Consumption of pondweed rhizomes by Yellowstone grizzly bears

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Abstract: Pondweeds (Potamogeton spp.) are common foods of waterfowl throughout the Northern Hemisphere. However, consumption of pondweeds by bears has been noted only once, in Russia. We documented consumption of pondweed rhizomes by grizzly bears (Ursus arctos) in the Yellowstone region, 1977–96, during investigations of telemetry locations obtained from 175 radiomarked bears. We documented pondweed excavations at 25 sites and detected pondweed rhizomes in 18 feces. We observed grizzly bears excavating and consuming pondweed on 2 occasions. All excavations occurred in wetlands that were inundated during and after snowmelt, but dry by late August or early September of most years. These wetlands were typified by the presence of inflated sedge (Carex vesicaria) and occurred almost exclusively on plateaus of Pliocene-Pleistocene detrital sediments or volcanic rhyolite flows. Bears excavated wetlands with pondweeds when they were free of standing water, most commonly during October and occasionally during spring prior to the onset of terminal snowmelt. Most excavations were about 4.5 cm deep, 40 cubic decimeter (dm³) in total volume, and targeted the thickened pondweed rhizomes. Starch content of rhizomes collected near grizzly bear excavations averaged 28% (12% SD; n = 6). These results add to the documented diversity of grizzly bear food habits and, because pondweed is distributed circumboreally, also raise the possibility that consumption of pondweed by grizzly bears has been overlooked in other regions.

Key words: excavation, foraging, grizzly bear, pondweed, Potamogeton, Ursus arctos, Yellowstone

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Pondweed (*Potamogeton*) is a genus of vascular hydrophytes that grow in shallow fresh or saline water worldwide (Cronquist et al. 1998). Depending on the species and growth stage, stems and foliage are completely submerged, floating, or emergent. Most pondweed species spread vegetatively by sprouting from stout subterranean rhizomes or detached turions ("tubers"; Pip 1987). Turions and some rhizomes contain high concentrations of simple carbohydrates that peak prior to depletion by sprouting and other growth that typically occurs during spring (Kantrud 1990).

The starchy rhizomes and turions of pondweed are an important food of bottom-feeding waterfowl and are palatable to humans and other mammals such as muskrats (*Ondatra zibethicus*; Harrington 1976, Kantrud 1990). Turions of sago pondweed (*Potamogeton pectinatus*) are one of the best-known foods of waterfowl (Kantrud 1990). Bewick's (*Cygnus columbianus bewickii*), tundra (*C. columbianus columbianus*), and trumpeter (*C. buccinator*) swans select for sago pondweed turions and rhizomes, select habitats rich in pondweed, and, at times, depend on excavated pondweed for much of their energy, most often during late fall and early spring (Bellrose 1976, Beekman et al. 1991). Excavated sago pondweed turions can comprise 20–40% of the winter and spring diet of trumpeter swans in the Yellowstone region of Wyoming (Squires and Anderson 1995).

Pondweed rhizomes can have high concentrations of soluble carbohydrates (50–60% dry weight) and high biomass (100–400 g m⁻²; Kantrud 1990), making them good candidates for bear food, especially for the digging-adapted brown bears (*Ursus arctos*) (Herrero 1978). However, despite extensive sympatry, to our knowledge there is only one reference to brown bears excavating and eating pondweed. Kaletskaya and Filinov (1986) described brown bears (*U. a. arctos*) in European Russia

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excavating pondweed during low water periods in September–November along the seasonally flooded margins of a major reservoir.

Here we describe spatial and temporal patterns of pondweed rhizome consumption by grizzly bears in the Yellowstone region of Wyoming during 1977–96, as well as features of excavated sites, individual excavations, and associated pondweed rhizomes. We also explain the distribution of observed feeding in terms of ecologic, hydrologic, and geologic factors and speculate about the use of pondweed rhizomes by brown bears in other areas.

