

EFFECTS OF CLIMATE, DUMP CLOSURE, AND OTHER FACTORS ON YELLOWSTONE GRIZZLY BEAR LITTER SIZE

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Abstract: Grizzly bears (*Ursus arctos*) in Yellowstone National Park fed heavily on garbage at open-pit dumps from about 1895 until the dumps were closed in 1968-71. Concurrent with dump closure, mean cub litter size declined 17%. Almost 20% of the decline was associated with coincidental worsening of the climate and nearly 80% with closure. Impacts of closure may have been compounded by the simultaneous increase in adult male abundance, to which litter size was negatively correlated.

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Across North America, grizzly, black (*U. americanus*), and polar bears (*U. maritimus*) supplement diets of natural foods with garbage (Craighead et al. 1974, 1976; Rogers 1976; Rogers et al. 1976; Craighead 1979; Bruemmer 1984). It is important to determine how much this artificial food source affects a bear population and how bears are likely to react if the garbage supply increases or decreases.

Rogers (1976) and Rogers et al. (1976) showed how litter size and age at 1st reproduction differ between black bears that feed at garbage dumps and those that do not. Their findings have not been replicated for other black bear populations, much less for other species, but data from Yellowstone National Park (YNP) provide the opportunity for doing so with grizzly bears.

For decades before 1968, abundant garbage was available to bears at several open-pit dumps in the vicinity of YNP. Then, during 1968-71, dumps within YNP and at the nearby town of West Yellowstone were progressively closed to bears, thereby greatly reducing availability of human food to bears. Associated with dump closure, mean cub litter size (cubs per litter, C/L; Table 1) dropped ($P < 0.001$) 17% or 0.38 C/L from 2.23 C/L in 1959-68 to 1.85 C/L in 1969-76, with a low of 1.5 in 1975. (Cub refers to juveniles less than 1 year old.)

Craighead et al. (1974, 1976) and Craighead (1979) attributed the litter size decline to effects of dump closure. Closure reduced the supply of food available to the bears and disrupted their social organization, increasing strife. However, neither garbage abundance nor strife was measured, so the correlations could not be quantified. Picton (1978), by contrast, revealed a significant correlation between litter size

and climate, then attributed the litter size decline to documented worsening of the climate.

After Picton's (1978) findings are reviewed, the relationship between litter size and climate will be reexamined from a different perspective, which quantifies the impacts of events associated with climatic change relative to those associated with dump closure. Among the events associated with closure are changes in garbage supply, adult male abundance, and perhaps, in female age-class ratios.

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CLIMATIC CHANGE AND NATURAL FOOD SUPPLY

Picton's (1978) index of winter-spring climate for YNP was calculated on the basis of monthly and long-term (1959-76) means for temperature and precipitation at the Mammoth weather station. The cumulative value for September-May (Picton, pers. commun.) each year was given a score according to how many standard deviations it departed from the long-term mean.

This winter-spring climate index (Table 1) was pos-

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Table 1. Litter size relative to Picton's climate index* for the previous winter-spring and adult male abundance.

Year of birth	Cubs per litter	Climate index	Adult males ^b
1959	1.86	3	—
1960	2.06	-7	43
1961	2.31	2	55
1962	2.29	-1	35
1963	2.50	10	18
1964	2.18	4	29
1965	2.11	-1	34
1966	2.13	-5	27
1967	2.50	11	29
1968	2.46	7	31
1969	2.00	2	44
1970	1.75	3	53
1971	1.94	-3	49
1972	2.00	1	—
1973	1.80 (1.85) ^c	-7	—
1974	1.73 (1.71)	-1	—
1975	1.50 (1.60)	-14	—
1976	2.06 (1.92)	3	—

* Data from Craighead et al. (1974), Cole (1974), and Knight et al. (1977). Figures for male abundance during some years estimated by regression on total adult abundance (Stringham 1983, 1985).

^b Abundance of adult males during the previous year. Thus, the number censused during year *t* are listed with litters born during *t* + 1 (e.g., 1959 males and 1960 litters).

^c Unduplicated (and cumulative) litter sizes, as defined in the text.

itively correlated with mean size of cub litters born that spring to resident grizzly bears (and censused at an average age of 0.5 year). The climate index accounts for 43% (r^2 , $P < 0.01$; Picton 1978) and 51% ($P < 0.001$) of variances in means for cumulative and unduplicated litter sizes during 1959–76. “Cumulative” refers to the means for sizes of all cub litters tallied during 1973–76, including what may have been repeated tallies of the same litters (Table 1). “Unduplicated” refers to the mean of tallies certain not to be duplicates. Whichever litter size measure one chooses, roughly half of its variance during 1959–76 is thus accounted for by the change in climate.

