FORAGING BEHAVIOR OF NORTH AMERICAN BEARS

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Predation on Land-Dwelling Prey

Even though all three North American bear species can be predators, the grizzly bear is more likely to kill larger terrestrial prey; either because of opportunity (compared to polar bears) or aptitude (compared to black bears). An adult grizzly is large enough to kill most adult ungulates, and equipped with claws, teeth, and power sufficient to deliver a killing blow. Meat's ready digestibility also means that the typical bear will reap considerable rewards from predation.

Bears locate larger land-dwelling prey, such as deer, elk, and moose, by a variety of methods and with varied intent. A certain number of encounters with potential prey are strictly by chance, apparently without deliberate stalk or search. This is typified by one incident where two grizzlies approached some elk behind a blind rise, without either species being aware of the other's presence. However, as soon as the elk came into sight, one of the bears lunged after them, but without success. This unfruitful result probably characterizes the vast majority of these chance encounters, however there are enough recorded kills in rolling terrain or otherwise visually opaque conditions to suggest occasional success under similar circumstances. On the other hand, the majority of observations suggest that both black and grizzly bears most often encounter their prey either after a deliberate search, characterized by movement in the direction of the hoped-for kill, or, with even greater forethought, by putting themselves in areas with concentrations of vulnerable prey. Elk and caribou calving grounds or traditional caribou river crossings are good examples of such areas where, either because of extreme young age, the preoccupations of birth, or the mass confusion of swimming animals, otherwise elusive ungulates become easy prey. This is most dramatically borne out by several graphic descriptions of observers such as Adolf Murie, Harry Reynolds, Kerry Gunther, and Steve and Marilyn French, of contemporaneous pursuits, kills, and confrontations by grizzlies concentrated on calving grounds in Alaska and Wyoming.

Bears clearly use all of their senses to track down prey. However, most observations suggest a prominent role for olfactory and audio cues. Bears have often been observed following scent trails associated with potential prey, sometimes for miles, or more convincingly, been seen killing calves at the culmination of a complex search mostly with nose to the ground. There are other phenomena that argue anecdotally for the prominence of hearing in tracking down meat. A number of hunters bugling for elk have surprised themselves by soliciting the apparently predatory interest of a grizzly bear. Concordantly, there is a consistently observed tendency world-wide for increased bear predation on both bull elk and bull moose during their fall ruts. Bears also seem to be attracted to the sound of gun-fire during the hunting season, one can only suppose with the intent of scavenging the gut pile and other remains of a hunter's kill. Although this likely orientation towards sound has not been conclusively demonstrated, it remains an intriguing possibility worthy of further study.

Bears can chase down prey in open country, and are more successful at this tactic after separating a young calf from a cow-calf herd. Capture usually occurs after the pursuing bear cuts the corner on a fleeing calf that has been foolish enough to turn. However, most successful bear predations are not the result of long pursuits, but rather the result of a short-range rush either from ambush or after a stalk. Given the relative slowness of bears, at least compared to most wild ungulates, there is a distance

at which this rush is more likely to be successful or, if not, then terminated. A number of records by different observers in different areas suggest that this "optimal" distance is around 20-50 m. Without the aid of mitigating conditions or tactics, it would be difficult for a bear to get this close to a reasonably alert and healthy ungulate, and so it should be no surprise that most kills are associated either with cover, conditions that hinder prey mobility, or the afflictions of exhaustion, disease, or raging sexual hormones in their prey. Thus, many documented predations have been in or near the edge of willow thickets and dense timber, often near running water; presumably under conditions that facilitate the unobserved approach of a predatory bear. Other predations occur on forest game trails, often as the prey negotiates deadfall or a small draw; under conditions where temporary imbalance or distraction would favor a successful ambush. Otherwise, bear researchers throughout the northern hemisphere have noted the remarkable success of bears preying upon winter-weakened ungulates in spring snow conditions. Surface crusts form that can support the weight of a broad-footed bear but not a larger-bodied ungulate such as an elk, moose, or muskox. Under these conditions the delivery of a killing bite is more often a constraint than over-taking the prey. Similarly, exhausted and/or hormonally-deluded bulls seem to make relatively easy bear prey during and after the fall ruts. One extraordinary story from Siberia recounts a brown bear that lured a rutting bull moose into a willow thicket by imitating the bull's mating roar.

