Attachment 1. Literature Cited

to accompany

David J. Mattson, Ph.D., Comments on the Draft Revised Plan (Publication No. R1-19-07) and associated Draft Environmental Impact Statement (Publication No. R1-19-08) for the Custer Gallatin National Forest

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Attachment 2. Primer on Nutritional Ecology of Bears

to accompany

David J. Mattson, Ph.D., Wyoming Wildlife Advocates, Comments on the US Fish & Wildlife Service proposal to remove grizzly bears in the Yellowstone ecosystem from the list of endangered and threatened wildlife protected under the US Endangered Species Act (ESA); Federal Register 81(48): 13174-13227; And Related Materials

Digestion

Bears are omnivores, which simply means that they eat a varied diet potentially comprised of either almost wholly meat or almost wholly vegetation. Yet they have the simple monogastric digestive tract of a carnivore lacking specialized chambers able to sustain anaerobic fermentation by symbiotic microbes. More to the point, they lack a rumen and a cecum, although there is evidence of some microbial fermentation in the bears' simple large intestine. As a result, they obtain little nutritional benefit from the fiber that they ingest. This fiber can comprise 10-30% of the foliage they graze or browse, which means, in turn, that their most digestible foods consist of those rich in either digestible protein or fat or containing high concentrations of simpler carbohydrates such as fructose, sucrose, or starch.

Comparative digestion in bears & herbivores

Figure 1 illustrates the general digestive plight—or strategy—of bears in contrast to fore- and hindgut fermenters (i.e, ruminants and non-ruminants), as well as in comparison to other carnivores. This graph illustrates the relative digestibility of several broad categories of foods by bears and other taxa (with percent digestibility shown as medians and interquartile ranges). For the purposes here, bears are parsed out in different ways, with giant pandas and grizzly bears differentiated for illustrating digestion of foliage and roots, and all bears lumped together as "ursids" for illustrating digestion of meat. These data come from multiple sources.

The basic patterns are pretty obvious. Bears are as well able as any other carnivore to digest most of the meat they eat--around 90% plus. By contrast, grizzly bears digest roughly 20% less of the foliage they consume compared to ruminants and 10% less when compared to non-ruminant herbivores. Starchy roots are digested by grizzly bears with about the same efficiency as foliage is digested by ruminants—which makes roots a comparatively beneficial vegetal food for bears, at least when reckoned simply in terms of digestibility.

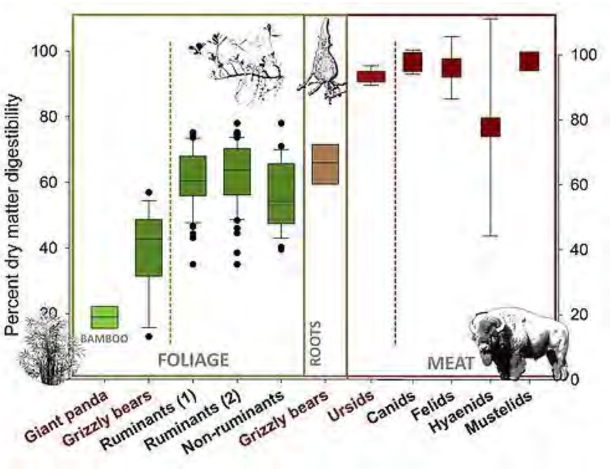

Figure 1. Percent dry matter digestibility of different types of foods by mammals of different higher-order taxa.

But the other key element of a digestive strategy is not just how well an animal can digest a given gram of ingested food, but also how many grams are being ingested in total. In other words, an animal can compensate to some extent for low digestibility by increasing the throughput of ingested food, which seems to be the strategy adopted by bears, especially giant pandas.

Figure 2 illustrates this pattern. Again, broad categories of animals are differentiated with non-ruminant herbivores separated by whether most fermentation of fiber occurs is the cecum versus the colon. Bears (i.e., ursids) are differentiated by whether they are ingesting foliage and fruit versus wholly meat. The top graph shows the rate at which these different types of animals ingest food, standardized to metabolism-corrected body mass, whereas the bottom graph shows the mean time that digesta is retained in the digestive tract (i.e., gut; the inverse of the rapidity of transit).

All of this suggests that, when possible, bears ingest vegetal material at a higher rate and retain it for a far shorter period of time compared to specialized herbivores, especially in contrast to foregut fermenters (i.e., ruminants). This would partly compensate for the lower efficiency with which bears digest most vegetal food. By contrast, bears ingest meat at a slow rate and retain it for roughly twice as long as they do their vegetal food. For the high digestibility of meat to be realized, bears probably need to retain it longer in the digestive tract, but still not as long as herbivores dependent on fermentation retain foliage or browse. Meat also probably passes through the gut more slowly simply because there is less accompanying fiber to hasten it along compared to when bears eat vegetation.

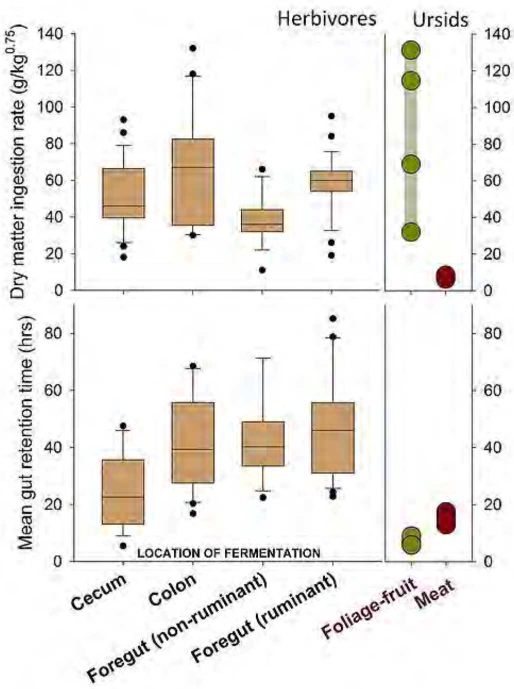

Figure 2. Ingestion rates and transit times for digesta by mammals with different digestive adaptations and by ursids eating meat versus vegetal foods.

The implications of these patterns for bears and bear foraging seem pretty obvious. Bears should prefer meat whenever they can get it, at least until sated, and up until a need to balance nutrient intake comes into play. Beyond that, roots (and berries) should be preferred vegetal foods, but only if the energy required for acquisition does not unfavorably alter the overall energetic equation--which, in the case of roots, is probably often the case because of the potentially considerable costs of excavation. Finally, bears should be able to profit from grazing only when they have access to large amounts of readily acquired and comparatively digestible foliage. And, as shown below, digestibilities of foliage can vary widely, not only among sites, but also among plant species and seasons.

Specific foods

In keeping with the broad patterns described above, the digestibilities of specific bear foods vary widely. Emblematic of this, Figure 3 shows the percent of energy contained in different foods that is digested by grizzly bears (the black, gray, and white dots). The varying shades of gray, from black to white, correspond to digestibilities during different seasons in instances where there is documented seasonal variability: black for spring, dark gray for estrus, light gray for early hyperphagia, and white for late hyperphagia. The reddish dots represent the percent of each food that is comprised of protein, again with seasonal variation denoted by varying shades: bright red for year-round or spring values; burgundy for mid-season; and white for late-season. All of these foods are specific to the Yellowstone ecosystem.

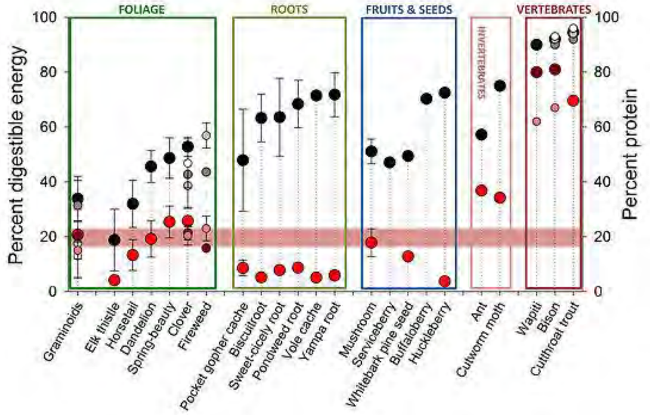

Figure 3. Percent digestible energy and percent protein for different grizzly bear foods common to the Yellowstone ecosystem.

Meat from any source is more digestible than other types of food. Roots, insects, and fruits and seeds are of comparable digestability, but with roots and fruits offering far less protein. Most of the digestable energy in these vegetal foods is contained in sugars and starches, with the proviso that much of the protein in ants, in particular, is bound up in chitin. Finally, the digestible energy in foliage varies widely, with forbs such as clover, fireweed, and dandelion offering the most, and elk thistle, horsetail, and grasses and sedges (i.e., graminoids) the least.

As a final note on Figure 3: The pinkish horizontal band corresponds to the optimal level of protein in bear diets; the point being that grizzlies would be hard-pressed to maintain an optimal level of protein intake if they subsisted solely on vegetal foods, especially roots, fruits, and seeds.

Protein & Energy Effects

Nutrition obviously entails more than just the digestibilities of different foods. The absolute and relative amounts of various macronutrients (e.g., proteins, lipids, and carbohydrates) are critical elements of nutrition, as are the absolute and relative amounts of digestible energy. Even though all of these additional nutrient-related aspects of nutrition are correlated with the digestion of various foods in the gut, there are additional consequences that play out through metabolic processes involved in the creation and use of body protein, fat, and glucose--i.e., protein biosynthesis and protealysis, lipogenesis and lipolysis, and gluconeogenesis and glycolysis. Moreover, the density of digestible energy in foods matters for reasons that transcend simple nutrient composition. Resting metabolism varies widely in close synchrony with nutrient-specific processes and related energy expenditure--with consequences for levels of heat production in the body (i.e., thermogenesis).

