IS GRIZZLY BEAR REPRODUCTIVE RATE DEPRESSED BY AGGREGATING AT CONCENTRATED FOOD SOURCES?

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Abstract: Especially when dispersed food sources are poor, grizzly bears (*Ursus arctos*) aggregate at concentrated sources -- fishing sites, berry patches, carrion, garbage dumps, etc. The largest and most durable aggregations known have been at McNeil Falls where bears catch salmon (*Oncorhynchus spp.*), and at garbage dumps in Yellowstone National Park (YNP). Although those "ecocenters" apparently enhanced nutrition, reproductive rates were lower than expected by Stokes (1970, pers. comm.). He attributed this to crowding-aggravated strife. To test for effects of strife, one has to distinguish them from effects of nutrition. Following Stringham (1990a), I did that by regressing mean rates of maturation and natality on adult female body weight for 9 dispersed populations. For hypothetical ones with the same weights as at McNeil and YNP, rates of maturation (0.17) and natality (0.63) would be exactly the same as the rates observed in the 2 aggregated populations. These relationships provide no support for Stokes' contention that reproductive rate is suppressed by aggregation -- at YNP and McNeil or elsewhere.

Key words: Aggregation, crowding stress, ecocenter, food concentration, reproductive suppression, *Ursus arctos*.

The abundant food at ecocenters can enhance nutritional status (Craighead et al. 1974, Rogers et al. 1976, Rogers 1987, Stringham 1985, 1989) -- tending to elevate reproductive rate. The positive relationship between nutrition vs. rates of reproduction and survival has been documented in all 3 species of North American bears (*Ursus arctos*, *U. americanus*, *U maritimus*) by comparing among populations or over time within populations (Baker 1912, Rausch 1961, Hatler 1967, Jonkel and Cowan 1971, Craighead et al. 1974, Rogers 1976, 1987, Stringham 1980, 1986, 1989, 1985, 1990a,b, Bunnell and Tait 1981, Blanchard 1987, Eiler et al. 1989, Elowe and Dodge 1989).

One might thus expect reproductive rate to be especially high in populations where bears utilize major food concentrations. But the effects of enhanced nutrition could be overwhelmed by those of crowding-aggravated social strife if a large number of bears gathered (Stokes 1970).

Enormous grizzly bear aggregations formed at garbage dumps in YNP from about 1900 until 1968-72, when the dumps were closed; moderate aggregations form each summer at McNeil Falls in Alaska, where salmon are caught in large numbers (see Stringham, in press *a*).

At YNP strife was highest during the breeding season. At McNeil aggregation occurred mainly after the breeding season, and strife was associated more with competition for food and space. (Hornocker 1962, J. Craighead, pers. comm., Stonorov and Stokes 1972, Egbert and Stokes 1976).

In other mammals, strife can produce severe physiological stress that can reduce resistance to malnutrition, disease and cold; it can impair natality, lactation, and maternal care (Selye 1956, 1976, Davis 1964). Strife can injure or kill relatively defenseless individuals, especially infants. Stokes (1970) hypothesized that crowding-aggrevated strife can have comparable effects in bears, lowering rates of reproduction and cub survival.

Stokes' hypothesis was consistent with seeming depression of reproduction and survival at YNP (Stokes 1970). Based on the data of Craighead and Craighead (1967), Stokes (p.1155) stated that: "The female grizzly is physiologically capable of breeding at 5 years, but in Yellowstone many do not breed until 6 to 7 years old. Likewise, a fourth of the potential breeding females do not breed ...."

It was in part to test his hypothesis that Stokes (pers. comm.) initiated research at McNeil -- where reproductive rate turned out to be even lower than at YNP.

Meanwhile, a fortuitous test occurred at YNP when the dumps were closed (1968-72) and the bears dispersed. Contrary to what one might expect from Stokes' hypothesis, reproductive rate declined. However, this contradiction does not refute Stokes, given that any effects of reduced strife could have been masked by the dramatic decline in food supply. Not only did availability of garbage crash (Craighead et al. 1974, Stringham 1985, 1986, 1990a), but natural food supply was apparently reduced by worsening climate (Picton 1978, Stringham 1985, 1986). To adequately test Stokes' hypothesis one has to distinguish the effects of nutrition, as is done here.

My work was supported by Wildwatch; the Blackfeet Indian Tribe; the Ecology Program, University of Tennessee, Knoxville; the State University of New York, CESF; A., J., J. and R. Stringham; C. and V. Nicolayeff; H. Strauss; L. and B. Lippincott.