Grizzly bears kill land-dwelling prey primarily one of two ways. Most often they maneuver to approach over the back, after which they grab the animal around the rib-cage and, if successful, deliver a killing bite to the back of the neck or skull. A bite to the small of the back may be a prelude to this finishing move, or an animal that escapes the first attempted neck bite may be severely wounded on the flanks by the bear's claws as they are disengaged from their hold. An approach from the rear is also the logical consequence of a chase, and on occasion the bear may use its weight to collapse the hind-quarters of an animal that has just been caught. The next most common kill technique involves a bite to the nose and face that at least paralyzes and possibly kills the animal. Either way, the animal does not offer subsequent resistance. Interestingly, there are only a few reports of bears delivering killing or debilitating blows with their paws, and in most cases their paws come into play for such things as pinning down a newly-captured calf or grasping larger prey to facilitate delivery of a killing bite.

Bears are able to consume between 12 and 40 kg of fresh meat in a day. However, consumption is not indiscriminate and typically reflects marked preference for some carcass parts. Almost universally, the most favored or at least first eaten portion of a female is the udder. After that, most bears eat the brisket and adjacent rib meat or the meaty proximal part of the front legs. Most carcasses are cleanly eviscerated soon after they are killed or found by a bear, with the heart, liver, and lungs selected for priority consumption. The skin, hair, rumen, and stomach are the most consistently unused soft parts of a carcass. In fact, a more-or-less neatly pealed off hide is one of the more diagnostic signatures of bear involvement. Bears are also one of the few consumers that can readily crack the major leg bones of a larger ungulate in pursuit of the marrow. Some bears even get into the habit of cracking the skull so that they can consume the brains.

There are other features that distinguish carcass use by grizzly bears. If there are enough edibles to warrant the investment, a bear will typically bury the entire carcass or selected parts of it by scraping adjacent soil and litter over the tidbit with its front paws. Presumably this inhibits decomposition and the dissemination of scent that might attract competitors. As further sign of ownership, you might even find a bear sprawled directly on top of a carcass, attempting to rest while at the same time prevent pilfering by other scavengers. A bear may also move an intact or even partly consumed carcass to a spot more to its liking. If the carcass is not fresh, a drag trail of shed ungulate hair will connect the new carcass location with the rumen contents left at the original site of death. In addition, there are often bear beds nearby and a bear trail leading to the nearest available water (an apparent necessity when consuming such a protein-rich diet).

As a final note on this type of predation - grizzlies exhibit marked preference for different sizes and species of ungulates. They are least likely to attack very large herd-dwelling animals that rely upon aggression for predator defense, epitomized by bison. Among the larger ungulates, they seem most likely to attack moose, presumably because of a solitary forest-dwelling existence that lends itself to ambush. However, within any given medium- to large-bodied prey species, bears preferentially prey upon young animals, especially the highly vulnerable neonates. On the other hand, although they are not

much larger than a calf elk or moose, adult deer are relatively infrequent bear prey, presumably because of their greater agility and endurance.

Predation on Spawning Salmonids

Bears apparently take spawning fish whenever and wherever they are vulnerable enough to be caught. Both black and brown bears congregate along streams during spawning runs, not only along the Pacific coast, but also under favorable circumstances in some inland areas (for example, currently in Yellowstone National Park and historically in central Idaho). The typical fishing bear is, however, the brown (. grizzly) bear. Where they have option, brown bears clearly orient towards spawners, most likely based on accumulated prior knowledge. However, selection of a specific fishing spot seems to not only involve knowledge of previous success, but also a complex social interplay among bears and humans based upon dominance and aggression; i.e., subordinate bears and species have to settle for second best, third best, or none at all. Setting these social factors aside, bears seem to preferentially select the kind of sites where probability of success is higher. Success is not only a function of fish abundance and size, but also stream characteristics such as depth, gradient, bank structure, and streamside debris. In short, bears seem to orient toward stream reaches where spawner density (i.e., the ratio of spawners to stream volume) is high, the water shallow (optimally, so that the fish's back protrudes), the current high (so that the fish's forward movement and vagility is impeded), and there is enough debris and bank structure to allow either ambush or containment of corralled fish.