Study area

Our 23,000 km² study area consisted of occupied grizzly bear range in the Yellowstone region of Wyoming, Montana, and Idaho, from 43°30' to 45°15'N latitude and 109°30' to 111°30'W longitude. High elevation (>2,100 m) rhyolite plateaus capped by deep Pleistocene till comprised the core of the study area, which was surrounded by geologically diverse higher-elevation mountains. Small ponds and lakes were common on the central plateaus, a result of recent (8,500-12,000 years before present [bp]) glacial deposits (Keefer 1976) and relatively young (300,000-600,000 bp) lava flows associated with fissures of the Island Park and Yellowstone calderas (Christiansen 2001). Annual precipitation on the central plateaus ranged from 50 to 70 cm, with a relatively uniform monthly distribution (Western Regional Climate Center 2004). Annual snowfall averaged 400-550 cm, with accumulations reaching 60-100 cm during January-April and terminal melt occurring during early May. Significant (>15 cm) enduring snow cover typically did not occur until November. With the exception of limited areas of grass and shrub cover on finetextured surficial Pleistocene lake deposits, most upland portions of the central study area were covered by lodgepole pine (Pinus contorta)-dominated forests (Despain 1990). Vegetated wetlands were typified by water sedge (Carex aquatilis), tufted hairgrass (Deschampsia cespitosa), and alpine leafybract aster (Aster foliaceus) (Mattson 1984). Wetlands with substantial water table fluctuations, indicated by abundant inflated sedge, comprised about 10% of wetlands on the central plateaus of our study area (Mattson 1984).

Methods

Bears were trapped, marked, and radiolocated according to methods described by Knight and Eberhardt (1985) and Blanchard and Knight (1991). We visited and described a subset of radiolocations according to methods in Mattson (1997*a*, 2000). We also described sites where grizzly bear feeding or bedding sign was encountered en route to and from telemetry locations. Among the many measures taken at each location, we listed individual plant species occurring within 10 m of plot center and ascribed to them an index of abundance (1-5; 1 = present but rare, 2 = scattered, 3 = common, 4 = abundant, and 5 = dominant). Many of the activity sites used in this analysis were not ascribed to a marked bear or radiolocation, and so constituted a potentially biased sample of grizzly bear activity influenced by variation in detectability of different signs and distributions of habitats characteristic of different activities relative to our travel routes.

We described all feeding, bedding, and rubbing signs and collected all feces (scats) encountered during 1977-96. During 1986–96, our descriptions of feeding activity included counts and measurements of excavations. We measured and multiplied length, width, and depth (all in dm) to estimate volume of excavation for pondweed rhizomes. We collected samples of pondweed rhizomes at 6 sites to estimate available biomass and nutrient content. We completely excavated 2-3 $1-m^2$ plots per site to a depth of 2.5 dm (the deepest observed excavation by a bear during this study) adjacent to areas excavated by bears. All pondweed rhizomes were collected and later oven dried at 40°C for approximately 12 hours. The dried rhizomes were weighed, by plot, and averaged by feeding site to obtain a site-specific estimate of dry mass (g) available/m². Rhizomes were also analyzed for percent ash, crude fiber, crude protein, and starch content. Ash, fiber, and protein estimates were determined by the standard proximate system of analysis (Van Soest 1982). Starch content was determined using a calorimetric method developed by K. Goering (Montana State University Analytical Lab, Bozeman, Montana, USA; Mattson 1997b). We also obtained 10 clawometer readings at each of 2 pondweed feeding sites. The clawometer is a 5-tined potato fork modified to resemble bear claws with a box spring scale attached to register maximum kg of resistance to extraction of the fork after being inserted in substrate at a 45° angle (Holcroft and Herrero 1984, Mattson 1997b). Clawometer readings can be used as a relative index of substrate resistance to excavation (Holcroft and Herrero 1984; Mattson 1997b, 2004).

We considered both proximal and distal effects in the analysis (Mattson 2000). Distal effects were those operational at broad temporal and spatial scales, whereas proximal effects were operational at the scale of the immediate site. Proximal effects were represented by measures taken at telemetry locations or other sites of grizzly bear activity. Distal effects were enumerated from other sources. We obtained monthly average temperatures (°C) and precipitation (cm) from regional monthly summaries published by the US National Oceanic and Atmospheric Administration (1977–96). We obtained date of snowmelt (first spring day with 0 cm of snow recorded on the ground) from records for Lake Yellowstone weather station—the station nearest most of the pondweed consumption observed during this study. We obtained maps of geology and caldera boundaries for the central plateaus of our study area from Christiansen (2001).