METHODS

Seasonally-standardized age/sex-specific body weight can serve as an index of nutritional status (Stringham 1990a,b). Stringham compared reproductive rate vs. body size among grizzly and black bear populations, demonstrating that reproduction tends to be highest where adults are largest. Here, using the same data on grizzly bears, new regression lines were derived for just 9 dispersed populations. Then data points for the 2 aggregated populations were tested for deviation from these regression lines. If Stokes' is right, maturation rate and natality should be lower relative to body weight at YNP and McNeil than in dispersed populations.

RESULTS

Natality (NAT: number of cubs per adult female per year) was estimated by dividing mean litter size by mean interbirth interval for each population. Age at first parturition is the reciprocal of maturation rate to adulthood (AFP = 1/MAT). (Stringham 1980, 1985, 1990a).

Contrary to Stokes (1970), absolute reproductive parameters were higher, not lower at YNP and McNeil (NAT: 0.63, MAT: 1/5.8 = 0.17) than in dispersed populations (NAT: 0.58, MAT: 1/6.8 = 0.15).

Each reproductive parameter had the same relationship to body weight for aggregated populations as for dispersed populations (Figs. 1 and 2). Regression equations for the dispersed populations are:

$$\log(NAT) = -1.66 + 0.66 \times \log(BW_F), \quad r^2 = 75\%, n = 8, P < 0.01$$
$$\log(MAT) = -2.46 + 0.78 \times \log(BW_F), \quad r^2 = 78\%, n = 9, P < 0.01$$
$$\log(AFP) = 2.46 - 0.78 \times \log(BW_F), \quad r^2 = 78\%, n = 9, P < 0.01$$

where BW_F = mean spring-fall body weight of adult females in a population: e.g., 152 kg at YNP and 159 kg at McNeil (Stringham 1990a). For each of the 3 regressions, standard error of the Y-intercept is 0.06; standard error of the slope is 0.16.

Predicted values for YNP and McNeil are, respectively, 0.62 and 0.64 for natality, 0.17 and 0.18 for maturation rate, 5.9 and 5.7 for age-at-first-parturition; corresponding means are 0.63, 0.17, and 5.8. These agree exactly with observed means for the two aggregated populations. The individual data points for the aggregated populations lie within the 95% confidence bounds for the dispersed-populations regression lines. Neither individually, nor in concert, do the data for aggregated populations differ significantly from those for dispersed populations.

DISCUSSION

Contrary to statements by Stokes (1970, pers. comm.), there is no evidence of reproductive suppression by social strife at YNP and McNeil Falls. Reproductive rates were consistent with body size and thus presumably with nutritional status.

If strife reduces reproduction at either site, it apparently operates by reducing nutritional status, for instance by excluding subordinates from the ecocenter, or motivating dams with young cubs to avoid the aggregation (Stringham 1985, Taylor et al. 1985). However, even Stokes impression of relatively low reproductive rates are contradicted by the larger sample of dispersed populations now available. Values for YNP and McNeil average higher, not lower, than those for dispersed populations.

These results refute Stokes' interpretation of data at YNP and McNeil, and thus most support for the general hypothesis that aggregation-induced strife impairs reproduction in bears. However, a definitive test of this hypothesis would require (a) data on more aggregated populations; (b) measures for degree of aggregation (e.g., how many bears were present per day over how many days, within how small an area?); (c) measures of food supply; and (d) measures of strife.

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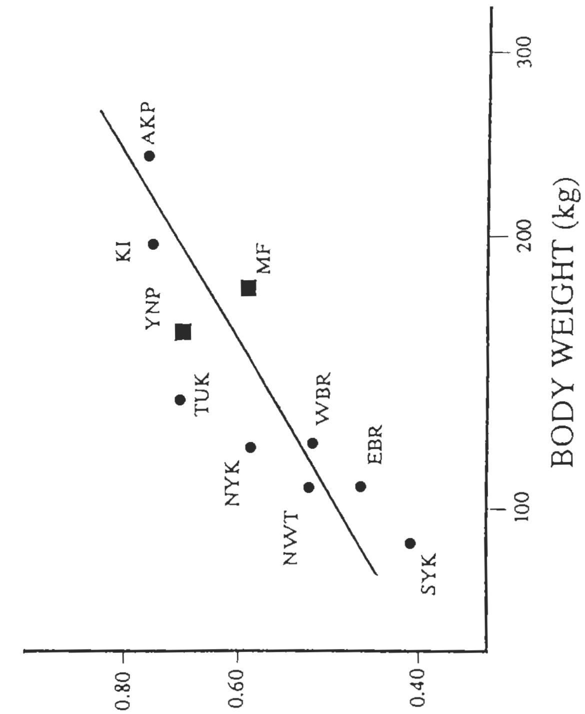

