URSID ONTOGENETIC RESPONSES TO VARIATIONS IN NUTRITION AND ADULT MALE ABUNDANCE

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Abstract: Even casual observation reveals wide variation in the rate of body growth and morphological development in bears. As a general rule, faster maturation accompanies faster growth – both of which are associated with better nutrition. However, much more needs to be learned about influences of nutrition and other factors. We need larger sample sizes even on familiar topics, as well as research on a greater diversity of topics. Among these is distinguishing relative impacts by nutrition vs. adult male abundance on variable survival among birth cohorts, and on underlying morpho-physiological ontogeny. For example, during which sensitive periods can nutritional deficit or adult male influences permanently alter the course of ontogeny and the ability of bears to survive from infancy at least to adulthood? We also need to know what development occurs during hibernation. These are questions which cannot be answered solely through field research. Studies on captives, for instance in zoos, is also essential.

DIFFERENTIAL SURVIVAL AMONG BIRTH COHORTS FROM INFANCY TO ADULTHOOD

From 1959-70, biologists John and Frank Craighead led a team studying grizzly bears in Yellowstone National Park. Each year, they counted bears of each age-sex class in the core of their study area (Craighead et al. 1974). Analysis of their data showed that the rate of each birth-cohort's survivorship from the first through sixth years postpartum was inversely related to adult biomass and directly related to food supply during the years of each cohort's gestation and infancy (Figure 1; Stringham 1983, 1985).

<u>Hypothesis 1</u>: Condition of a bear during its gestation and infancy (circumnatally) affects its likelihood of survival to adulthood.

<u>Hypothesis 2</u>: Condition of a bear during its gestation and infancy (circumnatally) was largely governed by maternal investment.

<u>Hypothesis 2a</u>: Mothers invest in cubs several ways, including nutrition – e.g., through nursing or sharing forage or prey. Maternal nutritional investment in cubs was governed by maternal nutritional balance, i.e., by her nutritional intake minus expenditures.

<u>Hypothesis 2a1</u>: Nutritional intake was governed by food supply per unit adult biomass, which was governed by total food supply divided by biomass of adults competing for it. (Adults have far more influence on competition than do other age-classes, and adult males usually have more influence than adult females, partly as a result of larger body size and physical domination).

<u>Hypothesis 2b</u>: Maternal investment in cubs was governed by another density-dependent factor such as local adult male abundance (which accounted for most variation in adult biomass). The more potentially infanticidal boars a sow encountered – ones with whom she did not mate -- and thus the greater the risk that her cubs would be killed, the less she invested in her litter nutritionally or in other ways. One physiological mechanism might have been analogous to the Bruce Effect, except that bears did not abort their cubs. (Stringham 1985).

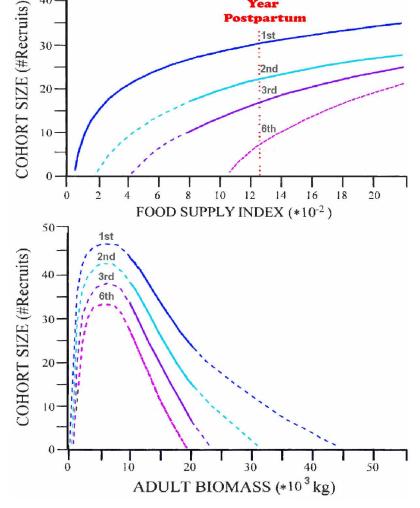


Figure 1. Cohort survival from infancy to the 6th year postpartum, relative to food supply and to adult biomass during the cohort's gestation and infancy. For a cohort produced during any given level of food supply or adult biomass, shrinkage of the cohort from year to year is seen by following a vertical line from one age class down to the next. Survivorship was inversely related to adult biomass and directly related to food supply during the years of each cohort's gestation and infancy.

Effects by nutrition and males should be tested with captives. Information needed includes:

- * Identify the degrees to which circumnatal nutritional deficit permanently impairs health, neural development and other traits affecting survivorship. During which periods is a cub most vulnerable to deficit and during which periods can a cub recover from deficit?
- * Test effects of a mother's nutritional status on her nutritional investment in cubs during gestation and infancy.
- * Test for impairment of mothers or cubs by exposure to adult males (peaceful interactions, antagonistic interactions, pheromones, etc.), both males with which a female has mated during the estrus when she was impregnated vs. those she has not.
- * Compare behavioral and morpho-physiological development among cohorts (even among individual cubs), including ontogeny of dentition, skull, and skeleton.

