GRIZZLY BEAR REPRODUCTIVE RATE RELATIVE TO BODY SIZE

STEPHEN F. STRINGHAM, Wildwatch Ecological Center, 12964 Foothill Rd., St. Ignatius, MT 59865-9709

Abstract: Mean adult body sizes (BS) and reproductive parameters were compared across 12 populations of grizzly bears (*Ursus arctos*). BS was assessed in terms of mean adult body weight (BW) and skull length (SL). BWs of adult males and females are positively related to each other and to SL. As BS increases, litter size (C/L) and natality (C/L/IBI) tend to increase, while interbirth interval (IBI) and age at first whelping (AFW) decrease. To the extent that IBI and AFW are inversely related to maturation rates to weaning and adulthood, respectively, these results indicate a positive relationship between maturation rate and BS in a population. Both BW and SL are inexpensive predictors of reproductive rate reliable enough for management purposes where reproductive data are lacking.

In both domestic and wild mammals, per capita rates of reproduction and survival tend to be positively related to nutritional status and to food supply (Sadlier 1969). This has been confirmed in black bear (*U. americanus*: Rausch 1961; Jonkel and Cowan 1971; Rogers 1976, 1977, 1983,1987; Beecham 1980a,b; Eiler 1981; Elowe 1987; and D.L. Garshelis, pers. commun.), polar bear (*U. maritimus*: Stirling et al. 1976, 1977), and grizzly bear (Stringham 1980, 1985, 1986; Bunnell and Tait 1981).

One index of nutritional status is sex-age specific body size. Frisch (1974, 1982, 1989) has shown positive relationships between reproductive success and maternal BW in humans. For white-tailed deer (*Odocoileus virginianus*), reproductive rate is highly correlated with adult female BW and yearling male antler-beam diameter (Moen 1978, Severinghaus and Moen 1983). The capacity to use BW or antler size data to estimate reproductive rate, with reasonable accuracy but negligible cost, is a valuable management tool for deer. To likewise facilitate management of bears, I have derived models relating reproductive parameters to BS.

I hypothesized that reproductive rate tends to be positively related to nutritional status, and thus to mean adult BS. In humans (Frisch 1974, 1982, 1989) and probably some other animals, extreme obesity is pathological and can impair reproduction; but in bears that is unlikely, because obesity is a necessary preparation for hibernation, one to which reproductive physiology has presumably adapted. Indeed, heavy fat accumulation may be critical to female reproduction (Rogers 1987). For bears, C/L, C/L/IBI, and maturation rate should therefore be positively related to BS. IBI and AFW tend to be inversely related to maturation rates to weaning and adulthood, respectively (Stringham 1980, 1985). So positive relationships of maturation rate to BS imply negative relationships of IBI and AFW to BS.

Males and females embody the same gene pool and are nourished by the same food supply. So I predicted a positive correlation between mean BSs of males and females. BW and SL are both facets of BS. I would expect heavier individuals to have larger skulls, on average, and so for populations with heavy mean BW to have a longer mean SL. If BW of males (BW_M) and females (BW_F) are positively related to each other, and mean BW for a sex is positively related to its mean SL, mean SL for each sex should be positively (but less strongly) related to mean BW for the other sex. In summary, these hypotheses are:

$$BW_M \propto BW_F, \quad BW_M \propto SL_M, \quad BW_F \propto SL_F,$$

$$BW_F \propto SL_M, \quad BW_M \propto SL_F, \text{ and}$$

$$\frac{C/L}{IBI} \propto BS \quad C/L \propto BS \quad \frac{1}{IBI} \propto BS \quad \frac{1}{AFW} \propto BS$$

This paper presents the results of my tests for most of these hypotheses. These findings were first presented at the 1986 congress of the International Association for Bear Research and Management. The research was supported by Wildwatch; the Shikar-Safari Club International; the College of Environmental Science and Forestry, State University of New York, Syracuse; the Salish-Kootenai College; A., J., J., and R. Stringham; C. and V. Nicolayeff; H. Strauss, and L. Lippincott.

METHODS

Hypothesis Testing

The best-documented measures of mean adult BS for grizzly populations are mean BW_F, BW_M and SL_M. Data on population-specific means for these size measures and for reproductive parameters (C/L, IBI, and AFW) were taken from the literature (Table 1); figures for C/L/IBI were calculated. I tested for relationships among BW_F, BW_M and SL_M using Minimum Variance regression. Then the population mean for each of the 4 reproductive parameters was regressed on BW_F, BW_M and SL_M — a total of 12 regressions. Significance tests for all of these relationships were 1-tailed because positive relationships between reproductive rate and nutritional status are typical for mammals. Relationships between reproductive

Table 1. Body size and reproductive parameters for grizzly bears; mean values from 12 North American populations.

Population	Body weight[a] (kg) F	Body weight[a] (kg) M	Skull length[b] (mm) M	Litter size (C/L)	Interbirth interval (IBI) (years)	Natality[c,d]	AFW[e] (years)
Kodiak Island (KI)[f]	200 (E)	300 (E)	397 (37)	2.23 (98)	3	0.74	5.0[e]
Lower AK Peninsula (AP)[g]	198 (63) [232	319 (21) 373]	403 (35)	2.30 (200)	3 (81)	0.77	4.4 (9)
McNeil River (MR)[h]	160 (E) [159	257 (E) 260]	377 (26)	2.10[c] (41)	3.6 (12)	0.58	5.9[e] (8)
Eastern Brooks Range (EBR)[i]	109 (26)	184 (19)	352 (4)	1.77[c] (13)	≥4[c]	0.44	10.1 (20)
Western Brooks Range (WBR)[j]	112 (48) [116	154 (38) 178]	334 (11)	1.98 (57)	≥4.1	0.48	7.4[c] (14)
Southern Yukon (SYK)[k]	95 (21)	140 (42)	330 (12)	1.70 (11)	≥4[c] (3)	0.42	≥7.5[c] (>10)
Northern Yukon (NYK)[l]	114 (42) [114	170 (54) 176]	335 (E)	2.00 (6)	≥4[c] (5)	0.57	7.0[c] (3)
Northwest Territories (NWT)[m]	110 (28)	148 (20)	335 (E)	1.83 (6)	3.8 (5)	0.48	≥8.0
Glacier N. Park, Canada (GNP)[n]	109 (E) [105 [128 {3}	165 (E) 165] 237} {5}	337 (10)	2.00 (108)			{≥5.0} (1)
Yellowstone Natl. Park 1959-70 (YNP)[o]	152 (72)	245 (33)	370 (E)	2.18[c] (173)	3.2 (68)	0.68	5.7 (16)
Tuktoyaktuk Peninsula (TUK)[p]	120 (50) [126	183 (25) 190]	335 (9)	2.30 (14)	≥3.3 (11)	≤0.70	6.4[c] (10)
Southcentral AK (SCA)[q]	133 (26) [156	248 (13) 290]	366 (16)	{2.8} (4)	3 (5)	{1.07}	5.0[e] (>6)

[a] Mean body weights for adults. F = female, M = male. (E) = estimate; derivation of each estimate is described below in the last footnote or in the Methods. (n) = sample size. [..] = sample size too small for data to be used in statistical tests — e.g., for BW in GNP. [...] = seasonally adjusted weight (see text for description of how the adjustment was done for AP, WBR, NYK, TUK, and SCA).