Picton attributes the correlation between litter size and climate to the effects of temperature and snowfall on energetic costs of thermoregulation, especially during the winter, and on access to 2 crucial foods: pine nuts before hibernation and carrion afterwards. Thus, he interprets the winter-spring climate index as an index of metabolic energy balance for the bears. The validity of his interpretation is still being tested (Knight, pers. commun.).

The annual plant food crops in YNP were not measured during 1959–76, but the National Park Service did keep records on ungulate carrion abundance each spring, beginning in 1966. Picton's com-

bined index for carrion and climate accounts for 58% ($P < 0.01$) of cumulative litter size variance for that period.

This increase in strength of the correlation is, however, largely an artifact of omitting litter sizes for 1959–65 due to lack of carrion data for that period (Stringham 1985). For the period 1966–76, climate alone accounts for 51% and 62% of variances in cumulative and unduplicated litter sizes, respectively. In other words, contrary to Picton's conclusion, addition of the carrion index to the climate index does little to increase its power for predicting litter size. Apparently carrion abundance was strongly correlated with climate, as Picton originally suspected, carrion being most abundant following severe winters.

Picton's results were phrased in terms of proportion of variance in litter size statistically accounted for by climatic change. However, it is neither variance nor annual variation, so much as the difference in means before vs. after closure, that needs to be explained. We need to learn how much of the actual decline in litter size associated with closure is accounted for by climate, compared to other events associated with closure, particularly the decline in garbage abundance. That is done here within the limits of available data.

METHODS

All analyses were done using Minimum-Variance/Least-Squares regression, Pearson product-moment correlation, and ANOVA procedures. Picton's analyses were based on a mixture of data for unduplicated (1959-72) and cumulative (1973-76) litter sizes. Mine are based solely on unduplicated sizes (1959-76).

RESULTS AND DISCUSSION

Dump Closure vs. Climate

Impacts of events associated with dump closure can be distinguished from those associated with climatic change by performing linear regression for unduplicated litter size vs. climate index (CI) separately for the preclosure vs. postclosure periods (analysis of covariance yields essentially identical results, because there is no "interaction"):

$$1959-68: C/L = 2.19 + 0.0238 \times CI \\ r^2 = 45\%, P = 0.03$$

$$1969-76: C/L = 1.89 + 0.0238 \times CI \\ r^2 = 56\%, P = 0.03$$

The 2 lines are parallel, with a vertical separation of 0.30 C/L, as indicated by the difference in their Y-intercepts (Fig. 1). This is 79% of the 0.38 C/L difference between the 2 periods. Had cumulative litter sizes or data from a longer or shorter time period been used instead, the relative percentages of litter size change associated with climate vs. closure would have differed slightly, but the basic result would be the same (Stringham 1985). Events associated with dump closure thus had roughly 4-fold as much impact as those associated with climate change on the litter size change before vs. after closure.

Controlling Factors

Causal links between climate and closure vs. litter size are not known and can only be inferred until confirmed by field research. However, the only obvious ways that this worsening of the climate might have affected litter size are by reducing natural food supply or increasing thermoregulatory costs of living (Picton 1978).

Changes in litter size associated with closure might be attributed to any of 5 factors.

1. Reduction in availability of garbage presumably lowered nutritional status of dams.

2. The coincidental increase in adult male abundance during the closure period might have increased their competition against dams and cubs for the diminishing food supply.

3. Dams may have adjusted litter size in direct response to male abundance.

4. Changes in age-class ratios among females, due for instance to deaths of those that became nuisances following closure, may have reduced the proportion of adult females that were in their prime.

5. Disruption of social relationships among the bears caused by closure (see Craighead and Craighead 1971) might have been severe enough to physiologically "distress" the animals and thereby impair production and rearing of cubs by females.

Only the 1st 4 factors can be discussed on the basis of available data. Lack of quantification for most of them prevents adequate partitioning of their respective influences.

