliminated that food supply for bears within Yellowstone National Park. Dumps serving communities adjacent to the Park were closed in 1982. Eliminating these food sources seriously affected the distribution and dynamics of the population (Knight and Eberhardt 1985). Effects of food supply changes on the size, weight, and growth patterns of bears from that population are reported here.

STUDY AREA

The study area is approximately 20,000 km^2, encompassing Yellowstone National Park and adjacent portions of Idaho, Montana, and Wyoming. Climate, physiography, and vegetative characteristics are described by Knight and Eberhardt (1985).

METHODS

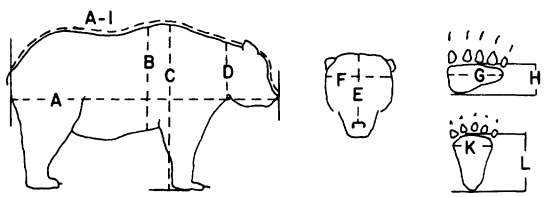
Weights and Measurements

From 1975 to 1985, bears were captured in culvert traps, foot snares, or "free darted" with immobilizing agents administered with a dart gun as part of the Interagency Grizzly Bear Study Team effort (Blanchard 1985). Immobilizing agents used were Sernylan (phencyclidine hydrochloride) or M-99 (etorphine). Ages were determined by examination of sectioned premolars for cementum annuli. Weights of live bears were determined with spring scales when possible; otherwise weights were estimated by experienced field personnel.

Weights of grizzly bears were estimated before administering immobilizing drugs, whereas scale weights were obtained after immobilizing the bear. Estimated and scale weights were recorded for 96 grizzly bears (53 males, 43 females). Paired *t*-tests indicated no statistical differences between estimated and scale weights ($P < 0.005$), and comparison analyses showed a high correlation between the 2 groups ($r = 0.95$). Estimated and scale weights were therefore combined for all further analyses. Weights of dead bears were obtained from necropsies performed by the Mont. Dep. of Fish, Wildl., and Parks.

Seven body measurements and 4 foot measurements were obtained from live bears (Fig. 1). All measurements were taken with a steel tape pulled snugly against the body and recorded along with sex and general body condition. Spring was April–June; summer, July–August; and fall, September–November. "Dump bears" refers to those bears known to use reliable supplemental food from human sources, such as garbage dumps; "nondump bears" refers to those not known to use such food sources. Adult bears were 5 years and older unless otherwise stated.

Methodology for calculating annual habitat quality indices is discussed by Mattson et al. (1986). One-way analysis of variance, the Student's *t*-test, and multiple comparisons were used to statistically test



A-I CONTOUR LENGTH: distance from base of tail to tip of nose with measuring tape following dorsal contour.

A TOTAL LENGTH: distance from tip of tail to tip of nose along side of body.

B GIRTH: circumference of chest just behind shoulder.

C HEIGHT: distance from top of shoulder along foreleg to lateral base of forefoot, with leg straightened to simulate a standing position.

D NECK CIRCUMFERENCE: measured posterior to jaws.

E HEAD LENGTH: distance between posterior protuberance of the parietal crest & tip of nose.

F HEAD WIDTH: distance between widest point of zygomatic arches.

G,K FOOT WIDTH: measurement at widest part of pad.

H,L FOOT LENGTH: distance from heel to front of pad.

Fig. 1. Measurements recorded from live grizzly bears, 1975–85.

differences in mean weights and measurements among sex and age groups. Analyses of annual and seasonal weight changes were performed on pooled samples.

RESULTS

Weight

Weights were recorded for 122 live grizzly bears immobilized 232 times, including 51 females and 71 males. Additional weights for 10 females and 19 males were obtained at necropsies. Nearly 70% of the weights were recorded during July, August, and September (Table 1). The heaviest adult female weighed 194 kg on 2 August 1981 as a 10-year-old; the lightest weighed 91 kg on 5 July 1984 as a 14-year-old. The heaviest adult male weighed 325 kg on 17 August 1977 as a 16-year-old, and the lightest weighed 98 kg on 11 August 1977 as a 10-year-old. The heaviest male and female recorded 1959–70 were 500 and 204 kg, respectively (Craighead and Mitchell 1982).

Male grizzly bears were consistently heavier than females within all age classes beginning at age 2 (P = 0.001–0.159) (Table 2). Sexual dimorphism in weights was apparent for northern interior Canadian grizzly bears at age 2 (Pearson 1975) and at age 1 for southwestern Alaskan coastal brown bears (Glenn 1980).