[b] Condylobasal length. All data from Rausch (1963) for males so mature that all sutures are ossified. Sites for these data are listed with the footnote for each population.

[c] Calculated from data provided by the author; see Methods.

[d] Natality = cubs/adult female/year = C/L/IBI.

[e] AFW = age at first whelping.
Sources for figures on reproductive parameters (R) and body weights (W) are given first, then sites for skull length (S) from Rausch (1963):

[f] KI: R: Hensel et al. (1969); W estimated from data provided by Troyer and Hensel, unpubl., cited by Blanchard (1987:Table 6). S Kodiak and Afognak Islands.

[g] AP: R: Glenn (1973); W spring data (Glenn 1980:Fig. 1); [W] = my estimate for mean spring-fall weight (see Methods). S Port Heiden-Lake Becharoff S = 402 (n = 10) and Lower Alaska Peninsula S = 404 (n = 25), yielding a mean of 403. Rausch measured skull length on cleaned skulls; by contrast, when head length for live bears was measured by Glenn (1980:Fig. 1), mean length was 423 mm for 26 males 7+ years old. To assure methodological standardization across populations, Rausch's figures were used here and wherever else they are available.

[h] MR: R Glenn (1973), Glenn et al. (1976); mean litter size was 2.1 C/L (Glenn 1973), not 2.5 as misprinted in Glenn et al. (1976); W I used skull length to estimate body weight — unadjusted and adjusted; S Kamishak Bay-Iliamna Lake.

[i] EBR: RW Reynolds (1976); S Upper Noatak River.

[j] WBR: R Reynolds (1983); W Reynolds (1981), mostly spring data; [W] = estimated spring-fall mean (see Methods); S Anaktuvuk Pass Region.

[k] SYK: RW Pearson (1975); S Southern Yukon.

[l] NYK: RW Nagy et al. (1983*a*); W data mainly from spring; [W] = estimated spring-fall weight (see Methods); S was assumed to be intermediate between values at Mackenzie Delta to the east (335 mm) and Anaktuvuk Pass region to the west (334 mm) of NYK.

[m] NWT: RW Miller et al. (1982). S assumed to be intermediate between values at Mackenzie Delta to the north (335 mm) and Southeastern Yukon to the south (334 mm) of NWT.

[n] GNP: RW Mundy and Flook (1973); litter size is the only reproductive parameter well enough documented to be included in statistical tests; the W figures are in curly brackets {..} because sample sizes are minuscule; weights used in regressions on litter size were estimated from skull length: W = estimated weights without seasonal adjustment; [W] = estimated adjusted mean spring-fall weights (see Methods); S Southeastern British Columbia.

[o] YNP: R Craighead et al. (1974, 1976); W Craighead and Mitchell (1982); S estimated from body weight, using the equation for unadjusted weight. Rausch's figure of 347 mm for Montana-Wyoming was not used since it is applicable to bears on predominantly natural diets, whereas Yellowstone grizzlies were unusually well fed on garbage.

[p] TUK: RW Nagy et al. (1983*b*); W most data collected in spring; [W] estimated mean spring-fall weight (see Methods); S Mackenzie Delta.

[q] SCA: R Ballard et al. (1982); litter size is for neonates. W spring data (Spraker et al. 1981; Miller 1988); [W] = estimated mean spring-fall weight (see Methods); S Talkeetna Mountains region.

parameters and BS are allometric; so regression models are log-log, as is conventional (McDonald 1984; Gittleman 1986). Weaknesses in available data limited me to preliminary tests of my hypotheses. More rigorous tests require more standardized data. This should be gathered.

Body Weight

Data on BW are for adults ≥5-years-old. BW varies seasonally, tending to be highest in late fall before hibernation and lowest sometime in spring after den emergence. For example, Pearson (1975) notes that grizzly bears in the southern Yukon Territory (SYK) may keep on losing weight, or at best hold their own, until late summer. Thus, before comparing BW data across populations, it is advisable to standardize by season. That is possible only to a limited degree using available information. My results are presented in 2 forms, the 1st using just the raw data, the 2nd incorporating seasonal weight adjustments for 5 populations, as described below.

Balancing Samples From Spring and Fall.—Data from most populations cover the entire period spring to fall, with varying emphasis on each season. But the degree of emphasis is known for only a few of the populations. Sampling was substantially heavier during spring than fall at the Tuktoyaktuk Peninsula (TUK), northern Yukon Territory (NYK), and western Brooks Range (WBR). To balance sampling emphasis between these seasons, I took the *unweighted* average of the mean spring (April-June) and fall (August-September) BWs. (July "summer" BWs are excluded to provide a clear separation between spring and fall). In WBR, females had mean BWs of 104 kg (n = 30) in spring and 127 kg (n = 9) in fall; the unweighted mean is 116 kg (= [104+127]/2); for WBR males the mean is 178 kg (= [147+209]/2).

TUK: F 126 = [105+148]/2, M 190 = [173+206]/2
NYK: F 114 = [88+141]/2, M 176 = [159+194]/2

Seasonally-adjusted weights presented in Table 1 are placed below unadjusted weights and enclosed in brackets.

Estimating Spring-Fall Weights from Spring Weights.—In southcentral Alaska (SCA) and the Alaska Peninsula (AP) south of McNeil River, BWs were measured during spring. So these spring BWs were converted to estimated spring-fall BWs. That was done by finding the ratio of spring-fall and spring BWs in NYK, WBR, and TUK (the only populations for which appropriate data exist), then multiplying the SCA and AP spring BWs by this ratio. For WBR F spring-fall/spring = 116/104 = 1.1; for M the ratio is 178/147 = 1.2.

TUK: F 126/105 = 1.2, M 190/173 = 1.1
NYK: F 114/88 = 1.3, M 176/159 = 1.1

For these 3 populations, the mean ratio is 1.17.

Spring SCA BWs of 133 kg for F and 248 kg for M were converted to estimated spring-fall BWs by multiplying with 1.17 = 156 kg for F and 290 kg for M. So too, AP spring BWs were multiplied by 1.17 (Table 1).