The net result of all of this is not only variation in the efficiencies of energy, protein, lipid, and glucose metabolisms, but also variation in the composition, efficiency, and total level of body mass accretion or loss. Different combinations of relative and absolute amounts of protein, fat, carbohydrates, and digestible energy in the diet can determine whether an animal gains or loses body mass, and whether that mass gain or loss is comprised of lean body mass or fat reserves.

With respect to bears, then, this amounts to a lot of complexity when it comes to understanding the ramifications of different diets.

Efficiencies, protein, & growth

Given that a bear eats a diet containing ample digestible energy (say 800 kcal per kg raised to the 0.75 power per day), it turns out that there can be both too little and too much protein when it comes to efficiencies of gain in body mass. The graphs in figure 4 are relevant to this point, adapted from those in a paper on which Joy Erlenbach was lead author—a paper in which she synthesized a lot of research specific to bear nutrition. Each figure features a bunch of dots of two different colors corresponding to the metabolic and accretional consequences for bears fed diets comprised of different macronutrients, including diets rich in protein or carbohydrates (salmon colored) as well as diets rich in protein or fat (burgundy).

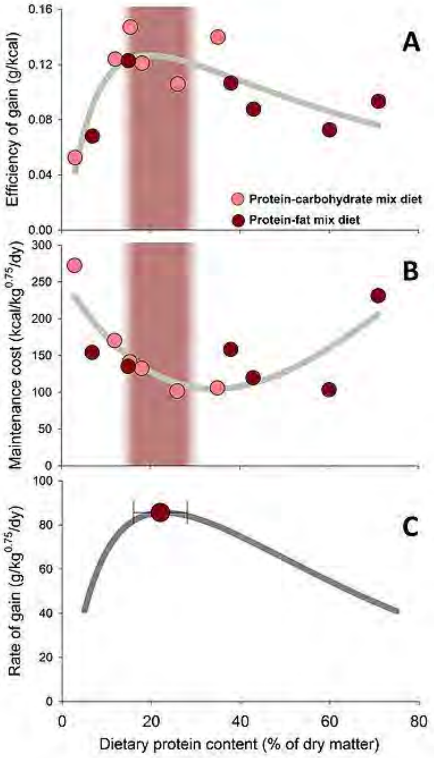

Figure 4. Effects of dietary protein content on (A) efficiency of mass gain, (B) energetic maintenance costs, and (C) rate of mass gain by grizzly bears fed diets of different protein content.

The main points? The top figure (A) shows that the efficiency of weight gain rises rapidly to a peak as diet protein increases from roughly 1% to 15% and then gradually declines, all of this with the density of diet energy remaining roughly the same. Correspondingly, the middle figure (B) illustrates a decline in resting metabolism (i.e., energetic costs of maintaining the body) as diet protein increases from 1% to roughly 30%, after which maintenance costs increase. When you put these two trends together you get the bottom figure (C) which shows the predicted total rate of gain per kg of body mass, standardized to the expected basal metabolic rate for carnivores (i.e., raised to the 0.75 power); a rapid rise as diet protein increases, followed by a steady decline.

It turns out that the predicted level of diet protein at which rates of gain in body mass peaks (roughly 21%) corresponds almost exactly with the mean diet protein content of diets selected by bears when given a free choice of what to eat (22% plus or minus 6%)--shown by the large burgundy dot and horizontal error bars in figure 4C.

From this a person could conclude that the optimal protein content of a bear's aggregate diet is around 22%, at least as far as growth of body mass is concerned--and without considering whether that growth is primarily in terms of lean body mass or fat; but with some important provisos. This rule of thumb for diet protein holds for a given energy concentration in the diet (in this case, around 800 kcal/kg 0.75/day) and for bears of intermediate body size. But bear size does affect nutrition in several ways, as does energy concentration of the diet (see below).

This all begs the question of why a diet protein content of around 20% yields greater growth rates than, say, 60%--all of this, of course, standardized to a given volumetric intake and to the metabolic rate expected at a given body mass. As a start, all else equal, elevated diet protein causes greater heat production in the body compared to elevated carbohydrates or fats. This thermic effect is called diet-induced thermogenesis (DIT). Much of this elevation in metabolic rate (as shown in figure 4B, above) is attributable to the thermic properties of protein synthesis, including increased heat production and reduced energetic efficiency. Depending on total diet composition, some of the increased heat production associated with a high-protein-content diet can be attributable to heightened formation of glucose (gluconeogenesis) above and beyond what would occur with a high-carb diet.

What about the effects of too little protein? Generally speaking, if a bear's diet is deficient in protein, it compensates by increasing the volume of intake, usually of foods rich in carbodydrates (think berries and roots; see Digestion). But the results above pertain to an isocaloric intake, that is, a constant or equal intake of calories. So the results explicitly pertain to differences in diet composition, not amount of energy intake. As figure 4B above shows, the metabolic rate of bears fed a low-protein diet increases substantially, which, because of the resulting increased energy expenditure, leads to decreased absolute and relative rates of gain in body mass. Why? Ultimately, because an increased proportionate consumption of fats or carbohydrates when bears are fed a diet low in protein leads to a chain of energy consumptive phenomena. The sympathetic nervous system is stimulated, which increases production of the hormone norepinephrine, which stimulates brown adipose tissue metabolism, which results in an elevated metabolic rate; in the end, more energy expenditure and less weight gain.

Intake, protein, and growth

At this point it is worth looking at what happens (unlike above) when the amount of dry matter ingested and digested by bears varies, adding to this variation in diet protein content. And, of course, the complement to variation in diet protein is complementary variation in diet fat or carbohydrates.

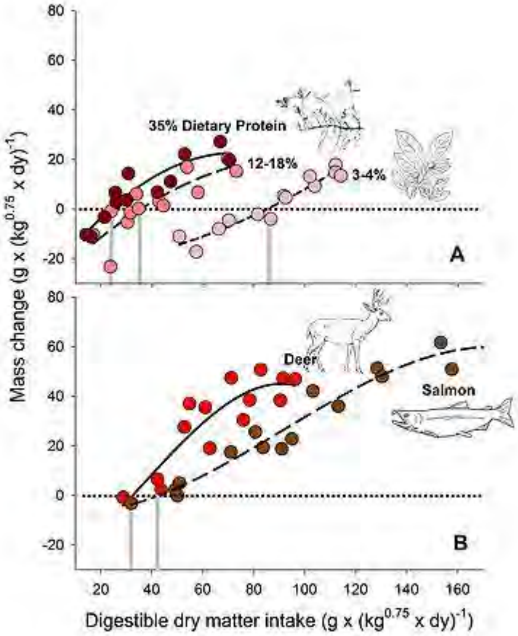

Figure 5. Change in mass of bears feed diets of different protein content as a function of total digestible dry matter intake.

The graphs in figure 5 summarize the results of several studies done in Charlie Robbins' lab, unified by a design that allowed bears to eat different amounts of digestable dry matter (the horizontal or x axis) while measuring responses in terms of change in body mass--i.e., growth (the vertical or y axis). All of this is standardized to the metabolism-corrected mass of the involved bear and considers diets with different amounts of protein, ranging from berries (3-4%) to deer and salmon (nearer 70% or more). In addition to the data points and curves describing the response in mass gain to variation in dry matter intake I've also benchmarked where each curve transitions from mass loss to mass gain (the vertical gray line).

The basic patterns are pretty obvious. In all instances weight gain tends to plateau (i.e., tends towards an asymptote) as intake increases. At some point, increased intake does not yield increased mass gain; the bears reach the limits imposed by internal metabolic processes. But this plateau is considerably higher (45-60 g per kg raised to 0.75 per day) for meat diets (B) compared to vegetal diets (nearer 20 g; A). Even so, the transition from weight loss to weight gain is similar (around 20-40 standardized ingested grams) for meat diets and vegetal diets having at least 12-18% protein content, the latter of which is within the lower range of optimal (see above). The biggest deviant is the low-protein-content diet comprised of berries. Weight gain only occurs when the standardized volumetric intake is high--in excess of 80 g, which is roughly 2-4 times higher than for other diets.

The implications? Even given the standardized metabolic inefficiencies associated with a protein-rich diet shown in figure 4, bears can grow much more rapidly on such a diet, especially if they have access to large volumes. The most notable example of this circumstance would be along salmon spawning streams during the height of spawning runs, which is why we see very large coastal brown bears. By contrast, bears with access primarily to berries have to eat relatively large volumes to gain mass and, even so, the potential for growth is relatively limited. This holds for bears in the interior regions of British Columbia, northeast Washington, northern Idaho, and northwest Montana. One important proviso to all of this is that there is no distinction made regarding the tissues in which weight gain occurs, principally whether in fat or lean body mass, which introduces the next topic.

Intake, protein, energy, & composition of growth

So a key question is whether the location of accreted (or lost) of body mass is as fat or lean tissue. Of relevance to this question, the graphs in figure 6 show differences in allocation of gain (or loss) for diets of two different protein contents: a berry diet comprised of 1.6-3.5% protein in A, and a mixed diet comprised of 15.4% protein in B. The red dots and associated trend line show changes in lean body mass (LBM) for each diet; the orange dots and associated trend line, changes in body fat.

All of the gain in body mass at a very low diet protein is as fat (A), whereas the majority of gain at moderate diet protein is in lean body mass (B). Moreover, bears eating a very-low-protein diet consistently lose lean body mass, which is an untenable situation. An important note: These patterns are as much a reflection of the fact that a vegetal diet low in protein (as in A) is necessarily rich in carbohydrates, whether glucose, sucrose, or starch (see Digestion). So the patterns in these figures reflect not only protein metabolism but also metabolic processes associated with varying concentrations of digestible carbohydrates, especially related to lipogenesis and protein biosynthesis.