Conditions at McNeil River Falls in Alaska are clearly favored by high spawner densities and dramatically retarded forward motion of the fish, and, accordingly, there is consistently a crowd of brown bears trying out their fishing skills. However, this picture that has been captured by photographers thousands of times, and that we consequently associate with bears fishing for salmon, is atypical. Most fishing occurs along the rapids and shallow riffles of medium-sized to small tributaries, often in forested or brushy reaches, and consequently in areas where log jams can sometimes be exploited for more sophisticated fishing techniques. Less commonly, bears may even "snorkel" for fish that are spawning along the beaches of inland lakes. Thus, most fishing is characterized by bears scattered up and down streams and rivers, sometimes moderately aggregated in favorable locations, but rarely stacked up like the crowd at McNeil River Falls.

Bears use many different fishing techniques that seem to vary not only with site-specific conditions and geographic area, but also idiosyncratically among individuals. In shallower water bears will bound from the shore, jump from the bank or a log jam, or stand silently in mid-stream waiting for passing fish. Some bears also herd fish into shallower water or hedge them against piled debris or a cutbank. In deeper water bears add the plunge and submerged scan to their repertoire. In all cases, bears attempt to take fish by surprise when they are most vulnerable or, conversely, somehow increase that vulnerability. At the extreme, bears in some areas primarily consume salmon that are already dead from the rigors of spawning, or are so weakened that the demand for fishing technique is minimal. Actual capture involves permutations of mouth and paw holds, ranging from first pinning the fish to the bottom with one or both front paws, to simply grabbing the fish directly with the canines. Less often, there have been descriptions of bears knocking passing fish out of the water with a broad and powerful sweep of the paw. In any case, most bears end up on shore, often ensconced in the brush, eating their catch. Bears are also apparently not fixated upon any given technique and fishing spot, and like any good angler often vary their approach.

As with other prey, bears are not ambivalent to the different parts of a captured fish. There is a clear pattern to the parts that bears leave uneaten; most often the jaws, gills, opercula, testes, and tail. On the other hand, bears consistently favor the skin and fatty eggs and brains. There have even been reports of bears selectively keeping and eating unspawned females, determined apparently by a combination of olfactory and visual cues, and presumably for the sake of the eggs. In another case where grizzlies were fishing for spawning suckers, they pinned their catches against a log to scrape off some of the scales prior to eating; a move not unexpected by anyone who has had the misfortune of eating sucker scales. When all is said and done, bears are capable of eating 20 to 40 kg of fish in a single day.

Excavating Rodents and Their Food Caches

Red squirrels, pocket gophers, and voles are often involuntary provisioners for bears because of a helpful tendency to accumulate large (1-5 liter) caches of roots and seeds, which the bears later raid at their convenience. In addition, the ground squirrels, gophers, and voles may themselves be a significant source of meat. But regardless of whether the bear's reward is a food cache or the animal itself, acquisition almost always requires some amount of excavation. As a consequence, black bears are less often the beneficiaries of rodents than grizzly bears, which are better built for digging.

Grizzlies enhance their chances of catching rodents apparently by seeking out areas with high densities of vulnerable rodents. Subsequent detection of this often subterranean prey is then typically dependent upon scent. This becomes especially clear when a bear digs down directly to a pocket gopher root cache buried under 1 m of snow and dirt in an otherwise featureless snow field, or when a bear is observed to stick its nose down a ground squirrel hole before committing itself to an excavation. However, scent is not the only means by which bears find rodents or their food stores. It is very likely that bears first orient toward the whitebark pine cone caches of red squirrels by listening for the chatter of these territorial creatures, which typically emanates from somewhere near their central hoard. Upon finding this spot, typically called a "midden", the bear then seeks out the cones typically buried in the spongy mass of debris that has accumulated from generations of squirrel meals, by a combination of scent and sight.

