

ROLES OF ADULT MALES IN GRIZZLY BEAR POPULATION BIOLOGY

STEPHEN F. STRINGHAM, Ecology Program, University of Tennessee, Knoxville, TN 37996

Abstract: Developing on my earlier work (Stringham 1980) and that of McCullough (1981), influences of adult male abundance on rates of reproduction and subsequent attrition (mortality + net emigration) were evaluated for grizzly bears (*Ursus arctos*) by analysis of the data of Craighead et al. from Yellowstone National Park 1959–70. Years when adult males were most abundant were also those in which (1) the litters conceived were smallest when censused at median age 0.5 year postpartum, and (2) the cohorts born were comprised of fewest litters at that age. Cohorts produced during years of peak adult male abundance were not only smallest at age 0.5, but showed the highest rates of attrition to at least age 2.5 years. Apparently adult male abundance and/or some closely linked factor, perhaps availability of food, governed not only abundance but quality of infants, which in turn governed survivorship and competitive ability for space and resources in Yellowstone National Park to age 2.5. That coincides generally with relationships between rates of reproduction and of attrition vs. abundances of adult males and of food observed by Rogers (1976, 1977) for black bear in Minnesota. McCullough (1981) reached some of these same conclusions.

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Due to steady decline in available habitat and to extensive hunting, only remnant populations of the grizzly bear remain south of the Canadian border. In 1975 these populations were officially listed as Threatened, under provisions of the Endangered Species Act; this status was renewed in 1980 for another 5 years. U.S. Federal mandate prohibits hunting of grizzlies outside of Montana (where most of these bears live), and limits harvest there to 25 grizzlies per year (Federal Register 20 May 1980, 45 FR 33768–81, 50 CFR, Section 17.40b0).

The ostensible necessity or advantage of current restrictions for protecting remnant grizzly populations has been questioned by both sportsmen and professional biologists. Many hunters consider grizzly/brown bears (*Ursus arctos horribilis* and *U. a. middendorfi*, hereafter collectively called grizzlies) the premier trophy carnivore of North America. Some protest against scarcity of opportunity to hunt grizzlies within the contiguous United States and seek greater access to remnant populations such as that in the Yellowstone area (e.g., Weiss 1980). Furthermore, there is belief that by hunting bear populations, consequent lowering of population density and/or depletion of adult males will increase rates of reproduction and/or survival (aside from gunshot mortality) (see Kemp 1972, 1976; Egbert and Luque 1975; Egbert and Stokes 1976). Is that really true? As biologists responsible for conservation of grizzlies, it behooves us to know whether and under what conditions hunting

would promote recovery of remnant populations rather than speeding their extinction.

Because adult male grizzlies are larger on average than adult females, and for other less objective reasons (see Stringham 1983a), males are the focus of trophy hunting. Even where hunters are not purposefully selecting for trophy bears—they may simply kill the first ones they can—adult males seem to be disproportionately vulnerable. This is partly because they travel more extensively than adult females (Craighead et al. 1974; F. Craighead 1979; J. Craighead 1980; Pearson 1975; Bunnell and Tait 1980). Similar information has been published for black bears *Ursus americanus* (Jonkel and Cowan 1971, Pelton and Burghardt 1976, Rogers 1977, Beecham 1980b). Therefore, a major facet of evaluating potential impacts of hunting on grizzly populations should be determining what roles adult males play in reproduction, as well as in the survivorship of immatures, dispersal by immatures from vicinity of their mother's home range, and emigration by them to other, perhaps poorer quality habitats.

There is still no evidence that adult males play any role in reproduction aside from siring cubs, or that they contribute directly to the welfare of their offspring after birth. At most, when adult males deter trespassers, they may *inadvertently* protect their own offspring from competition or murder by the intruders. Adult males sometimes kill and occasionally eat immatures—presumably those sired by rival males (Troyer and Hensel 1962; L.P. Glenn, unpubl. Rep. 1970 Brown bear

Studies, Alaska Fed. Aid Wildl. Rest. Proj., 1971; Egbert and Luque 1975; Glenn et al. 1976; Egbert and Stokes 1976; McCullough 1981; see also panel discussion by J. Craighead et al., in Herrero 1972:244–254). But direct evidence of infanticide by adult males is so sparse that one must rely on circumstantial evidence to quantitatively evaluate its impact on population dynamics. For example, comparison among 6 North American grizzly populations revealed inverse relationships between indices of reproductive and recruitment rates vs. proportion of adult males in each (Stringham 1980). Does the same thing hold within populations? Testing that was the goal of this study.

The only grizzly population on which adequate information is available for such an analysis is that in Yellowstone National Park (YNP), where data were collected by the Craighead research team during 1959–70 (see Hornocker 1962; Craighead et al. 1969, 1974, 1976; Craighead 1979, 1980). Analyses done by those authors and by Shaffer (1978, 1983) did not consider possible influences by adult male abundance on reproductive rate or on cohort size and attrition rate. McCullough (1981) also analyzed the YNP data, concluding that per capita rates of reproduction (measured at age 0.5 year postpartum) and recruitment were inversely related to abundance of total adults, with abundance of adult males having greatest influence. That coincides with the results of my findings from comparisons among YNP and 5 other populations (Stringham 1980), and my independent analysis of the YNP data on a year-by-year basis.

With a few exceptions, specified later, the scope of this paper is restricted to those aspects of my findings on YNP grizzlies that were achieved independently of any influence by McCullough's (1981) results, those aspects which are direct extensions of my earlier work (Stringham 1980). My subsequent findings, which were influenced by McCullough's results, are treated in separate manuscripts (e.g., Stringham 1983a).