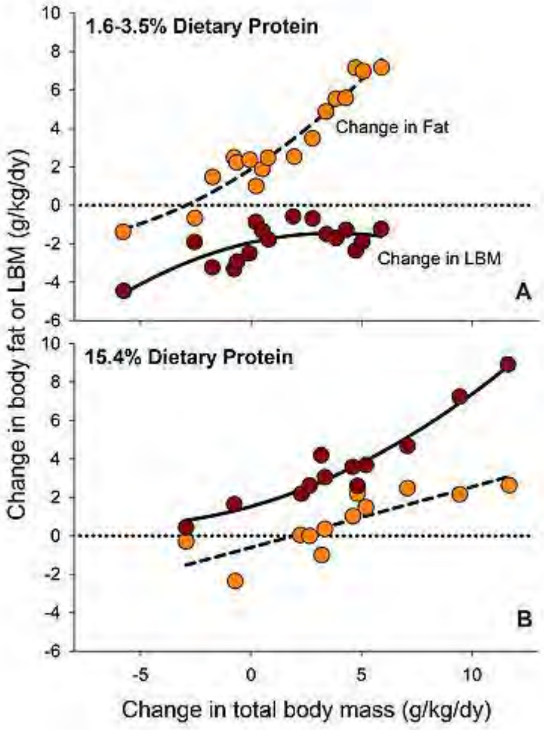

Figure 6. Change in lean body mass and body fat of bears fed diets of different protein content.

The implication? If a bear, eat a diet rich in carbohydrates and get fat while potentially losing lean body mass. Admix some amount of protein in the diet and you will maintain if not gain lean body mass. So a carbohydrate-rich diet with enough protein to maintain LBM makes more sense for a female needing to put on fat to reproduce; protein more sense for a male needing to grow physically large, which fits patterns of dimorphism among bears.

So now bring *diet energy* , as such, into the picture, and slightly recast the dynamics of total intake per day, at least for protein. Figure 7 shows the relation between standardized accretion of body fat and standardized ingestion of energy--regardless of the contributing macronutrient. And this for various diets comprised of very low (1.6-3.5%, the pink dots) and closer to optimum (15.4%, the red dots) concentrations of protein. In short, as intake of energy increases, so does accumulation of body fat. But more importantly, bears tend to gain more body fat (as above) on diets low in protein content, which is tantamount to saying on diets rich in either carbohydrates or fats. In fact, high-fat diets contain the highest concentrations of digestible energy, which translates into high rates of body fat gain.

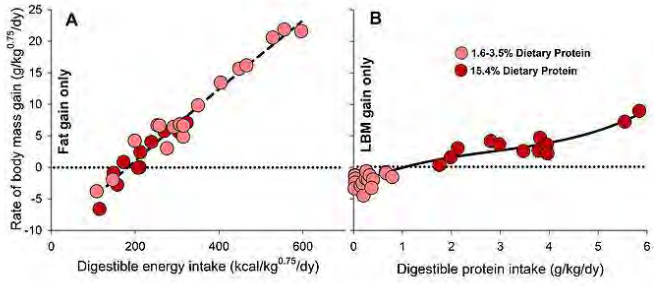

Figure 7. Rate of body mass gain standardized to metabolic rate as a function of total digestible energy and digestible protein intake for diets of two different protein compositions.

Figure 7B complements figure 7A by showing rates of lean body mass gain related to the total intake of digestible protein--with both values standardized. Not surprisingly, the more protein that a bear ingests and digests, the more lean body mass it accretes, with highest rates of both associated with diets containing a higher concentration of protein. And, as in the figure 6, protein intake on diets very low in protein content (1.6-3.5%, e.g., berries) does not allow even for maintenance of LBM. By contrast, the rate of LBM gain is remarkably high (8-9 grams per kg of body mass raised to the 0.75 power) at the highest rates of protein intake (around 6 grams per kg of body mass); in other words, in excess of a 1:1 translation.

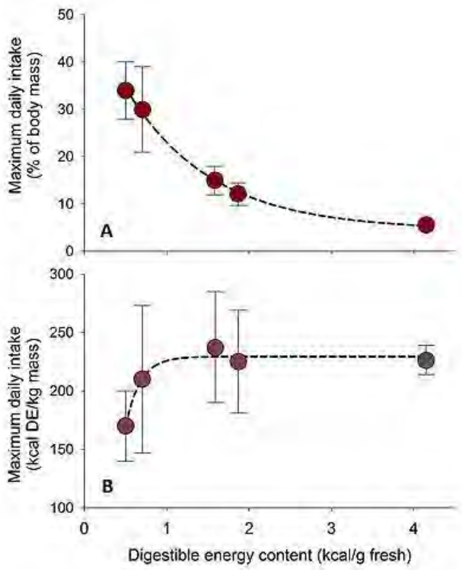

Figure 8.Maximum daily intake of digestible energy as a function of dietary digestible energy concentration.

Figure 8 illustrates an interesting phenomenon. Even when bears eat a diet increasingly rich in calories, overall intake of energy, standardized to body mass, doesn't correspondingly increase, especially once a threshold of 1 kcal of digestible energy per gram of fresh food is reached. This is most clearly illustrated in figure 8B; figure 8A shows the same trend standardized to body mass as percent of total mass.

Just to be clear, larger bears can and do ingest more absolute amounts of digestible energy during a given day, even as the digestible energy in the food they eat increases from 1 to 2 and even 4 kcal per gram. The point is that the energy *per kg of mass* doesn't increase and, as a percentage of total mass, even decreases, which pertains to efficiencies as much as anything.

To put this another way, a diet richer per gram in digestible energy--as would be the case with a diet rich in fat or protein--doesn't necessarily translate into a lot more digested energy for any kg of mass that a bear might be carting around. Related back to digestion, this pattern fits the much lower rates of transit and accompanying higher rates of digestion for ingested food for bears fed a diet of meat.

I conclude this section on the effects of nutrients, per se, with a few points that are either not adequately encompassed by the data presented above or that simply need additional clarification, and then end by quoting an elegant synopsis of nutritional fundamentals for bears that was included by Joy Erlenbach in her 2014 paper.

First, diets comprised solely of fruit are a potential problem for bears, especially if the involved bear is large in size. The low protein content and high glucose or fructose content of fruit diets require bears to eat exceptionally large volumes just to maintain LBM, but with resulting high rates of energy intake. This energy either needs to be dissipated as heat (diet-induced thermogenesis) or converted to body fat through lipogenesis, which is notably elevated on diets rich in fructose--one of the main sugars in blue- and blackberries. Large bears are notably much less efficient than small bears at harvesting any given concentration of fruit, which means that mass standardized consumption of fruit is maximized for large bears at rates far less than what they need to meet protein and even energy requirements. Hence, fruit-eating is more often a strategy of smaller bears or bear species (e.g., juveniles, females, and black bears) than it is of those that are larger (e.g., adult males and grizzly bears; for more on the implications of size see Foraging efficiency and Body mass effects below).

Second, bears prefer fat-rich foods and diets. In instances where captive bears had free access to diets of different composition they ended up eating diets from which they obtained roughly 68% of metabolisable energy from fats. Fats provide the highest concentrations of digestible energy of all macronutrients and are, in turn, the most efficiently converted of any to body fat. And ample body fat, to the point of obesity, is a center-piece of the bear life strategy. Moreover, unlike diets rich in protein or carbohydrates, diets rich in fat do not trigger auto-regulatory reductions in intake, which also contributes to high rates of body fat accumulation on high-fat diets. Or, put another way, diets comprised mostly of protein or carbohydrates are not optimal for most bears.

Third, related to the points immediately above, bears are energy maximizers. In fact, as noted by Joy Erlenbach, bears exhibit some of the highest levels of standardized energy intake observed for any mammal. When offered unlimited access to food these rates can be twice what some early researchers such as James Kirkwood considered to be the maximum rate likely or possible, and up to 18 times greater than the expected basal metabolic rate for carnivores, which is a lot of energy.

In conclusion, quoting Joy Erlenbach, bears live by three "rules" when it comes to intake of energy and nutrients:

(1) Maximize energy intake while optimizing dietary protein intake.
(2) Select lipids over digestible carbohydrates, which reduces dietary protein while maximizing food energy density.
(3) If lipids are not available, use digestible carbohydrates to optimize diet protein.

Body Mass Effects

The relationship shown in figure 9 is an interesting and compelling introduction to the effects of body mass on foraging efficiencies and weight gain of bears. Each dot represents the results of a controlled experiment involving one bear allowed free access to different kinds of foods. All of these data, again, are thanks to research by Dr. Charles Robbins and his graduate students at Washington State University.

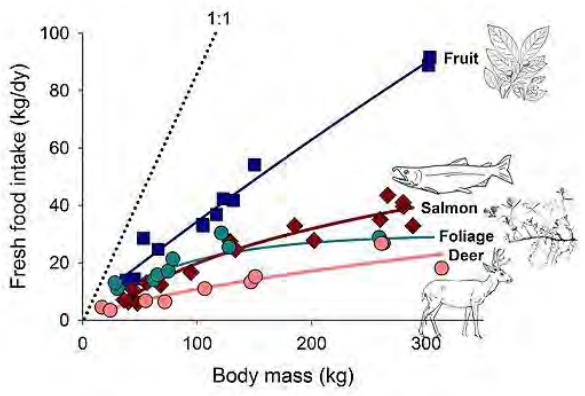

Figure 9. Total ad libitum fresh food intake as a function of mass of the involved bear.