Skull Length

Skull (condylobasal) length data, collected by Rausch (1963), come from approximately the same geographic regions as data on BW and reproductive parameters but from different animals, collected several years earlier. Skulls are from males with closed sutures which indicate termination of growth in SL. Based on data for known bears, those skulls with closed sutures were judged to be at least 7-years-old by Rausch.

Body Weight Relative to Skull Length

Reproductive data are available from 3 populations for which either BW or SL data are inadequate or absent. For Glacier National Park, Canada (GNP), sample sizes for BWs are too small to be usable (3 females and 5 males). There are no published data on BW at McNeil River (MR) or SL at Yellowstone National Park (YNP). Rausch (1963) gives a mean for SL_M in nearby Wyoming and Montana. This mean is apparently for bears on predominantly natural diets. So it is not applicable to YNP bears that ate substantial amounts of garbage; a

richer diet would have tended to increase BS and thus skull size.

Because SL and BW are highly correlated (see Results), it is possible to use one to estimate the other. (This use of regression assumes association between the BW and SL, not control of either by the other). Regressions of BW_F and BW_M on SL_M were done separately for seasonally adjusted and unadjusted (raw) data. Then each set of regressions was used to estimate seasonally adjusted and unadjusted BW at MR and GNP. The reciprocal regression of SL_M on unadjusted BW_M was used to predict SL_M in YNP.

Estimation of BWs or SL for these populations was done to get a more representative sample of relationships between reproductive parameters and BS. Use of an extrapolated value may slightly increase variance around a regression line, causing an *underestimation* of r^2, and perhaps slightly biasing regression and correlation coefficients. These disadvantages are outweighed by benefits of avoiding 2 other biases that arise if only known BWs and SLs are used — problems which tend to be negligible with large sample sizes but which can be major with such small samples. First, regression and correlation coefficients can be biased if one lacks data from the full ranges of BS and reproductive rate. Second, to the extent that regressions on BS include populations where one lacks SL data, and vice versa, this could generate spurious differences in how reproductive parameters appear to be related to BW as contrasted to SL (e.g., IBI on BW contrasted to IBI on SL).

Litter Size

When an author did not specify mean C/L (cubs-of-the-year per litter) the mean was readily calculated by dividing total cubs by total cub litters. The SCA mean of 2.8 C/L is based on a sample size of 4 neonate litters (Ballard et al. 1982); subsequent increase in sample size reveals a much smaller average (S. Miller, pers. commun.); so this 2.8 datum was not included in my statistical tests. Mean C/L may vary with litter age and maternal age; but data required to standardize by age are unavailable.

Interbirth Interval

The time interval between birth of 1 litter and birth of a mother's next litter is a function of at least 2 variables: 1) age at which the first litter dissociates from the mother, and 2) her capability to conceive her next litter and carry it to term. Only the YNP data (Craighead and Craighead 1969; Craighead et al. 1974, 1976) are extensive enough

to document successive litters for a large number of females ($n = 68$). There, most conceived a new litter the same year as they dissociated from the previous one — confirming the claim by Erickson and Nellor (1964) that a female normally does not come into heat again while she is lactating, although exceptions have been observed in black bear (LeCount 1983). Birth occurs the following winter. A female dissociating from cubs during their 3rd spring of life (age 2.5 years) would thus have at least 3 years between birth of that and her next litter. Mean age at which cubs dissociate (AD) is sometimes used to estimate the *minimum* mean interval between litters, where specific data are lacking (IBI ≤ AD + 0.5 year). When calculating IBI, most authors omit intervals known to have been truncated by whole-litter mortality, as I have done when estimating IBI from data provided by authors.

Derivation of IBI figures is described below. Where no description is given here, the tabulated figure is the author's. Inferences from an author's data are indicated in the text by an arrow "→". Abbreviations for population names correspond to those in Table 1.

AP: (Glenn 1973:9) IBI = 3.5 years for 6 marked litters surviving to weaning. Data are also available for 158 young in approximately 75 unmarked litters (75 = 61 1.5-year-olds + 54 2.5-year-olds + 43 3.5-year-olds, divided by the mean litter size of 2.1 at these ages). For these offspring, the proportions still with their dam at each age, and whether the dam was then in estrus, indicate that the normal interval was about 3 years — which is Glenn's (1973) estimate for mean IBI.

MR: 1 IBI at 2 years, 7 at 3 years, 2 at 4 years, 2 at 6 years → mean IBI = 3.6 years.

EBR: Young did not dissociate until at least age 2.5 and 1 not until age 4.5; so mean IBI ≥3.0 years. H. Reynolds (1976, pers. commun.) indicates intervals near 4 years are probably most common; ≥4 years is also consistent with the known relationships of IBI with C/L and AFW (Stringham 1980:Table 3); so the figure I used is mean IBI ≥4 years.

SYK: 1 IBI ≥3, 1 at 4, and 1 ≥5 → mean IBI ≥4 years.

NYK: the authors assumed that IBI = AD + 0.5 year: 1 at 5, 1 at ≥3, 3 at ≥4; so mean IBI ≥4 years.

SCA: Dissociation was normally at age 2.5 as seen in 5 litters; no dissociation of yearlings; all 2.5-year-olds already dissociated; so the authors concluded mean IBI = 3 years.

Age at First Whelping

Field researchers estimated AFW either from direct observations of cubs, condition of mammae, or other evidence of whelping; or on evidence of sexual maturity. Some females display signs of estrus and may even copulate as early as 1 year before their first confirmed conception (Craighead et al. 1974, Glenn et al. 1976). So estimates of AFW based on breeding are limited to cases where this is known to have resulted in pregnancy. First "successful conception" is abbreviated "FSC." AFW = FSC + 0.5 year. Estimation of mean AFW is described below.

KI: 5% of 3-year-olds were mature, 47% of 4-year-olds, and 100% of older females; so mean FSC = 4.5 years was assumed → mean AFW = 5.0 years.

MR: mean FSC = 5.4 years → mean AFW = 5.9 years.

WBR: mean 7.9 years for first summer with cubs → AFW = 7.4.

SYK: the author's data indicate minimum mean FSC = 7 years → minimum mean AFW = 7.5 years.

NYK: mean FSC = 6.5 years → mean AFW = 7.0.

TUK: mean FSC = 5.9 years → mean AFW = 6.4 years.

SCA: 3 FSC at 3.5 years; 1 other estrus at 3.5 years; 2 FSC at 4.5 years; all 4.5-year-old females without cubs were in estrus; 1 FSC at 5.5 years → rough mean AFW = 5 years.

