

BLACK BEAR REPRODUCTIVE RATE RELATIVE TO BODY WEIGHT IN HUNTED POPULATIONS

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Abstract: Litter size, natality (cubs per adult female per year), and maturation rate are positively related to body weights of adult males and females. This is shown by regressions of reproductive parameters on weight, using mean values from each of 7 hunted populations. Maturation rates to weaning and adulthood are, respectively, proportional to the inverses of interbirth interval and age at first whelping, generation length. Assuming that weight is an index of nutritional status, these findings for black bear (*Ursus americanus*) are consistent with the typical mammalian dependence of reproductive rate on nutritional status. Because body weights are commonly obtained by game managers, they may be a quick, inexpensive basis for estimating reproductive rate for populations where reproductive data are lacking.

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Per capita rates of reproduction and survival tend to be positively related to nutritional status and to food supply in various mammals (Sadlier 1969) including black bear (Rausch 1961; Jonkel and Cowan 1971; Rogers 1976, 1977, 1983, 1987; Beecham 1980a, b; Eiler 1981; Elowe 1987; Eiler et al. 1989; Elowe and Dodge 1989; D. L. Garshelis, pers. commun.), polar bear (*U. maritimus*; Stirling et al. 1976, Bunnell and Tait 1981), and grizzly bear (*U. arctos*; Stringham 1980, 1985, 1986, 1990; Bunnell and Tait 1981).

Findings on bears are not readily generalized from each population to others due to lack of a common measure for food supply or nutritional status. Rogers (1976, 1987), Eiler (1981), and Eiler et al. (1989) showed positive correlations between the proportion of adult females whelping each spring and indices of food supply during the previous summer or autumn, respectively. But more detailed comparison between their results is impossible. Eiler's (1981) index of acorn supply for the Smoky Mountains has nothing in common with Rogers' (1976, 1977, 1987) index of berry supply for Minnesota. Metabolizable energy or protein yields might be a common basis for some measures of food supply. But where measuring nutrient contents is unfeasible, an alternative approach is to follow the initiative of Moen (1978) and Severinghaus and Moen (1983). They used adult body weight or yearling antler-beam diameter in white-tailed deer (*Odocoileus virginianus*) as a common index of nutritional status governing reproduction and survival. Size data can be obtained much more readily and inexpensively than data on either nutrients or reproductive rate.

The utility of the body weight approach for bears was demonstrated by Rogers (1983): in northeastern Minnesota, 94% of all fertile adult female black bears weighing >80 kg on 1 October whelped during the following spring ($n = 34$). None weighing <67 kg whelped ($n = 17$). Whelping rates for 67-80 kg females were intermediate.

My work was done to provide more detail on how reproductive parameters are related to adult body weight so that mean weights for a population can predict its mean reproductive rate.

I hypothesized that mean reproductive rate for a bear population is positively related to mean body weights of adult males and females. Litter size (C/L), natality (C/L/IBI), and maturation rate therefore should be positively related to adult body weights. Interbirth interval (IBI) and age at first whelping (AFW) tend to be inversely related to maturation rates to weaning and adulthood, respectively. So positive relationships of maturation rate with adult body weight imply negative relationships of IBI and AFW with body weight. In summary, the 4 hypotheses are:

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

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METHODS

My hypotheses were tested by regressing the mean value for each reproductive parameter on mean body weights of adults of either sex, using Minimum Variance regression with 1-tailed tests of significance. The regression models fit to these data are log-log, as is conventional, because such allometric relationships tend to be geometric rather than arithmetic (see Peters 1983, McDonald 1984, Gittleman 1986). Data from 7 hunted populations (Table 1) were obtained from the literature.

Table 1. Mean values for reproductive parameters and adult body weights in North American black bear populations.

