

POSSIBLE IMPACTS OF HUNTING ON THE GRIZZLY/BROWN BEAR, A THREATENED SPECIES

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Abstract: Is hunting detrimental to bear populations? Or do harvests stimulate compensatory reproduction and decrease natural mortality among the survivors? When the literature was reviewed to evaluate support for the various sides of this controversy, data were found still inadequate for conclusions to be drawn. At best, available information can aid in distinguishing which additional data are most critical and which hypotheses are most likely to be heuristic. Among six *U. arctos* populations in North America, those with lowest proportions of adult males had highest reproductive potentials, and vice versa. Likewise, within Yellowstone National Park, there was a strong negative correlation between numbers of adult males during a given year vs. number of offspring. However, those populations with highest reproductive potentials were also in the best habitats. So whether the former relationships were due to (a) effects of adult males on conception and survivorship, or (b) a coincidental product of nutritional differences, must still be tested. For 2 black bear (*U. americanus*) populations in Idaho, 1 in good habitat which was hunted heavily and the other in poorer habitat that was hunted lightly, higher natality in the former was attributed not to hunting but to better nutrition. When trophy hunting was simulated on a formerly little-exploited population of black bears in Alberta, the natality rate was not obviously altered.

Dispersal of a once seasonally aggregated population of grizzly bears was apparently followed by marked increase in cub survival, perhaps because of lowered exposure of cubs to aggression by older bears. However, evidence does not confirm the idea that depletion of mature males substantially increases survivorship of cubs or otherwise offsets losses due to hunting. In fact, under some circumstances, trophy hunting may indirectly increase cub mortality. Aside from this aspect and the possible impacts of inverse culling on gene pools, trophy hunting may be less detrimental to bears than to certain ungulates, where fully-adult males regulate aggression by adolescent males and serve other important social roles.

Within the contiguous United States the grizzly is a "Threatened Species". One critical question for its management is whether we should allow any of the remaining populations to be hunted, and if so whether these should be trophy hunts concentrated on adult males or whether harvests should be unselective. Proponents of hunting partly justify their position by claims that aggression of adult males against other age-sex classes is detrimental to the populations. But this is just the opposite to what we find for at least some species of ungulates, where adult males play critical social functions; their depletion by trophy hunting can markedly lower viability of a population (Bubenik 1971; see also Stringham and Bubenik 1975). Would properly regulated hunting really enhance reproduction and survivorship in grizzly/brown bear populations? Or would it merely speed their extinction?

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Preliminary assessment of the stated problem was made by comparing 3 hunted populations with 3 pro-

tected populations. The former are on Kodiak Island (KI), Chignik-Black Lake (CBL), and the eastern Brooks Range (EBR) in Alaska. The protected populations are at McNeil River State Game Sanctuary (MRSGS) in Alaska, Kluane Game Sanctuary (KGS) in the Yukon, and Yellowstone National Park (YNP) in Wyoming. KI, CBL, and MRSGS are all mountainous coastal habitats; the latter 2 are on the Alaska Peninsula. The EBR encompasses part of the Brooks Range as well as tundra extending towards the Arctic Ocean. KGS and YNP are inland mountain habitats. Each summer for about 6 weeks, McNeil Falls within MRSGS hosts one of the largest aggregations of *U. arctos* in the world, as they fish for salmon. Comparable concentrations occurred at garbage dumps in YNP before they were closed (1968-70); hence, data before vs. after closure are treated separately where appropriate. In KI and CBL, bears were more dispersed along salmon streams; hunting pressure there is focused on trophy bears, especially adult males. In EBR, it is apparently less selective. Sanctuary bears (MRSGS, KGS, YNP) whose home ranges extend beyond sanctuary boundaries are also vulnerable to hunters; males tend to range more widely than females and are correspondingly more vulnerable. Among nuisance bears removed from YNP, there has been a small bias towards adult males. Troyer and Hensel (1964), Hensel et al. (1969), Craighead et al. (1969, 1974), Knight et al. (1975), Pearson (1975), Cole (1975, 1976), Egbert and Stokes (1976), Glenn et al. (1976), Glenn (1975),

Reynolds (1976). Hence, relative proportions of adults, even adult males, are at best rough indicators of intensity of trophy hunting (Table 1).

The difference in mean proportions of adult males between KI and CBL (4.8 percent) vs. MRS GS, YNP, and KGS (24.3 percent) is highly significant ($P < 0.005$) by the chi-square test. By contrast, relative proportions of females and immatures do not differ significantly. At EBR males are plentiful; adults constitute about two-thirds of the known population, despite hunting.

QUALITY OF THE DATA AND ESTIMATES

Reproduction

Maturation rate. — Evaluation of sexual maturity is based on condition of the mammae and external genitalia, estrus behavior, and age when the first known litter is produced. The fact (Craighead et al. 1969; Glenn et al. 1976) that some females display signs of estrus and may even copulate as early as one year before their first confirmed conception, adds to the uncertainty of assessing maturity level. But we cannot yet estimate how much this may bias inter-population

comparisons. For the purposes of this preliminary analysis, puberty was assumed to have occurred one year prior to production of the first confirmed litter, and vice versa in cases where the author did not provide a definite figure. The most extensive and reliable data on female maturation rates (Table 2) come from KI (Hensel et al. 1969), YNP (Craighead et al. 1969, 1974), and MRS GS (Glenn et al. 1976). Glenn (pers. comm.) is also preparing a detailed report for CBL; for now, all we have is an estimated mean. Figures from KGS (Pearson 1975) and EBR (Reynolds 1976) are questionable. Three KGS females had not conceived by age 6, nor is it known when they did. So minimum age at puberty for them was at least 7, giving a minimum mean for the entire female population ($n = 8$) of 6.85, and more likely older; a mean of 7 years was assumed for this analysis (Table 2). Data from EBR cover only two years, so in order to obtain a reasonable sample size, Reynolds estimated age at first litter for several females (aged by tooth annuli). While the estimates are reasonable, each could be off by a year.