RESULTS

All my hypotheses were confirmed by the regression tests. Mean BW_F and BW_M are positively interrelated ($r^2 \geq 90\%$, Table 2, Fig. 1). Mean BW_F and BW_M are positively related to mean SL_M ($r^2 \geq 88\%$, Table 3, Fig. 2). Mean C/L, IBI, C/L/IBI, and AFW are all significantly related to mean BW_F and BW_M ($r^2 = 61-78\%$) and to SL_M ($r^2 = 37-64\%$, Table 4, Figs. 3-6). Relationships of reproductive parameters with BW_F and BW_M are of comparable strength; relationships with available SL_M data are weaker. Strengths of these relationships (r^2) found using seasonally adjusted data tend to be 5-10% stronger than those found with unadjusted (raw) data.

DISCUSSION

BW_F, BW_M, and SL_M are all positively related to C/L and C/L/IBI, but inversely related to IBI and AFW. It is already known that IBI depends strongly on rate of cub maturation to weaning; slow-maturing cubs tend to be weaned later (Jonkel and Cowan 1971; Stringham 1980,

Table 2. Relationships between mean body weights of adult males and females. Data from Table 1 (n = 10 populations).[a]

Regression equation	r^2	P	±SEI[b]	±SES
Raw data				
$\log(BW_F) = 0.23 + 0.82x\log(BW_M)$	90	<0.001	0.04	0.09
$\log(BW_M) = -0.03 + 1.10x\log(BW_F)$			0.04	0.13
Seasonally adjusted data				
$\log(BW_F) = 0.12 + 0.86x\log(BW_M)$	94	<0.001	0.03	0.08
$\log(BW_M) = 0.02 + 0.08x\log(BW_F)$			0.04	0.10

[a] Weights are not known for MR and GNP; weights for those populations given in Table 1 are estimates based on skull length. Only known weights are used in these regressions.
[b] SEI = standard error of intercept; SES = SE for slope.

1985). So, all else being equal, IBI and AFW are inversely related to maturation rate — IBI being shorter and females younger at first whelping where maturation is fastest (Stringham 1980, 1985). The results presented here are thus consistent with the hypothesis that maturation rates to dissociation and adulthood are positively related to adult BS.

The fact that reproductive parameters were not as strongly related to SL as to BW is not necessarily typical. The bears whose skulls were measured are from only the same general regions as those whose BWs and reproduction were assessed; and more than a decade separated measurement of the SLs from collection of BW and reproductive data. Thus, to have found such strong relationships here for SL with BWs and reproductive parameters indicates that yet stronger relationships exist where all data are for bears in the same exact areas and
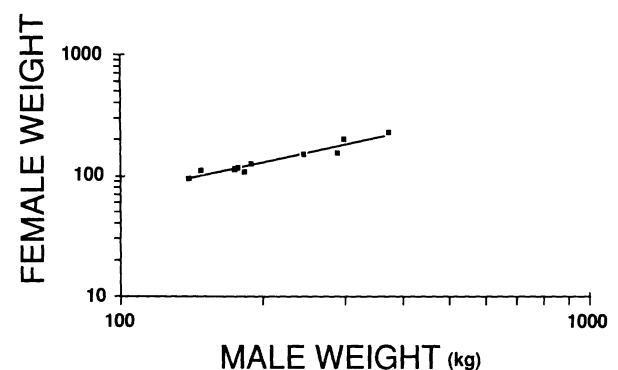

Fig. 1. Female body weight relative to male weight in adult grizzly bears; comparison across population means (n = 10), using seasonally adjusted data (see Table 2 for further details).

$\log_{10}(BW_F) = 0.12 + 0.86x\log_{10}(BW_M)$, $r^2 = 94\%$, $P < 0.001$

Table 3. Regressions of mean body size on mean skull length and vice versa; data from Table 1.[a]

Regression equation	r^{2b} (%)	P	±SEI[c]	±SES
Raw data[d]				
$\log(BW_F) = -6.09 + 3.22x\log(SL_M)$	90	<0.001	0.04	0.40
$\log(SL_M) = 1.96 + 0.28x\log(BW_F)$			0.01	0.04
$\log(BW_M) = -7.36 + 3.79x\log(SL_M)$	94	<0.001	0.04	0.37
$\log(SL_M) = 1.98 + 0.25x\log(BW_M)$			0.01	0.02
Seasonally adjusted data[e]				
$\log(BW_F) = -7.30 + 3.70x\log(SL_M)$	90	<0.001	0.04	0.47
$\log(SL_M) = 2.03 + 0.24x\log(BW_F)$			0.01	0.03
$\log(BW_M) = -8.07 + 4.07x\log(SL_M)$	88	<0.001	0.06	0.57
$\log(SL_M) = 2.05 + 0.22x\log(BW_M)$			0.01	0.03

[a] $n = 9$; there are no data on BW from MR and GNP, or on SL from YNP.
[b] Regression of A on B and of B on A yield exactly the same r^2 and P values. So the values are listed here only once for each pair of regressions between BW and SL.
[c] SEI = standard error of intercept; SES = SE for slope.
[d] BW_F = body weight for adult females; BW_M = body weight for adult males; SL_M = skull length for adult males.
[e] Seasonally adjusted weights are used for 5 populations.

times, and perhaps for the same individuals. Such data should be gathered.

Anomalous Data.—Some populations have anomalously high or low values for some reproductive parameters relative to BS. If the causes of anomaly could be identified, and these factors monitored, adding the factors to regression models could increase the exactness with which rates of reproduction (and survival) are predicted. New research should be focused on deriving this information.
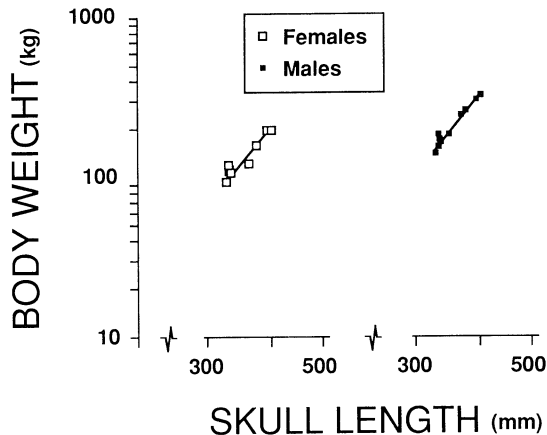

Fig. 2. Body weights of adult female and male grizzly bears relative to male skull length; comparison across population means ($n = 9$), using seasonally adjusted BW data (see Table 3 for further details).
$\log_{10}(BW_F) = -6.09 + 3.22x\log_{10}(SL_M)$, $r^2 = 90\%$, $P < 0.001$
$\log_{10}(BW_M) = -7.36 + 3.79x\log_{10}(SL_M)$, $r^2 = 94\%$, $P < 0.001$
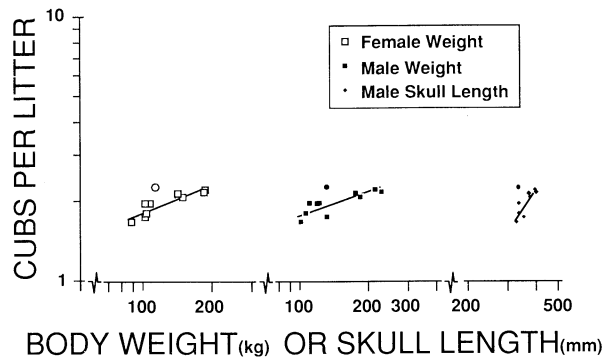

Fig. 3. Litter size relative to adult body weights and skull length for grizzly bears; comparison across population means ($n = 11$) using seasonally adjusted BW data. Each regression line shown was calculated without the anomalously high TUK litter size datum (circle). Regression equations are given in Table 4.