Population	Mean body weight (kg)		Litter size (C/L) ^a	Interbirth interval (IBI) (yrs.)	Natality	Age at first whelping (AFW) (yrs.)
	F	M				
Western Montana (WM) ^c	57 (76)	96 ^b (43)	1.70	≥3.0 ^b (14)	0.57	6.6 ^b (5)
Northeastern Minnesota (MN) ^d	78 ^b (58)	171 ^b (15)	2.38 (52)	2.28 (36)	1.04	6.3 (17)
Lowell, Idaho (LI) ^e	52 ^b (59)	86 ^b (45)	1.65 (23)	3.57 ^b	0.46	5.0 ^b (7)
Council, Idaho (CI) ^f	62 ^b (81)	106 ^b (58)	1.90 (11)	3.23 ^b	0.59	4.8 ^b (9)
North Carolina (NC) ^g	89	167	2.45 ^b (22)	2.16 ^b	1.13	4.0 ^b (5)
Kenai Peninsula (KP) ^h	62 ^b (36)	107 ^b (25)	1.9 ^b (15)	2.56 ^b	0.74	4.4 ^b (8)
Pennsylvania (PN) ^j	92	181	2.90	2.00	1.45	3.6 ^b

^a Litter size for cubs of the year.

^b Values calculated by me from data provided by the authors. R = reproductive data; W = weight data.

^c RW Jonkel and Cowan (1971).

^d R Rogers (1987; females on natural diets); W L. L. Rogers. (pers. commun.).

^e R Beecham (1980b, pers. commun.), Reynolds and Beecham (1980); W Beecham (1980a).

^f R Beecham (1980b); W Beecham (1980a).

^g R Collins (1974), W Collins (unpubl., cited by Alt 1980).

^h RW Schwartz et al. (1983).

^j R Kordek and Lindzey (1980), Alt (1982); W Alt (1980). The abbreviation identifying a population in this Table also identifies it in the text.

Body Weight

Data on body weights are for adults, bears ≥5-years-old. Weight varies seasonally, tending to be highest in late fall, just before hibernation, and lowest sometime in spring after den emergence. In some populations this seasonal variation is large (Jonkel and Cowan 1971, Schwartz et al. 1983), in others it is small (Hellgren et al. 1989). Before comparing weight data across populations, it would be preferable to standardize by season (Schwartz et al. 1983). But that is not feasible using available information. Data from most populations cover the entire period spring to fall, with varying emphasis on each season—an emphasis not specified for any populations except Pennsylvania (PN) and Alaska's Kenai Peninsula (KP). For consistency across populations, all weight data are used in calculating means, irrespective of season.

Where authors did not provide mean weights, but did

provide raw weight data, I calculated means. Abbreviations given below for population names correspond to those in Table 1. Inferences from an author's data are indicated in the text by an arrow "→".

KP: Schwartz et al. (1983:Table 24) present means by season: spring (May) 53 kg for 6 females, 104 kg for 6 males; summer (June-July) 59 kg for 23 females, 90 kg for 19 males; fall (August-October) 75 kg for 7 females, no data for males. To estimate spring-to-fall average weights without over-emphasizing any season, I used the *unweighted* mean across those seasons: $(53+59+75)/3 = 62$ kg for females. Due to lack of fall weight data for males, their spring-to-fall average was estimated by assuming that the ratio of unweighted spring-to-fall vs. spring-summer weights for both sexes were comparable: $(SPR-SUM-FALL)/(SPR-SUM) = 62/56$ for females = $X/97$ for males; $X = 107$ kg.

LI and CI: Beecham (1980a) provided age-specific weights and sample sizes, from which I calculated weighted means.

MN: L.L. Rogers provided unpublished raw data from which I calculated means.

Mean weights for the other populations were provided by the authors.

Litter Size

Where a value for mean litter size (cubs-of-the-year per litter) was not provided by an author, it was calculated. For prenatal litters, total corpora lutea were divided by total pregnant females. For postnatal litters, total cubs were divided by total cub litters.

Mean size of litters in a population tends to vary over time. Older litters may have suffered more partial attrition, which would tend to reduce their size. Conversely, smaller litters may suffer a higher rate of complete attrition, due perhaps to maternal abandonment (Tait 1980); this would tend to increase mean size of remaining litters. Corpora luteal litter size is not necessarily larger than summer litter size; in Great Dismal Swamp (GDS), 5 corpora luteal litter sizes averaged 1.8, compared to 2.3 for 7 cub litters (Hellgren and Vaughan 1989).