Results

During 1977–96, 7,459 scats were collected and 2,134 telemetry locations from 175 radiomarked bears were investigated to determine activity of the associated animal. Feeding sign was found at a total of 3,101 sites, including 1,940 sites not associated with a telemetry location. Remains of pondweed rhizomes were found in 18 scats, and excavations for pondweed rhizomes were found at 25 sites. Six sites were associated with telemetry locations of 5 different radiomarked bears. One of the marked bears was an adult male (>4 years old), 1 was a subadult male, and 3 were adult females (>4 years old or, if younger, known to have reproduced). We visually observed a grizzly bear excavating and consuming pondweed on 2 occasions. Excavations for pondweed rhizomes were documented during 7 of the 20 years of this study; 6 of these years occurred during the last decade. The highest observed frequency of use during any one year (n = 10) occurred in 1977.

Even though pondweed use was detected in either scats or at activity sites during all months of the bears' active season (Mar–Oct), peak relative frequencies of pondweed use, as indicated by both scats (1.1, SE = 0.5%) and activity sites (4.6, SE = 1.8%), occurred during October. A secondary peak in use during spring was more ambiguously suggested by excavations observed during March (3.3, SE = 1.5%) and by pondweed roots in feces from April (1.3, SE = 0.8%). Percent frequency of pondweed excavations at activity sites during May, June, July, August, and September was 0, 0.7, 0.3, 0.2, and 0.9; percent frequency of occurrence in feces for these same months was 0.4, 0.4, 0, 0.1, and 0.2. All of the March– May use was detected prior to 1981.

The tendency for pondweed consumption to occur late in the active season was consistent with an observed tendency for pondweed excavation to be proportionally more common <62 and especially >117 days after

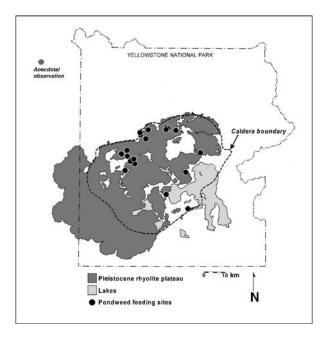


Fig. 1. Sites where Yellowstone grizzly bears excavated pondweed rhizomes, 1977–96, relative to the Yellowstone caldera boundary and associated Pliocene–Pleistocene rhyolite plateaus, including an anecdotal observation of pondweed feeding west of Yellowstone National Park (gray dot) and feeding sites documented (black dots). White areas within the caldera boundary consist largely of Pleistocene sediments.

terminal snowmelt. For quintiles of the data, with mean time since snow melt of 12, 45, 76, 103, and 140 days, percent frequency of pondweed excavations was 1.0, SE=0.3; 0.7, SE=0.4; 0, SE=0; 0, SE=0; and 1.4, SE=0.5. Median number of days since snow melt was 144 for pondweed feeding sites and 75 for other sites with feeding or bedding sign.

All of the sites where grizzly bears excavated pondweed rhizomes occurred in pothole wetlands within the boundary of the Yellowstone caldera (Fig. 1) and lacked standing water at the time of excavation. All 9 of the sites reliably classified to wetland type were high moisture flux wet meadows (Mattson 1984). All but 1 of the sites occurred on rhyolite bedrock produced by Pliocene–Pleistocene volcanic events. Inflated sedge was observed at 7 of the 9 sites where graminoid species were reliably identified, Canada reedgrass (*Calamagrostis canadensis*) and water sedge at 6 sites, and short-awn foxtail (*Alopecurus aequalis*) at 5 sites.

Proportions of activity sites with excavations for pondweed rhizomes were positively related to abundance of pondweed. Percent frequency of pondweed excavations was 0.2, SE = 0.1 (n = 2701); 50.0, SE = 35.4 (n = 2); 25.0, SE = 21.7 (n = 4); 75.0, SE = 15.4 (n = 8); and 100.0, SE = 0.0 (n = 4) at sites where pondweed abundance was indexed as 0, 1, 2, 3, and 4, respectively. Pondweed was not judged to be dominant (index = 5) at any sampled site. Pondweed stems and leaves were desiccated at the time grizzly bear feeding activity was documented, making identification of species for an already problematic genus (Cronquist et al. 1998) all the more difficult. In the 3 instances where we could determine species, specimens keyed to either *Potamogeton natans* or *P. nodosus*.