Interval between litters. — The time interval between birth of 1 litter and birth of the next is a function

Table 1. Age-Sex Structure of Six North American *Ursus arctos* Populations.

	Number and percent () of Population						Adult sex ratio M/100F
	Cubs	Yearlings	Other Immatures	Male Adults	Female Adults	TOTAL	
HUNTED							
Kodiak Island ^a	42 (25.8)	36 (22.1)	44 (27.0)	9 (5.5)	32 (19.6)	163 (100%)	28
Chignik-Black Lake ^b	140 (25.0)	84 (15.0)	169 (30.2)	23 (4.1)	143 (25.6)	559 (100%)	16
Eastern Brooks Range ^c	-----32----- (32.3)			33 (33.3)	34 (34.3)	99 (100%)	97
PROTECTED							
McNeil River ^d	9.7 (15.0)	6.0 (19.3)	8.7 (13.5)	17.7 (27.4)	22.4 (34.7)	64.5+ (100%)	79
Yellowstone Natl. Park 1959-70 ^e	31.4 (17.5)	22.6 (12.6)	43.8 (24.5)	37.7 (21.1)	43.8 (24.5)	179 (100%)	86
Kluane Game Sanctuary ^f	3 (7.3)	7 (17.1)	13 (31.7)	10# (24.4)	8# (19.5)	41 (100%)	131#

References:

^aTroyer and Hensel (1964)

^bGlenn (1975)

^cReynolds (1976)

^dGlenn et al. (1976)

^eCraighead et al. (1974)

^fPearson (1975)

*Figures calculated from data in source cited.

+ Excluding 5 bears of unknown age.

Rough estimate for use in this preliminary analysis.

Table 2. Statistics for density, reproduction, and cub-vs.-yearling litter size differences.

	Mean value, standard deviation; and sample size ()											
	1 density (km ² /bear)	Females: Age at		Litter size		Litter size difference		Interval between litters (years)	Potential Natality Index t ₁₁		Sood supply	Dispersal
		puberty	first litter	Cubs	Yrlgs.	Cubs vs. Yrlgs. (percent)	PNI		lnPNI			
HUNTED												
Kodiak Island	1.6 ^a	4 ^b	5 ^b	2.23 ^b ±0.87 (98)	2.00 ^b ±0.74 (103)	-10 ^b (201)	3 ^b	7.04	1.95	good	medium	
Chignik- Black Lake ^{c,d}	15 ⁺	4	5	2.20	2.02 ^o	-9 (342)	3	6.92	1.93	good	medium	
Eastern Brooks Range ^e	260	9 ⁺ ±1.36 (20)	10	1.8 (13)	2.0 (7)	+10 (20)	4	2.53	0.93	poor	high	
Lake Becharof ^f				2.0	2.0	0						
PROTECTED												
McNeil River ^c	--	5 ±1.07 (8)	6	2.1 (41)	1.8 (69)	-13 -38 (110) (13)#	3.58 ±1.24 (12)	5.12	1.63	good	low	
Yellowstone Natl. Park 1959-70 ^g 1959-68 ^g	13.5	5.14 ±1.10 (14)	6	2.18 ±0.23 (173) 2.23 ±0.20 (147) 1.87 ±0.12 (83)	1.5 ⁺	-31#	3.21 ±1.17 (68)	5.49	1.70	good	low	
1969-74 ^{h,i}										fair?	medium?	
Kluane Game Sanctuary ^j	27	7 ⁺ (>6.89)*	8 ⁺	1.7 (11)	1.5 (11)	-12	3 ⁺ (3-5)	3.60	1.28	poor	high	
Glacier Natl. Park, U.S.A. ^k				1.7 ±0.68 (35)	1.8 ±0.66 (30)	+6						
Mountain Parks, ^l Canada				2.0 ±0.70 (108)	1.93 ±0.72 (45)	-4						
Katmai Natl. Monument ^f				2.0	1.8	-10						

References:

- ^aTroyer and Hensel (1964)
- ^bHensel et al. (1969)
- ^cGlenn et al. (1976)
- ^dL. Glenn (1975, personal communication)
- ^eReynolds (1976)
- ^fTroyer (cited by Faro 1977)
- ^gCraighead et al. (1969, 1974)
- ^hCole (1975, 1976)
- ⁱKnight et al. (1975)
- ^jPearson (1975)
- ^kMartinka (1974)
- ^lMundy and Flook (1973)
- *Figure calculated from data in source cited.
- + Rough estimate for used in this preliminary analysis
- ^oCombined figure for yearlings and older young still accompanying an adult female
- # Only these data are from known litters compared at ages 0.5 vs. 1.5 years. Hence, the figure for sample size at McNeil of 13 is equivalent to 26 litters of unidentified cubs vs. yearlings.

of at least 2 variables: (1) age at which the cubs are weaned and dissociated from the mother, and (2) capability of the mother to conceive and gestate progeny. Only the YNP data (Craighead et al. 1969, 1974) (Table 2) are extensive enough to document successive litters for a substantial number ($n=68$) of females. 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 does not come into heat again while she is lactating. Birth occurs the following winter. A female dissociating from cubs during their third spring of life (age 2.5 years) would thus have at least 3 years between birth of that and the next litter. So mean age at which cubs dissociate is sometimes used to estimate the *minimum* mean interval between litters, where specific data on inter-litter interval are lacking. However, the reliability of such estimates is questionable, since under certain circumstances black bear females may remain barren one or more additional years after dissociation (Rogers 1976). Figures for inter-litter interval from YNP, KGS (Pearson 1975), and MRS GS (Glenn et al. 1976) are derived from data; those from the other populations are primarily estimates based on age at which mothers dissociate from their cubs. Reynolds (1976) reported a range of 2.5 to 4.5 years for age of young at weaning in EBR, with emphasis on longer durations. So the mean minimum interval was roughly estimated as 4 years for this paper (Table 2). Pearson (1975) gave a range of 3-5 years for KGS, with only 1 female each at the 4 year and 5 year intervals; a rough mean of 3 years was estimated by me. Because of the uncertainties in determining inter-litter intervals and small sample sizes for some populations, there is no basis yet for concluding that the intervals vary significantly between the populations.