There is case-to-case variation in whether mean litter size for a population tends to decrease or increase between conception or birth and censusing up to a year later. Without information on mortality patterns in each population and on ages of litters, litter size cannot be standardized relative to these factors when comparing among populations.

Only prenatal litter size is available from North Carolina (NC), in-den litter size from PN, and den-emergence litter size from KP. Other postnatal litter sizes are for "summer."

The mean size of litters produced by females tends to increase as the females age (Collins 1974, Eiler 1981, Alt 1982). Of the authors whose data is analyzed here, only Alt (1982) specified mean litter size for mothers of each age. So I could not standardize litter size for maternal age across populations.

Interval Between Litters

The time interval between birth of a litter and birth of the female'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. Little information is available on this. Age at dissociation seems inversely related to maturation rate of the offspring (Stringham 1980, 1985).

When calculating IBI, most authors omit intervals known to have been truncated by whole-litter mortality, as I have done where possible when estimating IBI from data provided by authors.

One index of IBI is the inverse of the proportion of females accompanied by cubs each year. At CI, for instance, this proportion was 31% (Reynolds and Beecham 1980), suggesting a mean interbirth interval of roughly $1/31 = 3.23$ years. At LI it was "a few percent lower" (J. Beecham, pers. commun.) \rightarrow roughly $1/28 = 3.57$ years.

Other IBI figures were derived as follows:

WM: known IBI: $n = 2$ at 2 years, 9 at ≥ 3 years, 2 at 4 years \rightarrow mean IBI ≥ 3.0 years.

NC: 67% of the mature (≥ 3 -year-old) females harvested each year were pregnant. If hunters killed only females without cubs, 67% pregnancy would indicate roughly 67% of cubless females breeding at 2-year intervals and 33% at ≥ 3 -year intervals \rightarrow mean IBI ≥ 2.33 years. Alternately, if vulnerability to hunting was unrelated to whether a female bore cubs the year she was killed, mean IBI would be < 2.33 years, perhaps as short as 2 years. The ratio $1/67 = 1.5$ years is unrealistically short for an IBI and perhaps a statistical artifact of synchronous breeding. If synchrony occurs, pregnancy rate could be much higher in alternate years than in intervening years, and thus bias any estimate of mean pregnancy rate based on an odd number of years of data. Collins (1974) has data from just 3 years. The true mean is probably between 2.00 and 2.33; the median of this range is about 2.16 years, which is my estimate for IBI in NC.

KP: 39% of mature females were accompanied by cubs; $1/39 = 2.56$ as a rough IBI figure.

Age at First Whelping

Age at first whelping/parturition is equivalent to generation length—the span of time between the birth of a female and the birth of her own first offspring (or her first female offspring). Maturation rate to adulthood is the inverse of generation length (Stringham 1980, 1985). Authors determined whether a female was sexually mature or had whelped by traits such as presence of corpora lutea, placental scars, or cubs; or condition of the genitalia and mammae.

Some authors listed ages at which females are known to have first successfully conceived (FSC); these females would have given birth the following spring:

$$AFW = FSC + 0.5 \text{ year.}$$

I estimated AFW from the proportions of females known to have bred or whelped by each age. For example, in PN, no females were found to have bred before age 2.8 (Kordek and Lindzey 1980). Based on examination of reproductive tracts, the authors conclude that all females >2.5 years had the potential to breed. Therefore, one can reasonably assume that most females that did not breed by age 2.5 did breed by 3.5, and all that did not breed at 3.5 had bred at 2.5. The proportions of females with evidence of current breeding at ages 2.8 and 3.8 were 38% ($n = 36$) and 68% ($n = 25$), respectively. The total number of females that bred at either age is 51, of which 35% ($18/51 = 10/26 + 8/25$) bred at 2.5, and 65% ($33/51 = 16/26 + 17/25$) bred at 3.5. Calculating $(35\%)(2.5 \text{ years}) + (65\%)(3.5 \text{ years}) = 3.15$ years for FSC \rightarrow AFW = 3.65 years.