Bear excavations for rodents are quite variable. Although grubbings for voles are typically shallow and often of limited extent, they can also be so extensive that a field may look like it has been plowed. Pocket gopher excavations similarly vary, in a seasonally predictable manner. Digs are shallowest but most extensive in spring, when the gophers are restricted to shallow depths by frozen ground and saturated soils, and deepest but least extensive in mid-summer, when the gophers are established at greater depths. Different types of digs are also diagnostic of whether a bear has been seeking a root cache or pursuing an animal. A grizzly in pursuit of a pocket gopher or vole that is escaping down a tunnel will literally hop side-ways while furiously excavating a runway with its front paws. On the other hand, excavation of a root cache is a more leisurely affair and involves the studied digging of more circular holes that often reveal both a nest and a cache. Bears will typically rake through a cache before consuming the roots directly off their claws, presumably as a means of reducing the amount of ingested dirt. They may be so relaxed that they lay on their bellies while engaged in this activity.

Bears most often capture rodents with their paws, typically by pinning them to the ground but occasionally by stunning them with a swat. Not unlike the canids, bears will also pounce on above-ground rodents prior to pinning them, and sometimes achieve this despite an obscuring blanket of snow. Adolf Murie described the use of a similar pounce by grizzly bears that was directed at the remaining over-burden of soil between them and an elusive ground squirrel, presumably with the intent of startling the squirrel into making its escape. In any case, a bear usually makes short work of eating a rodent after capturing it.

This small reward has mystified a number of researchers trying to understand the benefits that bears derive from using rodents. The "carloads" of earth moved by some grizzlies in pursuit of a relatively diminutive ground squirrel has especially caused its share of wrinkled brows. This seeming paradox is perhaps best resolved by invoking normal bear behavior and the potential power of habit. For example, most excavations for ground squirrels occur in the spring and fall, when they are most vulnerable, and may take only a few minutes each. However, many observations of bears digging for squirrels are made during mid-summer, when grizzlies are more likely to undertake 30-60 minute digging marathons. Furthermore, excavations for the even smaller pocket gophers and voles are rewarded not only by their capture but also by the discovery of root caches. It is therefore likely that the high costs ascribed to rodent use by the casual observer may be the result of both unrepresentative observations and, indeed, the tendency for bears to engage in traditional activities even under energetically unfavorable conditions; much like the human who walks an additional two blocks to a favorite restaurant for a cup of coffee.

Excavating Roots

Root are the diagnostic food of grizzly bears, and indeed, where black and grizzly bears live together, many differences in diet can be ascribed to root grubbing by grizzlies. This is not to say that black bears never dig roots, as some eastern black bears do when excavating jack-in-the-pulpit corms during the spring, but rather that this is an uncommon activity for them. However, even for the better adapted grizzlies, the extraction of roots is a dynamic and sophisticated problem in balancing energy expenditure with energy return. We consequently see some of the most compelling evidence for highly selective feeding when grizzly bears eat roots.

The quality and abundance of roots vary both within and among sites, as does the earthen matrix within which they are imbedded; and we accordingly see temporal and spatial variation in bear grubbing that predictably maximizes benefits to the bear. For example, take the case yampah, a member of the carrot family that produces small but very tasty roots rich in starchy energy. Grizzlies from the Yellowstone area seem to love this root. However, they don't dig it at all times or in all places. As might be expected from the preamble, peak grubbing occurs after the roots have reached peak starch content, shortly after the plants flower. There is also a secondary peak in use during early spring, just prior to the draw-down of starch reserves that accompanies the first flush of spring growth. Even during the season of peak grubbing, use roughly tracks episodes of rainfall and the easier digging conditions that follow. Bears are also not indifferent to varied conditions at any given point in time, and consistently favor sites where yampah is denser and more easily dug. Not only that, they further select for the most easily dug microsites where they can excavate more than one plant at a time; and even more remarkably, they select the largest plants (which also happen to have the largest roots) in a patch to dig. Generalizing on the example of yampah, it is clear that grizzlies seek to maximize returns on their investment at all levels of selection when they feed on roots. And, indeed, this is corroborated by observations of grizzlies digging for sweetvetch and biscuitroot roots. Although some details, such as peak season of use, vary from that of yampah grubbing, the observed differences can all be explained in terms of corresponding differences in the timing of peak starch content or optimal digging conditions.