Litter size. — In the black bear populations where many females give birth in alternative years, there is roughly a biannual fluctuation in cub production (Free and McCaffrey 1972; Kemp 1976). In the year of most numerous litters, cubs tend to be most frequent but yearlings least so, and vice versa. Among grizzly/brown bear, where inter-litter interval averages at least three years, fluctuations in number of litters could be even more complex. Effects of that on natality could be compounded by variations from year to year in mean litter size, as documented at YNP (Craighead et al. 1974). These could be important sources of bias in estimating mean cub production in a population from which data are available for less than one full "cycle". Substantially different estimates might be obtained ac-

ording to which years were sampled. So some of the differences between population sample means could be attributable to this. Ideally, litter sizes should be measured over at least two or three times the length of the mean inter-litter interval. Where that has not been possible, inter-population comparison of combined data for cubs, yearlings and other immatures might help avoid this bias (e.g., in EBR), despite the possibility of another bias: inter-population differences in age-sex specific mortality and migration rates. Due to lack of detail in some published findings, one cannot fully analyze litter size variance within vs. between populations. But when we compare the distribution of mean litter sizes between populations with that from year to year in YNP, neither the (unweighted or sample-size weighted) means nor the variances differ significantly. (Unless otherwise stated, all means given are unweighted; when sample size figures are unavailable, weighting cannot be done even if appropriate). Comparison of litter sizes can also be biased by inter-population differences in infant mortality, since censusing is not done until the cubs are at least 0.5 years old.

Mortality and Survivorship

The most reliable data on cub mortality are for MF and YNP 1959-70 (Table 3), where individually known litters could be compared from week to week and year to year. Among those litters, loss, but not necessarily death, of young were 38 percent and 31 percent, respectively (Glenn et al. 1976, Craighead et al. 1974). This included the loss of all cubs from some litters — a decrement not detectable merely by comparing mean sizes of cub vs. yearling litters. Thus, figures obtained by the latter method could substantially underestimate the number of cubs separated from their mothers between ages 0.5 and 1.5 years (Glenn et al. 1976). If complete yearling litters are easier to observe than complete cub litters, this would also promote underestimation — as Martinka (1974) suggested to help account for the fact that observed yearling litters averaged larger than cub litters seen in Glacier National Park of Montana. These two sources of bias might largely explain why Glenn et al. found only a 13 percent net decline at MRS GS when they also took into account an additional 41 cub litters and 69 yearling litters that were not individually identified. The known litters spent a greater amount of time at MF than the others; although they may have suffered a higher rate of mortality as a consequence (Glenn et al. 1976), most cub losses occurred *after* the bears had left MF for the

Table 3. Correlation matrix for density and reproduction parameters: simple Pearson Product-Moment Linear correlations, r = correlation coefficient; p = confidence level; \ln = natural logarithm.

	Age at puberty females (A)	Cub litter size (L)	Interval between litters (I)	L/I	Potential Natality Index (PNI)	\ln PNI	Percent in Population		Density of	
							cubs	yrllgs.	cubs	yrllgs.
% adult males in population	0.811 0.05	-0.694 0.13	0.775 0.07	-0.921 0.009	-0.945 0.004	-0.906 0.01	-0.877 0.05	-0.645 0.24	-0.587 0.42	-0.542 0.46
% adult females in population	0.383 0.45	-0.096 0.86	0.888 0.02	-0.599 0.21	-0.494 0.32	-0.500 0.31	-0.094 0.88	-0.902 0.04	-0.493 0.51	-0.539 0.46
% adults (M+F) in population	0.726 0.10	-0.528 0.28	0.902 0.01	-0.890 0.02	-0.864 0.03	-0.839 0.04	-0.695 0.19	-0.865 0.06	-0.746 0.25	-0.724 0.28
Adult sex ratio M/F	0.737 0.09	-0.831 0.04	0.340 0.51	-0.754 0.08	-0.861 0.03	-0.796 0.06	-0.954 0.01	-0.125 0.84	-0.527 0.47	-0.484 0.52
Density of population (D)	-0.552 0.83	0.537 0.35	-0.387 0.52	0.572 0.31	0.615 0.27	0.578 0.31	0.563 0.44	0.896 0.10		
$\ln D$	-0.883 0.05	0.713 0.18	-0.813 0.09	0.896 0.04	0.864 0.06	0.883 0.05	-0.691 0.31	0.797 0.20		
Density of adult males	-0.553 0.33	0.512 0.38	-0.460 0.44	0.576 0.31	0.557 0.33	0.562 0.32	0.372 0.63	0.779 0.22		
Density of adult females	-0.579 0.31	0.568 0.32	-0.400 0.50	-0.598 0.29	0.642 0.24	0.605 0.28	0.590 0.41	0.882 0.12		
Density of Adults (M+ F)	-0.580 0.31	0.563 0.32	-0.418 0.48	0.601 0.28	0.613 0.25	0.603 0.28	0.553 0.45	0.872 0.13		
Density of yearlings	-0.494 0.51	0.427 0.57	-0.320 0.68	0.534 0.47	0.553 0.45	0.523 0.48	0.544 0.46	0.909 0.09		
Density of cubs	-0.540 0.46	0.474 0.53	-0.308 0.69	0.579 0.42	0.596 0.40	0.568 0.43	0.588 0.41	0.891 0.11		
Percent yearlings in population	-0.125 0.84	0.0000 1.000	-0.846 0.07	0.519 0.37	0.453 0.44	0.388 0.52	0.381 0.53			
Percent cubs in population	-0.953 0.01	0.893 0.04	-0.292 0.63	0.969 0.006	0.994 0.0005	0.999 0.0001				
\ln PNI	-0.974 0.001	0.878 0.02	-0.753 0.08	0.990 0.0001	0.989 0.0002					
Potential Natality Index (PNI)	-0.938 0.006	0.877 0.02	-0.720 0.11	0.983 0.0005						
Annual unit natality rate (L/I)	-0.941 0.005	0.831 0.04	-0.811 0.05							
Interval between litters (I)	0.695 0.13	-0.360 0.48								
Cub litter size (L)	-0.882 0.02									