Much of the variance in the regressions of C/L and C/L/IBI on BS comes from the "anomalous" 2.3 C/L mean at TUK. It is not only unusually large *per se* (Nagy et al. 1983*b*), but much larger relative to BS than for other populations. Two causes have been hypothesized. First, females may have been unusually well nourished during at least 1 spring of that study — such that C/L was affected more than other reproductive parameters or BS. Second, high hunting pressure on males may have reduced their abundance and thus their aggression toward cubs (Nagy et. al 1983*b*). Negative relationships for adult male abundance with C/L, C/L/IBI, and maturation rate were demonstrated by Stringham (1980, 1983, 1985). If the TUK datum is omitted, seasonally-adjusted BW accounts for about 20% more of the *remaining* variance in C/L than of the *total* variance; figures for C/L/IBI rise comparably. To best represent trends for typical populations, a 2nd set of regression equations for C/L and C/L/IBI were calculated without the TUK datum (Table 4). It is these equations which are best used for predicting C/L from BW in other populations.

AFW in EBR (10.1 years) is not only the oldest yet recorded, but the oldest relative to BS — especially to BW_M and SL_M. Anomalously late maturation was also found among black bear populations in Montana and Minnesota (see Stringham 1990), populations which had been subjected to multi-year famines during the study periods (Jonkel and Cowan 1971; Rogers 1977, 1987). Perhaps a multi-year famine also occurred in EBR.

Closer correlations of BW_F with C/L and IBI than with AFW suggest that food scarcity may affect BW and reproduction by adult females less than it affects growth and maturation by immature females. This hypothesis of reduced vulnerability as females reach maturity is consis-

Table 4. Relationships[a] between population means for 4 reproductive parameters and adult body weight or skull length in 12 grizzly bear populations.[b]

Regression equation		r^2	P	±SEI	±SES
LITTER SIZE					
All populations ($n = 11$)					
$\log(C/L)$	$= -0.30 + 0.28x\log(BW_F)$	61	<0.01	0.03	0.08
	$= -0.30 + 0.26x\log(BW_M)$	59	<0.01	0.03	0.07
	$= -1.85 + 0.84x\log(SL_M)$	37	<0.05	0.04	0.37
Without Tuktoyaktuk Peninsula ($n = 10$)[c]					
$\log(C/L)$	$= -0.32 + 0.29x\log(BW_F)$	78	<0.001	0.02	0.06
	$= -0.33 + 0.27x\log(BW_M)$	78	<0.001	0.02	0.05
	$= -2.37 + 1.05x\log(SL_M)$	64	<0.01	0.03	0.28
NATALITY					
All populations ($n = 10$)					
$\log(NAT)$	$= -1.72 + 0.69x\log(BW_F)$	77	<0.01	0.05	0.13
	$= -1.66 + 0.61x\log(BW_M)$	71	<0.01	0.06	0.14
	$= -5.82 + 2.18x\log(SL_M)$	55	<0.01	0.07	0.70
Without Tuktoyaktuk Peninsula ($n = 9$)[c]					
$\log(NAT)$	$= -1.79 + 0.72x\log(BW_F)$	93	<0.001	0.03	0.08
	$= -1.75 + 0.64x\log(BW_M)$	87	<0.001	0.04	0.09
	$= -7.01 + 2.65x\log(SL_M)$	83	<0.001	0.04	0.45
INTERBIRTH INTERVAL (All populations $n = 11$)					
$\log(IBI)$	$= 1.40 - 0.40x\log(BW_F)$	73	<0.005	0.03	0.08
	$= 1.36 - 0.35x\log(BW_M)$	72	<0.005	0.03	0.07
	$= 4.01 - 1.36x\log(SL_M)$	59	<0.01	0.04	0.3
AGE AT FIRST WHELPING					
All populations ($n = 11$)					
$\log(AFW)$	$= 2.45 - 0.77x\log(BW_F)$	78	<0.005	0.05	0.14
	$= 2.36 - 0.66x\log(BW_M)$	74	<0.005	0.06	0.13
	$= 7.14 - 2.48x\log(SL_M)$	57	<0.01	0.07	0.72
Without Eastern Brooks Range ($n = 10$)[c]					
$\log(AFW)$	$= 2.23 - 0.67x\log(BW_F)$	89	<0.001	0.03	0.08
	$= 2.20 - 0.60x\log(BW_M)$	96	<0.001	0.02	0.05
	$= 6.83 - 2.37x\log(SL_M)$	84	<0.001	0.04	0.37

[a] Log_{10}-log_{10} regressions, based on the data set including seasonally adjusted weights from 5 populations (Table 1). Using unadjusted weights for those 5 populations, similar regression lines are obtained, but r^2 values tend to be 5-10% lower.

[b] Although some data are available from all 12 populations, there are none on C/L for SCA or on IBI and AFW for GNP. Thus, $n = 11$ for regressions of C/L, IBI, or AFW on body size, and $n = 10$ for regressions of natality (C/L/IBI) on body size.

[c] The C/L datum for TUK is anomalously high relative to body size. The AFW datum for the EBR is anomalously late relative to other reproductive parameters and to body size. Regressions derived without these anomalous data appear more representative for the trends among other populations.

Fig. 4. Natality relative to adult body weights and skull length for grizzly bears; comparison across population means ($n = 10$) using seasonally adjusted BW data. Each regression line shown was calculated without the anomalously high TUK litter size datum (circle). Regression equations are given in Table 4.