Grizzlies are remarkably efficient at getting a root out of the ground, and find the desired root by a combination of sight and smell. As indicated above, size is a factor in their selection as is the advent of flowering for some species. However, in cases where several other species resemble the target food plant, sight may allow for only the first level of discrimination. At these times and at times when the plant's above-ground portions are withered and gone, scent becomes the primary means by which bears target a prospect. Again taking yampah as an example, this interplay of sight and smell proceeds as follows: the bear moves towards a cluster of small white flowers which may either be of yampah or yarrow (another species that commonly grows admixed with yampah). The bear smells the plant, and if yampah, then grasps the slender stem side-ways in its mouth, scoops the root out with a shallow dig while still grasping the stem, moves the root up into its mouth with its tongue and a sideways movement of the head, bites the root off, and finally spits out the remains. Thus, it is common to find rootless stems with a kink in them from the mouth hold lying atop or nearby a relatively small paw-sized excavation. Art Pearson and Adolf Murie have also described the more labor-intensive excavation of larger sweetvetch roots by grizzly bears in the Yukon and Alaska. The actual digging requires greater exertion by the main body, and involves a rocking motion after the claws of one or both front claws have been engaged. The excavated root is then lifted out of the hole or from beneath the over-turned clod either with the claws or teeth. The culminating move consists of the bear firmly grasping the top of the plant with its teeth and pulling the rest of the root through its firmly clasped claws, shredding the root prior to moving it into the mouth, "...by alternate tooth and tongue movements". All of this may take as little as 20 seconds. When all is said and done, they can proceed at a pace of 1 root/minute for sweetvetch and as many as 14 roots/minute for the much smaller yampah.

Pursuing Ants and Hornets

Bears eat their share of ants, hornets, wasps, and bees, especially in drier climates where these Hymenoptera seem to flourish. During especially dry years a novice summer-time observer might even

conclude that some bears were insectivores. Ants are the most commonly eaten insect, and sight probably plays an important role in helping bears track down likely spots to eat them. The logs, debris mounds, and rocks typically excavated or over-turned by bears in their pursuit of ants are usually prominent and are no doubt readily discernable to the eye of a bear. In any case, a typical bear's approach to using ants, once a likely spot has been found, is anything but haphazard given the uncertain rewards often hidden beneath a mound or log and the uncertain costs associated with getting there.

Bears sample a lot of logs and ant hills, and as a consequence, you find a lot more small ant digs than you do big ones. Several factors seem to influence where bears end up expending a substantial amount of effort to acquire ants from logs, including its size and hardness, its aggregation with other suitable logs, its exposure to the sun, and the numbers and size of ants contained within. Thus, the canonical excavated log is >5 dm diameter, moderately decomposed under a moderately brittle rind, located in a forest opening surrounded by numerous other favorably endowed logs, and contains large numbers of large ants. There are plausible reasons why all of these features favor bear use, but ultimately they devolve down to one key issue: the greatest ant biomass in return for the least energetic investment. A similar diagnosis of excavated anthills shows disproportional bear use of large hills containing large numbers of large ants, and ultimately leads to the same conclusion.

Bears rely upon their claws to gain access to ants, whether they are under a rock or in a log or hill. In fact, 3 to 5 parallel gouges on the upslope side of a log or anthill dig is diagnostic of bear involvement. Paws are also used to facilitate the capture of ants once access to a nest has been gained. Typically, a bear will let the ants swarm over its paw and then lick them off (a handy way to minimize the ingestion of soil), or if the ants are less aggressive, it will lick them directly off the substrate. The high fraction of dirt and wood debris associated with ant remains in bear feces, however, is testimony to the fact that the consumption of undigestible material is an unavoidable by-product of ant use.

The benefits that bears derive from eating ants is another topic that has defied the ready comprehension of most researchers. Individual ants are small and, in total, typically comprise a small part of feces that result from bears foraging on them. The rest of these feces is typically nest debris. The energy required, especially to break into ant nests sheltered in logs, is also not trivial. This is graphically brought home to anyone who has tried to emulate a bear's efforts with a modified five-pronged potato rake, dubbed the "clawometer" by researchers who developed it. It is thus hard to understand how bears can come out ahead energetically on much of the ant grubbing that they do. Researchers have consequently invoked other non-energetic explanations, such as nutrient requirements, a taste for formic acid, or possible aids to digestion. Many ants have a pleasant, almost citric, flavor eaten raw and might appeal to afficiandos of lemons, and they can provide protein to bears during times of year when protein is remarkably deficient in the rest of their diet, but this speculation is far from convincing, and any more confident conclusions will have to await further study.