Other values presented in Table 1 were derived as follows:

WM: known AFW: $n = 1$ at 6 years, 1 at 7 years and 1 at 8 years; 1 other female first whelped no earlier than 6 years; a 5th female may have first whelped as early as 5 years, but perhaps not until 7 years \rightarrow mean AFW ≥ 6.6 years.

LI: Beecham (1980b) FSC: 2 at 3.5 years, 4 at 4.5 years, and 1 at least 6 years, so mean FSC = ≥ 4.5 \rightarrow AFW ≥ 5.0 years.

CI: Reynolds and Beecham (1980) FSC: 3 at 3.5 years, 5 at 4.5 years, and 1 at 5.5 years, so mean FSC = 4.3 years \rightarrow AFW = 4.8 years.

NC: FSC = 3.5 (Collins 1974) \rightarrow AFW 4.0 years.

KP: AFW: 6 at 4 years, 1 at ≥ 5 years, 1 at ≥ 6 years, so mean AFW ≥ 4.4 years.

Natality

Natality, the number of cubs per adult female per year, is estimated by dividing litter size by interbirth interval (Stringham 1980, Bunnell and Tait 1981).

RESULTS

Regression analyses (Figs. 1-4) confirm the positive relationships of litter size and natality with body weights for adults of either sex ($r^2 \geq 94\%$, $P < 0.001$). The relationship for natality embodies the positive relationship of litter size with weight and a negative relationship of interbirth interval with weight. Results also confirm a negative correlation of age at first whelping with weight. Correlations are of comparable strength for adults of both sexes, whose weights are highly correlated ($r^2 = 96\%$, $P < 0.001$; Fig. 5).

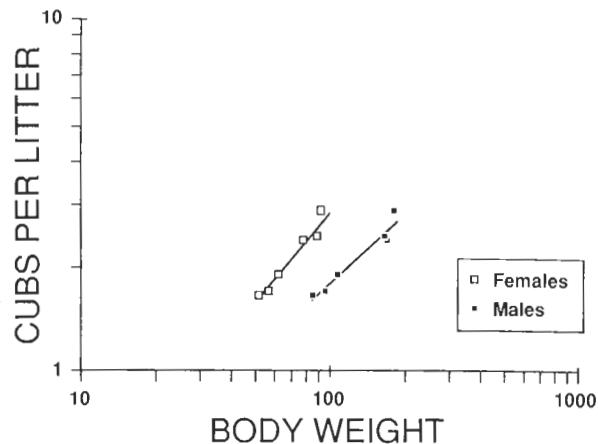


Fig. 1. Litter size relative to body weights of adult black bears; comparison across population means ($n = 7$; note complete overlap of CI and KP data).

$$\begin{aligned} \log(C/L) &= -1.06 + 0.66 \times \log(BW_w), R^2 = 94\%, P < 0.001, \\ &SEI = 0.02, SES = 0.07. (SEI = \text{standard error of intercept;} \\ &SES = SE \text{ for slope}) \\ &= -1.37 + 0.92 \times \log(BW_w), R^2 = 96\%, P < 0.001, \\ &SEI = 0.02, SES = 0.09. \end{aligned}$$

DISCUSSION

Reproductive Rate vs. Body Weight

For C/L, IBI, and natality relative to weight, data from all populations are consistent with straight-line relationships ($r^2 \geq 88\%$, $P < 0.01$). That is true for AFW in only 5 of the 7 populations. Relative to body weights, AFW is far older in WM and MN than in the other populations; AFW is also older relative to C/L and IBI.