Garbage Supply and Nutritional Status

We know that roughly 50%-75% of Yellowstone grizzly bears fed at the dumps (Craighead et al. 1974, McCullough 1981), which contained many tons of edible garbage daily. During 1959-61, this averaged

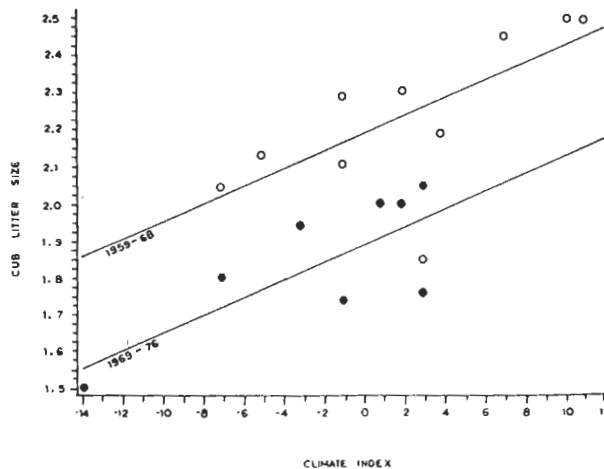


Fig. 1. Cub litter size relative to climate. Litter size (C/L) is regressed on Picton's (1978) Index of winter severity (CI), separately for 1959-68 vs. 1969-76. The former period precedes closure of the Yellowstone garbage dumps, and the latter encompasses and follows closure. The vertical distance between these lines, as represented by the difference in their Y-intercepts, represents the 0.30 C/L litter size decline associated with dump closure.

$$1959-68: C/L = 2.19 + 0.0238 \times CI \quad r^2 = 45\%, P = 0.03$$

$$1969-76: C/L = 1.89 + 0.0238 \times CI \quad r^2 = 56\%, P = 0.03$$

an estimated 60 kg garbage available per day per grizzly bear censused there between June and September (Stringham 1985). We also know that dump closure largely eliminated garbage from the diets of most of these bears, but we have no data on the amounts of garbage actually eaten by the whole population or per bear before or after closure. We can only show a rank correlation between reduction in garbage supply vs. litter size without being able to quantify it. This is comparable to findings by Rogers (1976) on black bears.

Rogers (1976) and Rogers et al. (1976) compared black bears found at dumps to those found elsewhere in Minnesota and in the Upper Peninsula of Michigan. Bears using dumps tended to be larger within each sex-age class, to mature earlier ($\bar{x} = 4.4$ years, $N = 5$ vs. $\bar{x} = 5.6$ years, $N = 9$), and to have larger litters ($P < 0.01$). In Michigan, cub litter sizes averaged 3.1 at dumps during that study compared to 1.99 elsewhere on the Peninsula during the research by Erickson et al. (1964). In Minnesota, 4 females using dumps had litters of 4 cubs each, which was extremely rare elsewhere. Apparently, females eating garbage gave birth to larger litters or their cubs had higher survivorship than in families subsisting primarily on natural forage. Rogers (1976, 1977) also showed that among bears subsisting primarily on natural forage, the proportion of dams whelping each year and survivorship of their cubs were directly related to nutritional status.

Direct relationships between litter size and maternal nutritional status have been documented in numerous mammals with immediate implantation of blastocysts; less is known about those with delayed implantation. Litter size can be affected through changes in ovulation rate, proportion of ova that become implanted embryos, prenatal mortality of embryos or fetuses, and postnatal mortality before 1st censusing.

Longhurst et al. (1952) reported a positive correlation between litter size vs. prebreeding nutritional status and body weight of the dam in mule deer (*Odocoileus hemionus*). Positive correlations between ovulation rate and nutritional status were found in domestic swine (Robertson et al. 1951, Self et al. 1955); domestic sheep (Reid 1960); white-tailed deer (*O. virginianus*) (Cheatum and Severinghaus 1950; Verme 1965, 1969; Kirkpatrick 1975); snowshoe hare (*Lepus americanus*) (Vaughan and Keith 1981); and lynx (*Felis canadensis*) (Brand and Keith 1979). Rats deficient in protein or energy have fewer, smaller

litters than controls (Stewart and Sheppard 1971, Widdowson and Cowan 1972); whether this involves decreased ovulation rate is not known, but undernourished rats have more deformed or degenerating ova (Platt et al. 1969). Mortality of entire litters of implanted embryos or fetuses may be linked to maternal nutritional status. However, I have found no clear indication that such a link exists for the proportion of implanted embryos or fetuses lost from individual litters. Evidence of a positive correlation between prenatal or postnatal food supply or maternal nutritional status (indexed, for instance, by body weight) vs. neonate body weight, growth rate, or survival has been presented for numerous mammals, including domestic species (see Russell et al. 1967; Natl. Res. Council 1968:47; Maynard and Loosli 1969; Slee 1971), wild sheep (*Ovis* spp.) (Geist 1971, Seip and Bunnell 1985), wapiti (*Cervus elaphus*) (Thorne et al. 1976), white-tailed deer (Verme 1977, 1979), black-tailed deer (*O. hemionus*) (Mueller and Sadlier 1980), snowshoe hare (Vaughan and Keith 1981), and lynx (Brand and Keith 1979).