The sight of a hornet's thorax or head protruding from a bear feces is a somewhat disconcerting sight. Few people do not pause and contemplate the potential unpleasantries of eating a hornet, including graphic images of the angered meal administering stings to the esophagus. Nonetheless, bears do eat substantial numbers of hornets, especially during dry years when hornet numbers multiply. Nests of the ground-dwelling hornets typically used by bears are not as obvious as those of ants, and the most likely means of detection is by scent, perhaps in combination with tracking hornets that are leaving or entering a nest. Bears excavate the paper nests typically from a recess at the base of a tree or from under semi-decomposed deadfall, and may consume nest and hornets together. Based strictly upon circumstantial evidence, it is probable that bears minimize personal discomfort and maximize meal sizes by more often attacking nests during the chill early morning hours, when hornets are lethargic and more likely to be home. This tactic has similarly been observed to work when bears eat similar-sized grasshoppers and mormon crickets, with greatest success during cool days or the cooler crepuscular hours. Peter Krott also observed some brown bear cubs that he was raising in the European Alps to sneeze or blow at hornets when they were eating them, perhaps as a means of keeping them at bay until they could be eaten.

Acquiring Fruits and Seeds

The main problem that confronts bears in their pursuit of fruits and seeds is getting them off the bushes or out of the tree tops either before other competitors get there or before the fruits decompose. After finding a suitable patch, a bear may face more immediate problems such as gaining access to fruits and seeds elevated above the ground, removing seeds from some undigestible protective covering, gleaning fruits from out of a less digestible matrix of leaves and twigs, or simply the rate at which it can consume and digest readily accessible berries. But ursids are as well equipped as any organism to deal with these difficulties and draw upon an acute sense of smell, relatively well-developed color vision, facile lips, paws, and tongue, and varied climbing capabilities to ingest sometimes phenomenal amounts, 10-45 kg, of energy-rich fruits and seeds in a given day.

The simplest foraging scenario for a bear eating fruits is probably the removal of berries from ground-hugging or nose-level bushes. In this case the bear often tries to maximize the number of berries ingested relative to leaves and twigs. This endeavor is obviously limited by energetic considerations and, at some point, it is not worth the extra time and effort to be picky. However, this break-even point clearly varies among individual bears (depending upon their skills and tolerances) and with the abundance and type of berry being consumed. Although it has not been clearly demonstrated, there are observations supporting the logical expectation that bears are more selective when sated or when foraging upon large abundant berries. Observers have thus reported behavior ranging from the sloppy to the fastidious. Some bears wrap their lips around a stem and indiscriminately strip off leaves, twigs, and berries. Other bears daintily pluck berries out from among less desired portions by a combination of lip and tongue work, sometimes aided by manipulation of stems with their paws. Accordingly, we find berry feces that sometimes contain nothing but the remains of fruits and others that contain mostly leaves.

Bears also consume a substantial number of tree fruits and seeds that have fallen to the ground, either by their own efforts (as described below), wind and natural dehiscence, or the efforts of competitors. They detect such things as acorns and whitebark pine cones by sight and scent, and move along alternately nose to the ground and scanning the nearby forest floor. They typically use their lips and tongue to pick up nuts from the ground litter, crush the shells in their mouth, and spit out the hull. Acquisition of seeds from whitebark pine cones can be a little more complicated, but can be as simple as chewing and swallowing the cone, seeds and all. At the other extreme, bears often break the cone bracts off with their claws or teeth, after bracing the cone with another paw, and facilely lick the seeds out of the debris with their tongue. The opportunity to indulge in this more fastidious consumption of seeds seems to be greater when bears are raiding cone caches made by red squirrels compared to when they are scavenging sometimes rancid seeds from cones dispersed over the forest floor. We accordingly see feces that consist wholly of crushed seeds when bears are using squirrel middens and messier feces containing lots of other cone remnants when bears are engaged in the energetically more costly pursuit of wind-thrown cones.