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During the period 1964–70, when sexes of adults were discriminated, most variation in number of adults was due to variation in number of adult males (*AdMM*); the number of adult females (*AdFF*) was nearly constant (see McCullough 1981). Respective means and standard deviations for males and females are about $38 \pm 27\%$ vs. $44 \pm 6\%$. As McCullough suggested, abundances of adult males for 1959–63 can be estimated from the relationship between numbers of adult males vs. total adults. The equation used here ($r = 0.981$, $P = 0.0001$) is:

$$AdMM = -33.4 + 0.868 \cdot (AdMM + AdFF)$$

RESULTS

Reproduction

Number of cubs censused each year was a product of rates of not only of ovulation, conception, implantation, and natality, but subsequent attrition until the time of censusing at median age about 0.5 years postpartum. Conventionally, reproductive rate refers to number of offspring present at the earliest age that they can be censused, whether pre- or postnatally. It is not necessarily synonymous with fertility, fecundity, or natality. Hence, for purposes of this analysis, variables assessed as indices or components of reproductive rate include mean cub litter size each year (*C/L*), abundances of cub litters (*L*), and of cubs (*C*), as well as interbirth interval (i.e., mean interval until females who bore litters in year *t* bore again), and rate of maturation to weaning, puberty, and first reproduction.

During 1960, total adults and probably total adult males in YNP peaked at levels otherwise approached only in 1968–70. Corresponding values for numbers of cubs and of cub litters censused in 1960, and litter size and interbirth interval measured in 1961, were all higher than is

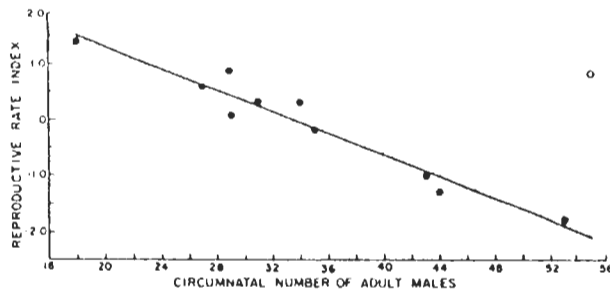


Fig. 1. Reproductive rate index derived as the 1st principle factor (f) for 3 reproductive components (litter size, litter abundance, and interbirth interval [IBI]) in years t and $t+1$ relative to abundance of adult males in each year t ($AdMM_t$). Note that the datum (o) corresponding to abundance of adult males in 1960 is highly anomalous (see text); so it was not allowed to influence determination of the given regression line:

$$f = 4.922 \cdot \ln(C/L)_{t+1} + 3.695 \cdot \ln(IBC)_{t+1} + 1.505 \cdot \ln(L)_t \\ = 18.43 - 0.0980 \cdot \ln(AdMM)_t$$

consistent with the pattern for other years. (In each Figure, the anomalous datum is distinguished by an open circle "o", and the other reproductive data by closed circles "●"). The net impact of this anomaly on reproductive rate is revealed when the 1st Principle Factor for interbirth interval, litter size, and litter abundance is regressed against adult male abundance; deviation of the anomalous point from the regression line is 15-fold the average deviation for the other data points (Fig. 1). Variance remaining after deletion of the anomalous datum for each index is referred to as its "typical" variance. For example, whereas mean number of adult males during the year of each cohort's conception and gestation (i.e., "prenatally"), accounts for only 37% of the total variance in litter size, it accounts for nearly twice as much of typical variance ($r^2 = 72\%$ typ). It is not known why the 1960 value for adult male abundance or corresponding values for reproductive components were anomalous. That may stem from censuses being less reliable during the first 2 years of the study (1959 and 1960) than later, when a larger proportion of the population was individually identified; or some intervening variable, such as unusually good food supply, may have masked influences by adult male abundance on reproductive rate during that period. Additional analyses of data are underway to find an answer. In any event, results presented here are from analyses done both with and without inclusion of the anomalous datum.

Table 1. Reproductive components relative to percent of adult males in each of 6 grizzly populations (after Stringham 1980). Pearson product-moment correlation (r) and P an index of probability that the correlation and slope are either zero or positive. All relationships are approximately linear.

Reproductive Component	Proportion of Adult Males	Reproductive Component	Proportion of Adult Males
Rate of maturation to puberty	-0.811 0.025	Potential natality index	-0.945 0.002
Rate of maturation to weaning (W)	-0.775 0.035	Proportion of cubs	-0.877 0.025
Cub litter size (C/L)	-0.694 0.065	Proportion of yearlings	-0.645 0.12
(C/L) · W	-0.921 0.0045		

Results of my earlier comparison among 6 populations (Stringham 1980; Table 1) indicate that rates of both reproduction and recruitment are elevated in those populations where adult males are scarcest. So too within YNP, rates of reproduction and recruitment were highest when adult males were scarcest (Table 2). (Signifi-

Table 2. Reproductive components relative to number of adult males in Yellowstone National Park, 1959-70. Significance level (P) is for hypotheses that correlation and slope are either (a) zero or negative (in the case of number or proportion of adult females without cub litters) or (b) zero or positive (in the case of other variables).

Reproductive Component (RC)	Number of Adult Males			
	Without Outlier		All Data	
	Prenatal	Postnatal	Prenatal	Postnatal
Number of cubs ^a	-0.482 0.08	-0.715 0.006	-0.456 0.08	-0.554 0.03
Cub litter size ^b	0.848 0.0005	-0.512 0.05	-0.649 ^c 0.01	-0.517 ^d 0.045
Interbirth interval ^e	-0.750 0.006	-0.504 0.06	-0.511 0.05	-0.606 0.02
Numbers of cub litters and of adult females with them ^a	-0.081 0.41	-0.566 0.035	-0.153 0.33	-0.342 0.14
Number of adult females without cub litters ^a	+0.222 0.29	+0.424 0.095	+0.263 0.22	+0.423 0.085
Proportion of adult females without cub litters ^a	+0.223 0.28	+0.523 0.05	+0.208 0.27	+0.407 0.095