In general, males appeared to steadily gain weight annually until at least 15 years of age (Fig. 2). Mean annual rate of weight increase for males aged 4–15 years (5.6%) was markedly less than for males aged cub through 3 years (42.1%). One-way analysis of variance and multiple comparisons indicated mean weights of males 4 years and older belonged to 1 population. The mean weight of 5-year-old males was less than expected but could be explained by the small number of fall weights for this age class (1 of 9).

Annual weight patterns of females were less clear than those for males. Mean annual rate of weight increase for females aged cub through 3 years (36%), was also much greater than for females aged 4–13 years (5.2%). Females steadily increased in weight through age 13 (Fig. 2). At 6 years, mean weight dropped, partially due to a lack of fall weight samples. Mean weights of subsequent age classes suggest this drop in weight may be real, probably a reflection of the mean age of 1st cub production of 6.15 years in this population (Knight and Eberhardt 1985) and the subsequent nutritional drain on still growing, lactating females. Multiple comparisons of mean age class weights indicated females aged 4–7 belonged to 1 population, and females aged 8–13 years belonged to another. Limited data indicated females declined in mean weight after 13 years.

Females with cubs-of-the-year weighed an average of 129 kg compared to 140 kg for females with yearlings and 134 kg for lone adult females. These weight differences were not statistically significant. Troyer and Hensel (unpubl. data) found that the heaviest female grizzly bears on Kodiak Island were usually those without young.

Approximately 62% of the variation in male weight could be explained by age using linear regres-

Table 1. Captures by month of weighed grizzly bears, 1973–85.

	Males		Females		Total	
Month	*N*	%	*N*	%	*N*	%
Apr	2	1.32	0	—	2	0.76
May	20	13.16	7	6.31	27	10.27
Jun	17	11.18	13	11.71	30	11.41
Jul	25	16.45	25	22.52	50	19.01
Aug	41	26.97	32	28.83	73	27.76
Sep	30	19.74	29	26.13	59	22.43
Oct	12	7.90	5	4.50	17	6.46
Nov	4	2.63	0	—	4	1.52
Dec	1	0.66	0	—	1	0.38
Total	152		111		263	

Table 2. Mean weights of female and male grizzly bears by age class, 1975–85.

	Females				Males			
	N	Mean (kg)	Range	Coefficient of variation	*N*	Mean (kg)	Range	Coefficient of variation
Cub	8	22.2	5.9 – 30.9	16.1	16	24.2	5.9 – 52.2	23.3
1	13	58.3	25.0 – 77.2	11.9	18	63.0	45.4 – 99.0	12.3
2	11	84.4	54.5 – 122.6	11.7	19	98.4	68.1 – 124.9	7.4
3	9	100.2	77.2 – 120.3	7.9	17	137.9	99.9 – 181.6	8.7
4	8	116.0	90.8 – 158.9	10.9	14	154.0	90.8 – 242.9	12.9
5	9	125.1	102.2 – 161.2	6.5	9	149.1	102.2 – 240.6	13.7
6	5	115.3	100.0 – 127.1	5.2	8	185.7	147.6 – 219.7	6.0
7	7	120.3	109.0 – 136.2	3.8	7	189.4	158.9 – 227.0	6.7
8	7	126.8	102.2 – 181.6	9.2	5	172.1	158.9 – 181.6	2.8
9	4	143.6	115.8 – 181.6	8.7	6	199.0	136.2 – 272.4	11.9
10	6	146.3	102.2 – 194.3	12.5	5	168.9	97.6 – 204.3	11.6
11	6	152.5	103.5 – 193.0	9.6	7	224.0	145.3 – 288.3	10.6
12	4	134.5	102.2 – 158.9	8.8	4	199.0	170.3 – 244.3	7.7
13	5	170.7	129.4 – 190.7	6.4	2	261.1	249.7 – 272.4	2.8
14	2	97.6	90.8 – 104.4	4.5	2	233.8	190.7 – 276.9	11.9
15	2	138.5	136.2 – 140.7	1.0	1	301.9	—	—
16	2	113.5	102.2 – 124.9	6.4	2	259.9	195.2 – 324.6	16.0
17	—	—	—	—	1	147.6	—	—
18	1	181.6	—	—	—	—	—	—
20	—	—	—	—	1	215.7	—	—
22	2	125.8	90.8 – 160.7	17.8	1	238.4	—	—
Ad (5+)	63*	134.5	90.8 – 194.3	10.0	65*	193.3	97.6 – 324.6	11.4

*Sample sizes include 1 female and 4 males aged only as "adult."

sion analysis, whereas only 48% of the variation in female weight could be attributed to age. Correlations between weight and age for females were higher for cubs through 4 years ($r^2 = 0.67$) compared to the adult (5+ years) group ($r^2 = 0.05$). Less difference was observed for subadult and adult males ($r^2 = 0.75$ and 0.21, respectively) reflecting the steady annual weight increase for adult males.