Correlations are between population means, not between individual observations. In most cases, $N=6$ populations. But as will be noted from Tables 1 and 2, certain data are missing from some populations. Corresponding correlations are based on only 5 or 4 populations. Hence, the relatively low confidence levels in some cases despite high correlation coefficients. Any association significant with N based on number of populations should still be significant when correlations are done on raw data; but some which are not yet known to be significant may be found significant when raw data become available for analysis.

year (Egbert and Stokes 1976). The larger sample size for the 110 unidentified litters suggests that those figures are more representative of cub vs. yearling litter sizes than are values for the 13 known litters; but that does not make the former a better estimate of cub loss. Annual fluctuation in mean litter size renders the cub vs. yearling litter size comparison method even less reliable as an estimator of mortality.

DISCUSSION

The fact that figures for maturation rate, inter-litter interval, litter sizes, and survivorship, may be seriously biased, certainly does not demonstrate that they are. The uncertainties restrict the confidence we can place in conclusions drawn from these data; but uncertainties should not preclude an interim face-value analysis of the data. We need to derive as much information as

possible from past research as a basis for planning new investigations and evaluating current management practices. So a tentative picture of relationships should be much more heuristic than none at all. It is within these constraints that the following statistical analysis should be interpreted.

Potential vs. Realized Rates of Natality

Natality (birth) rate per unit number (N) of fertile females is a function of (a) age when the first litter is produced *G* (generation length) relative to age a puberty *A*, (b) interval between births of successive litters *I*, and (c) litter size *L*. In addition to considering each of these parameters separately, it is particularly revealing to examine inter-population differences in their combined effects. This is done using the summation formula given below. The following assumptions were made for the purposes of this paper: (1) 50:50 natal sex ratio; the mean number of female cubs produced per litter per year is thus 0.5(*L/I*); (b) the fraction of adult females producing cubs each year is 1/*I*, (c) mean values of *L*, *I*, and *G* are stable through the index period; (d) rates of breeding, fertility, and survivorship for females are 100 percent; every female produces young when mature, none dies within the index period; and (e) there is no migration in or out of the population. This provides an index of *potential*, as proposed to *realized*, natality. Starting with *N* (e.g. 1,000) adult females at made for the purposes of this paper: (a) 50:50 natal sex descendents born during the index period were computed. The index period used is 1 generation — the mean length of time it takes females born in year *t*₁ to produce their own first litters (year *t*_{*G*+1}) — in the slowest reproducing population. That is EBR, where females don't bear until age 10 years (*t*₁₁) on the average; so the index period is 11 years. This computation yields the coefficients for the Potential Natality Index (PNI) given in Table 3(e.g., 7.04 *N* for KI) — indicators of total female descendents born between years *T*₁ to *t*_{*i*}:

$$\begin{aligned}
 \text{PNI } (t_i) &= \text{daughters} + \text{grand-daughters} + \text{great-grand-daughters} + \dots \\
 &= N \left[(t_i)R + \sum_{i=1}^k (t_i-G)R^2 + \sum_{j=1}^k \sum_{i=1}^j (t_i-2G) R^3 + \dots \right]
 \end{aligned}$$

Note that the natural logarithm (ln) of PNI, rather than PNI as such, will be used for comparing populations. This is done to minimize geometric exaggeration of

errors in estimating differences in *A*, *L*, and *I*. Such exaggeration might otherwise occur since PNI is based on geometric population growth.

Realized natality is the actual number of cubs born each year, a value estimated by censusing at age 0.5 year (so, as with *L* values for 0.5 year, bias by inter-population differences in rates of infant mortality and migration cannot be ruled out). This index is symbolized by *RNI*.

$$\text{RNI} = \left[\frac{\# \text{ females bearing cub}}{\text{litters}} \times \text{mean natal litter size} \times \text{survivorship to age 0.5 yr.} \right] + \left[\frac{\text{net immigration of cubs}}{\text{of cubs}} \right]$$

Correlations (Table 3) among *A*, *I*, and *L*, are only moderately strong; knowledge of one is not a precise predictor of the others. However, annual unit natality rate *L/I* is highly correlated (*r* = -0.94; *P* < 0.005) with *A* for females and with lnPNI. *A* is similarly correlated with lnPNI. Inter-population differences in *L/I*, *A* and lnPNI, are highly correlated with percent cubs at age 0.5 years (RNI) (*r* = 0.95 to 0.999; *P* < 0.01 to 0.0001). The very close association between PNI vs. RNI suggests that net inter-population differences in rates of impregnation, prenatal survivorship, natal sex ratio, etc. were minor. By contrast, within YNP (Craighead et al. 1974), annual differences in litter size *L* showed only moderate relationship with RNI, as measured by either percent (*r* = 0.48; *P* < 0.11; *N* = 12) or density/number (*r* = 0.60; *P* < 0.02; *N* = 15) of cubs at age 0.5 year (Stringham et al., in preparation). Now let us consider some of the factors which control reproductive rate.