WM and MN are unusual in being subjected to multi-year famines during the study periods (Jonkel and Cowan

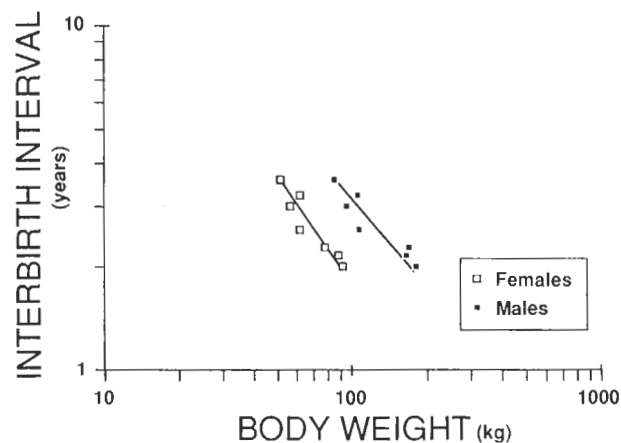


Fig. 2. Interbirth interval relative to body weights of adult black bears; comparison across population means ($n = 7$).

$$\begin{aligned} \log(IBI) &= 1.81 - 0.66 \times \log(BW_w), R^2 = 88\%, P < 0.002, \\ &SEI = 0.04, SES = 0.11. \\ &= 2.11 - 0.92 \times \log(BW_w), R^2 = 88\%, P < 0.002, \\ &SEI = 0.04, SES = 0.15. \end{aligned}$$

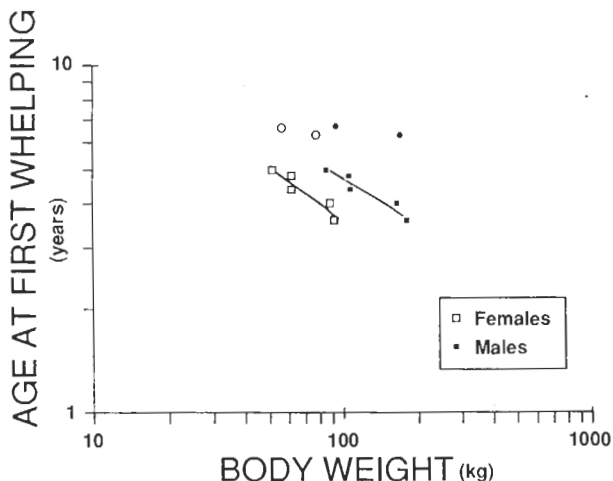


Fig. 3. Age at first whelping relative to body weights of adult black bears; comparison across population means. The anomalous data from WM and MN are marked with circles rather than squares. All populations ($n=7$) (regressions not plotted):

$$\log(\text{AFW}) = 1.27 - 0.28 \times \log(\text{BW}_f), R^2 = 15\%, P > 0.05, \text{SEI} = 0.10, \text{SES} = 0.30,$$

$$= 1.65 - 0.53 \times \log(\text{BW}_m), R^2 = 28\%, P > 0.05, \text{SEI} = 0.09, \text{SES} = 0.38.$$

Excluding WM and MN ($n=5$) (regressions plotted):

$$\log(\text{AFW}) = 1.57 - 0.51 \times \log(\text{BW}_f), R^2 = 89\%, P < 0.01, \text{SEI} = 0.02, \text{SES} = 0.10,$$

$$= 1.48 - 0.40 \times \log(\text{BW}_m), R^2 = 92\%, P < 0.01, \text{SEI} = 0.02, \text{SES} = 0.07.$$

1971; Rogers 1977, 1987). Perhaps females just reaching maturity are more vulnerable to famine than are females that have bred before. Decreasing vulnerability with maturity is shown by the fact that females in their prime are less likely than younger mothers to skip reproduction

in years when food is scarce, despite the fact that prime females tend to produce larger litters (Eiler 1981, Alt 1982). Mothers in their prime tend to be somewhat larger in body size, often with heavier fat reserve (Collins 1974, Eiler 1981, Alt 1982). Perhaps prime-age mothers have better home ranges, or are able to forage on these ranges more efficiently.

If we consider just the 5 populations that did not suffer multi-year famines during the study periods, body weights of adults account for 92% (M) and 89% (F) of remaining variance in AFW, contrasted to only 15% and 28%, respectively, of the total variance. Prediction of AFW from body size for a population is thus greatly enhanced if one knows whether this population has been subject to multi-year famines during the periods when weights were taken.