Mean monthly weights by sex and age class indicated adult grizzly bears lost weight from den emergence through July, generally regaining emergence weight by August (Fig. 3). Mean seasonal weight gains for subadults 2–4 years old were less clear, although limited data suggested emergence weights were generally not regained until September.

Pooled samples indicated weaned yearlings steadily lost weight July–September, whereas unweaned yearlings gained weight during the same period (Fig. 3). By September, weaned yearlings weighed an average 21.7 kg less than unweaned yearlings ($N = 4$). The 2-year-old age class demonstrated the lowest spring-to-fall weight gain, with females gaining only 7% of their final weight during the year and males only 2% (Fig. 3). Low weight gains at this age probably reflected the stress of weaning during late spring and subsequent dispersal from the maternal home range, particularly for males (Knight et al. 1984).

Females exhibited greatest average spring-to-fall weight gains as 3- and 4-year-olds (30% and 29%, respectively). Males demonstrated greatest average spring-to-fall weight gains as 4- and 5-year-olds (39%

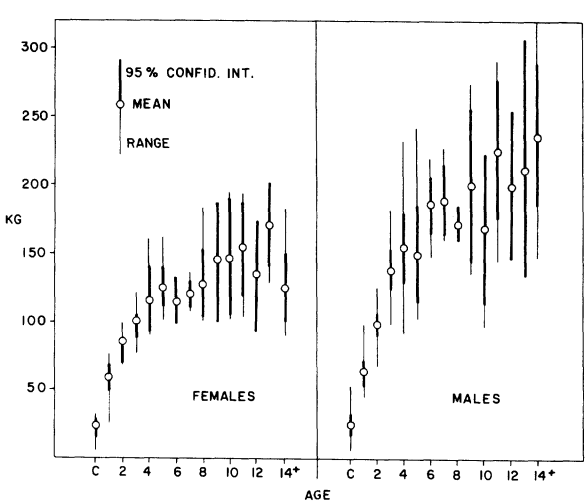


Fig. 2. Male and female grizzly bear weights by age class, 1975–85.

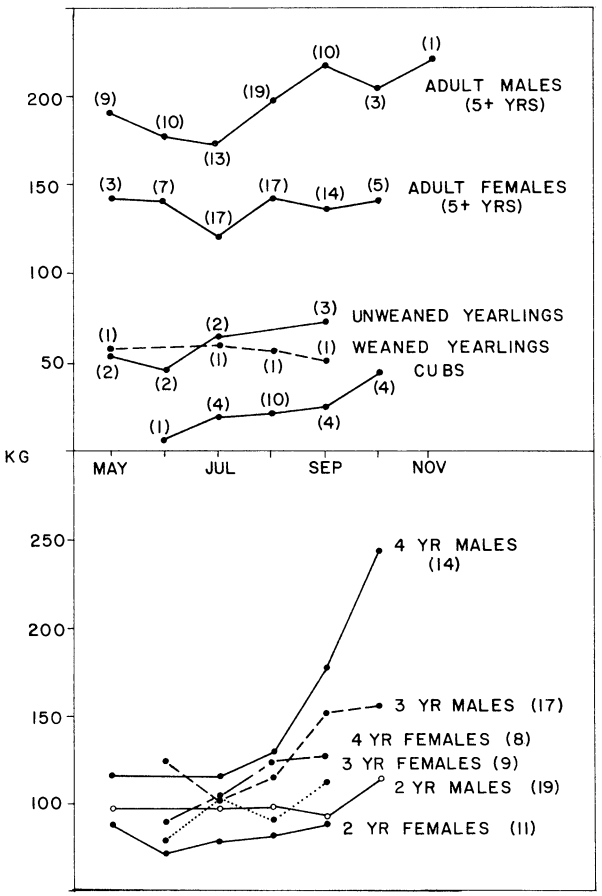


Fig. 3. Seasonal weight changes by sex and age class. Sample sizes are given in parentheses.

and 34%, respectively). Males aged 6 and older gained an average 15% of their final weight spring–fall. Greatest daily weight gain of 1.3 kg/day was recorded for 2 3- year-old males, 1 between 3 September and 20 September 1982, and 1 between 22 August and 13 September 1978. Lowest daily weight gain of 0.1 kg/day was recorded for 2 adult females, a 10-year-old with no young between 27 May and 25 August 1981, and a 6-year-old with cubs between 16 June and 5 July 1984. From 1 July to fall, males gained an average 1.0 kg/day compared to 0.4 kg/day for females (N = 11).