^a Log-log relationship: $\ln(RC) = a + b \cdot \ln(AdMM)$

^b Linear relationship: $(C/L) = a + b \cdot (AdMM)$

^c Relationship previously reported by Schaffer (1978)

^d Relationship previously reported by McCullough (1981)

^e Semi-log relationship: $\ln(IBC) = a + b \cdot (AdMM)$

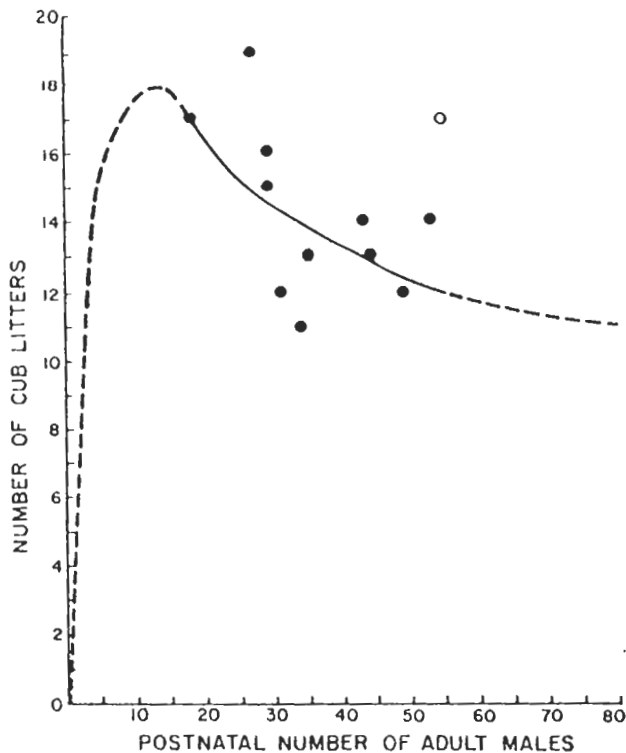


Fig. 2. Postnatal abundance of cub litters relative to postnatal abundance of adult males:

$$L = 3.69 \cdot AdMM^{-0.299}$$

Interpolation between the origin and empirical data is schematic. Extrapolation beyond empirical data follows the exponential curve obtained by least-squares regression on log-transformed data. The corresponding dose-response curve is:

$$L = 1.67 \cdot AdMM \cdot e^{-0.0397 \cdot AdMM}$$

cance levels specified are for 1-tailed tests of the hypothesis that lowering abundance of adult males elevates rates of reproduction by females and recruitment of their offspring.) Numbers of adult females with cub litters ($r^2 = 29\%$ typ; Fig. 2) and without them ($r^2 = 17\%$ typ) each year were related to postnatal abundance of adult males but not to their prenatal abundance (Table 2). The same thing was true ($r^2 = 26\%$ typ) for proportions of adult females with and without cub litters. By contrast, litter size ($r^2 = 72\%$ typ; Fig. 3.) and interbirth interval ($r^2 = 56\%$ typ) were more strongly related to prenatal abundance of adult males. The 1st 5 relationships are exponential; the 6th is linear. The combined response of mean cub litter size, abundance of cub litters, and interbirth interval (at the time lags indicated above) was even stronger, judging from regression of their 1st Principle Factor vs. adult male

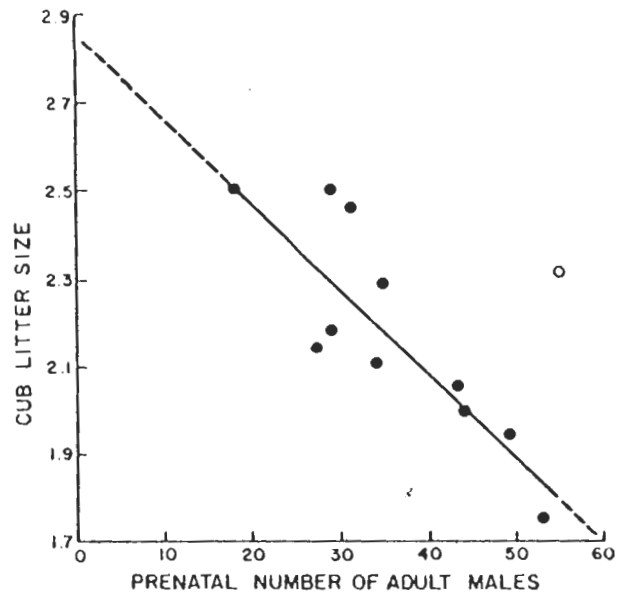


Fig. 3. Mean annual cub litter size relative to prenatal abundance of adult males:

$$C/L = 2.87 - 0.0196 \cdot (AdMM)$$

abundance ($r^2 = 94\%$ typ, $P = 0.0001$; Fig. 1). Comparable results are obtained from multiple correlation ($r^2 = 88\%$ typ, $P = 0.0002$ for the full model and $P \leq 0.003$ for each of the 3 reproductive components individually).

Mathematically, ($C = \{L\} \cdot \{C/L\}$); so, ($\ln\{C\} = \ln\{L\} + \ln\{C/L\}$), where variances in $\ln\{L\}$ and $\ln\{C/L\}$ respectively correspond to 56% and 40% of the variance in $\ln\{C\}$. Because cub abundance was related to litter abundance more strongly than to litter size, and because litter abundance was related only to postnatal abundance of adult males, cub abundance was also more strongly correlated with postnatal than prenatal abundance of adult males (Fig. 4). But it is the mean abundance of adult males for the pre- and postnatal periods, i.e., their "circumnatal" abundance, that is the best predictor of postnatal (age 0.5 year) cub abundance ($r^2 = 51\%$ typ; $P = 0.007$; Table 2). These data were fit with a declining exponential curve (linearized by log-log transformation; Figs. 4 and 5), in conformance with the relationship for abundances of cub litters vs. adult males.