A number of berries are produced towards the top of tall bushes. Mountain ash, elderberry, chokecherry, and hawthorn are good examples of this type of fruit that is potentially quite abundant but often beyond immediate reach of tongue and lips. Bears resolve this problem quite simply by squatting or standing on their hind legs and pulling more flexible fruit-laden stems to within range of their mouth. More robust stems may be subdued by either grabbing them with the paws and pulling on them until they break or walking along them from proximal to distal end until either the branch breaks or the fruit is reached.

Bears employ variations on this technique to get fruits and seeds out of trees. There are many incentives to make a trip into the tree tops, including potential meals of sugar-rich cherries and fat-rich acorns and beechnuts that would otherwise have to wait until later in the year, or be sacrificed altogether to competing rodents and birds. The option of arboreal foraging is largely denied to grizzly and brown bears, and is perhaps the price they pay for being able to live in austere northern habitats where digging and large body size are important to survival. This not to say that grizzlies never climb trees, and, in fact, some closely-related European brown bears have been observed to forage for fruits or leaves in tree canopies in Norway, the Alps, and Afghanistan. Nevertheless, tree foraging is the definitive domain of the smaller-bodied black bear, whether in North America or Asia.

Once in a tree, black bears most often try to get the items of gastronomic interest down from the canopy by either breaking or chewing off branches or by simply shaking the fruit off. They then descend to eat on the ground. Under other ill-defined circumstances, black bears will stay in the canopy to feed. This type of foraging is characterized by the bear securing itself in a fork or on a broad branch near fruit-laden stems, and then consuming the fruits from branches that have been pulled inward with the paws. Branches thus handled often break, and are then either dropped or accumulated in a pile beneath or near the bear. This accumulation has often been described as a "bear nest", but has nothing to do with either rearing young or resting, and is simply an artifact of feeding. In any case, black bear foraging is usually clearly betokened not only by claw marks on tree trunks, but also by broken limbs on the ground and dangling in the canopy.

Grazing and Browsing

Bears are not able to digest much of the fiber that they eat. This fact is key to understanding how, when, and where bears graze grasses and forbs or browse the leaves and flowers of shrubs, given that all these items have a relatively fleeting period in their seasonal development when fiber content is low enough that bears can benefit by much of what they ingest. This low digestibility, as well as minimal mastication, is reflected in the bulk and structure retained by foliage in bear feces. The basic strategy employed by most bears when grazing seems to be: eat large volumes when the net energetics of digestion are in your favor, and incur as few additional costs associated with acquisition and processing as possible. As with roots, we thus see a lot of selective feeding when bears are serious about grazing. Bears are unstudied about some grazing, but this could be fairly characterized as "incidental" or "auxiliary". In the latter case incentives may be to aid digestion or clear the digestive tract, and is often the interpretation applied to grazing that accompanies use of meat.

Early in the growing season bears seem to be limited more by the biomass and height of grazable foliage than they are by its quality. Grasses and forbs usually emerge through the dried-up remnants of last-year's growth, or "hay", which limits access to this more nutritious new growth. On rare occasions bears have been seen raking or muzzling through detritus to expose spring growth, but more often bears either graze where the new foliage is more robust or where there is less obscuring hay. Bears most often graze with their incisors, aided by manipulations of their flexuous lips and tongue, and are capable of cropping material as low as 4-8 cm. In the colder climates typical of most current bear range, this minimal growth is typically first achieved on exposed south-facing slopes where the snow melts first and where much of the previous year's foliage has been removed by winter-active herbivores. It is thus common for bears to be seen grazing on this kind of site during early spring, literally throughout the northern hemisphere.

It isn't long, however, before nutritional quality and growth characteristics of the forage begin to limit where bears can beneficially graze. Among the grasses and sedges bears seem to favor species that have broader succulent leaves concentrated farther up the main flowering stems, and avoid species that concentrate short slender leaves at the base of taller sparse culms. Bears also begin to restrict their grazing to moist and shaded sites or sites at higher elevations where plant maturity, and associated increase in fiber content, is delayed. They also tend to shift their grazing to broad-leaved species, or "forbs", which tend to be more nutritious later in the growing season. Clover is a favorite mid- and late-summer forage, and in some places bears graze mixed patches of bluegrass and clover so intensively that they look as if they've been mowed by a ground's keeper. However, the typically numerous bear feces are a dead give away to the true cause.