Adult male grizzly bears (4+ years) lost a greater percent of body weight over winter than adult females (5+ years) (18% and 8%, respectively). Kingsley et al. (1986) also recorded that males in northern Canada lost a greater percent of body weight over winter compared to females. Weight losses may have been greater than indicated for Yellowstone bears, because only 2 bears were captured before 1 May and only 4 after 1 November.

Measurements

Body measurements were recorded for 127 male and 100 female grizzly bears (Tables 3 and 4). The largest adult male measured 241 cm long (measurement A, Fig. 1), 117 cm at the shoulder (C), 95 cm around the neck (D), and had a hind foot pad 170 mm wide (K) and 216 mm long (L). The largest female was 193 cm long (A), 103 cm at the shoulder

Table 3. Mean body measurements of male grizzly bears by age class, 1975–85.

Age	N	Length (A)	Contour length (A-1)	Girth (B)	Height (C)	Neck (D)	Head		Front pad		Rear pad	
							Length (E)	Width (F)	Width (G)	Length (H)	Width (K)	Length (L)
Cub	13	88.3	108.7	72.5	54.3	42.1	26.9	14.4	86.6	50.9	80.0	112.4
1	16	127.6	157.4	91.8	71.9	52.7	32.9	17.5	116.8	60.0	104.1	141.9
2	17	129.2	159.3	103.9	80.1	59.7	35.4	20.9	122.7	59.5	116.5	166.9
3	15	152.4	182.5	112.9	88.8	67.4	39.4	20.6	133.9	70.7	121.6	171.6
4	11	158.8	183.0	116.6	94.0	68.9	39.5	23.3	137.0	68.4	123.9	173.1
5	8	152.7	188.0	114.4	92.3	65.8	40.2	22.6	135.0	74.0	127.8	186.0
6	8	166.7	191.8	139.5	95.5	82.5	42.3	25.3	146.4	81.5	135.5	185.0
7	4	159.7	188.5	131.0	92.3	78.5	41.7	28.0	150.0	70.0	134.0	173.3
8	5	162.8	189.0	126.8	97.0	77.0	38.0	26.0	147.8	73.5	134.8	172.0
9	5	160.0	200.0	142.0	94.0	87.0	43.0	28.0	147.4	75.0	140.4	192.8
10	3	164.7	195.3	133.0	97.5	80.3	41.0	29.3	155.0	81.7	139.0	192.0
11	5	152.8	213.7	131.0	98.5	80.3	42.3	26.3	149.3	77.0	132.0	191.8
12	3	164.0	192.0	126.3	92.5	75.0	40.5	30.0	144.0	67.5	135.5	201.5
13	2	177.0	191.0	150.0	83.0	84.0	42.0	30.0	142.0	82.0	130.0	196.0
14	2	161.0	213.0	137.0	105.0	81.0	45.0	23.0	159.0	86.0	146.0	213.0
15	1	241.0	—	—	—	74.0	—	—	165.0	89.0	—	—
16	2	189.5	197.0	134.5	92.0	76.5	43.0	30.0	154.5	79.0	143.5	208.0
17	1	144.0	197.0	116.0	97.0	68.0	46.0	23.0	145.0	76.0	135.0	197.0
20	1	165.0	205.0	142.0	99.0	91.0	42.0	26.0	150.0	70.0	155.0	205.0
22	1	165.0	211.0	147.0	97.0	91.0	44.0	28.0	148.0	80.0	140.0	190.0
Ad (5+)	55	164.3	196.5	130.5	95.2	78.6	41.7	26.5	147.4	76.6	135.6	189.3

Table 4. Mean body measurements of female grizzly bears by age class, 1975–85.