The observed inverse relationships of IBI and AFW with body weight are consistent with the expected positive correlation between maturation rate and body weight. My results thus substantiate the finding by Rausch (1961) that better nourished black bears tend to grow larger, faster, and to mature at an earlier age.

Signs (+ vs. -) of these correlations for reproductive parameters with body weights of black bears agree with those on grizzly bears (Stringham 1990). For both species, the positive relationships of natality, litter size, and maturation rate with body weight agree with other findings on black and grizzly bears concerning reproductive rate relative to food supply or nutritional status (Jonkel and Cowan 1971; Rogers 1976, 1983, 1987; Stringham 1980, 1985, 1986; Bunnell and Tait 1981;

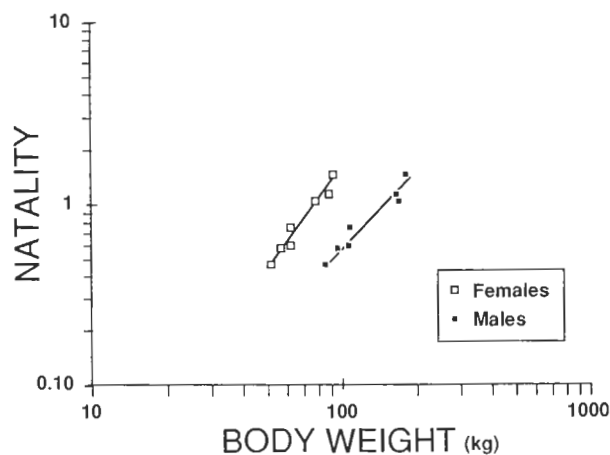


Fig. 4. Natality (C/L/IBI) relative to body weights of adult black bears; comparison across population means ($n=7$).

$$\log(\text{NAT}) = -2.87 + 1.32 \times \log(\text{BW}_f), R^2 = 95\%, P < 0.001, \text{SEI} = 0.05, \text{SES} = 0.14,$$

$$= 0.043 + 1.83 \times \log(\text{BW}_m), R^2 = 95\%, P < 0.001, \text{SEI} = 0.04, \text{SES} = 0.18.$$

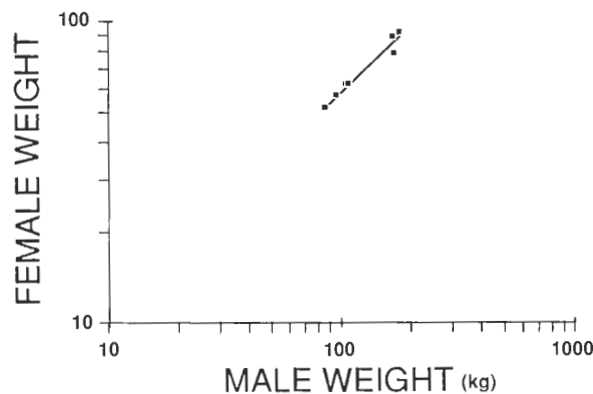


Fig. 5. Relative body weights of adult male and female black bears; comparison across population means ($n=7$; 2 data points overlap).

$$\log(\text{BW}_f) = -0.39 + 1.35 \times \log(\text{BW}_m), R^2 = 96\%, P < 0.001, \text{SEI} = 0.03, \text{SES} = 0.13,$$

$$\log(\text{BW}_f) = 0.35 + 0.71 \times \log(\text{BW}_m), R^2 = 96\%, P < 0.001, \text{SEI} = 0.02, \text{SES} = 0.07.$$

Eiler 1981; Elowe 1987; Eiler et al. 1989; Elowe and Dodge 1989).

Differences in body size and reproductive rate for bears in different habitats are commonly attributed to differences in total food supply (e.g., eastern deciduous vs. Rocky Mountain conifer forests; coastal vs. inland habitats) (Stringham 1980, Bunnell and Tait 1981). But this has never been confirmed by measuring differences in supplies of foods or nutrients.