At one level, figure 9 shows something that might be considered self-evident: larger bears tend to ingest greater volumes when given unlimited access to food. But, then, they would need to given their greater energetic needs, even accounting for the lower rate at which metabolic needs increase relative to each increment of body mass (at roughly the 0.75 power). Energy consumption, even at rest, increases nonetheless.

But the interesting thing is that the rate at which intake increases varies substantially among foods, but especially for berries in contrast to everything else. You might expect intake of protein-rich foods such as deer or salmon to increase at a lesser rate as body mass increases. Each gram of such a food delivers a substantial amount of digested energy entailing a comparatively slow rate of passage through the gut, with gut length and passage rate scaling at less than a 1:1 rate with body size (see Digestion). And intake of deer is probably less than intake of salmon at any given body mass because of the comparatively greater effort required to process a gram of tissue from a deer compared to a more easily ingested and chewed gram of fish.

It would be reasonable to expect that intake of foliage would increase at roughly the same rate as intake of berries given that both of these are vegetal foods. So, why is the intake of foliage so depressed compared to berries for large bears? For the answer, see the section below on Foraging Efficiencies. But, in short, when bears graze, ingestion is partly limited by the time it takes to chew a mouthful of fibrous foliage, which means that bite rate drops as a function of bite size; which means that bears need large standing volumes of tall-statured foliage to increase total ingested volumes in defiance of the limits imposed by chewing time--which rarely happens.

Insofar as berries are concerned, figure 9 only pertains to bears offered unlimited access to food. Which begs the question of why such large volumes are ingested as body mass increases? Unlike with foliage, processing time for berries, once ingested, is not of great consequence. Moreover, bears are highly motivated to ingest large volumes of protein-deficient berries (see Digestion) in an effort to meet their protein requirements, but with a resulting glut of digested energy which is either expended as heat or stored as body fat (see the section above on Protein and Energy Effects).

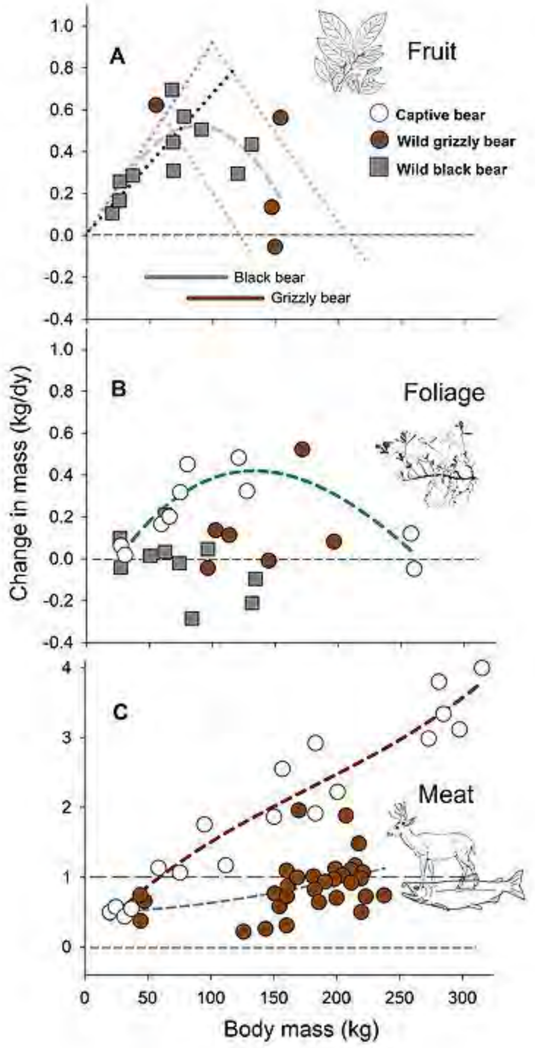

Figure 10. Daily change in body mass as a function of beginning body mass of the involved bear for (A) fruit. (B) foliage, and (C) meat, differentiating salmon (open dots) from deer (solid brown dots).

But where things get really interesting is when you look at per day rates of gain in body mass as a function of bear size--especially under circumstances where the involved bears did or did not have access to unlimited amounts of different kinds of food.

The graphs in figure 10 summarize this relationship for a number of individual bears that ate fruit (A), grazed foliage (B), and consumed meat from either deer or salmon (C). The open circles denote the results for captive bears; the brown dots, results for grizzly bears in the wild; and the gray squares, for black bears in the wild. Importantly, the captive bears had access to unlimited amounts of the various foods, whereas the wild bears typically did not.

Going over these graphs in reverse order, from bottom to top starting with meat: notice that, unlike with foliage and fruit, the trend lines for captive (dotted) and wild (solid) bears increase without reaching a plateau or peak, which means that bears are able to grow increasingly large even as their body mass increases. When fed unlimited amounts of meat, these gains can be phenomenal--upwards of 4 kg per day for a 300 kg bear. Moreover, no bear lost body mass eating a diet comprised mostly of meat. And, it is worth emphasizing that these gains were mostly as lean body mass, and despite the depressed per kg energetic efficiencies of a high protein diet (see Protein and energy effects).

With foliage, it is perhaps not surprising that a number of wild bears seemed to lose body mass when subsisting almost wholly on such a food. Foliage is not very nutritious or digestible (see Digestion). No wild bear but one gained much weight. But, the important trend is the one documented for captive bears with access to unlimited amounts of foliage (the dashed line). These captives were able to gain weight up until around 125 kg of body mass, after which gains declined, even into negative territory around 250 kg. In other words, the modest increases in ingested volumes of foliage that occurred at large body masses (see above) could not offset the increased energetic needs of a large bear, even given a less than 1:1 scaling of unit volume metabolic rate with body mass.

Something very similar was evident for wild bears subsisting on berries. Gains increased, peaking for bears of around 100 kg mass, and thereafter declined, even into negative territory for one c. 150 kg grizzly. To explain this pattern requires additional explanation of figure 10A. The ascending dotted red and blue lines denote the theoretical maximum rates of gain for bears eating unlimited quantities of serviceberries and huckleberries;

that is, for captive bears. But this theoretical maximum is obviously not achieved, primarily because of the limits imposed by foraging inefficiencies under field conditions; for example bite sizes and bite rates. These limits are described by the descending gray lines--the farthest left associated with a bite size of 1.7 berries and a bite rate of 55 per minute, the farthest right with a bite size of 2.5 berries and a rate of 90 per minute. The point being that foraging efficiencies take a major toll on what bears can realize from eating berries, with major implications for even modest-sized bears. Notably, though, at peak, daily gains for wild bears eating berries were over three times greater than gains for wild bears eating foliage: roughly 0.5 versus 0.15 kg per day.

There are some important implications of all this: Most important, if you are a bear weighing much in excess of 100 kg, weight gains are going to be greatest on a meat diet, not a berry or foliage diet. And much of these gains will be in lean body mass (see Protein and energy effects). So, given the consistently greater size of adult males compared to other bears--typically in excess of 150 kg--you would expect adult males to eat disproportionate amounts of meat, which is indeed the case. And, adopting such a strategy, you would expect males to grow ever larger over time, which seems to be the case as well. But all of this is with an important proviso: If you are female weighing somewhere between 100-150 kg, rates of body fat accumulation will probably be greatest on an energy-rich but protein-poor berry diet, as long as you can eat large volumes, closer to 2.5 berries per bite, at 90 bites per minute.

One important additional proviso: None of the graphs above deal with foods rich in fat, but containing adequate protein. More concretely, we don't have a clear picture of the nutritional benefits entailed for bears eating army cutworm moths and whitebark pine seeds: two of the most important bear foods in the Yellowstone ecosystem. Even so, it is not too hard to imagine that these foods are among the best bear foods of all.

Diet Meat Effects

Meat is handy shorthand for denoting a food comprised mostly of protein and fat. As I describe in the section devoted to digestion, protein and fat are the most digestible of all nutrients and, because of that, the essential ingredients of an energy-rich diet. Put a slightly different way, meat is the most concentrated form of protein and fat commonly eaten by bears. Given that we can only rarely directly measure the nutrient composition of bear diets, it is useful at times to use the fraction of meat (or berries, for that matter, to denote little protein) as a proxy and, from that, get a general sense of how a protein- and energy-dense diet affects outcomes such as body size and female reproduction, which is what I address below.

It is worth noting that not all meat is equal. Fractions of water, protein, and fat vary with the season and from prey animal to prey animal. Emblematic of this variability, I've created a summary in figure 11 of variation in the mass of edibles, including body fat and metabolisable energy, for a representative source of meat: female mule deer.

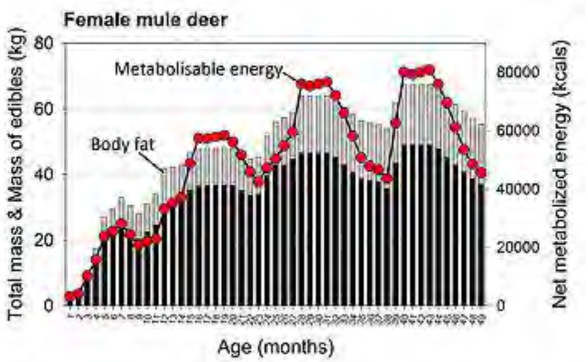

Figure 11. Total mass, amount of fat, and total metabolisable energy of female deer carcasses as a function of deer age.

The amount of edibles increases (obviously) with animal age, up to around age 4 in the case of mule deer; the fraction of body fat varies with the season; and, with all of this, the amount of metabolisable energy available to a carnivore such as bears varies substantially seasonally and with age of the prey animal.

The graphs in figures 12 and 13 show data that I assembled from North American study areas reporting both the body mass of grizzly bears captured for research purposes as well as information sufficient to determine the percent of the bear diet that was comprised of meat. On the meat front, Garth Mowat was the primary source, based on either direct measures or estimates derived from interpolation of one form or another. I differentiate adult males from adult females, and areas where bears had access to abundant spawning salmon from those where the primary source of meat was land-dwelling herbivores. I also denote the Yellowstone area with a white-centered dot.