Age	*N*	Length (A)	Contour length (A-1)	Girth (B)	Height (C)	Neck (D)	Head		Front pad		Rear pad	
							Length (E)	Width (F)	Width (G)	Length (H)	Width (K)	Length (L)
Cub	6	87.3	110.3	64.5	51.3	39.3	26.0	15.8	87.8	43.5	80.5	110.0
1	13	107.5	138.4	85.5	64.3	51.7	31.4	16.4	106.1	48.9	97.3	135.1
2	11	117.8	151.8	98.0	76.0	59.4	34.8	19.6	113.0	56.4	108.7	150.3
3	8	130.4	162.3	98.4	83.1	57.4	35.6	20.4	119.4	60.7	111.3	150.9
4	7	128.2	178.4	110.6	86.6	66.5	37.4	19.6	124.7	62.0	106.8	161.6
5	9	154.8	173.5	110.4	86.6	65.1	38.3	20.1	120.3	67.2	113.2	163.8
6	4	131.3	181.0	108.0	90.0	64.3	38.0	22.0	122.3	61.0	110.7	166.0
7	5	149.6	180.5	114.8	87.0	67.4	38.5	23.5	131.8	66.6	118.8	167.0
8	5	151.5	184.7	120.0	89.0	62.8	37.3	21.7	118.7	64.7	109.0	152.3
9	4	154.7	183.3	119.3	90.7	63.8	38.3	25.0	132.8	72.8	125.8	169.0
10	6	152.0	188.3	119.7	86.7	63.3	38.7	22.7	127.7	67.3	121.3	164.3
11	5	172.5	179.5	121.0	93.5	68.0	38.0	24.0	132.7	70.0	127.3	170.3
12	4	144.7	177.0	109.0	87.0	68.7	39.7	21.0	122.0	67.0	115.3	167.7
13	6	154.0	175.6	122.3	85.7	66.7	36.3	22.7	128.7	68.0	124.0	157.0
14	2	136.5	165.5	106.0	90.0	59.0	35.5	24.5	120.5	66.5	111.5	146.5
15	2	136.4	165.0	108.0	87.0	63.0	38.0	23.0	131.0	64.0	123.5	164.0
16	2	143.5	175.5	109.0	86.0	68.0	37.0	24.5	123.0	70.5	119.0	151.5
AD (5+)	55	151.1	177.8	114.6	87.4	65.4	37.8	22.4	125.5	67.0	117.5	163.1

(C), 74 cm around the neck (D), and had a hind foot 135 mm wide (K) and 190 mm long (L).

Sexual dimorphism in body measurements was apparent in cubs and became significant in 8 of 11 measurements by the yearling year ($P < 0.170$) and in 10 of 11 by age 2 years. The 11th measurement, neck circumference, became different by 3 years ($P = 0.003$). Male grizzly bears on the central Alaska peninsula were also significantly larger than females at age 3 in 6 body dimensions recorded (Glenn 1980). Measurements of adult males in this study were 8%–17% greater than those of adult females, compared to a 29% difference in weights. The greatest difference was in neck circumference and the least in height at the shoulder. Glenn (1980) reported a 19% difference in mean total body size and 88% difference in weights of males and females on the central Alaska peninsula.

Females attained mean adult size in 5 of the 11 body dimensions by 4 years (contour body length, height at the shoulder, neck circumference, head length, and front pad width) and in all 11 by age 7 years. Males reached mean adult size in 7 of the 11 dimensions by 6 years (body length, girth, height at the shoulder, neck circumference, head length, front pad length, and rear pad width) and in all 11 by 9 years. Overlap in ranges of all measurements occurred in every age class for both males and females.

Girth was the measurement most closely correlated with weight for both male ($r = 0.87$) and female ($r = 0.91$) grizzly bears. High correlations between weight and girth have also been reported for grizzly bears in 3 geographic areas of Canada (Nagy et al. 1984), Jasper National Park (Russell et al. 1979), and the central Alaskan peninsula (Glenn 1980).

Head length and front pad width measurements showed least variation for both males and females. Both dimensions were relatively short and consequently subject to less error in measurement and less subject to extremes in fat deposition and loss. Greatest variation was evident in total body length for both sexes.

Effects of Food Availability on Weight

Adult grizzly bears feeding at garbage dumps weighed more than bears relying on natural food sources. The majority of weights of dump bears (17 of 18) were recorded July–September. Comparisons with weights of nondump bears recorded during the same months revealed 13 adult males feeding at dumps weighed an average 222 kg compared to 184 kg for 29 adult males not known to use dumps ($t = 2.26$, $P = 0.015$). Fourteen adult females using dumps weighed an average 142 kg compared to 130 kg for nondump females ($t = 1.26$, $P = 0.106$). This dump-vs.-nondump weight difference was apparent for females with cubs and yearlings but not for lone adult females (Table 5). The heaviest adult male (325 kg) and female (194 kg) consistently foraged at the Cooke City, Mont., dump during summer months for the entire period they were monitored (3 and 7 years, respectively). Grizzly bears feeding at dumps in Jasper National Park, Alberta, also weighed more than bears using natural foods only (Russell et al. 1979), as did black bears in Minnesota (Rogers et al. 1976).

Table 5. Mean weights (kg) of adult male and female grizzly bears not known to feed at dumps compared to weights of dump foragers, 1975–85.