PHYSICAL ONTOGENY

Observations to be Explained or Questions to be Answered

- 1. Differential survival among cohorts.
- 2. Which morphological traits (e.g., dentition or morphology of the skull/head and skeleton/body) allow reliable assessment of a bear's age, maturity class or sex? Which require measurement of the bear itself vs. which can be determined from photos or by eye?
- **3.** Bears exhibit an unusually high degree of intra-specific diversity in morphology of the skull and perhaps skeleton. To what extent is this diversity due to phenotypic plasticity, perhaps related to diet?
- **4.** What morphological development occurs during hibernation?

Dentition

Several investigators have published sequences of tooth eruption in North American bears. But those several cases are far too few to reveal the range of individual variation, much less how variation is linked to factors such as nutritional status and age. By the 9th month postpartum, body weight of black or grizzly/brown bears may range from 5 kg to 50+ kg, depending on nourishment. How this affects rate of dental ontogeny is unknown. This knowledge could ease determining the age of infants by reference to dentition plus nutritional indices.

Skull Growth

First year cubs typically have a relatively short muzzle, which lengthens as the bear progresses towards puberty. Then, during adolescence and especially adulthood, the skull increases in relative width and depth – as is particularly marked with males. One result is that relative spacing between the ears (e.g., as measured in ear-width units) increases progressively (Figures 2 & 4), peaking in old boars.

Whereas these patterns of change are well known, I find no record where head size and body weight have both been documented frequently (e.g., at monthly intervals) for even a single bear, much less for many bears. Is most variation in developmental sequence governed endogenously or exogenously, perhaps by nutrition?



Figure 2. Variation in head shape with age: infant vs. yearling brownies. The ratio of ear size to head size increases during the first year, then declines into adulthood (excerpted from Stringham 2009).

Nearly a century ago, geographic variation in skull morphology led C.H. Merriam (1918) to describe what he considered to be over 80 species of grizzly/brown bears in North America. Although subsequent taxonomists concluded that these are but varieties of one genetic species, *Ursus arctos*, the variation documented by Merriam remains unexplained. Is the variation primarily genetic, or a result of phenotypic plasticity? Which variations in morphology are linked together vs. which change independently of one another? To the extent that skull morphology is plastic, what effect is exerted by the resistance of food to mastication? Does eating tough food (e.g., chewing plant roots or cracking ungulate limb bones) promote development of larger temporalis and masseter muscles? How is muscle size related to skull

width, depth and length; to the massiveness of skull bones; and to the amount of surface area for muscle origins and insertions on the mandible, cranium, occiput and other parts of the skull, including crests and flanges? What other influences might nutrition have on skull morphology?

To answer these questions, if and when a bear dies, measure dimensions of all bones, including those of the skull. Measure surface area for attachment of muscle origins and insertions on the mandible, cranium, and other parts of the skull, including crests and flanges. Relate this to size of the masseter and temporalis muscles. Relate those features to the bear's diet, particularly to how tough the food was to masticate (chewing, bone crushing, etc.). Also, measure brain size and, if possible, size of various lobes.



Figure 3. **Polar bear skull.** Note sagittal crest and flanges on the occiput and mandible, increasing surface area for muscle attachment.

What variation occurs in relative sizes of skull bones at each age from gestation and infancy through adolescence to adulthood? Which bones of the skull are growing fastest during each stage of development? In many mammals, relative growth rates of different skull bones change during ontogeny. If the normal growth spurt for a given bone coincides with a nutritional deficit, is growth of that bone permanently retarded relative to other bones whose growth spurt occurs during a period of nutritional abundance? Does variation in other stressors have similar effects? Reciprocally, do relative sizes of different bones in an adult bear reveal anything about nutritional status or other physiological conditions at any prior ages/stages? During which stages of life is growth of each bone plastic enough that previous retardation can be reversed?

In some mammals, brain size is directly related to nutritional status (Geist 1979). Is that also true for bears? Is the cranium of a scrawny bear disproportionately smaller than that of a robust bear? Which lobes of the brain are smaller? How does this relate to the age at which nutritional deficit occurs? Are the impacts of an impoverished diet greatest during gestation and infancy? What implications does such phenotypic plasticity have for intelligence and learning ability?