Figure 12 shows trends towards larger size among populations of grizzlies that consume more meat, but more so for males than for females. The trend among females that eat terrestrial meat is barely discernable, and that of salmon-eating bears is substantially greater than the trend among populations of grizzlies that eat terrestrial herbivores.

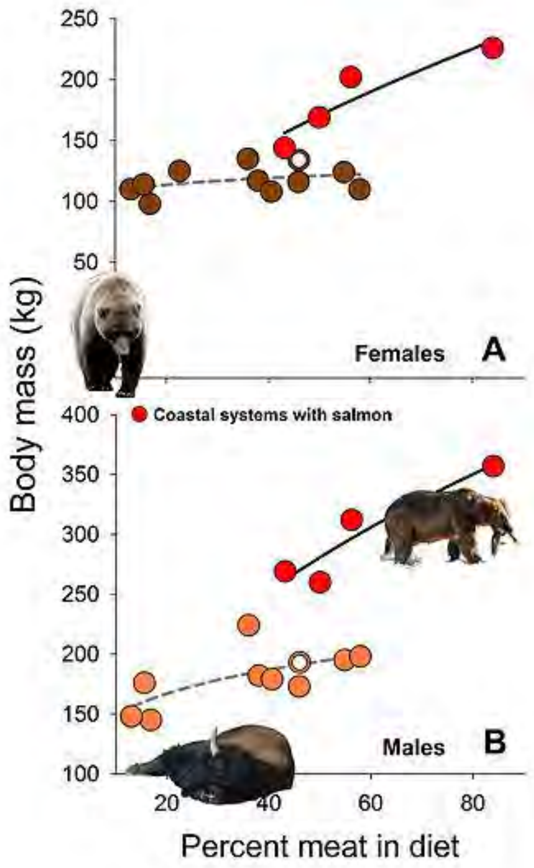

Figure 12. Population-averaged body mass of female (A) and male (B) grizzly bears as a function of population-averaged meat in the diet.

Figure 13 shows an increase in the ratio of male body mass to female body mass as the percentage of meat in the collective bear diet increases. In other words, size dimorphism of the sexes is greater where bears eat more meat, especially terrestrial meat (the burgundy dots). This is just a different way of representing the lesser response of females versus males to increasing amounts of dietary meat, noting, again, that the trend is greater among interior versus coastal salmon-eating populations. The dampened trend for all populations, including coastal ones, is shown by the solid line whereas the trend for interior populations alone is shown by the dashed line.

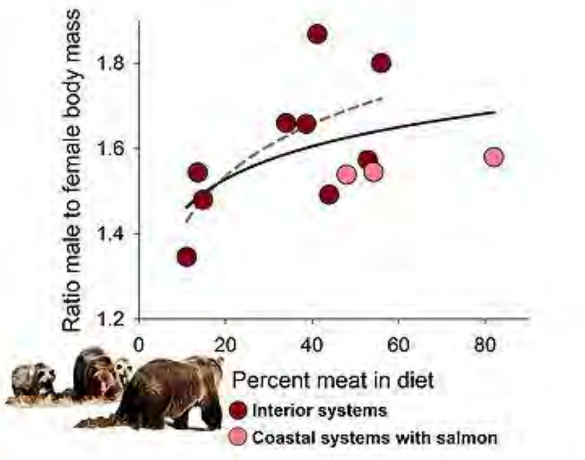

Figure 13. Ratio of population-averaged male and female body mass as a function of population-average meat in the diet.

The different responses of males versus females and of coastal versus interior populations to increased dietary meat beg for explanation. I can only speculate, but I suspect that differences between the sexes have to do with differences in diet within any given population, as well as differences in sex-linked physiological responses to dietary protein--all driven, in turn, by differences in the reproductive strategies of male versus female grizzlies.

More specifically, although responses of the two sexes to dietary protein have not been explicitly studied (or at least reported) for bears, we do know a fair amount about this phenomenon in two other omnivores: swine and humans. In both *Sus scrofa* and *Homo sapiens*, males and females fed the same amount of protein differ in the efficiency with which they accumulate lean body mass. Not surprisingly, males are more efficient than females. So if such were true for bears as well, this phenomenon could plausibly contribute to the greater population-level response of male versus female grizzly bears to elevated dietary meat.

Moreover, study after study has shown that, on average, male grizzlies eat more meat compared to female grizzlies in any given population. This could partly be a result of motivation and resulting dietary preferences. It could also partly be the consequence of on-average larger males being better able to dominate a concentrated food source, as is typical of packages of meat. So, differences in diet between males and females could also explain some differences in population-averaged body size between the sexes.

But what about the differences between coastal and interior ecosystems; between areas with spawning salmon compared to areas without? As I describe in the section devoted to the effects of diet protein, bears fed as much salmon as they can eat can grow to a much larger size (albeit at a slower rate) compared to bears fed deer. As the research in that section also shows, a diet exceedingly rich in protein (as would be the case with salmon) actually leads to less efficient accretion of body mass. But this lesser efficiency (as perhaps manifest in the lesser rate of gain among salmon-fed bears) can be more than offset by access to large volumes of food, as would certainly be the case--and for sustained periods of time--in most of the Pacific coastal areas with multiple runs of spawning salmon. So, the point here is that the greater response of population-averaged body mass to increasing dietary meat among grizzlies with access to salmon may simply be a consequence of these bears having access to a veritable glut of energy-rich food perhaps more than it has anything to do with protein content of salmon, as such.

Foraging Efficiency

The rate at which a bear of a given size can ingest, masticate, and swallow food is a critical aspect of nutrition. It sets the stage for how much can be passed through the gut, which is particularly important when it comes to vegetal foods. Bears depend upon passing large volumes of foliage through their digestive tract if they are to stay ahead energetically when eating such a fibrous food (see Digestion). And, when it comes to berries and roots, they likewise need to ingest large volumes to compensate for the very low protein content of these foods--but with the derivative benefit of ingesting relatively high concentrations of digestible energy (see Protein & energy effects).

Given this imperative to ingest large volumes when bears eat vegetal foods, it is with such foods that the consequences of fine-scale variation in foraging efficiency are starkest--at the scale of bite size and bite rate, which is why researchers such as Charlie Robbins and Lisa Shipley have focused on berries and foliage in their investigations of foraging efficiency by bears. And it is their research that I feature here, most of which was executed under Dr. Robbin's tutelage by Christy Welch and Karen Rode.

Effects of forage density & stature

Figure 14 shows the effects of berry density on the size and rate of bites by bears. Bite rate and size are perhaps self-evidently the two immediate determinants of the total rate at which food is ingested, at least as far as the mouth cavity. After that, the rate and efficiency of mastication take over; e.g., chewing.

The two graphs in figure 14 feature two berry-producing species that are of widespread importance to bears: serviceberry (*Amelanchier alnifolia*; salmon-colored dots) and huckleberry (*Vaccinium membranaceum*; blue dots). There are substantial differences between these two species in how berries are presented to a potential forager. Serviceberries grow in attenuated terminal bunches which allow large-mouthed foragers such as bears to harvest multiple berries in a single bite. By contrast, huckleberries tend to grow singly and dispersed, which means that bears need to employ a strategy of taking numerous small bites that are often contaminated with the accompanying detritus of leaves.

These morphologic differences are clearly evident in the relations of bite rate (A) and bite size (B) to variations in berry density for each species, where each dot represents one feeding trial involving a single bear. Put succinctly, bite size, but not bit rate, increases substantially as densities of serviceberries increase. The opposite is true for huckleberry. Bite rate, but not bite size, increases with density. More to the point, different strategies are imposed on bears by physical configurations of the berries they eat. As a result, morphologic features are as important as digestible energy in determining the overall energetic benefits of exploiting different patches of berries.

The same is true for grazed foliage. Figure 15 shows how bite sizes of clover vary with both the size of the involved bear and, more to the point here, with stature of the grazed plant--this under circumstances where the clover is uniformly dense. Basically, the relatively small sizes of bites taken by small bears are essentially unaffected by the stature of the grazed plant. By contrast, even though large bears are constrained to bites no larger than those of small bears when grazing plants <9-13 cm (3.5-5") tall, they reap huge comparative benefits (at least in terms of bite size) if they can find patches of herbaceous plants that average >15 cm (6") tall.

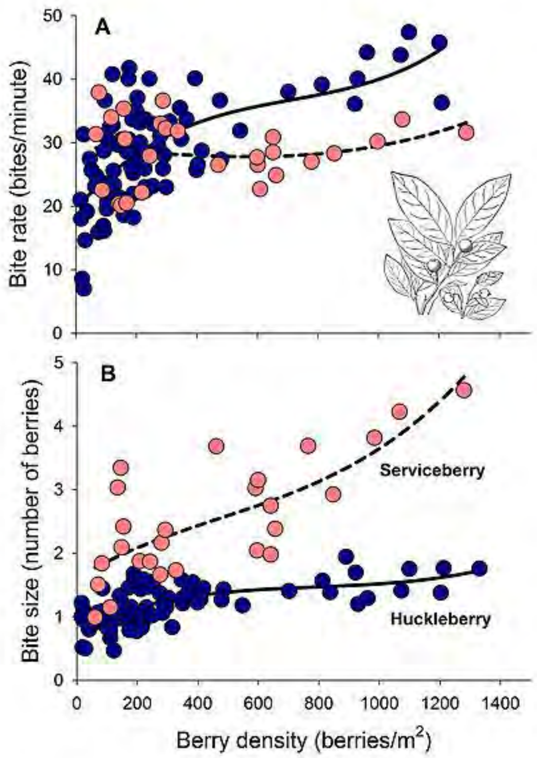

Figure 14. Bite rate and size of serviceberry and huckleberry by bears as a function of berry density.