Fig. 5. Interbirth interval relative to adult body weights and skull length for grizzly bears; comparison across population means ($n = 11$) using seasonally adjusted BW data. Regression equations are given in Table 4.
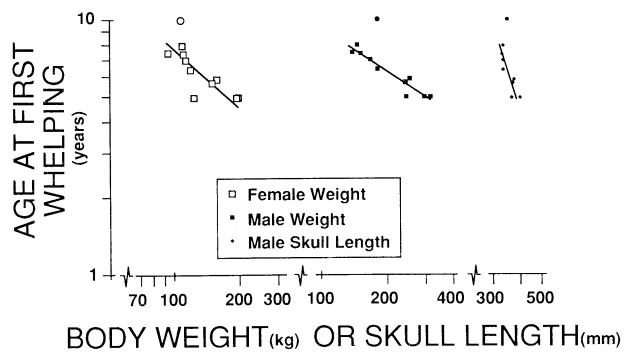
Fig. 6. Age at first whelping relative to adult body weights and skull length for grizzly bears; comparison across population means ($n = 11$) using seasonally adjusted BW data. Each regression line shown was calculated without the anomalously late AFW datum from EBR (circle). Regression equations are given in Table 4.

tent with the further reduction as mature females reach their prime — IBI tends to decline, despite increasing C/L (Couturier 1954, Craighead et al. 1974), just as is found in black bears (Eiler 1981; see Stringham 1990). Mature females tend to be larger, which may provide them with a greater body reservoir of nutrients for reproduction. Mature females may also have better home ranges, or the ability to forage more efficiently. Unfortunately, data on BW of females around the age of puberty are too scarce
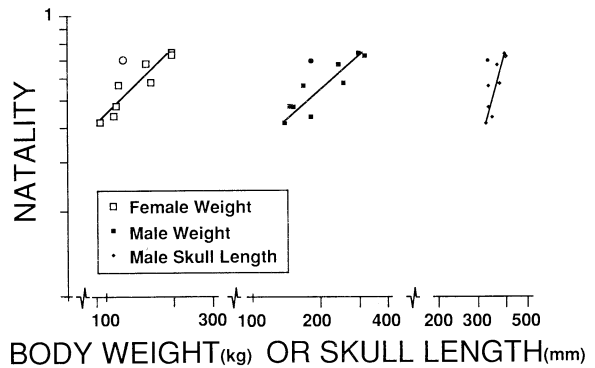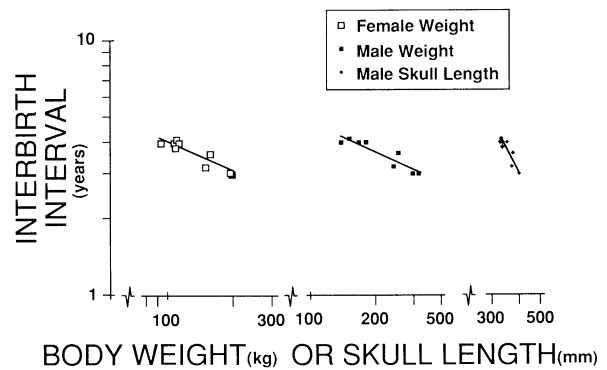
for one to test whether AFW is more closely correlated with pubescent BW than adult BW.

Limits to Standardization of Data

Lack of information on seasons of weight measurements for several of the populations prevents seasonal weight adjustment for them. Were such adjustments possible, the slope, intercept, and coefficient of correlation obtained (e.g., for BW_M with SL_M or with C/L) might change somewhat from what is found without thorough standardization. But limited standardization is not likely to have significantly biased my results. I made 12 tests, involving regressions of 4 reproductive parameters on BW_F, BW_M, and SL_M. It is highly probable that 1 of 12 relationships tested could yield a "significant" correlation by chance. But likelihood of correlations being spurious declines as the number of tests increases, being negligible for 4, much less 12 tests. All of these parameters were sampled independently; even the ratio of C/L to IBI (i.e., C/L/IBI = natality) is effectively independent since it is a ratio. So probability of all 12 tests yielding spurious correlations at $P < 0.05$ is roughly $0.05^{12} = 2 \times 10^{-16}$. For black bears, these same 4 reproductive parameters were regressed on BW_F and BW_M (Stringham 1990), bringing the total number of independent tests to 20. The chance of 20/20 spuriously significant relationships is about $0.05^{20} = 1 \times 10^{-26}$. Given that the individual P values found are generally ≤ 0.01, and $0.01^{20} = 1 \times 10^{-40}$, the overall significance of these findings must be astronomically high even if independence among the variables is <100%.

All data contain noise; valid data also contain information. The value of these data depends not on an absence of noise, but on a high information-to-noise ratio. One way of increasing this ratio is to combine data, either successive replicates from a single study or different studies. If the noise is random, combining the data sets tends to average out the noise. This occurs, for instance, when one calculates a mean, and with most other statistical analyses, including regression. The information-to-noise ratio here is apparently very high, judging from the consistently strong relationships found and the astronomical overall significance level.

High information-to-noise ratios are typical in relationships of reproductive parameters to BS, even when one is comparing not across populations but across species, using even unstandardized data (Eisenberg 1981, Peters 1983, McDonald 1984, Gittleman 1986).

Results with poorly standardized data can be used as 1st approximations. But they should eventually be replaced by more precise regressions as more standardized data are gathered and other variables affecting reproduc-

tive parameters can be included in regression models (see Gittleman 1986).

MANAGEMENT APPLICATIONS

Predicting Reproductive Parameters from Body Size

Estimates of reproductive parameters based on BS data have reasonably narrow confidence bounds, judging from the high r^2 and significance levels obtained. The bounds for AFW can be narrowed even farther where one can partition data from populations subjected to a recent multi-year famine from those which weren't — as is done here by omitting the EBR datum. Thus, 2 sets of regressions on AFW are provided, a 1st with the EBR datum, the 2nd without. The latter should be used to estimate EBR for populations not subjected to recent famine.

The reliability of predicting reproductive parameters from BS can be illustrated for Yellowstone grizzly bears. Figures for their adult BW and reproduction in Table 1 come from years 1959-70 (Craighead et al. 1969, 1974; Craighead and Mitchell 1982). During 1974-80, adult BWs were lighter: a 25% drop to 183 kg for adult males, and a 16% drop to 127 kg for adult females (see Knight et al. 1981, Stringham 1985). Lower BW is apparently due to reduced food supply. From the early part of this century, bears fed regularly on garbage at open pit dumps in YNP; between 1968-70, the major dumps were closed to bears (Cole 1976, Craighead and Mitchell 1982).

My regression equations for BW_F and reproduction can be used to predict declines in reproduction at YNP associated with dump closure. The predicted decline in C/L from 2.2 to 1.9 agrees exactly with the observed mean of 1.9 during 1974-80 (calculated from the data of Knight et al. 1981). The predicted delay in AFW from 5.7 to 6.6 years differs negligibly (6%) and non-significantly from the mean of 6.2 years observed during 1974-84 (Knight and Eberhardt 1985).