Fig. 1. *Natality (cubs per adult female per year) as a function of adult female body weight -- mean values for grizzly bear populations (data from Stringham 1990a). The regression line represents just the dispersed populations (o). Data points for 2 aggregated populations -- YNP and MF -- are marked with squares. (YNP = Yellowstone National Park, MF = McNeil Falls, AKP = Alaska Peninsula, EBR = Eastern Brooks Range, WBR = Western Brooks Range, KI = Kodiak Island, TUK = Tuktoyaktuk Peninsula, NYK = northern Yukon Territory, SYK = southern Yukon Territory, NWT = Northwest Territories).*

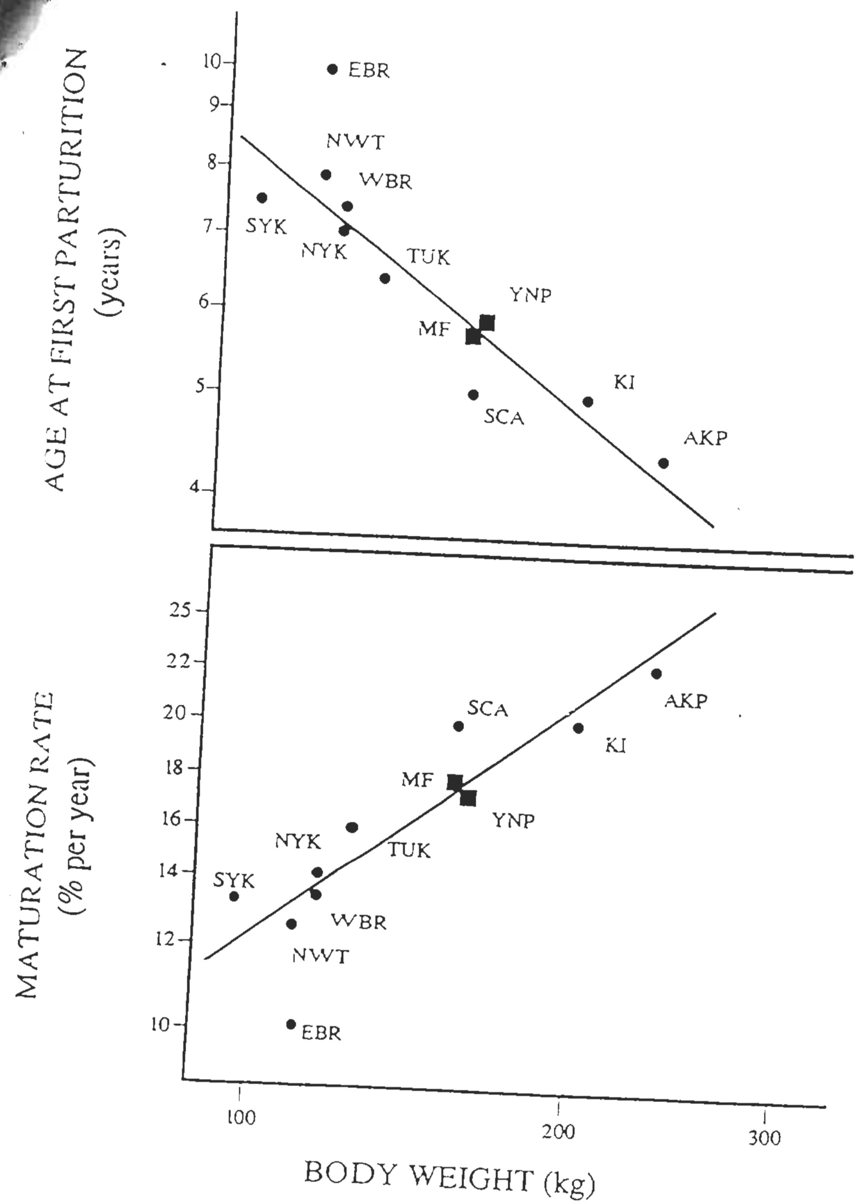

Fig. 2. *Age-at-first-parturition and maturation rate as functions of adult female body weight -- mean values for grizzly bear populations (data from Stringham 1990a). The regression lines represent just the dispersed populations (o). Maturation rate is the mathematical inverse of age-at-first-parturition (e.g., in South Central Alaska [SCA] it takes 5 years to reach maturity and give birth; maturation rate is 1/5 [20%] per year).*

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