Extrapolation to higher abundances of adult males can be done using those same regression lines. At lower abundances of adult males, the regression line for litter size provides reasonable

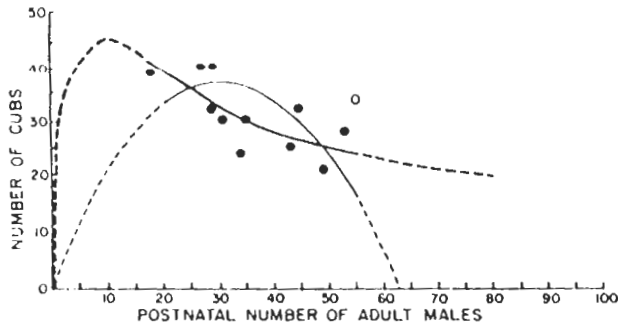


Fig. 4. Postnatal abundance of cubs relative to postnatal abundance of adult males. Comparison of fits to data obtained using a parabolic model derived by regression of $C/AdMM$ vs. $AdMM$ (after McCullough 1981) versus that using an exponential model. Coefficients of determination for these models are respectively 5% and 31%. Interpolation between the origin and empirical data for the exponential curve is schematic. The parabolic, exponential, and dose-response models are, respectively:

$$C = 2.37 \cdot AdMM - 0.0378 \cdot AdMM^2$$

$$C = 4.93 \cdot AdMM^{-0.418}$$

$$C = 3.47 \cdot AdMM \cdot e^{-0.0375}$$

estimates even when there are as few as 1 adult male in the population (i.e., 2.85 C/L). However, exponential regression lines for numbers of cub litters and of cubs must be modified to begin at the origin; for if there are no adult males in a population to sire cubs, there can be no cubs. That is shown in Figs. 2 and 4. Such curves can be approximated closely with the "dose response" form of a Ricker stock-recruitment model.

$$R = a \cdot (AdMM) \cdot e^{-b \cdot AdMM}$$

where R is number of recruits or litters.

Recruitment

The size of a cohort past age 0.5 year is a function of both initial (0.5 year) size and subsequent attrition. As one would expect, influence of initial cohort size on subsequent size diminished with age, accounting for almost 60% ($P = 0.003$) of variance in cohort size at age 1.5 years, but less than 40% ($P = 0.003$) of that at 2.5 years. Diminishment was a function of intercohort differences in rates of attrition (mortality + net emigration); at least 50% ($P = 0.01$) of variance in size at age 2.5 was accounted for by attrition since age 0.5.

Using parabolic models for recruitment to ages 0.5 to 2.5 years, McCullough (1981) (Fig. 4) indicated that recruitment between ages was also an inverse function of postnatal abundance of total

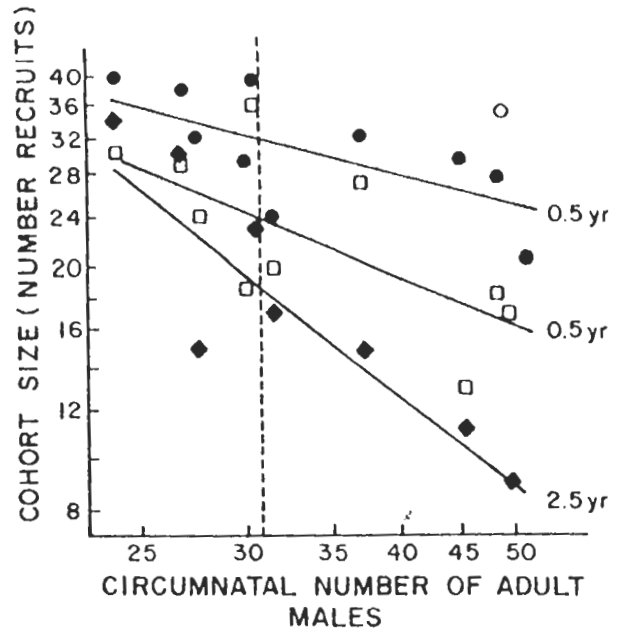


Fig. 5. Cohort sizes at ages 0.5 to 2.5 years, relative to circumnatal abundance of adult males. Each cohort is represented by a vertical line through the recruitment curves; its intersections with the curves give its sizes at ages 0.5, 1.5, and 2.5 years. A vertical line cutting through 31 adult males yields a recruitment curve nearly identical to that shown in Fig. 6.

$$\ln(0.5 \text{ yr size}) = 4.93 - 0.418 \cdot \ln(AdMM) \quad r^2 = 31\%$$

$$\ln(1.5 \text{ yr size}) = 6.07 - 0.843 \cdot \ln(AdMM) \quad r^2 = 50\%$$

$$\ln(2.5 \text{ yr size}) = 8.49 - 1.615 \cdot \ln(AdMM) \quad r^2 = 82\%$$

adults, at least within the range of available data; so attrition rate between those ages was directly related to postnatal abundance of adults. Results of this analysis, involving exponential models, show the same thing as a function of circumnatal abundance of adult males, but with markedly different predicted values for number of recruits remaining vs. lost at each age, and for coefficients of determination and confidence levels (Figs. 4 and 5).

According to the exponential models, fluctuations in circumnatal abundance of adult males accounted for 77% ($P = 0.0001$) of variance in percentage attrition in cohort size between ages 0.5 and 2.5. This is illustrated by comparing vertical distances between recruitment curves (Fig. 5) at different abundances of adult males. As circumnatal abundance of adult males doubles from 25 to 50, attrition rate between ages 0.5 and 2.5 triples from 22% to 67%. Furthermore, at 25 adult males, the attrition rate for cubs is almost 9-fold that for yearlings (26%:3%). But whereas cub attrition would rise only 1/3 as adult male

abundance doubles, yearling attrition would rise 14-fold. Because of these correlations between circumnatal abundance of adult males vs. initial size and subsequent attrition of cohorts, adult male abundance accounted for 50% ($P = 0.01$) of total variance in cohort sizes at age 1.5 and over 80% ($P = 0.0004$) at age 2.5. Because Craighead et al. (1974) lumped data on older immatures, one cannot test for influences on attrition and recruitment to those ages by circumnatal abundance of adult males (see Stringham 1983a).