Bears are especially picky when it comes to eating forbs. Compared to grasses and sedges, bears are much more selective about the species that they eat, both because of variable nutritional quality and highly variable levels of potentially noxious secondary compounds. These compounds may not only complicate digestion, they may also be mildly toxic. By contrast, use of grasses and sedges is limited primarily by the amount of indigestible fiber and silica. Thus, we see little or no use of most forb species and relatively heavy consumption of a select few, including cow-parsnip, angelica, and sweet-cicely at mid-latitudes, and boykinia and sourdock farther north.

However, selection is not limited to choosing a species, but is also extended to the parts of a plant that are eaten. Bears seem to relish dandelion flowers, and in most places restrict themselves to the stems, blossoms, and petioles of cow-parsnip except during early spring. This selective consumption of plant parts is especially evident when bears eat thistle. Thistle stems are quite succulent shortly after elongation and can taste like the sweetest celery. However, from a bear's point of view this otherwise tasty morsel is disadvantaged by a spiny exterior, and the bear accordingly tries to maximize ingestion of the succulent interior while minimizing ingestion of spines. A bear will do this one of several ways. One approach is to knock the spiny flower head off with a swat of the paw and strip off the equally spiny leaves with the claws prior to eating the stem, or eat the stem, leaves and all, but spit the leaves back out. Alternately, some bears will break the stem over, strip the leaves off of the facing surface with their claws, and then eat the exposed stem by precise nips with their incisors. This behavior is fascinating not only because of the involved technique, but also, like much bear behavior, because of the varied approaches taken by different bears.

As a final item, it is worth noting that bears browse the leaves and flowers of trees and shrubs, especially during early spring. Bears are most commonly observed eating the leaves and catkins of aspen and willow throughout higher latitudes, but can also be seen eating the leaves of such plants as devil's club in coastal Alaska and beech trees in the northeastern United States. Some of this browsing is complicated by comestibles that are beyond immediate reach. In these cases bears employ the same techniques that they use to get berries from tall shrubs or small trees: they either bend the branches to within mouth's reach, walk out along more robust branches to the succulent growth, or break the branches down. Again, flexible paws are key to these strategies.

Consuming Cambium

Both black and grizzly bears have the annoying habit of eating cambium from commercially-valued trees. Cambium is the succulent and spongy growth that conveys most of the tree's nutrients between roots and leaves, just beneath the tree's bark. Simple carbohydrates are part of this arboreal freight, and spring sugar content of cambium in some tree species can be as high as that of berries. So there is an understandable impetus for bears to use cambium, but with the unfortunate side-effect of retarding tree growth or even killing a tree if the cambium is exposed and eaten around the entire trunk (i.e., "girdled"). Regardless of the fact that this usually antagonizes foresters and other people who hope to profit from the production of wood fiber, the means by which bears gain access to cambium is fascinating.

Bears seem to prefer different trees for a variety of reasons related to bark thickness, tree size, and sugar and ash content of the cambium. Nutrient content varies by season, species, and vigor of the individual tree. We accordingly see bears preferentially stripping bark in the spring or early summer, when sugar content is highest, from more vigorously growing trees, as in stands that have been thinned or fertilized, of species that tend to have thinner bark and higher average sugar content. Trees 15-50 years old and 15-50 cm in diameter typically fill this bill, as does Douglas-fir, lodgepole pine, redwood, and various species of true firs.

Bears most commonly gain access to cambium by working their claws under the bark near the base of the tree and pulling back and upward. A series of tugs with claws and teeth eventually pulls off an elongate vertical strip of bark 10-15 cm wide and 6-30 dm long. These strips tend to be broader at the base and taper to a point where the bark either detaches and falls to the ground or remains dangling by an attenuated connection. Less often bears will start stripping from the top and initiate the tear with their teeth. Whatever the specific technique, bears will almost always attack from uphill if the tree is on a steep slope. After removing the bark, most bears then consume the cambium by vertical scrapes with their lower incisors. Some bears apparently do not eat the cambium, and merely lick the exposed sap, whether because of the particular tree species or idiosyncratic behavior is not clear. In any case, a bear may content itself with one tear or progressively work its way around the entire tree, in which case the tree inevitably dies.