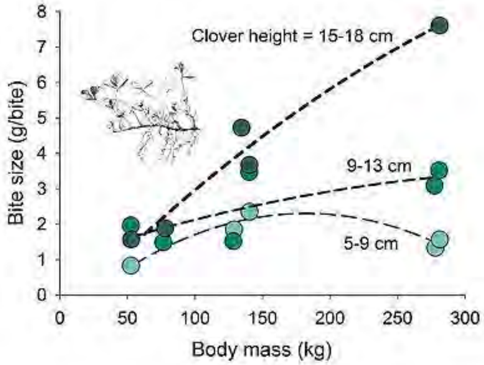

Figure 15. Size of bites of clover as a function of clover height and mass of the involved bear.

In short, the small dentition and jaws of small bears mean that they don't benefit from increases in the stature of grazed foliage, whereas the larger dentition and jaw of large bears allow them to exploit and benefit from greater vertical expression of biomass; which amounts to a constraint imposed by foliage stature on large but not small bears. This, in turn, exacerbates the intrinsic energetic problems for large bears when they try to subsist on a diet of stems and leaves. Which is to say, they typically can't, whereas small bears more commonly can (see Body mass effects).

Bite rate vs Bite size

The relationship between bite size and bite rate further elucidates the basic mechanics of bear grazing and, along with this, some fundamental constraints imposed on bears trying to subsist on foliage. Figure 16 shows this relationship; again, each dot represents a single trial involving a single bear.

The inverse relationship is not surprising. A larger bite requires more processing time, which intrinsically constrains bite speed (i.e., bite rate). But the important feature here is the rapid diminishment in bite rates with increases in bite size.

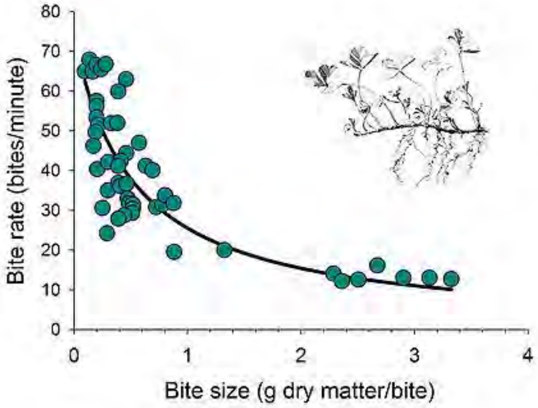

Figure 16. Bite rate as a function of bit size of clover for bears of a given size and clover of a given stature.

The implications? If a bear, it probably makes more sense to seek out patches of foliage to graze that allow for small rapid bites. And, if you are large, you are probably not going to benefit much in the end from being able to take larger bites of taller-statured foliage (as above), which partly explains why, in places such as Yellowstone, smaller bears seek out and heavily graze very dense short-statured patches of clover and bluegrass--commonly referred to as "grazing lawns."

Total rate of intake

Regardless of proximal biomechanics, the bottom line for bears is the total rate at which they can ingest foliage, berries, or any other vegetal food. Again, total rate of intake is especially critical for bears when it comes to vegetal foods (see above), in contrast to when they eat foods such as meat.

The graphs in figure 17 show total rate of intake (grams of dry matter per minute) as a function of key constraining factors. In the case of both serviceberry and huckleberry (B) intake (not surprisingly) increases with the density of each type of berry in a given patch. But the response for serviceberry is dramatically greater than the response for huckleberry because serviceberries (as I describe above) grow in terminal clumps that make it much easier for bears to harvest when compared to the more dispersed single berries of a huckleberry bush. That being said, huckleberry is considerably more digestible than serviceberry (see <u>Digestion</u>), which probably negates the benefits of the latter species rooted solely in ingestible volumes.

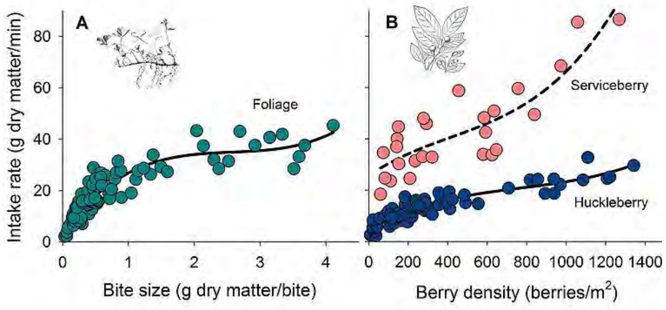

Figure 17. Intake rate of (A) clover and of (B) serviceberry and huckleberry as a function of bite size and berry density, respectively.

Figure 17A shows intake rate as a function of bite size for clover, one of the choicest of grazed bear foods. Why bite size rather than forage density? Simply because the research that produced these data essentially held density constant by insuring that bears had access to thick patches of foliage within which researchers varied composition and stature. Perhaps the point of this is that anything less would presumably be a non-starter for a food as fibrous and relatively indigestible as foliage (see <u>Digestion</u>). But the key point of graph A is that ingested volumes increase with bite size at first, but then rapidly reach a plateau (i.e., asymptote). This pattern is consistent with the depressive effect of bite size on bite rate (see above), ultimately rooted in the limits imposed by a need to chew foliage and then, after that, rate of passage through the gut.

Attachment 3. Primer on Taxonomy & Biogeography of *Ursus arctos*

to accompany

David J. Mattson, Ph.D., Wyoming Wildlife Advocates, Comments on the US Fish & Wildlife Service proposal to remove grizzly bears in the Yellowstone ecosystem from the list of endangered and threatened wildlife protected under the US Endangered Species Act (ESA); Federal Register 81(48): 13174-13227; And Related Materials

Evolutionary relations

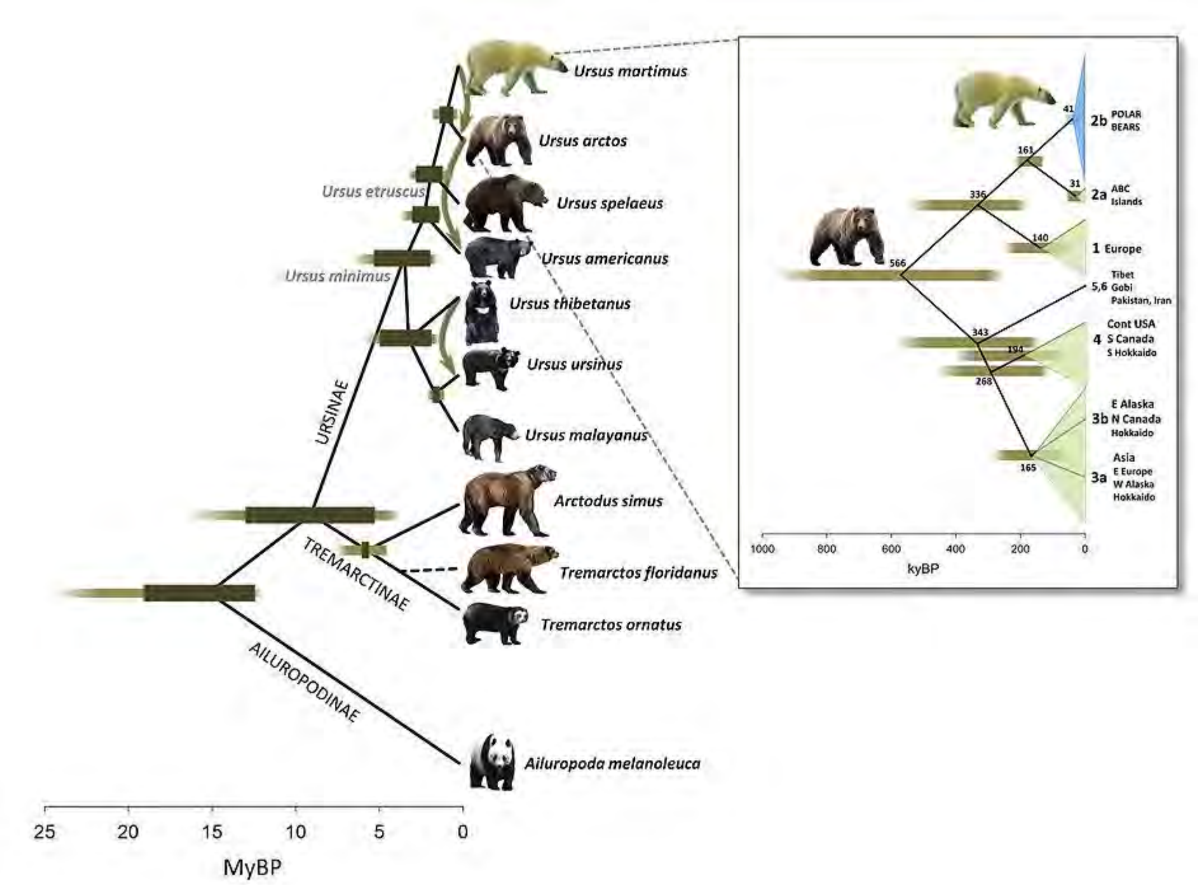

Figure 1. Consensus tree on the phylogeny of Ursidae, including an inset showing relations between Ursus maritimus and U. arctos as well as the diversification of U. arctos into various Clades. Gene flow subsequent to species separations is shown by the green arrows. Ranges of uncertainty in times of divergence are denoted by the length of the horizontal green bars at each node. Source are given below.