Although biologists might prefer to always base management on observed rather than predicted rates of reproduction, that is not often feasible. Even where observations can be made, sample sizes are sometimes too small to be reliable. Reliability depends on how widely sampling is distributed through the regional population, the number of bears whose reproduction is assessed each year, and the number of years over which assessment continues. Management of an entire state or provincial population may be based on data gathered in a small fraction of that region, one not necessarily representative of the whole region. Or data may be gathered for only a brief period that does not reflect subsequent

changes in habitat quality or other environmental factors. So the question is less often whether management will be based on *predicted* reproductive rate, than how the predictions can be made most reliably. In lieu of adequate field data on reproduction, basing estimates on BS seems to be the best method now available. Indeed, predictions of reproductive parameters based on a large sample of BWs may prove more reliable than estimates based on a small sample of observed C/L, IBIs and AFWs. This needs to be investigated.

My log-log regression models provide local approximations for average values of reproductive parameters relative to adult BS within the ranges of size considered here. But they may not apply at larger or smaller sizes; extrapolation should be done cautiously. For example, there may be absolute limits to reproduction — thresholds beyond which changes in BS no longer affect reproduction. For the populations considered here, mean natality did not exceed 0.77 cubs per adult female per year; females did not reproduce before mean age 4.4 years. These may approximate thresholds.

Before other data sets on BS are used to estimate reproductive parameters with my regression models, methods of measurement need to be standardized or data converted to a standard format. To predict reproductive rate from the mean size of hunter-killed bears, one needs to convert from the weight of each dead and perhaps dressed bear to its estimated live weight. Before predicting from SLs measured on live bears (e.g., Glenn 1980), one needs to subtract for hair and tissue covering the skull, and for any shrinkage that normally occurs when a skull is cleaned and dried. Measurements of SL made by tape measure following skull contours need to be converted to caliper lengths. If appropriate equations for these conversions are not yet available, they should be developed.

Monitoring Population Dynamics

Natality and maturation rate together determine the net contribution by reproductive rate to population growth rate (i.e., reproductive vigor, as reflected by the Potential Natality Index [Stringham 1980]). The higher the body growth rate and adult sizes, the more vigorously a population tends to reproduce. Cub survivorship may also be enhanced. Rogers (1976, 1987) documents positive relationships of cub survivorship with BW of cubs and their mother in black bear.

Theoretically, annual fluctuation in BS could be used to estimate annual changes in reproductive rate and nutrition-limited survivorship. Monitoring adult BS might thus provide a basis for monitoring population dynamics

and fine-tuning harvest quotas for bears, as is already done for some ungulates.

CONCLUSIONS

My findings should leave no doubt but that body measurements and reproductive parameters are strongly interrelated. This and my previous findings (Stringham 1980) demonstrate a much higher information-to-noise ratio than many biologists would have expected when comparing data among bear populations. Nevertheless, increasing that ratio should both tighten up the relationships already found and reveal new insights. Comparison among populations is best done with fully comparable data. Increasing standardization of data collection and analysis should become a higher priority in our field. Where standardization is prevented by financial or logistic factors, we need better methods of converting results from each non-standard measurement to approximate what would have been found with a standard measurement (e.g., adjustment of BWs in spring to approximate weights in fall). This may require collection of multiple measurements in some populations so that we can directly evaluate the effect of measurement differences on results (e.g., reweighing some animals in both spring and fall to determine how much their weights change, so that we can estimate potential fall weights of animals measured only in spring).

Another priority is preservation of more raw data so that different data sets can be more fully integrated with minimal loss of information. Where raw data sets are too lengthy for journal publication, they should be archived in a central location where they are available to colleagues. This is already common practice in other fields of science.

LITERATURE CITED

BALLARD, W.B., S. MILLER, AND T.H. SPRAKER. 1982. Home range, daily movements, and reproductive biology of brown bear in Southcentral Alaska. Can. Field Nat. 96:1-5.

BEECHAM, J. 1980*a*. Some population characteristics of two black bear populations in Idaho. Int. Conf. Bear Res. and Manage. 4:201-204.

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

BLANCHARD, B.M. 1987. Size and growth patterns of the Yellowstone grizzly bear. Int. Conf. Bear Res. and Manage. 7:99-107.

BUNNELL, F.L., AND D.E.N. TAIT. 1981. Population dynamics of bears - implications. Pages 75-98 *in* C.W. Fowler and T.D. Smith, eds. Dynamics of large mammal populations. John Wiley and Sons, New York. 477pp.

COLE, G.F. 1976. Management involving grizzly and black bears in Yellowstone National Park, 1970-75. Nat. Resour. Rep. 9. U.S. Dep. Inter., Natl. Park Serv. 26pp.

CRAIGHEAD, J.J., AND F.C. CRAIGHEAD, JR. 1969. Reproductive biology of young female grizzly bears. J. Reprod. Fert., Suppl. 6:447-475.

_____, _____, AND J. SUMNER. 1976. Reproductive cycles and rates in the grizzly bear, Ursus arctos horribilis, of the Yellowstone ecosystem. Int. Conf. Bear Res. and Manage. 3:337-356.

_____, AND J.A. MITCHELL. 1982. The grizzly bear. Pages 515-556 in J.A. Chapman and G.A. Feldhamer, eds. Wild mammals of North America: biology, management, and economics. Johns Hopkins Univ. Press, Baltimore. 1147pp.

_____, J.R. VARNEY, AND F.C. CRAIGHEAD, JR. 1974. A population analysis of the Yellowstone grizzly bears. Mont. For. Conserv. Exp. Stn. Bull. 40. 20pp.

EILER, J.H. 1981. Reproductive biology of black bears in the Smoky Mountains of Tennessee. M.S. Thesis. Univ. Tenn., Knoxville. 128pp.

ELOWE, K.D. 1987. Factors affecting black bear reproductive success and cub survival in Massachusetts. Ph.D. Thesis. Univ. Mass., Amherst. 71pp.

EISENBERG, J. 1981. Mammalian radiations: an analysis of trends in evolution, adaptation, and behavior. Univ. Chicago Press, Chicago. 610pp.

ERICKSON, A.W., AND J.E. NELLOR. 1964. Breeding biology of the black bear. Pages 1-45 in A.W. Erickson, J. Nellor, and G.A. Petrides, eds. The black bear in Michigan. Mich. State Univ., Agr. Exp. Stn., East Lansing. Res Bull. 4. 102pp.

FRISCH, R.E. 1974. Menstrual cycles: fatness as a determinant of minimum weight for height necessary for their maintenance or onset. Science 185:945-951.