Factors Affecting Natality

Inter-population differences in maturation rate, inter-litter interval, and litter size could all be genetically controlled. But in lieu of information on heritability, analysis will be confined to other endogenous and environmental influences. These include hunting pressure, social strife, population density and dispersal, nutrition, and age of the mother.

Hunting pressure, social strife, and population dispersal. — When maturation rate, inter-litter interval, cub litter size and lnPNI are compared between the hunted (KI, CBL, EBR) vs. protected (MRS GS, YNP, KGS) populations, significant differences are not found. The same is true when we compare populations having low (KI, CBL) vs. high (MRS GS, YNP,

KGS, EBR) proportions of adult males, in terms of A , I , and L ; only the difference in $\ln PNI$ is significant ($P < 0.03$). Nevertheless, all 4 reproductive parameters are strongly correlated with proportion of adult males (Table 3). Particularly striking are those for L/I , $\ln PNI$ ($r = -0.91$; $P < 0.01$) and percent cubs ($r = -0.88$; $P < 0.05$). Correlations involving just those populations with high proportions of adult males are comparable; so inclusion of depleted populations, despite lack of data from populations with intermediate proportions of adult males, has not appreciably biased the coefficients.

Note that significance figures given for correlation coefficients are based on the number of populations (6), rather than number of observations; some of the population means represent hundreds of observations. So if and when the investigators pool their raw data for statistical analysis, some of the correlations should attain much higher significance.

Re-analysis of the Craighead et al. (1974) data indicates that peak cub production would be achieved with about 65 adults (38 percent of the mean population size) (McCullough, in press). It is not clear what proportion of the adults should be males. Litter size, number of litters, and percent cubs were not significantly correlated with either the current density or percent of adult males, although there was a significant correlation between litter size at age 0.5 year vs. number of adult males during the previous year, when conception occurred ($r = -0.83$; $P < 0.02$; $N = 7$) (Stringham et al., in preparation). Thus, while findings are somewhat similar to those between populations, the relationships are not quite the same. Caution should be used in trying to draw conclusions about intra-population relationships from inter-population analysis.

The strong negative correlations for interpopulation differences in maturation rate, annual unit natality rate (L/I) and potential natality index vs. percent adult males are consistent with the hypothesis that adult males depress reproduction. Among grizzly/brown bears, they tend to dominate other age-sex classes. Many fully adult males are highly feared by subordinates (Hornocker 1962; Stonorov and Stokes 1972; Bledsoe 1975, personal communication; Egbert and Stokes 1976). They may restrict access by adult females to food at sites of feeding aggregations and through inducing psychologically mediated stress could disrupt their reproductive physiology.

It has been observed among a wide variety of vertebrates that social strife can stress an animal both through the physiological dimension of the emotions/states it arouses (e.g., fear) (Selye 1956, 1976; Davis

1964) and through the activities of strife (e.g., chasing and fighting), as well as any consequent injuries. If extreme enough and chronic, strife like any other stressor can arouse the Selye "General Adaptation Syndrome" (G.A.S.); at least the pre-acclimation and exhaustion phases can lower rates of reproduction, maturation, and survivorship. But is this true for bears? When captive black bears are reared in small groups, maturation of subordinates is not known to be retarded (Rogers 1976). But domination of subordinates does not necessarily stress them enough to arouse the G.A.S. appreciably. Domination by a constant companion in captivity may be less stressful than domination in the wild.

Nutrition, habitat quality and population density. — Nutrition can affect natal litter size evolutionarily or directly. It can select for genotypes promoting large litters in good habitat and small ones in poor habitat, which could result in geographic differences in mean litter size (e.g., coastal vs. inland bear habitat). It can maintain genetic polymorphism within a given habitat whose carrying capacity, and thus optimum litter size, fluctuate strongly from year to year (Lack 1954; Geist 1974). Nutrition can also influence natality through direct alterations of reproductive physiology (Sadler 1969; Hafez 1974).

Among the ways in which malnutrition or starvation can proximally affect a female vertebrate is through arousal in her of the G.A.S. That, along with more specific effects of nutritional deficit, tends to impair reproduction and recruitment. Conception and prenatal survivorship may decline, maternal care and lactation can be inhibited. Rate of maturation by offspring can be retarded (Selye 1956, 1976; Davis 1964).

These symptoms of the G.A.S. are comparable to what Rogers (1976) observed about effects of restricted diet in black bear. He found that litter production or nonproduction by a mature female black bear and the cubs' rates of (a) weight gain, (b) survival, and (c) sexual maturation were all strongly related to nutrition, as evidenced primarily by body weight. His own well-fed captive black bears matured earlier than garbage-eating wild black bears, which in turn were better nourished and matured earlier than wild black bears with no access to garbage. Litter size also seems to have been positively correlated with nutrition, as a function of postnatal survivorship and perhaps birth rate.

This is consistent with observations by other biologists. Beecham (1980) compared 2 black bear populations in Idaho, 1 in good habitat that was hunted

heavily and a second in somewhat poorer habitat that was hunted lightly. Densities and sex ratios (all ages combined) were comparable, but maturation rate [$1/(4.25 \text{ years})$ vs. $1/(4.50 \text{ years})$] and mean litter size (1.90 vs. 1.65) were higher in the former. He attributes the greater natality per female not to hunting but to a better habitat, as also evidenced by higher age-specific body weights. The direct relationship between nutritional status and speed of maturation to puberty has previously been documented for bears by several investigators (Baker 1912, Rausch 1961, Jonkel and Cowan 1971; summarized by Pearson 1975) and for many other mammals (Sadler 1969, Giest 1971, Hafez 1974). In numerous species, weaning is partly governed by loss of juvenile appearance and behavior as the young mature (Ewer 1968, Lent 1974), so age at weaning tends to be directly related to age at puberty. Growth and rate of maturation are in turn functions of nutrition. Jonkel and Cowan (1971) reported 1 case where a poorly nourished cub was nursed at least 9 months longer than was typical in a northern Montana population. A female typically mates again during the same spring-summer that she weans her previous litter, and if adequately nourished (Rogers 1976), gives birth about 7 months later. However, if she is too depleted after rearing a litter, 1 or more additional years may pass before she can produce another.