	Dump		Nondump		t-test	
	N	Weight	*N*	Weight	*P*	*t*
Ad F + cubs	3	153	10	122	.055	1.740
Ad F + yrlngs	3	149	11	137	.293	0.557
Lone Ad F	8	135	27	132	.461	0.099
All Ad F	14	142	48	134	.139	1.093
All Ad M	14	222	49	193	.012	2.300

Adult bears were heavier before 1970 when open pit garbage dumps were available within Yellowstone Park (Craighead and Mitchell 1982). During that period, 33 adult males weighed an average 53 kg more than adult males from this study. Males feeding on garbage during this study weighed only 23 kg less than during the earlier period, whereas nondump males weighed 52 kg less. Weight differences were not as great for adult females, with 72 adult females from the earlier period weighing an average 17 kg more than adult females from this study. Females feeding on garbage during this study weighed 10 kg less than during the earlier period, whereas nondump females weighed 18 kg less. Differences of less than 20 kg were not considered significant. Four-year-old females from the earlier period had reached 87% of their mean adult weight compared to 86% for 4-year-old females during this study. However, 4-year-old males from the earlier period had attained only 62% of their mean adult weight compared to 80% for 4-year-old males during this study.

Mean annual weights of nondump adult females were highly correlated with annual habitat quality indices (Mattson et al. 1986) for Yellowstone Park ($r = 0.710$; $F = 4.19$; $0.50 < P < 0.10$) (Fig. 4). Similar trends were not recorded for nondump adults males ($r = 0.330$). Adult females foraging at dumps were consistently heavier than nondump females, except during 1980 when optimum seasonal natural foods were available.

DISCUSSION

Yellowstone grizzly bears were smaller and weighed less in this study than they did during 1959–70, when major garbage dumps were available as a food source within and adjacent to Yellowstone Park. Natural adaptation to the loss of that stable, high-energy food source was probably the major cause of reduced body size, delayed sexual maturity in females, and smaller litter sizes in the current population. One adult female (26) feeding at a dump weighed 182 kg in September 1977, a very poor natural food year when nondump females weighed a mean of 120 kg. The dump was removed the following year, and the same female was radio-monitored for 3 consecutive years during which she did not use garbage as a food source. She was recaptured in July 1981 and weighed 91 kg, whereas dump females weighed a mean 160 kg during that same year. Beecham (1980) reported similar findings for 2 black bear populations in Idaho. Seven species of berries were available to 1 population, whereas only 1 species was available to the 2nd, which was characterized by smaller bears, smaller litter sizes, and females first breeding 1 year later. Other researchers have suggested that an additional factor influencing litter size in Yellowstone has been a change in climate (Picton and Knight 1986).

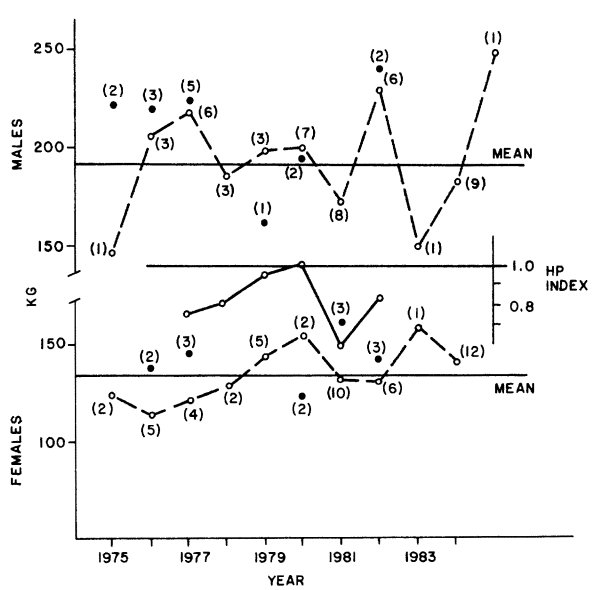


Fig. 4. Annual variation in mean weights of dump and nondump adult male and female grizzly bears in relation to annual habitat productivity (HP). Sample sizes are given in parentheses, and dump weights are shown as solid dots.

Table 6. Comparisons of mean and maximum adult weights, age of 1st cub production, and mean cub litter size among 9 North American grizzly bear populations.