Recapitulating: Correlations between circumnatal abundance of adult males vs. recruitment and attrition rates increased as cohorts matured to at least age 2.5. This trend seems to be an extension of events initiated before birth; for litter size was more strongly related to prenatal than to postnatal abundance of adult males, whereas litter abundance was related only to postnatal abundance of adult males. When cubs are lost from a litter, litter size is affected when even the first cub goes. So one would expect litter size to be affected at an earlier age than litter abundance. That occurrence of this trend is not even clearer during the circumnatal period maybe due to masking by the following bias: Mean values for litter size were based only on litters with at least 1 cub, and thus fail to show the impact of whole-litter losses. The fact that litter abundance was related to adult male abundance postnatally but not prenatally, indicates that loss of final cubs from litters was caused primarily by postnatal influences, irrespective of how many other cubs had already been lost from those same litters due to prenatal influences. Fig. 6 summarizes the findings, showing the proportion of variance (r^2) in cohort size (recruitment) and attrition at ages 0.5 to 2.5 accounted for by (a) circumnatal abundance of adult males and by (b) an index of what may be prenatal winter/spring energy balance for the mother (see Discussion concerning Picton's [1978] "Climate Index").

The above considerations indicate that conditions (e.g., adult male abundance) affecting each cohort circumnationally had more impact on probability of death or emigration by its members as yearlings and 2-year-olds than did conditions (e.g., adult males abundance) concurrent with their attrition. That is corroborated by lack of

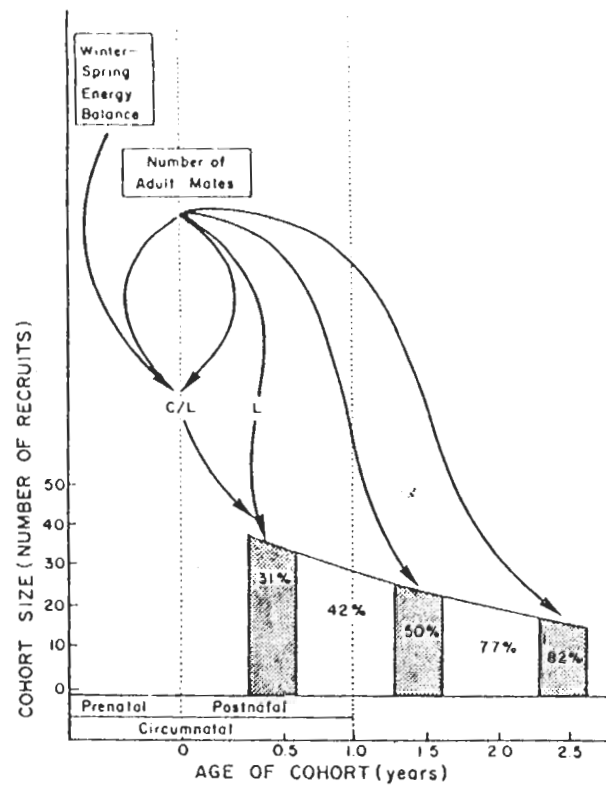


Fig. 6. Mean cohort size at ages 0.5 to 2.5 years. The recruitment curve represents the average for all cohorts 1959-70 (based on Tables 1 and 9 of Craighead et al. 1974). Cohort size (number of recruits remaining) at each age is approximately that for a cohort produced when there was a mean circumnatal abundance of 31 adult males (see Fig. 5). Percentages represent contributions (r^2) by circumnatal abundance of adult males to cohort sizes at ages 0.5, 1.5, and 2.5 years (vertical bars), and to attrition rates between those ages. Also indicated are influences on initial cohort size via influences on litter size (C/L) and abundance (L) by adult male abundance and by Picton's (1978) index of what may be winter-spring energy balance (see text).

relationships between adult male abundance vs. concurrent abundances of yearlings ($r = -0.030$, $P = 0.47$) and 2-year-olds ($r = -0.169$, $P = 0.30$), even when both age-classes are considered together ($r = -0.137$, $P = 0.34$). This agrees with the findings by McCullough (1981).

It is concluded, therefore, that circumnatal abundance of adult males, or some other factor closely linked to it, (1) directly influenced natality and/or cub attrition, and (2) indirectly influenced the probability that members of each cohort would die or emigrate from YNP as yearlings or 2-year-olds—dominating direct influences on their attrition by factors such as concurrent abundance of adult males.

DISCUSSION

Other Analyses on Roles of Adult Male Bears

Yellowstone Grizzlies. — McCullough (1981) also analyzed some of the same relationships between rates of reproduction and recruitment vs. adult and adult male abundances. Our results coincide in indicating that both absolute levels and per capita rates of reproduction and recruitment were inversely related to postnatal adult (male) abundance, within the range of values for which data are available. (Note that prior to reading McCullough's paper, this author had not gotten to the point of extrapolating below the range of observed adult [male] abundances. So this author's eventual extrapolation of curves through the origin (0,0) may have been influenced by McCullough's despite the fact that in retrospect it is self evident).