So far, we have no physiological evidence on nutritional status from the 6 grizzly/brown bear populations. While clues might eventually be gotten from data on body weight, stature, and fat deposits, those data were not collected consistently for all the populations; nor are all the data published yet. We also lack detailed comparisons of habitat quality. At best, we have rough impressions that good quality food has been abundant (a) on the coasts of KI and the Alaska Peninsula (CBL, MRS GS), where salmon and berries are plentiful during part of the year, and (b) at YNP 1959-68 (J. Craighead, personal communication). Apparently, garbage is a good supplemental source of nutrition for bears (J. Craighead, personal communication; Rogers 1976). KGS and EBR have been described as having very poor sources of food (Pearson 1975, Reynolds 1976).

Splitting these 6 populations into 2 classes according to food supply, good vs. poor, reproductive rates in the 2 classes can be contrasted (Table 3). Mean age at puberty was lower ($4.5 < 8+$; $P < 0.03$), cub litters were larger ($2.29 > 1.75$; $P < 0.03$), and thus reproductive potential ($1n\text{PNI}$) was higher ($1.805N > 1.103N$; $P < 0.03$) in the 4 best habitats KI, CBL,

MRS GS, and YNP 1959-68, compared with KGS and EBR. Furthermore, following closure of the garbage dumps in YNP, the size of cub litters dropped 24 percent from the 1959-68 mean of 2.23 to a low of 1.7 in 1974 (Knight et al. 1975). The difference between the two periods 1959-68 vs. 1969-74 is highly significant ($2.33 > 1.87$; $P < 0.001$).

Of course, the assumed drop in food supply may not have been the only influence retarding reproduction. When black or grizzly/brown bears concentrate at feeding sites, aggression between these normally dispersed animals can become intense. This aggression has been documented at the YNP garbage dumps and at salmon streams, including the McNeil River (Hornocker 1962, Stonorov and Stokes 1972, Frame 1974, Egbert and Stokes 1976). While the YNP dumps were being closed (1968-71), the progressive reduction in available garbage supposedly (Cole 1975) accentuated competition and strife at those dumps still open. Intensification of strife, alone or in combination with reduction in food supply, may have elevated physiological stress and the G.A.S., thereby lowering rates of conception or raising prenatal and postnatal mortality — accounting at least in part for the drop in mean size of litters censused at age 0.5 year. Conversely, closure of dumps and consequent dispersal of the bears may have eventually lowered the vulnerability of cubs (mostly over 0.5 years old during the tourist-garbage season) to murder; there was an apparent increase in rate of survivorship between ages 0.5 and 1.5 years from 61 percent (1959-68) to 69 percent (1959-70) to 93 percent (1974) (Craighead et al. 1969, 1974; Knight et al. 1975). But as mentioned above, this trend may be exaggerated or spurious because whole-litter losses may have gone undetected after 1970.

We have no evidence that nutrient supplies at MRS GS or YNP (1959-68) were poorer than at KI and CBL. MRS GS is rich in salmon, berries, sedges, and other natural forage; YNP offered spring carrion in addition to natural vegetation and garbage. So the fact that rates of maturation by females to puberty averaged 1 year slower at MRS GS and YNP than at KI and CBL, despite seemingly abundant food, may indeed be due to effects of strife at feeding aggregations (see also Stokes 1970, Cole 1975). In other words, maturation rate is hypothesized to be a function of both strife (as related to dispersal and other factors) and nutrition. At KI and CBL dispersal is at least moderate; at KGS and EBR it is high. Hence, now that the YNP dumps have been closed and the bears dispersed, we would have expected maturation rate to increase there, all other

factors being equal; however, the loss of garbage as a substantial source of food may have counteracted this effect of dispersal.

As Glenn (personal communication) has also noted, contrasting density figures between populations can be misleading since they are calculated per unit land area, rather than per unit habitat or resource (e.g., food). They were determined by a variety of methods whose results are only roughly comparable. The bears travel so widely that it is extremely difficult, for instance on the Alaska Peninsula, to obtain a meaningful estimate of density for any subunit. Lastly, the fact that data on only five populations spans two orders of magnitude ($1/1.6 \text{ km}^2$ to $1/260 \text{ km}^2$), with three of the values clustered centrally ($1/15 \text{ km}^2$ to $1/27 \text{ km}^2$), prevents us from making meaningful correlations between densities (as opposed to percents or numbers) within each age-sex class (e.g., cubs vs. adult males); interpopulation differences in density are so great that the density-density autocorrelation overwhelms differences in population structure. Nevertheless, even with this limitation in mind, it is interesting to note that density (D) is significantly correlated with reproductive potential ($\ln D$ vs. $\ln PNI$; $r = 0.88$; $P < 0.05$). Not only is density a function of natality, but both density and natality are presumably functions of nutrition.