To the extent that skull and brain development are vulnerable to any given environmental stressor, must the stressor occur during the development of the individual or might it occur during a sensitive stage in the life of its parent or grandparent? Conversely, how do stresses, including nutritional deprivation or excess, on each generation affect the next few generations, for instance via epigenetic inheritance?

Research on wild bears may never be able to monitor nutrient intake and expenditures, body growth, and other variables, in enough detail to answer these questions. However, coordinated data collection across a host of captive facilities might. Ideally, weight and size measurements should be supplemented by periodic photos ("mug shots") so that people can learn to recognize main maturational stages by eye (Figure 4). Photos should be made from standard angles (e.g., front, rear and from each side) of each bear's head and body, at monthly intervals. Then, using photos, one should measure relative sizes of the ears, head, muzzle, neck, legs, hands, feet and torso.



Figure 4. **Maturational changes in head shape for grizzly/brown bears**. As a general rule, muzzle length tends to increase with age, especially for males. Note the extreme length of the muzzle of the old alpha male at lower left. His two profile views illustrate the difference before (left) vs. after (right) shedding his jaw-line ruff. (All age-sex classes approximately to scale, except for the alpha boar which is 33% scale.

Skeletal Growth

How do rates of bone growth vary seasonally and ontogenetically? When wild cubs enter hibernation, they are typically of stocky build. The following spring, many seem lanky – like adolescent boys during a growth spurt. Have the length ratios of limbs vs. other bones actually increased? Or is that merely an illusion resulting from catabolism of body fat during hibernation and perhaps to shedding of winter fur?

How does growth of the neck, shoulders and pelvis vary with maturity, age and sex? Is it universally true that adult males tend to have relatively longer necks, as well as broader shoulders and hips, than do other age-sex classes; how much longer and broader? Physical conformation should be photographed from standard angles throughout ontogeny.

Attempts to lump skeletal dimensions into compound factors via statistical analysis should be done in terms of the logarithm of each dimension, so that lengths, areas, and volumes or masses can all be compared and contrasted without distortion. Otherwise, lengths may tend to cluster with other lengths, areas with other areas (related to length squared), and volumes/masses with one another (related to length cubed), masking more heuristic relationships.

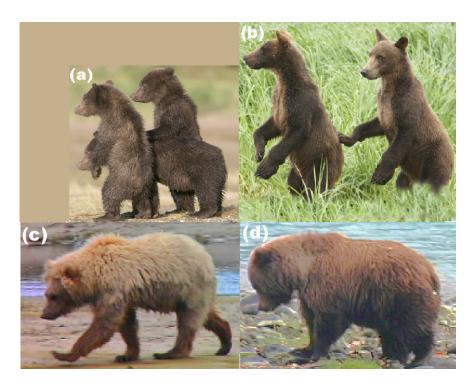


Figure 5. **Statures of infants vs. yearlings** are most obvious when both have short fur. (a) Infants before they have ever grown long fur. (b) Yearlings just after they have shed their infantile fur. (c) A typical yearling prior to shedding its infantile fur in June. (d) By October, a well-fed cub appears almost as well rounded as a beer keg due to fat deposits and heavy fur. (From Stringham 2009)