The fact that reproductive rate and body weight tend to rise together indicates that they are in turn correlated with population differences in nutrient-energy income and/or in efficiency of physiological processes (maintenance, growth, and reproduction). Nutrient-energy income, governed largely by per capita food supply, seems the most likely cause; but data needed to test this hypothesis have yet to be gathered.

Environmental vs. Genetic Influences

For no bear species do we know how the relationship of reproductive rate with body weight is influenced by genetics. Genetic selection could affect the nutritional efficiency of living, i.e., the amount of maintenance, growth, and reproduction achieved per unit nutrient-energy expenditure. Or genetics might affect physiological thresholds for allocation of nutrient resources to each activity.

An effect of genotype on lower or upper body weight thresholds for reproduction could cause differences in thresholds across populations. Recall the 67 and 80 kg thresholds for black bear in MN (Rogers 1983). Yet, in some populations, females reproduce at mean weights down to at least 50 kg; in others, reproduction is not necessarily maximized below a mean of 90 kg. So some populations have basement thresholds lower or ceiling thresholds higher than in Minnesota, where the spread between thresholds was 13 kg. My results do not reveal width of spread for any other population, or how width varies among populations.

Limited Standardization of Data

Had it been possible to standardize data more thoroughly, values for reproductive parameters could probably be predicted more precisely from body weight. The regression equations obtained with more standardized data would probably have less data variance around regression lines, and thus narrower confidence bounds around the slope and intercept, higher r^2 , and lower P .

But current limits on standardization apparently do not seriously bias accuracy, as evidenced by the high

consistency of my results. Tests were made on 4 relatively independent reproductive parameters; even natality, calculated by dividing litter size by interbirth interval, is independent, because it is a ratio. Each reproductive parameter was regressed on body weights for adults of both sexes, a total of 8 tests for black bears. These same parameters for grizzly bears were regressed on body weights of adult females and males, as well as on adult male skull length—another 12 tests, for a total of 20. The chance of 20/20 spuriously significant relationships is roughly $0.05^{20} = 1 \times 10^{-26}$. Thus values for reproductive parameters predicted from body weights with my equations will tend to be accurate, but less precise than if the data could have been more thoroughly standardized.

MANAGEMENT IMPLICATIONS

Monitoring Demographic Vigor

The regressions derived here can be used to predict a population mean for each reproductive parameter from a mean for adult body weight of either sex. Analogous regression models for grizzly bears successfully predicted the amount of decline in litter size and age at first whelping accompanying reduced body size after closure of garbage dumps at Yellowstone National Park (Stringham 1990)—a change attributed to reduced nutritional status (Craighead et al. 1974; Craighead and Mitchell 1982; Stringham 1985, 1986, 1990; Blanchard 1987). Likewise, it might be possible to estimate annual changes in reproductive rate from changes in mean body weight of harvested bears. A conversion would, of course, have to be made between the live-weights used here, and carcass weights of harvested bears.

Modeling Population Dynamics

Rogers (1983, 1987) has shown positive relationships of cub survivorship with body weights of cubs and mother—weight differences that apparently depended on nutritional status. Thus, it should eventually be possible to base models of population dynamics on body size. Data from bears killed during the fall of a 1st year might be used to estimate sustainable harvest for a 2nd year, and so on. A comparable approach is already being applied to some ungulates (A. Moen, pers. commun.).

A Word of Caution

Application of the body weight approach to estimate reproduction, survival, and harvestable yield would be most appropriate in cases where field data on reproduction and survival cannot be obtained. Until this weight

approach is verified and shown to be reliable enough for management purposes, it should *not* be used as an excuse for not collecting the field data. Nutritional status may affect reproduction in ways not fully reflected by adult body weight, as illustrated here with the retarded maturation rates in WM and MN. Furthermore, factors other than nutritional status, such as hunting pressure and social strife, may also affect rates of cub production, emigration and survival (Jonkel and Cowan 1971; Beecham 1980a,b; Stringham 1980, 1983, 1985). I suspect that reproductive rate is reduced in hunted populations, in part through harvest of older, more productive females (Stringham, in prep.).

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