Productivity of females as a function of age. — On the basis of data published by Craighead et al. (1969, 1974), intervals between successful matings and between litters did not differ as a function of age in females 4.5 to 9.5 years old. However, there was an age-related difference in mean litter size. The 5.5- and 6.5-year-old mothers ($N = 7$) had 2 cubs each, whereas 7.5- to 9.5-year olds averaged 1.8 ($N = 8$), or 1.4 if we exclude an a typical litter of 4 cubs (perhaps enlarged by adoption). Whether the decline in litter size ($P < 0.01$) as a female ages is typical of North American *Ursus arctos* is unknown. It may be that females which reach maturity latest also produce smaller litters. Couturier (1954, cited by Mundy and Flook 1973) reported that female European brown bears 5-7 years old usually had only 1 cub, those at their reproductive peak had 2 or 3, and old females had 1 or 2.

MORTALITY vs. SURVIVORSHIP AND MIGRATION

Mortality Induced by Adult Males

Sexually mature males, especially full adults — those that have completed puberty and are also mature

in most other socially important morpho-physiological and behavioral traits (for ungulates see Bubenik 1971, Geist 1971, and Stringham and Bubenik 1975; for *U. arctos*, Egbert and Stokes 1976) — seem to be dangerous to juveniles at least when not protected by their mothers. Adults force egress of subadults; full adults may eject adolescent adults. If the emigrants have to live in marginal habitat, their chances of survival and reproduction are diminished accordingly. So it has been suggested that removal of large males through trophy hunting would increase survivorship of juveniles and subadults (Glenn, cited by Egbert and Luque 1975; Kemp 1976).

That assertion is plausible, but available data on grizzly/brown bears provide little support for it. I have found reference to less than 2 dozen confirmed murders (J. Craighead, personal communication; Murie 1961; Glenn et al. 1976). The aggressor is rarely known to have been an adult male. Murie saw an adult female kill cubs of another mother after the two litters had mixed and the former sow was trying to recover her own young. Nor has definitive evidence yet been published that survivorship of cubs between ages 0.5 to 1.5 years is higher in the 2 populations with few adult males than in the 4 with many, hunted (EBR) or not.

Litter Size Declines

Recall that figures solely on loss of cubs from known litters are available only from YNP (31 percent) and McNeil Falls (38 percent). These are also the only habitats of the 6 with sites where the grizzly/brown bears aggregated in large numbers to feed — sites where aggression between these normally dispersed animals was very high. Hence, because of differences in both methods and dispersal, these mortality estimates cannot be compared directly with figures from other populations based strictly on contrasting mean sizes of mostly unidentified cub vs. yearling litters. The only data from MRSGS which can be used are for the 110 unidentified litters.

Comparative data on cub and yearling litter sizes are thus available from 9 populations (Table 3). Lacking sample size figures for Lake Becharof (hunted) and Katmai National Monument (protected), these two populations cannot be included in the comparison of cub to yearling litter size declines. Among the others (using the 13 percent figure for MRSGS), the decline averaged 8.7 percent ($s^2 = 127$; $N = 3$)* in hunted

*sample-size weighted means

populations, contrasted to 3.1 percent ($s^2 = 78$; $N = 4$) in the protected ones. Comparing litter size declines between populations with few adult males (KI and CBL: 9.4 percent; $s^2 = 0.5$) vs. those with many (MRS GS, KGS, and ERB: 9.9 percent; $s^2 = 136$), the difference is not significant. These comparisons provide no basis for concluding that cub mortality rates between ages 0.5 and 1.5 years could be reduced by hunting adult males. Under some conditions, hunting adult males may even increase cub mortality, as will be discussed later.

We also do not know the extent to which these declines in litter size between ages 0.5 and 1.5 years reflect mortality. Some young may become independent before they can be censused as yearlings. Johnson and LeRoux (1973) reported that a cub orphaned at age 7 months survived at least until the next year. Others are adopted, at least temporarily. Adoption is a well documented and fairly common phenomenon at MRS GS and YNP (1959-70) (e.g., Erickson and Miller 1963, Craighead et al. 1969, Bledsoe 1975). Indeed, yearling litters at EBR averaged 10 percent larger than cub litters. Whether this finding represents sampling error (e.g., due to annual fluctuations in cub litter size), migration or adoption remains to be determined.

In view of these considerations, we cannot be sure that mortality rates at YNP before dumps were closed and at MRS GS were significantly higher than for other populations or for YNP after 1970. Nor is there yet any basis for claiming that juvenile mortality is higher in populations with many adult males than in those with few. Even where adult males do induce mortality, we do not yet know to what extent this is due to strife-induced, psychologically-mediated stress disrupting fetal development or inhibiting lactation and maternal care, for instance via the General Adaptation Syndrome, rather than to direct murder. Re-analysis of the Craighead et al. (1969, 1974) data shows that the ratios of yearlings or 2-year-olds to adults are more highly correlated with number of adults in the year each cohort was born than in subsequent years (McCullough, in press); correlations with year of conception are comparable (Stringham et al., in preparation).

Evidence on juvenile mortality relative to percentage of adult males is also provided by Kemp's (1976) simulation of trophy hunting for black bears at Cold Lake, Alberta. After removal of most mature males, population density doubled within 2 years — a result that some sportsmen construe as experimental confirmation that trophy hunting is beneficial. But no evidence has been presented that increased density cannot

be explained by enhanced immigration and lower egress. No increase in reproduction was demonstrated. We have no data on murder rate. However, if a "territorial" matrix was intact before the simulated hunting, there is reason to expect (Rogers 1976) that murders would have *increased* after removal of resident males disrupted the matrix, allowing a consequent influx of other males. Furthermore, after the peak, density declined over the next 3 years to a level only 25 percent above the original (G. Kemp and R. Ruff, personal communication). I do not know whether the decline continued beyond that time; nor had its cause yet been established. The decline is consistent with what would be expected if (a) the initial density rise had led to overpopulation and deterioration of the habitat, and/or (b) if a "territorial" matrix was reestablished, forcing egress of "surplus" males.