Differences in these 2 sets of results and approaches are detailed below: (1) This analysis includes a number of relationships which McCullough's (1981) analysis did not, both among components of reproduction and recruitment, and between them vs. adult (male) abundance (see Table 2). For instance, (1a) McCullough, using an arithmetic model, found that *proportion* of adult females with cub litters each year is more strongly correlated with cub abundance than is litter size. The same basic conclusion resulted here from use of a logarithmic model for absolute *number* of adult females with litters (i.e., L). Although this distinction is otherwise trivial, it has importance for what the latter correlation indicates about pre- vs. postnatal influences by adult male abundance. (1b) McCullough did not consider influences by prenatal abundance of adult males. (2) Furthermore, he used a different method of statistical regression on most of the relationships; so his results yield substantially different quantitative estimates of how reproduction and attrition rates varied as functions of adult males abundance (Fig. 4). (3) In 1977 at the 4th International Conference on Bear Research and Management and in the resultant publication (Stringham 1980), this author considered two major hypotheses as possible explanations for negative correlations between rates of reproduction and recruit-

ment vs. abundance of adult males: (3a) Abundance of male adults may have been the factor actually controlling rates of reproduction and recruitment, via resource competition, exile, infanticide, or socially induced physiological stress. (3b) Alternately, adult male abundance in itself may have been only an index of control by other factors such as food supply. By contrast, McCullough (1981) discussed only resource competition and infanticide.

McCullough's analysis of recruitment was based on relationships between numbers of recruits (R) to each age-class per adult, relative to postnatal abundance of adults (N), that is, R/N vs. N . These and other relationships, such as abundance of 3- and 4-year-olds per 2-year-olds, were evaluated by regressions of form Y/X vs. X . It is a statistical artifact that coefficients of determination and confidence level were usually high, as exemplified by the values for C/N vs. N ($r^2 = 71.4\%$, $P = 0.0005$). The artifact arises from the presence of N on both ordinate and abscissa. Indeed, coefficients of correlation and significance from any regression with 1 or more variables on both axes are suspect (Ranney and Stringham, unpublished results). At the very least, confidence tests for Y/X vs. X regressions should be based not on whether the slope is significantly different from zero, but whether it is significantly different from the strongly negative slope obtained even if there is no correlation between Y vs. X .

The remainder of McCullough's analysis is only moderately affected by those flaws, despite the fact that the Y/X vs. X regression was used to generate equations for stock-recruitment parabolas of form Y vs. X . Similar equations are obtained by direct least-squares regression of Y vs. X if each curve is forced through the origin (see Ricker 1975, p. 352). Nevertheless, parabolic stock-recruitment models account for no more than half as much of the variance in empirical data as do the exponential/dose-response modes.

According to this author's calculations, with a parabolic model, abundance of adults accounts for only 5% ($P > 0.50$) of the total variance in abundance of cubs. By contrast, exponential regressions for abundances of cubs vs. adult males or total adults circumnatally or just postnatally, account for at least 6 times (30% to 31%) ($P < 0.05$) as much of the variance in abundance of

cubs (Fig. 5). The same is true for corresponding dose-response models. Likewise, with parabolic models, postnatal abundance of adults accounts for 22% and 41% of total variance in number of recruits reaching ages 1.5 and 2.5 years, respectively; corresponding values for exponential/dose-response curves are about 50% and 80%. Those figures apply to fits of the curves only to the empirical data. If fit to the origin is also included, each coefficient of determination is grossly inflated because the origin lies so far from the empirical data points (e.g., to >70% for the parabola and >95% for the dose-response curve for cubs).

Comparison among grizzly populations. — The inverse correlations between rates of reproduction and recruitment vs. abundance of adult males presented in my earlier paper (Stringham 1980) were derived from comparison among 6 populations — populations whose densities ranged over 2 orders of magnitude. Such great variance prevented analyses from being done in terms of absolute abundance or density of adult males; instead proportion of adult males was used. Confidence levels for 1-tailed tests of hypotheses were above 90% for all correlations between reproductive components vs. proportion of adult males (Table 1). In YNP, correlations vs. proportion of adult males were not quite that reliable, by contrast to the even stronger and more reliable correlations vs. absolute abundance or density of adult males. In other words, there is general although not perfect agreement between results of inter- vs. intra-population analysis of reproductive rate vs adult male abundance.

Census-sample data from populations other than YNP are less detailed, lumping abundances of immatures older than yearlings. So attrition rate can be evaluated only for cubs. This can be approached in 2 ways. One can compare either abundances of cubs vs. yearlings or sizes of cub litters vs. yearling litters. The former may be biased by incompleteness of censuses and the latter by failure to take into account whole-litter losses; both can be biased by comparisons between cubs vs. yearlings from different cohorts rather than within the same cohort (see Stringham 1980). In YNP and another population that also had over 21% adult males, mean difference in abundances of cubs vs. yearlings (33%) was higher than in 2 populations with less than 6% adult males (28%).

Likewise, in the populations with at least 21% adult males, percentage decline in mean cub to yearling litter sizes ($9.9\% \pm 12\%$) was slightly higher than in those populations with under 6% adult males ($9.4\% \pm 0.7\%$). Although these differences are not significant at the $P = 0.10$ level, these results are compatible with those from inter-year analyses for YNP grizzlies; for they indicate positive correlations between cub attrition vs. adult male abundance.

Experimental simulation of hunting impacts. — The only study to experimentally test the effects of lowering adult male abundance on recruitment of immatures was that with black bears by Kemp (1972, 1976). Most adult males were removed from an area of habitat near Cold Lake, Alberta, Canada. Within 2 years, population density doubled; then, over a period of 3 more years, it returned to level only 25% above the original. Density change seems to have been due primarily to immigration into the study area while there were too few resident adult males to prevent it, then re-emigration as new adult and subadult males established home ranges there. No relationship was detected between survivorship of immatures vs. adult male abundance (Ruff and Kemp, unpubl. data).

Interpretation of comparisons among years within YNP and among populations. — As an initial working hypothesis, let us suppose that it was actually abundance and behavior of adult males that controlled rates of reproduction and recruitment in the manner and degree discussed above, then test that hypothesis against data. Afterwards, evaluation will be done on support for the alternative hypothesis that both rates of reproduction and recruitment, as well as abundance of adult males, all varied as functions of other factors, perhaps food supply and weather.