Figure 1 illustrates what taxonomists call a "consensus tree" describing relationships and timing of divergence among species within the family Ursidae, as well as (in the inset) relationships and divergence times for various subgroups of the species *Ursus arctos* (the brown and grizzly bears). The polar bear *Ursus maritimus* is included here for reasons that will be addressed shortly. This so-called consensus has been reached only within the last few years, and may be revised in light of new research. But the main part of it will likely hold over time. An important feature to be noted, in addition to the main branching, is the green arrows. These arrows indicate on-going gene flow between "species," which has led to some of the confusion and disagreements over relations and dates of divergence among different species. Note the gene flow from polar bears to grizzly bears, and from grizzly bears to black bears, which suggests inter-fertile breeding, albeit under presumably rare circumstances.

Surviving bear species of the family Ursidae are, for the most part, relatively recent in origin. The most ancient surviving derivative is the giant panda (*Ailuropoda melanoleuca*) which, although most closely related to bears, is so different as to have led taxonomists to put into a separate family, or even cluster it with raccoons. Another main split is between species of the subfamilies Tremarctinae and Ursinae. This split happened about 6-13 million years ago (mya), giving rise to bear species that evolved and survived mainly in North America (the Tremarctine bears), and those that evolved primarily in Eurasia (the Ursine bears). The only surviving bear of the Tremarctine lineage is the Spectacled bear (*Tremarctos ornatus*) of South America, although prior to the end of the last Ice Age a number of Tremartine bears had existed and flourished. Perhaps the most spectacular of these bears was the Giant short-faced bear (*Arctodus simus*), which was a giant as much as 6 feet tall at the shoulder that survived until roughly 13,000 plus or minus 300 years ago (this in years corrected for bias in carbon dating).

But the main focus here is the species *Ursus arctos*, which encompasses the grizzly bears living in Yellowstone. Grizzlies and their kin the Polar bear and Eurasian cave bear (*U. spelaeus*) split from the lineage giving rise to the American black bear (*U. americanus*) roughly 3 mya. These species all shared a common ancestor called *U. minimus*, which gave rise as well to an intermediary form called *U. etruscus*. Barring the American black bear, these species are all best represented by fossils that have been found in Europe and western Asia.

More recently, the branch giving rise to the cave bears split from the brown bear lineage in Eurasia roughly 1-3 mya and, more recent yet, the polar bear lineage split from brown bears about 200-500 thousand years ago (kyBP). There is persisting disagreement among those who study phylogeny regarding when "the" polar bear split happened--some arguing as long as a million years ago, others as recent as 300 thousand years ago. The waters remain muddy because this so-called split has continued to be blurred by interbreeding among brown and polar bears. Whatever the conclusion, polar bears are closely related to brown bears.

But even before the divergence of polar bears, brown bears began to diversify into lineages, or clades, most of which have survived to the present. The major split between brown bears that live in Europe (Clade 1, along with an anomalous bunch on the ABC Islands of Alaska--Clade 2a) and brown bears that live elsewhere (Clades 3-6) occurred around 300-900 kyBP. The reasons for this complex of Clades has a lot to do with how various lineages of brown bears were split and more-or-less isolated during the course of the Ice Ages, which is covered immediately below under Evolutionary biogeography. Of particular relevance to Yellowstone's grizzlies: all of them belong to Clade 4, which appears to have been isolated in central North America when, according to Chris Stokes and collaborators, the Pleistocene ice sheets of North America coalesced across the northern span of the continent for the last time roughly 70 kyBP, albeit with what seems to have been a temporary opening around 55 kyBP. Clade 4 split from the various lineages of Clade 3 (currently concentrated in Asia and Alaska) around 200-350 kyBP. Clade 4 currently survives nowhere other than the in the center of North America and on the island of Hokkaido, which testifies to the Eurasian ancestry of all brown bears, including bears of this clade.

Information in this section is based on a host of sources, including for the carnivoran supertree, Bininda-Emonds et al. (1999) and Nyakatura & Bininda-Emonds (2012); phylogency of Ursidae writ large, Waits et al. (1999), Lorielle et al. (2004), Yu et al. (2004), Krause et al. (2008), Pages et al. (2008), and Kutschera et al. (2014); the unrelenting discourse on relations between polar bears and other bear species, Lindqvist et al. (2011), Cronin & MacNeil (2012), Hailer et al. (2012), , Miller et al. (2012), Nakagome et al. (2013), Liu et al. (2014), and Cahill et al. (2015); and on divergence and nature of brown bear clades, Waits et al. (1998), Leonard et al. (2000), Shields et al. (2000), Matsuhashi et al. (2001), Miller et al. (2006), Hirata et al. (2013, 2014), and Solomashkina et al. (2014).

Evolutionary biogeography

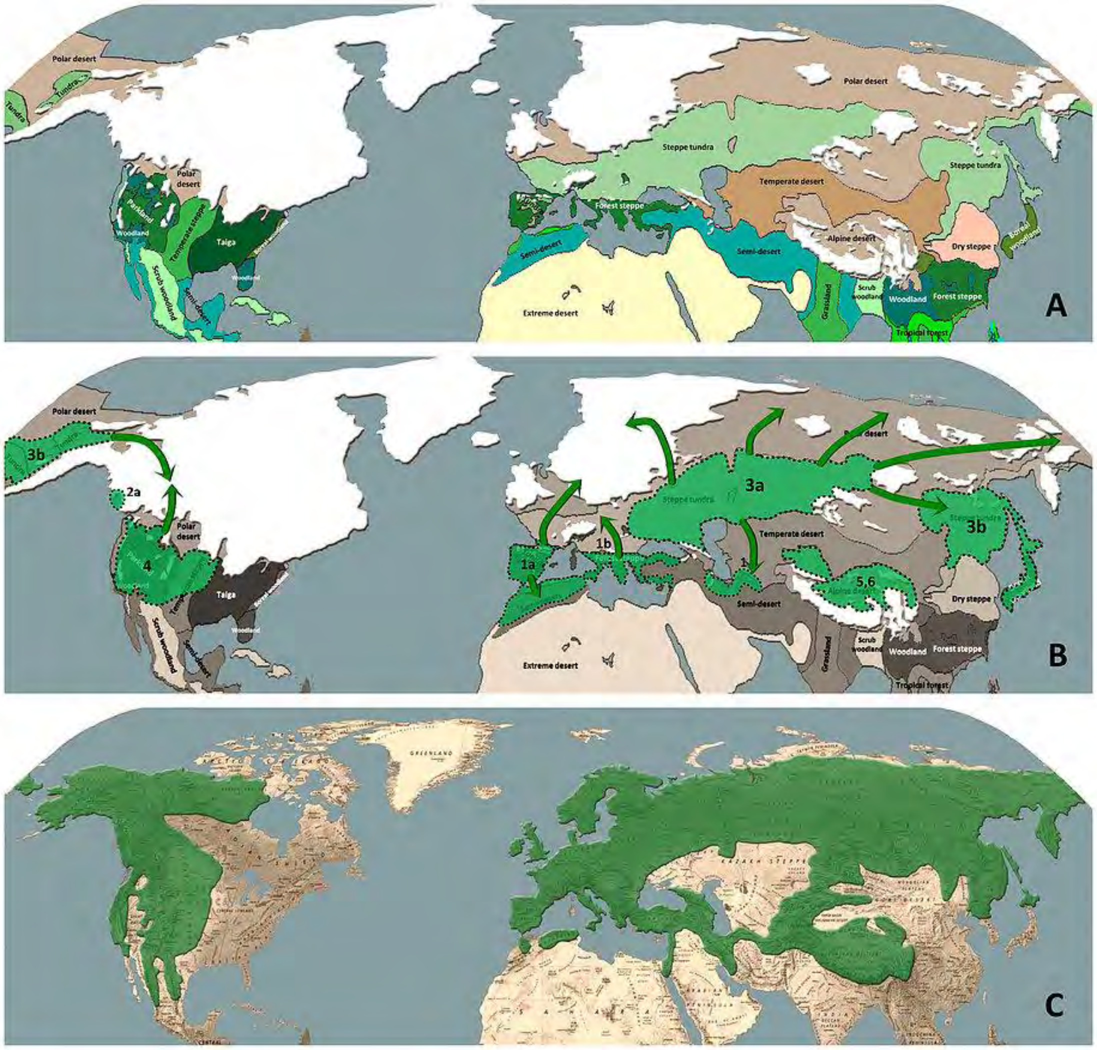

Figure 2. A somewhat speculative reconstruction of the Pleistocene biogeography of Ursus arctos, with (A) a reconstruction of Northern Hemispheric vegetation during the Last Glacial Maximum (LGM); (B) the LGM distribution of Ursus arctos, by Clade, including glacial refugia and subsequent recolonizations; and (C) the distribution of U. arctos circa 10,000 year bp.

The three maps in figure 2 attempt to summarize much of what's relevant to understanding the current population-level genetic diversity evident among today's brown and grizzly bears--all included within the single species *Ursus arctos*. Most of what's presented in these maps is a result of the synthesis published by Davison and his colleagues in 2011. Parenthetically, the notion of "subspecies" has passed out of favor in application to brown bears, and been replaced instead with the concept of "clades," each of which represents enough genetic differentiation to warrant speculations about reasons for the divergence. This recent convergence by taxonomists on the notion of clades is in stark contrast to a 1918 publication of C.H. Merriam in which he described over 70 "species" of grizzly bears in North America alone. The shift has been a result of both increased reliance on information from the genome along with increased appreciation for how plastic brown bear morphology can be (morphology of the skull was the main basis for Merriam's distinctions).

One key to understanding the current genetic diversity of brown bears resides in understanding the distribution of this species during the last Ice Age, which was, in turn, a reflection of vegetation and climate--especially the distribution of ice sheets and exceptionally harsh polar climates. Geneticists speculate that the main explanation for current differences in genomes of bears living in different parts of Eurasia and North America has to do with where their ancestors found refuge--often in isolation--during the different Ice Ages of the Pleistocene, and how they moved and mixed during warmer intervals, especially the current warm period that led to terminal melt of ice sheets between 18,000 and 6,000 years ago.