Numbers and sizes of excavations for pondweed varied greatly among sites, although characteristics of pondweed rhizomes did not. Median total excavated soil volume (n =8) was 40 dm³ (19–234 interquartile range), distributed among a median of 4.5 digs (1–8.5 interquartile range). Maximum total excavated volume was 2,381 dm³. Median volumes and depths of individual digs were 11.7 dm^3 (1.9–94.5 interquartile range) and 4.5 cm (4.5– 4.5 interquartile range), respectively. Mean dry weight mass of rhizomes (n=6) was 24.7 g/m² (SD=12.4 g/m², maximum=40.7). Mean starch content (n=5) was 28.5% (SD = 11.8%, maximum = 48.4) and crude fiber from 2 samples was 5.9% and 6.9%. Mean digestibility, based on starch content (Mattson et al. 2004), was 68.4% (SD = 8.6%). Mean clawometer readings were 19.9 and 25.5 kg at the 2 sites where this measure was taken.

Discussion

Although consumption of pondweed rhizomes by Yellowstone grizzly bears occurred regularly throughout our study and was relatively common during 1977, this activity was rare overall. Even so, estimated starch content and digestibility of pondweed rhizomes did not differ substantially from starch contents (32-36%) and digestibilities (62-72%) of biscuitroots (Lomatium cous) and yampah roots (Perideridia gairdneri), the 2 most common root foods of Yellowstone grizzly bears (Mattson et al. 2004). Root yield per unit volume of excavated soil (0.25–0.5 g/dm³, assuming an excavation 0.5–1 dm deep) was also comparable to, if not higher than, root yields of biscuitroot and yampah (0.2 g/dm³; Mattson 2004). So, why was excavation of pondweed rhizomes by grizzly bears so uncommon during our study?

The answer to this question probably has to do with limited pondweed availability. Excavation by bears only occurred when sites supporting pondweed were drained. Complete drainage only occurred at sites with high water table fluctuations, as indicated by the presence of inflated sedge and short-awn foxtail (Mattson 1984). However, even in high moisture flux wetlands, the 0.5-7 dm of standing water in early summer typically did not disappear until late August or September (Mattson 1984). Shortly thereafter, soil surfaces hardened. This hardening was indicated by the high clawometer readings (20-26 kg) obtained from pondweed excavation sites 1-2 weeks after the activity had occurred. This contrasts with the much lower clawometer readings obtained from biscuitroot and yampah root excavation sites (6-9 kg; Mattson 2004). Grizzly bears probably had only a short period to gainfully excavate pondweed roots, between the time of drainage and soil surface drying. This limited temporal availability was probably exacerbated by the limited extent of high moisture flux wet meadows and limited abundance of pondweed within our study area (Mattson 1984).

The consumption of pondweed by grizzly bears observed during March and April of 1977–80 is intriguing. This activity occurred prior to the onset of terminal spring snowmelt. Several sites were also in areas with geothermal warming in the Nez Perce and Rabbit Creek drainages of Yellowstone National Park. This combination of circumstances may have resulted in potholes free of substantial standing water and with thawed yet moist soils, increasing the likelihood that excavation of pondweed roots would be profitable for bears.

Nearly all grizzly bear excavation of pondweed rhizomes occurred on rhyolitic plateaus built from volcanic extrusions along fissures associated with the Yellowstone caldera. This concatenation was probably a result of both topography and hydrology. Pothole wetlands are relatively common on the central Yellowstone plateaus because of broadly flat terrain and irregular glacial deposits (Mattson 1984). Moreover, with the exception of somewhat circumscribed lacustrine deposits, most of the glacial debris consists of deep coarsegrained till or kame (US Geological Survey 1972). Although not conclusively known, drainage is probably accelerated on this coarse-grained substrate compared to finer-grained substrates more common in the study area. Accelerated drainage is indicated by the greater frequency of high moisture flux wetlands on the central plateaus (Mattson 1984) compared to other parts of the study area such as northern Yellowstone National Park (Hansen et al. 1988).

Given the extensive overlap of pondweed and brown bear ranges, there is potential for as yet undocumented consumption of pondweed rhizomes by brown or grizzly bears in boreal and arctic regions of the Northern Hemisphere. However, exploitation of pondweed rhizomes probably does not occur except where it is abundant and accessible. Pondweed is most abundant where there are numerous pothole wetlands, estuaries, or slow-moving rivers (Pip 1987)-common conditions in much of boreal and arctic Eurasia and North America. Seasonal drainage is likely to be the factor that most limits bear consumption. Substantial water table fluctuation is not a common feature of natural wetlands on permafrost or fine-textured substrates. Thus, the best prospects for excavation of pondweed rhizomes by brown bears are probably along the margins of reservoirs, as documented by Kaletskaya and Filinov (1986), or in regions, such as the Yellowstone caldera, with undulating topography, coarse-textured substrate, and without permafrost.

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