Region	Age used for mean adult wt.	Mean adult weight (kg)				Max. wt. (kg)		Female age at 1st litter (*N*)	Mean cub litter size	Major high energy foods[a]	
		F	*N*	M	*N*	F	M				
Northern interior Canada (Pearson 1975)	"Mature"	95	21	139	40	125	240	6.5 (min.) 8.0 (mean) (6)	1.7	Roots Berries	0.55 1.00
East Brooks Range, Alaska (Reynolds 1974, 1976)	8+ years	104	20	174	30	141	272	6.5 (min.) 10.1 (mean) (19)	1.8	Roots Berries	0.55 1.00
West Brooks Range, Alaska (Reynolds 1981)	5+ years	112	48	155	38	182	234	8.1 (mean) (16)	1.93	Roots Berries Caribou	0.55 1.00 0.80
Southcentral interior Alaska (Spraker et al. 1981, Ballard et al 1980)	5+ years	117	20	243	18	170	289	4.5 (min.)	2.8	No data	
Jasper National Park, Alberta (Russell et al. 1979)	6+ years	134	7	221	17	213	356	7.0 (min.)	2.0	Garbage	0.80
	"Dump"	213	1	306	3	—	—			Roots	0.55
	"Nondump"	121	6	203	14	—	—			Berries	1.00
Yellowstone National Park (this study)	5+ years	135	63	192	64	194	325	6.3 (mean) (12)	1.9	Pine nuts	0.89
	"Dump"	142	14	222	14	—	—	5.8 (mean) (4)		Elk	0.80
	"Nondump"	134	48	193	49	—	—	6.3 (mean) (8)		Garbage	0.80
Yellowstone National Park (Craighead and Mitchell 1982)	5+ years	152	72	245	33	204	500	5.5 (min.) 6.1 (mean) (15)	2.24	Garbage Pine Nuts Elk	0.80 0.89 0.80
Kodiak Island, Alaska (Troyer and Hensel, unpubl. data; Hensel et al. 1969)	6+ years	200[b]	16	300[b]	10	300	611	—	2.23	Salmon Berries	0.80 1.00
Coastal Alaska Peninsula (Glenn et al. 1976, Glenn 1980)	9+ years	207	25	389	5	277	442	6.0 (mean)	2.5	Salmon Berries	0.80 1.00

[a] Annual diet item value (Mattson et al., unpubl. data) of major late summer/fall food items.
[b] Approximate weight based on data given.

Food with the highest nutrient values available to Yellowstone grizzly bears during summer and fall were the nuts of whitebark pine (*Pinus albicaulis*); berries, primarily buffaloberry (*Shepherdia canadensis*) and globe huckleberry (*Vaccinium globulare*); and ungulates (Mattson et al., unpubl. data). Whitebark pine had the highest value of all foods during the fall but unfortunately was characterized by disjunct and meager habitat and highly variable, unreliable productivity. Berry-producing areas were typically specific to limited habitat of also variable, unreliable productivity.

Use of ungulates was typically characterized by a peak in spring, when bears primarily scavenged on winter-killed animals and preyed on weakened ones. Predation on newborn calves during June and on rutting bulls during fall was fairly common. Recent data indicate increased predation on prime condition elk (*Cervus elaphus nelsoni*) during summer (Mattson et al., unpubl. data). Adaptation to the use of this reliable, high-energy food source during summer and fall could compensate for the loss of garbage once available during the same period. However, adult females known to prey on elk during summer weighed only 100 kg compared to the mean adult female weight of 135 kg and the dump female weight of 142 kg. Adult females that were successful moose (*Alces alces*) predators in south-central Alaska (Ballard et al. 1980, Spraker et al. 1981) were similar in mean weight (117 kg) to females that preyed on elk in Yellowstone. Although the Alaskan females were relatively small, they had 1 of the largest mean cub litter sizes recorded (Table 6). Adult males in Yellowstone known to prey on elk during the summer weighed more than the nondump adult males (235 kg and 193 kg, respectively). Alaskan males preying on moose were similarly heavier than expected (243 kg).

Comparisons of mean adult female weights and productivity among 9 studies of North American grizzly populations are listed in Table 6. A high correlation between mean adult female weight and mean cub litter size was apparent ($r = 0.92$) when the south-central interior Alaskan population was omitted. When that population was added to the regression, the correlation became only moderate ($r = 0.48$). A small sample of 4 was used to calculate the high litter size of 2.8 for that population. Limited data indicated smaller adult females tended to produce their 1st cubs at a later age. A moderately high negative correlation existed between mean adult female weight and mean age at 1st cub production ($r = -0.52$ for 5 populations).

During this study 9 females not known to use garbage as a major food source had a mean reproductive rate of 0.469 compared to 0.800 for 2 females that relied on garbage as a food source (Knight et al. 1986). Mean cycle length was 3.56 years and mean litter size 1.92 cubs for the nondump females, compared to 2.5 years and 2.17 cubs for the 2 females feeding on garbage. In general, females with reliable, high-value foods (meat, berries, and garbage) during summer and fall tended to attain larger body sizes, mature at an earlier age, and have larger cub litters compared with females with relatively low-value foods, such as roots.