With that in mind, the map in Panel A, above, shows a plausible reconstruction of ice sheets and vegetation during the height of the last glaciation, roughly 25,000-15,000 years ago. You can see that much of the main range of brown bears in Eurasia was covered by polar desert and what many have called steppe tundra--a kind of tundra with substantially more grass than is common in boggy shrub-dominated tundras of today. This abundance of grass meant that a corresponding abundance of large herbivores could live there, including horses, mammoths, rhinos, giant bison, and more. Overall, though, the main range of Eurasian brown bears (the vast majority of the brown bears alive at the time) was quite dry and bitterly cold.

The map in Panel B shows a speculative reconstruction of the Ice Age distributions of the various modern-day clades, each denoted by its own number (see Evolutionary relations for more details). As you can see, Clade 1 was hunkered down in the southern part of Europe while Clade 3 was distributed throughout the steppe tundra of Asia. Clades 5 and 6, which persist as the genetically and morphologically distinct bears of the Tibetan Plateau and Gobi Desert, were thought to be more or less isolated in high-elevations of south-central Asia. Note that Clade 4 is the sole representative south of the North American ice sheet. More on where and when Clade 4 got there a little later. Also of interest, the green arrows in Panel B show how each of the clades spread and colonized during the late Pleistocene and early Holocene (our current warm period). Clade 1 moved north to occupy most of Europe, but Clade 3 was the big winner, with bears of this lineage spreading into eastern Europe and surging once again into Alaska via Beringia. Clade 3 bears also moved south in North America to mingle with Clade 4 bears moving north in what is now Alberta.

The final map above, in Panel C, shows (in green) how the distribution of brown bears settled out after all of the surges and retreats that occurred with warming and ice melt--by roughly 1000-2000 years ago. Of note, brown bears occurred in the Atlas Mountains of Africa as well as in Mediterranean coastal mountains of the Middle East. They also spread south into Mexico in North America and ended up retreating to an eastern boundary on this continent that aligned with the Great Plains.

Figure 3. Somewhat speculative routes and timings of migrations by Ursus arctos Clades from Eurasia to North America during the late Pleistocene along with a reconstruction of ice sheets prior to the Last Glacial Maximum, including a potential ice-free corridor that could have allowed for early passage of Clade 4 bears south.

The map in Figure 3 provides a little more detail on when and how the various clades of grizzly bears represented in North America arrived. The earliest colonists were apparently of Clades 2 and 4, along with a sprig of Clade 3 called 3c. Clade 4 continued south, occupying west-central North America prior to closure of the last ice-free corridor, which some think might have happened as early as 70,000 years ago (kyBP), although with a brief opening perhaps around 55 kyBP. During this same period bears of Clade 2 (specifically, 2a) made it to the ABC (Admiralty, Baranof, Chichigof) Islands of Alaska. The early southward movement of brown bears into the region encompassing Yellowstone is evidenced by current distributions of the various clades, as well as by a single find of skeletal remains near Edmonton, Alberta, that dates to roughly 32 kyBP (corrected for bias in carbon dating).

Interestingly, of these early colonizing clades, 2a and 4 survived in their interior continental and island refuges whereas 2c and 3c eventually disappeared.

The final colonists, all across Beringia into and via Alaska, were of Clade 3. Clade 3b comprised an earlier wave of colonization that occurred perhaps during and immediately after the last glacial maximum, whereas Clade 3a represents the most recent and last wave of migrants, arriving just prior to when the land bridge of Beringia disappeared. (Remember from the Map in Panel B above, Clade 3a bears had farther to go compared to Clade 3b bears before reaching Beringia.) Modern-day grizzly bears in eastern Alaska consist of descendants of the Clade 3b colonists, whereas those in western Alaska consist of descendants of the Clade 3a new-comers.

The main source of information for the material in this section is Davision et al. (2011), but augmented by the numerous publications that describe Pleistocene refugia and related brown bear lineages in Eurasia, including Taberlet & Bouvet (1994), Matsuhashi et al. (2001), Saarma et al. (2007), Sommer & Benecke (2005), Valdiosera et al. (2007), Keis et al. (2013), Kutschera et al. (2014), and Salomashkina et al. (2014). Mathues et al. (2001) describe the U. arctos remains found near Edmonton, Alberta. Stokes et al. (2012) are the source for delineations of ice sheet margins prior to the Last Glacial Maximum.

Early prehistory: 70,000-10,000 years ago

Up until the early 2000s most scientists thought that grizzlies had not arrived in the middle part of North America until after the last continental Ice Sheets had melted enough to allow passage of bears from Beringia (which included all of modern-day Alaska) through an ice-free corridor along the eastern edge of the Rocky Mountains (see the maps below)--probably around 13,000 years ago (all of the ages here are corrected for biases in radiocarbon age). However, the discovery of grizzly bear remains near Edmonton, Alberta, dating to roughly 32,000 (or 32k) years ago turned this assumption on its head. Recent analyses of genetic material from North American grizzly bears have reinforced the idea that grizzlies arrived much earlier, probably during the last opening in the Alberta ice-free corridor, prior to closure at the height of the last Ice Age, roughly 55,000-18,000 years ago. Recent research by Chris Stokes and his colleagues suggests that a long-lasting opening between the Crodilleran (to the west) and Laurentide (to the east) continental ice sheets occurred between 80k and 65k years ago, with a possible brief opening again around 55k years ago. So, grizzlies probably arrived--and presumably then persisted--as early as 70k or as late as 55k years ago.

As I noted in the previous section, figure 3, above summarizes current thinking about the several migrations of brown bears from Asia into and through North America (parenthetically, grizzlies are brown bears, all *Ursus arctos*). An early wave of bears carrying genetic material identified with Clades 2a, 2c, 3c, and 4 (roughly the equivalent of subspecies) arrived in eastern Beringia around 70k years ago, having successfully crossed over the Bering Land Bridge. Of those bears, those of Clade 4 managed to successfully complete the journey into the middle part of the continent, presumably along the eastern edge of the Rocky Mountains. They were then isolated with closure of the ice-free corridor, intermingling with other grizzlies of the newly-arrived Clade 3b only after reopening of the ice-free corridor around 14-11k years ago (see the maps below). Shortly after, the Bering Land Bridge was closed to additional migrants by rising sea levels. Parenthetically, some researchers have theorized that grizzlies also got to the mid-continent by following ice-free coastal areas of modern-day Alaska and British Columbia--prior to the opening of Alberta's ice-free corridor. Land levels at these ice free margins were dramatically elevated as a compensatory ("forebulge") response to depression of the Earth's crust by the ice sheet farther inland. Migrating coastal grizzlies presumably subsisted largely on marine resources.

Figure 4 shows the distributions of grizzly bear remains from two different periods: In panel A, from 32-10k years ago, with all but the ones near Edmonton dating to less than 15.5k years ago; and, in panel B, from 10k to 200 years ago--up to essentially historical times. In panel A the extent of the ice sheets and bordering glacial melt lakes are shown at 13.5 and 11.5k years ago. Note Lake Agassiz (see the discussion above about climate). Most of the remains are not radiocarbon-dated.

The map in panel A constitutes pretty conclusive evidence that grizzly bears occurred in eastern North America between roughly 15.5 and 11k years ago. But by 10k years grizzlies seem to have been gone in the East. All of the specimens post-10k roughly coincide with the historical distribution of grizzlies. The one exception is the Utz site in Missouri. This specimen was apparently found during excavations of a prehistoric Indian settlement. I tried to track down the original publication documenting this find, but without success. My current suspicions are that either: (1) the specimen was misidentified or, if authentic, then (2) the result of a series of trades among tribes that transported grizzly bear remains from farther west to this site in Missouri.

In addition to the sources that I mention in the section on biogeography, I also reference Guilday (1968), Loring & Spiess (2007) and Harington et al. (2014) for more information on *Ursus arctos* in eastern North America. The Utz site is described by Berry & Chapman (1942).

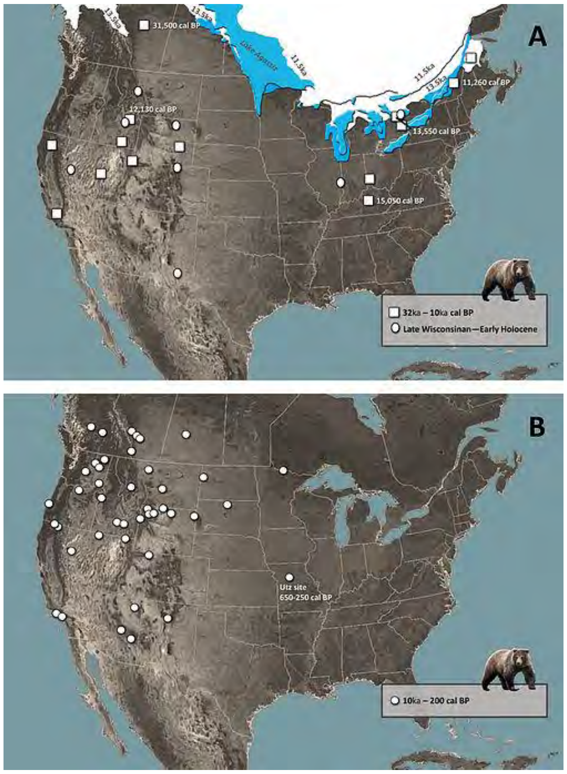

Figure 4. Locations of *Ursus arctos* remains in central North America for two different time periods: (A) 32-10k years bp; and (B) 10k-200 years bp. Locations are shown as either white dots or white squares.