The Roles of Social Organization in Enhancing Survivorship

Social organization is, in general, evolutionarily specialized for optimizing resource income while minimizing the costs of living and reproducing. This capability elevates the number of individuals that can be sustained by a given amount of resource. While social behavior may limit density below the highest level that it could attain temporarily, it can substantially raise (maximize?) the long-term average (Rogers 1976), which is equivalent to increasing the carrying-capacity (K) of the habitat.

Hence, a distinction is drawn between *potential* vs. *realized* carrying capacity (PK vs. RK). PK represents the theoretical maximum number of animals that can be sustained by a given supply of resources — a maximum that can be approached only more or less asymptotically in practice. By contrast, RK represents the actual number that can be supported. RK is a function of (a) available resources and efficiency in (b) obtaining and (c) utilizing them, which in turn influences *per capita* requirements. RK is also a function of (d) efficiency in, and effectiveness of, stress avoidance.

In the mountain sheep (*Ovis* spp.) of North America and Iran and in the ecologically similar chamois (*Rupicapra rupicapra*) of Europe, fully adult rams play a number of vital roles besides impregnation. Limiting aggression by adolescent adults is 1 of the most important roles; so depletion of fully adult males through hunting can markedly lower viability of a population (Grubb, personal communication to Sadlier 1969:34; Bubenik 1971, Geist 1971, Schröder 1971, Stringham and Bubenik 1975, Valdez and Stringham, in prepara-

tion). Do adult male bears also play this role? Apparently not. The limited data available on grizzly/brown bear social behavior (Murie 1961, Hornocker 1962, Craighead et al. 1969) provide no evidence that adult males enhance the viability of a population other than by siring offspring. The same may be said of black bears, except perhaps in cases where a resident male excludes transient males from his home range. This inadvertently prevents them from endangering the cubs of females which share his home range — cubs likely to be his own offspring (Rogers 1976).

SUMMARY AND CONCLUSIONS

Limitations in quality and detail of published data preclude rigorous analysis. However, preliminary analysis leads to the following tentative interpretations: Differences in reproductive potential between six North American grizzly/brown bear populations are directly related to differences in food supply and density, but negatively correlated with differences in proportions of adult males; there is also evidence of a negative correlation within YNP. Whether adult males actually depress birth rate and survivorship by disrupting reproductive physiology of mothers, perhaps via social strife, or whether lowered reproductive potential is a co-effect of other variables, remains uncertain. The interpopulation correlation between natality vs. deficit of adult males could arise because harvests reduce population density below realized carrying capacity of the habitat and elevate access to prime food by females and young, thereby increasing *per capita* nutrition. Alternatively, the correlation could be spurious, arising from the concentration of harvest in areas of peak carrying capacity where bears are largest, most numerous, and easiest to find. Beecham (1980) likewise attributed to nutrition, rather than to hunting, differences between his 2 black bear populations, 1 in good habitat that was hunted heavily, and a second in poorer habitat that was lightly exploited. When Kemp (1976) simulated trophy hunting on a formerly little-exploited population of black bears, the natality rate was not noticeably altered.

There is no solid evidence that removing adult males raises the survivorship of juveniles. Although such enhancement probably does occur under certain circumstances, under others the reverse may be true. According to Rogers (1976), in dispersed populations, a resident male black bear inadvertently protects his offspring by excluding transient males from his home range. Removal of a resident male would permit an influx of subadult and adult males from the periphery of his range, which could result in increased murder of

resident young. The same situation may arise among dispersed grizzly/brown bear populations where individuals have stable home ranges. However, it can be hypothesized that where either species is nomadic or hierarchical, natality and survivorship of offspring may be enhanced by depletion of adult males — providing the number remaining are sufficient to breed most of the fertile females. This critical minimum adult sex ratio has yet to be determined but is probably proportional to dispersal of the population. The more widely females are scattered, the more adult males will be necessary to assure maximum impregnation without excessively taxing individual males. Within any population there might be an optimum proportion of adult males at which reproduction and recruitment are maximized.

Thus, despite some preliminary evidence, utmost caution should be exercised in removing adult males to stimulate recovery of an endangered population. Not only do data limitations weaken the analysis, but there is no *proof* that aggression by adult males significantly lowers either natality or survivorship. Less than 2 dozen murders have been confirmed, and the aggressor is rarely known to have been an adult male. Adult females also kill cubs. Nor do we know what determines *which* adult males kill a significant number of young; perhaps most of the killers are the highest-ranking and/or transient males. If so, they alone should be removed. We know little about variations in intensity and amount of male-induced strife under different ecological and social conditions, except that it may be greater amidst feeding aggregations. We also need to learn the extent to which trophy hunting is detrimental — by biological and trophy criteria — to a population's gene pool, via selection against the qualities that make for trophy animals and consequent reduction in the number of cubs produced by trophy-quality bears. For this calculation, we need data on heritability and selection coefficients. Lastly, trends found between populations do not necessarily hold within them.

Removal of adult males from a population seems to decrease emigration of subadults. Decreased emigration would benefit hunters to the extent that it increases the number of potential emigrants that could be harvested within a core area on a sustained-yield basis. Conversely, decreasing egress could eventually reduce harvestable yield in cases where (a) hunting is concentrated on the periphery of a core area (for instance a wilderness) and emigrants are the most available class of bears to harvest, and where (b) emigration serves to prevent overpopulation in the core area or to (c) re-

populate peripheral areas depleted by hunting. In such cases, it would be advantageous to maintain adult males in the core area. Note that dispersal of subadults from an area does not necessarily indicate that the area has reached carrying capacity, even from a long-term standpoint. Dispersal is not a reliable indicator that density should be reduced. Harvest should be governed by more reliable evidence on how closely a population has approached the realized carrying capacity of its habitat.

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