LITERATURE CITED

BALLARD, W. B., S. D. MILLER, AND T. H. SPRAKER. 1980. Moose calf mortality study. Alaska Dep. Fish and Game, Final Rep., Fed. Aid in Wildl. Restor., Proj. W-17-9, W-17-10, W-17-11, and W-21-1. Job 1.23R. Juneau. 123pp.

BEECHAM, J. J. 1980. Population characteristics, denning, and growth patterns of black bears in Idaho. Ph.D. Thesis, Univ. Mont., Missoula. 101pp.

BLANCHARD, B. 1985. Field techniques used in the study of grizzly bears. Interagency Grizzly Bear Study Team Rep. 24pp.

CRAIGHEAD, J. J., AND J. A. MITCHELL. 1982. Grizzly bear. Pages 515–556 *in* J. A. Chapman and G. A. Feldhamer, eds. Wild mammals of North America. The Johns Hopkins Univ. Press, Baltimore, Maryland.

——, J. R. VARNEY, AND F. C. CRAIGHEAD, JR. 1974. A population analysis of the Yellowstone grizzly bears. Mont. For. and Conserv. Exp. Sta. Bull. 40. Univ. Mont., Missoula. 20pp.

GLENN, L. P. 1980. Morphometric characteristics of brown bears on the central Alaska peninsula. Int. Conf. Bear Res. and Manage. 4:313–319.

——, J. W. LENTFER, J. B. FARO, AND L. H. MILLER. 1976. Reproductive biology of female brown bears (*Ursus arctos*), McNeil River, Alaska. Int. Conf. Bear Res. and Manage. 3:381–390.

HENSEL, R. J., W. A. TROYER, AND A. W. ERICKSON. 1969. Reproduction in the female brown bear. J. Wildl. Manage. 33:357–365.

KNIGHT, R. R., B. M. BLANCHARD, AND D. J. MATTSON. 1986. Yellowstone grizzly bear investigations: annual report to the Interagency Study Team, 1985. U.S. Dep. Int., Natl. Park Serv. 58pp.

——, AND L. EBERHARDT. 1985. Population dynamics of Yellowstone grizzly bears. Ecology 66:323–334.

MATTSON, D. J., R. R. KNIGHT, AND B. M. BLANCHARD. 1986. Derivation of habitat component values for the Yellowstone grizzly bear. Pages 222–229 *in* G. P. Contreras and K. E. Evans, eds. Proceedings—grizzly bear habitat symposium. U.S. Dep. Agric., For. Serv., Gen. Tech. Rep. INT-207. 252pp.

NAGY, J. A., M. C. KINGSLEY, R. H. RUSSELL, A. M. PEARSON, AND B. C. GOSKI. 1984. Relationships of weight to chest girth in the grizzly bear. J. Wildl. Manage. 48:1439–1440.

PEARSON, A. M. 1975. The northern interior grizzly bear Ursus arctos L. Can. Wildl. Serv. Rep. Ser. 34. 84pp.

PICTON, H. D., AND R. R. KNIGHT. in press. Using climate data to predict grizzly bear litter size. Int. Conf. Bear Res. and Manage. 6:

RAUSCH, R. L. 1963. Geographical variation in size in North American brown bears, Ursus arctos, as indicated by condylobasal length. Can. J. Zool. 41:33–45.

REYNOLDS, H. 1974. North slope grizzly bear studies. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor., Prog. Rep., Proj. W-17–6, Jobs 4.8R, 4.9R, and 4.11R. Juneau. 26pp.

———. 1976. North slope grizzly bear studies. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor., Final Rep., Proj. W-17–6 and W-17–7, Jobs 4.8R, 4.9R, 4.10R, and 4.11R. Juneau. 20pp.

———. 1981. North slope grizzly bear studies. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor., Prog. Rep., Proj. W-21–1, Job 4.14R. Juneau. 27pp.

ROGERS, L. L., D. W. KUEHN, A. W. ERICKSON, E. M. HARGER, L. J. VERME, AND J. J. OZOGA. 1976. Characteristics and management of black bears that feed in garbage dumps, campgrounds, or residential areas. Int. Conf. Bear Res. and Manage. 3:169–175.

RUSSELL, R. H., J. W. NOLAN, N. W. WOODY, AND G. ANDERSON. 1979. A study of the grizzly bear (*Ursus arctos L.*). Can. Wildl. Serv., Edmonton. 136pp.

SPRAKER, T. H., W. B. BALLARD, AND S. D. MILLER. 1981. Game management unit 13 brown bear studies. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor., Final Rep., Proj. W-17–10, W-17–11, and W-21–1, Job 4.13R. Juneau. 57pp.