Presumably in bears, too, litter size at ovulation depends on concurrent maternal nutritional status, and adjustment of litter size to postpartum status occurs postnatally. However, more empirical research is needed before this can be accepted.

Abundance of Adult Males

Cub litter size for Yellowstone grizzly bears was negatively correlated with abundance of adults, especially males (Shaffer 1978, 1983; McCullough 1981; Stringham 1983, 1985). Abundance of adult males in the population (1959–70) during the gestation of each of the 1960–71 cub cohorts statistically accounted for 42% ($P = 0.02$, $N = 12$) of variance in cub litter size. If 1 outlier (due perhaps to intervening effects of climate or garbage supply) is removed, this correlation (r^2) rises to 72% ($P < 0.001$, $N = 11$) (Stringham 1983).

Some of the litter size decline associated with closure might thus be attributable to the nearly 50% higher density of adult males during 1968–70 ($\bar{x} = 49$ males, range 44–53) than during the previous 9 years ($\bar{x} = 33$, range 18–55; Table 1; Stringham 1983). Males might have affected litter size through food competition, killing of offspring, or inducing dams to adjust litter size to avoid wasting investment in cubs likely to be killed by the males (Stringham 1985). Because cub litter size is correlated with male

abundance prenatally much more strongly than post-natally, infanticide by males is unlikely to account directly for the correlation. These hypotheses need to be tested empirically.

Effects of events associated with fluctuations in male abundance can be partitioned from those associated with fluctuations in climate through multiple regression. That is done here for the period 1959–70, because those are the only years for which adult male abundance (#AdM) was estimated ($r^2 = 57\%$, $P = 0.01$):

$$C/L = 2.52 + 0.0177 \times CI \\ - 0.00985 \times \#AdM$$

The slope P values are 0.05 for CI and 0.04 for #AdM.

This equation indicates that the increase in mean adult male abundance by 16, from 33 to 49 males, would have tended to decrease litter size 0.16 C/L ($= 0.00985 \times 16$), or about half of the 0.30 C/L decrease associated with closure. However, this quantity could have been distorted by the overlapping effects of garbage decline during closure. Although this regression helps partition effects of male abundance from those of climate, it is only a 1st step toward partitioning them from effects of garbage supply and possibly female infrastructure.

Maternal Age and Female Age-class Ratios

Craighead et al. (1969, 1974, 1976) and Knight et al. (1981) provide data showing an age-related change in litter size for Yellowstone grizzly bears. Similar trends have been documented in European brown bear (Couturier 1954), polar bear (Lentfer et al. 1980, Stirling et al. 1980), and black bear (Collins 1974, Eiler 1981, Alt 1982). The general pattern in these and other homeotherms is increasing litter size during a female's adolescence, a peak or plateau during her prime, then a decline during senescence (Stringham 1987).

If events associated with dump closure, such as removal of females that became nuisances, substantially lowered the proportion of females in their prime, this could have lowered mean litter size. Unfortunately, we lack the data on female infrastructure needed to test this hypothesis. We must also question whether age-related litter sizes were themselves unaffected by events associated with dump closure.

The physiological mechanisms and cues linking litter size to maternal age are unknown. One possi-

bility is that the link is simply maternal nutritional status or body size, as is believed to occur in moose (*Alces alces*) (Markgren 1969, Saether and Haagenrud 1983). Female bears grow somewhat after puberty. That, and any attendant increase in social rank and experience, may increase their ability to obtain enough additional food to support larger litters. However, for now, we have no conclusive evidence that bear litter size changes with maternal age independently of nutritional status and body size.

SUMMARY

Demographic data on Yellowstone grizzly bears have been collected by Craighead et al. (1974, 1976), Cole (1974), and Knight et al. (1977). Associated with closure of the garbage dumps within Yellowstone National Park and West Yellowstone during 1968–71 was a decline in mean annual cub litter size. Craighead et al. (1974) attributed this to impacts of dump closure, reducing bear food supply and elevating social strife. Picton (1978), by contrast, demonstrated a direct correlation between litter size and climatic favorability; he thus attributed the litter size decline to climatic worsening rather than to dump closure. Reanalysis of this correlation, however, shows that climate can account for only about 20% of the litter size decline, whereas events associated with dump closure account for the other 80%.

Events associated with closure include near elimination of garbage from diets of most of the bears and thus presumably a decrease in their nutritional status, temporary social disorganization and increased strife, and coincidentally increased adult male abundance. Litter size was negatively correlated with male abundance. The possibility that age-class ratios for females also changed cannot be ruled out. Lack of quantitative data on garbage supply, female infrastructure, and strife prevents adequate partitioning of their respective influences on litter size.

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