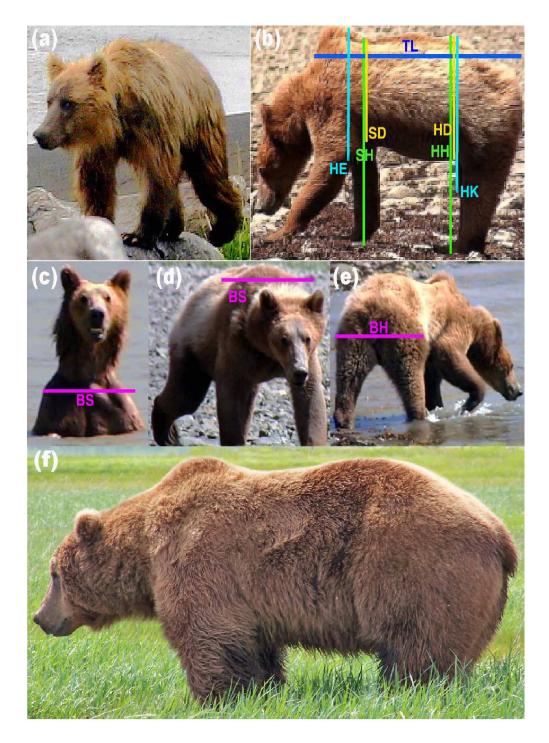
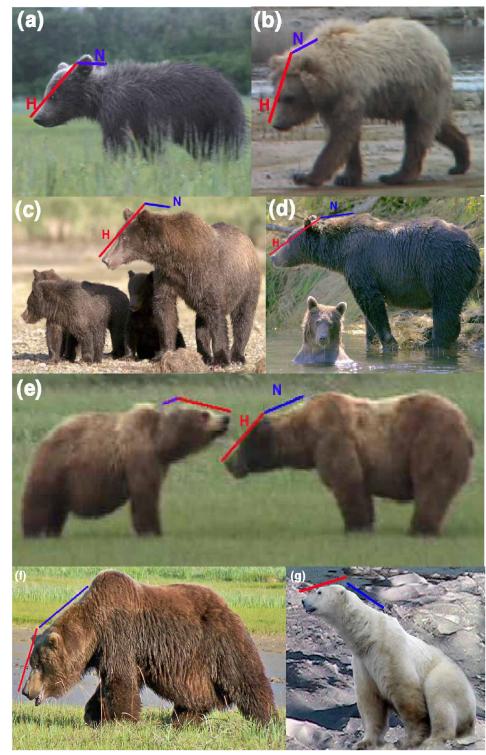


Figure 6. **Torso proportions**. Adolescent female and male. (a) Female at age 4 years, in July before she began putting on fat. (b-e) Male at age 3, during June, just after being abandoned by his mother, as she was being courted by two boars. Some of the most useful measures made without physical contact are [1] torso length (**TL** front of shoulders to back of hips, [2] torso depth and height just behind the shoulder (**SD** & **SH**) or in front of the hind legs (**HD** & **HH**). [3] If the bear's feet are not visible, then measure from the top of the back to the elbows (**HE**) or from hips to knees (**HK**). [4] Torso breadth at shoulders (**BS**) and hips (**BH**). (f) No measurements are needed to distinguish an adolescent from a prime boar like the one at left. However, measurements can be essential for more subtle discriminations. (From Stringham 2009)

Figure 7. Relative length of neck vs. head and body. In my study areas: As a brown bear matures, its neck (N) gets longer relative to its head (H). Head length is measured from the tip of the nose to the back of the skull. Neck length is measured from there to the front of the shoulder hump. Although mean ratios vary between regions and species, boars typically have the highest average N/H ratio. (a) Whipple as an infant (August) and (b) as a yearling (June). (c-d) A sow's neck usually quits growing around puberty, before it reaches 2/3rds her head length (i.e., N/H < 2/3). (b) A boar's neck, however, keeps growing. Male N/H is usually >2/3 by adolescence. (e) The sow at left has an unusually short neck (N/H < $\frac{1}{2}$), whereas the alpha boar has a ratio of N/H > 2/3, as well as massive muzzle, hips, and arms - all typical of an ultra prime boar. (f) "Gooseneck" is the only brown bear I've seen with N>H, (g) By contrast, among polar bear boars, N>H is common. Hopefully, captive studies can more fully document variations in N:H ontogeny.



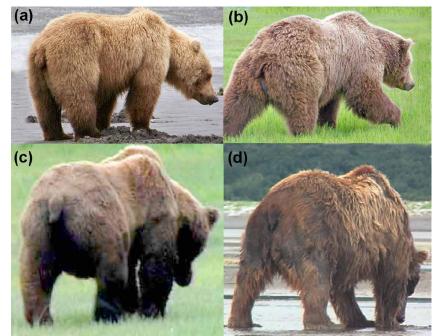


Figure 8. Rear view of adult brownies. (a) Adolescent sow. (b) Prime estrous sow. (c) Alpha boar who is aging and beginning to lose muscle mass, so that his pelvis and shoulder blades are prominent. (d) A lower ranking but physically prime boar, with heavy musculature. Note the exceptional pelvic breadth vs. height ratio in these prime boars. The ratio is smaller, not greater, for sows. (From Stringham 2009).

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