_____. 1982. Malnutrition and fertility. Science 215:1272-1273.

_____. 1989. Body weight and reproduction. Science 246:432.

GITTLEMAN, J.L. 1986. Carnivore life history patterns: allometric, phylogenetic, and ecological associations. Am. Nat. 127:744-771.

GLENN, L.P. 1980. Morphometric characteristics of brown bears of 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.

JONKEL, C.J., AND I.M. COWAN. 1971. The black bear in the spruce-fir forest. Wildl. Monogr. 27. 57pp.

KNIGHT, R.R., AND L.L. EBERHARDT. 1985. Population dynamics of Yellowstone grizzly bears. Ecology 66(2):323-334.

_____, B.M. BLANCHARD, AND K.C. KENDALL. 1981. Yellowstone grizzly bear investigations. Annu. Rep. Interagency Study Team, 1980. U.S. Dep. Inter., Natl. Park Serv. 55pp.

LECOUNT, A. 1983. Evidence of wild black bears breeding while raising cubs. J. Wildl. Manage. 47:264-268.

McDONALD, J.N. 1984. The reordered North American selection regime and late Quaternary megafaunal extinctions. Pages 404-439 in P.S. Martin and R.G. Klein, eds. Quaternary extinctions. Univ. Ariz. Press, Tucson. 892pp.

MILLER, S.D. 1988. Impact of increased hunting pressure on the density, structure, and dynamics of brown bear populations in Alaska's Game Management Unit 13. Alas. Dep. Fish Game, Fed. Aid Wildl. Restoration Proj. W-22-6. 151pp.

MILLER, S.J., N. BARICHELLO, AND D. TAIT. 1982. The grizzly bears of the Mackenzie Mountains, Northwest Territories. Completion Rep. 3. Mimeo. 118pp.

MOEN, A.N. 1978. Seasonal changes in heart rates, activity, metabolism and forage intake of white-tailed deer. J. Wildl. Manage. 42(2):715-738.

MUNDY, K.R.D., AND D.R. FLOOK. 1973. Background for managing grizzly bears in the National Parks of Canada. Can. Wildl. Serv. Rep. Ser. 22. 35pp.

NAGY, J.A., R.H. RUSSELL, A.M. PEARSON, M.C.S. KINGSLEY, AND B.C. GOSKI. 1983a. Ecological studies of grizzly bears in the Arctic Mountains, Northern Yukon Territory, 1972-75. Can. Wildl. Serv., Edmonton. 104pp.

_____, _____, _____, _____, AND C.B. LARSEN. 1983b. A study of grizzly bears on the barren-grounds of Tuktoyaktuk Peninsula and Richards Island, Northwest Territories, 1974-78. Can. Wildl. Serv., Edmonton. 136pp.

PEARSON, A.M. 1975. The northern interior grizzly bear Ursus arctos L. Can Wildl. Serv. Rep. Ser. 34. 86pp.

PETERS, R.H. 1983. The ecological implications of body size. Cambridge Univ. Press, New York. 329pp.

RAUSCH, R.L. 1961. Notes on the black bear, Ursus americanus, Pallas, in Alaska, with particular reference to dentition and growth. Z. Saugetierk. 2:65-128.

_____. 1963. Geographic variation in size in North American brown bears, Ursus arctos L., as indicated by condylobasal length. Can. J. Zool. 41:33-45.

REYNOLDS, H.V. 1976. North Slope grizzly bear studies. Alas. Dep. Fish Game, Final Rep., Fed. Aid Wildl. Restoration Proj. W-17-6 and W-17-7. 14pp. + App.

_____. 1981. North Slope grizzly bear studies. Alas. Dep. Fish Game, Proj. Prog. Rep., Fed. Aid Wildl. Restoration Proj. W-21-1. 18pp.

_____. 1983. Grizzly bear population biology in the Western Brooks Range, Alaska. Paper presented at the 6th Int. Conf. Bear Res. and Manage.

ROGERS, L.L. 1976. Effects of mast and berry crop failures on survival, growth, and reproductive success of black bears. Trans. North Am. Wildl. and Nat. Resour. Conf. 41:431-438.

_____. 1977. Social relationships, movements, and population dynamics of black bears in northern Minnesota. Ph.D. Thesis. Univ. Minn., Minneapolis. 194pp.

_____. 1983. Effects of food supply, predation, cannibalism, parasites, and other health problems on black bear populations. Pages 194-211 in F.L. Bunnell, D.S. Eastman, and J.M. Peek, eds. Symposium on natural regulation of wildlife populations. Proc. No. 14, For. Wildl. Exp. Stn., Univ. Idaho, Moscow. 225pp.

_____. 1987. Effects of food supply and kinship on social behavior, movements, and population growth of black bears in northeastern Minnesota. Wildl. Monogr. 97. 72pp.

SADLIER, R.M.F.S. 1969. The ecology of reproduction in wild and domestic mammals. Methuen and Co., Ltd., London. 321pp.

SEVERINGHAUS, C.W., AND A.N. MOEN. 1983. Prediction of weight and reproductive rate of a white-tailed deer population from records on antler beam diameter among yearling males. N.Y. Fish and Game J. 30(1):30-38.

SPRAKER, T., W. BALLARD, S. MILLER, S. EIDE, AND K. TAYLOR. 1981. Feeding behavior of interior brown bears. Alas. Dep. Fish Game, Proj. Prog. Rep., Fed. Aid Wildl. Restoration Proj. W-17-10, W-17-11, W-21-1. 57pp.

STIRLING, I., A.M. PEARSON, AND F.L. BUNNELL. 1976. Population ecology of polar and grizzly bears in Canada. Trans. North Am. Wildl. and Nat. Resour. Conf. 41:421-429.

_____, C. JONKEL, P. SMITH, R. ROBERTSON, AND D. CROSS. 1977. The ecology of the polar bear (*Ursus maritimus*) along the western coast of Hudson Bay. Can. Wildl. Serv. Occas. Paper 33. 64pp.

STRINGHAM, S.F. 1980. Possible impacts of hunting on the grizzly/brown bear, a threatened species. Int. Conf. Bear Res. and Manage. 4:337-349.

_____. 1983. Roles of adult males in grizzly bear population biology. Int. Conf. Bear Res. and Manage. 5:140-151.

_____. 1985. Responses by grizzly bear population dynamics to certain environmental and biosocial factors. Ph.D. Thesis. Univ. Tenn., Knoxville. 456pp.

_____. 1986. Effects of climate, dump closure, and other factors on Yellowstone grizzly bear litter size. Int. Conf. Bear Res. and Manage. 6:33-39.

_____. 1990. Black bear reproductive rate relative to body weight in hunted populations. Int. Conf. Bear Res. and Manage. 8:425-432.