Possible Impacts of Adult Male Abundance

Infanticide. — Hrdy (1979) identified 3 ways that male mammals might enhance their fitness by eliminating (killing or exiling) immature conspecifics other than their own offspring: (1) Reducing reproductive competition from fathers of the immatures; (2) reducing competition from the immatures for resources; or (3) cannibalism. In both grey langurs (*Presbytis*

entellus) and African lions (*Panthera leo*), adult females live in permanent harem groups with their offspring. Each harem is "owned" by one or more adult males. When harem lords are deposed by rivals, typically some or all offspring sired by the former lords soon die or disappear. Elimination of all of a female's unborn or unweaned offspring is thought particularly advantageous for a new lord because it induces each mother to ovulate sooner than if she had reared any of her offspring to weaning, thereby shortening the delay until she can be bred by the new lord (Schaller 1972; Hrdy 1974, 1979; Bertram 1975; see also Bruce 1959). Consequently, Hrdy predicts that infanticide as a tactic of intermale reproductive competition will focus on unborn and unweaned offspring. It should be aimed at elimination of whole litters.

There is evidence of infanticide and cannibalism in YNP grizzlies (J.J. Craighead and F.C. Craighead, Jr., unpublished rep., Environ. Res. Inst. and Mont. Coop. Wildl. Res. Unit, 1967; J. Craighead in panel discussion in Herrero 1972:244–254; see also McCullough 1981). But how often adult males are the culprits and how many immatures are lost this way is unknown. No more than half the grizzly litters were weaned before age 2.5, judging from the proportion of the 68 documented interbirth intervals that were less than 3 years long. Note that weaned offspring apparently are not protected by their mothers, and should be even more vulnerable than unweaned young to cannibalism and direct competition from adult males. Thus, Hrdy's 1st hypothesis predicts greatest attrition among unweaned young, whereas her 2nd and 3rd predict it among weaned ones. Neither singly nor jointly do these hypotheses explain why, for YNP grizzlies, abundance of adult males was correlated with concurrent abundance of cubs but not of yearlings or 2-year-olds. Nor do they explain why cohort sizes at ages 1.5 and 2.5 years were even more strongly correlated with circumnatal abundance of adult males than was cohort size at age 0.5 years.

Pre- vs. postnatal quality and attrition of offspring.—There is no obvious way that circumnatal abundance of adult males could have exerted sufficiently durable and powerful modifications on the environment to continue influencing attrition from each cohort for at least 2 subsequent years, much less that such influences

would actually be magnified rather than attenuated with time. To have had such a lasting impact on immatures, something must have influenced not only quantity but quality of the young during gestation or infancy, in such a way as to affect their long-term capacity to compete for space and resources and generally to survive.

The fact that litter size and litter abundance were, respectively, correlated most strongly with pre- vs. postnatal abundances of adult males, also indicates time-lagged effects explicable in terms of pre- and postnatal quality of offspring. This hypothesized relationship between quality vs. attrition rate of bears is analogous to the well-known pattern for machines. For example, if groups of several brands of off-road vehicles were driven in an endurance competition cross-country through rugged mountains, all might complete the 1st leg of the race, fewer the 2nd leg, and so on, until only the best machines remained. The better the quality of a cohort or brand of machine, the lower its average rate of attrition. (See Geist [1978] for a review on phenotypic quality in wildlife populations.) Let us now consider factors that might have governed not only quantity but quality of grizzly cubs.

Physiological stress, competition, and social strife.—That natality, maternal care, and lactation can be impaired in stressed mothers has been demonstrated for a wide variety of mammals (Selye 1956, 1976; Sadlier 1969; Hafez 1974; Christian 1980) and may also be true in bears. That is consistent with the hypothesis that quality of offspring has governed rates of attrition from infancy if not gestation through at least age 2.5 years, judging from findings summarized above. Physiological stress could have had such an effect even if it was not adult males that induced the stress.

Among the ways that adult males might have influenced levels of maternal stress are: (1) social strife, and (2) restricting availability of food for females and immatures by (2a) consuming it themselves or by (2b) restricting access to critical sources (e.g., prime fishing sites on salmon streams, berry patches, or garbage dumps). Some females, primarily those accompanied by offspring, outrank some males. However, those without cubs, most of whom are presumably pregnant, are lower ranking. On average, adult males dominate females in food competition, tending to take first choice of times and places to

feed and probably usurping choice items. At food concentration sites where food supply is low relative to the number of adult males, females and their offspring may be able to obtain little. But at sites where food is relatively abundant and available over enough space and time throughout the day, adult females and their offspring feed extensively. Such sites have included the main YNP garbage dumps and a prime fishing site at McNeil River Falls in Alaska. These impressions on patterns of food competition between adult males vs. females are derived from the findings by Hornocker (1972), Stonorov and Stokes (1972), Egbert and Luque (1975), Egbert and Stokes (1976), Rogers et al. (1976), L.L. Rogers (pers. commun.), Craighead (1979, 1980), and Herrero (1983); see also McCullough (1981).

Possibly objections to the hypothesis that adult males impair reproduction by females via strife-induced physiological stress and resource competition might arise from 2 sources: (1) Rogers (1976, 1977) observed no reproductive impairment among subordinates in groups of captive black bears reared together. However, as has been discussed in more detail elsewhere (Stringham 1980, 1983), that does not preclude the possibility that adult males grizzlies stress adult females under quite different (natural) social and ecological conditions. (2) The above hypotheses would be most plausible if there was a direct relationship between total number of adult males censused (primarily at dumps) each summer vs. the mean number of them seen at dumps each day or week during the summer. Until census data have been analyzed in enough detail to demonstrate such a relationship, assuming its validity is risky (J. Craighead, pers. commun.).

With those considerations in mind, let us now evaluate the possibility that other factors controlled both abundance of adult males and rates of reproduction and recruitment.

Habitat Carrying Capacity

One alternative hypothesis is that annual variations in the amount of food available to adult females and their offspring in YNP may have been less a function of adult male abundance than of habitat carrying capacity, and that adult male abundance was highest when the supply of natural foods was lowest because that is when more of the males regularly fed at garbage dumps—the sites where most censusing was done.

During 1968–70, 3 of 4 years when adult males were most abundant, garbage was scarcest due to closure of the YNP dumps. This substantially lowered the carrying capacity of YNP for grizzlies (Craighead et al. 1974, 1976; Craighead 1979, 1980). Following closure of dumps, litter size dropped 24% from the 1959–68 mean of 2.24 to a low of 1.7 in 1974, with a mean of 1.84 for 1969–76 (R. Knight et al., unpublished rep., U.S. Dep. Inter. Natl. Park Serv., 1975). The difference between means for the 2 periods is highly significant ($P < 0.001$). Furthermore, Picton (1978) devised a climate index accounting for 43% ($P < 0.01$) of variation in litter sizes for 1958–76, though only 33% for 1958–70. He attributes that to effects of temperature and snowfall on energetic costs of hibernation and on access to 2 crucial foods, pine nuts before hibernation and carrion afterwards. If an index of carrion abundance for 1966–1976 is also taken into account, 58% ($P < 0.01$) of litter size variance for that period is explained. Rogers (1976, 1977, pers. commun.) showed that rates of reproduction and recruitment between ages 0.2 to 2.5 years in a Minnesota black bear population were inversely related to circumnatal supplies of berries and mast (nuts), and directly related to maternal body weight—and thus probably nutritional status—during pregnancy and lactation. The same is probably true for grizzlies. However, note that even on Roger's study area, years of high food supply were also those of low abundances of adult males and total adults, and of low adult sex ratio (Stringham 1983a). Thus, unfortunately, available data on both black bears and YNP grizzlies are insufficient for statistically partitioning influences of food supply from those of adult male abundance, and for distinguishing their relative influences on rates of reproduction and recruitment.

This same impasse was reached in earlier analyses (Stringham 1980) because grizzly populations with the fewest adult males and highest rates of reproduction seemed to have had the best food supplies. Age at puberty and litter size respectively averaged 4.5 years and 2.29 C/L in 4 habitats with "good" food supplies, compared to ≥ 8 years and 1.75 C/L in 2 habitats with "poor" supplies. So "reproductive potential" was higher ($1.805 > 1.103$) in the 4 best habitat ($P < 0.03$ for all 3 comparisons). Beecham (1980a) made a similar comparison among 2 black bear populations in Idaho whose densities and overall sex ra-

tios (all ages combined) were similar to each other. In the population where age-specific body weights were highest and adult males scarcest, maturation rate and litter size averaged 4.25 years and 1.90 C/L, compared to means of 4.50 years and 1.65 C/L in the other population ($P < 0.10$). Inverse relationships between nutritional status vs. age at puberty have previously been documented for bears by several investigators (Baker 1912; Rausch 1961; Jonkel and Cowan 1971; Rogers 1976), as well as for other mammals (Sadlier 1969; Hafez 1974; Geist 1978).

SUMMARY AND CONCLUSIONS

Available data provide no indication that adult male grizzlies contribute to the welfare of their own offspring, except perhaps when deterring other males from trespassing on their home ranges inadvertently protects their offspring from the intruder males (Rogers 1976, 1977; Stringham 1980). Although adult males are known to kill and sometimes eat immatures, inconsistencies between predictions from the infanticide hypotheses of Hrdy (1979) vs. demographic observations in YNP suggest that frequency of infanticide and/or exile to marginal habitats for bears no more than 2.5 years old were little affected by variations in concurrent adult male abundance.

However, high abundance of adult males prenatally and postnatally seems to impair reproduction and recruitment of offspring. Abundance of adult males prenatally, and to lesser extent postnatally, is inversely related to mean postnatal cub litter size. Postnatal abundance of adult males is inversely related to postnatal abundance of cub litters. Mean number of adult males for those 2 years, i.e., circumnatally, also seems to impair recruitment rates to at least age 2.5 years.

It is hypothesized that sizes of each cohort from infancy through age 2.5 years within YNP, 1959–70, were predominantly governed by the condition of young during gestation and infancy, which was in turn strongly influenced by some social or ecological factors, perhaps abundance of adult males and/or of food during that period. On the one hand, this "quality of young" hypothesis accounts for all of the above relationships between abundance of adult males vs. components of reproduction (litter size, interbirth interval, number of litters, number of cubs) and vs. recruitment rate to age 2.5 years. On the other hand, the possibility exists that it was availability of natural foods that ultimately controlled

quality of young, and thus (1) rates of reproduction and recruitment as well as (2) abundance of adult males at censusing locations—sites where garbage was obtainable. Rogers (1976, 1977) observed a similar trend among black bears due to variations in food supply. In either case, effects of annual differences in natural food availability on dump usage and competition for garbage by adult males may account for at least part of the correlation for rates of reproduction and recruitment vs. adult male abundance.

Until impacts of adult male abundance can be distinguished from those of nutritive balance, effects of harvesting adult males cannot be reliably predicted. Some progress towards that goal can be made through further analysis of data already collected; that is underway. But the primary requirement is additional research on a broader scope than has previously been feasible. It is essential to obtain data on phenotypic quality (Geist 1978) and physiology of reproduction, stress, and nutrition, as well as on food supply.

Even if it does turn out that fluctuations in rates of reproduction and recruitment in YNP during 1959–70 were determined more by variations in adult male abundance than by those in food supply, that will not necessarily be true in YNP at other times or in other populations. In cases where adult male abundance is more stable, its impact might be largely masked by that of food supply variation. Likewise, the fact that variations in adult female abundance had negligible effects on rates of reproduction and recruitment does not imply that this is typical in bear populations. Had abundance of adult females been as unstable as that of adult males, it might have had even more impact on rates of reproduction and recruitment.

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