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Use of Whitebark Pine (*Pinus albicaulis*) seeds by GPS-collared Grizzly Bears (*Ursus arctos*) in Banff National Park, Alberta

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Abstract

Seeds of Whitebark Pine (*Pinus albicaulis*) are a major food for Grizzly Bears (*Ursus arctos*) in the Yellowstone ecosystem. In Canada, Grizzly Bears are known to eat Whitebark Pine seeds, but little additional information, such as the extent of such use and habitat characteristics of feeding sites, is available. Because Grizzly Bears almost always obtain Whitebark Pine seeds by excavating cones from persistent caching sites (middens) made by Red Squirrels (*Tamiasciurus hudsonicus*), it is possible to infer Whitebark Pine feeding when bears are located near excavated middens in Whitebark Pine stands. During 2013–2018, I conducted a retrospective study in Banff National Park using data from 23 Grizzly Bears equipped by Parks Canada staff with global positioning system (GPS) collars. My objectives were to use GPS fixes to determine the percentage of these bears that had been located in close proximity to excavated middens containing Whitebark Pine seeds and to describe the habitat at these excavated middens. I linked 15 bears (65%) to excavated middens and, by inference, consumption of Whitebark Pine seeds. Excavated middens occurred on high-elevation (mean 2103 ± 101 [SD] m), steep (mean 26° ± 8°) slopes facing mostly (96%) north through west (0–270°). Use of Whitebark Pine seeds by at least 65% of the 23 studied Grizzly Bears suggests that conservation of Whitebark Pine in Banff National Park would concomitantly benefit the at-risk population of Grizzly Bears.

Key words: Banff National Park; Grizzly Bear; midden; *Pinus albicaulis*; Red Squirrel; seeds; *Tamiasciurus hudsonicus*; *Ursus arctos*; Whitebark Pine

Introduction

The large seeds of Whitebark Pine (*Pinus albicaulis* Engelmann) are an important seasonal food for Grizzly Bears (*Ursus arctos*) in the Yellowstone ecosystem, Wyoming and Montana, USA (Kendall 1983; Mattson *et al.* 1991). Whitebark Pine seeds weigh about 175 mg, or ~35 times those of Lodgepole Pine (*Pinus contorta* Douglas ex Laudon), and contain ~50% lipid and ~20% protein—a ratio close to that identified as an optimal autumn Grizzly Bear diet (Lanner and Gilbert 1994; Erlenbach *et al.* 2014). Grizzly Bears typically obtain Whitebark Pine seeds by excavating the persistent cone-caching sites (middens) of Red Squirrels (*Tamiasciurus hudsonicus*; Kendall 1983; Mattson and Reinhart 1997; Costello *et al.* 2016).

Although Mattson and Reinhart (1997) stated that Yellowstone Grizzly Bears fed almost exclusively on Whitebark Pine seeds when cones were available, an analysis of movement data from 72 individual global positioning system (GPS)-collared Grizzly Bears recorded in Yellowstone during 2000–2011 revealed that about a quarter of the autumn home ranges used by these bears did not contain Whitebark Pine habitat (Costello *et al.* 2014). Overall, a third of the sampled Grizzly Bears made little or no use of habitat with Whitebark Pine, even though the data were about equally divided between males and females and between years with good and poor cone production and came from areas and years showing variable amounts of Whitebark Pine mortality caused by Mountain Pine Beetle (*Dendroctonus ponderosae*).

Recent study has shown that Grizzly Bears in the Canadian Rocky Mountains also excavate Red Squirrel middens to obtain seeds of Whitebark Pine (Raine and Riddell 1991; Hamer and Pengelly 2015). However, beyond confirmation of use, little additional information is available on the importance of Whitebark Pine seeds to Grizzly Bears outside the Yellowstone ecosystem (Ciarniello 2018). Because Red Squirrel middens tend to be persistent and conspicuous features on the landscape and because evidence of excavation by bears tends to persist, I used available locations of GPS-collared Grizzly Bears in Banff National Park to retrospectively investigate these bears' use of Whitebark Pine seeds cached in squirrel middens. My

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objectives were to determine the percentage of collared Grizzly Bears that could be linked to excavated middens containing Whitebark Pine seeds and to describe habitat characteristics associated with these putative feeding sites. I assumed that Grizzly Bears located during August–November at sites containing excavated Red Squirrel middens in Whitebark Pine habitat could be categorized as having most likely fed on Whitebark Pine seeds.

Study Area

My study area was defined by the home ranges of GPS-collared bears (*n* = 26) that fell within Banff National Park. I also included some GPS locations to the south and west, in Kootenay and Yoho national parks, within 2 km of the Banff National Park boundary. Because bears were GPS-collared for a study of mortality associated with train strikes (Hopkins *et al.* 2014), most bears were captured in the Trans-Canada Highway–Canadian Pacific Railway transportation corridor running through the centre of Banff and Yoho national parks. The home ranges of the collared bears were mainly in the Bow Valley and adjacent watersheds, in the central portion of Banff National Park. The Bow Valley transportation corridor runs 70 km northwest–southeast, from the eastern boundary of Banff National Park in the Front Ranges of the Rocky Mountains to the British Columbia–Alberta boundary on the Continental Divide, in the Main Ranges of the Rocky Mountains.

There is a diminishing moisture gradient between the Continental Divide, which intercepts moist air moving inland from the Pacific Ocean, and the more arid rain-shadow of the Front Ranges. Subalpine forests in Banff National Park are dominated by Interior Spruce (*Picea engelmannii* Parry ex Engelmann var. *engelmannii* × *Picea glauca* (Moench) Voss), Subalpine Fir (*Abies lasiocarpa* (Hooker) Nutall), and Lodgepole Pine. Subalpine Larch (*Larix lyallii* Parlatore) and Whitebark Pine occur in some upper subalpine stands (Achuff 1982; Corns and Achuff 1982). Limber Pine (*Pinus flexilis* E. James), a species normally found in wind-swept, arid sites at lower elevations, occasionally occurs in the upper subalpine with Whitebark Pine on some steep, south- and west-facing Front Range sites exposed to solar insolation and desiccating foehn (Chinook) southwesterly winds (Hamer 2016). Whitebark Pine has greater abundance in the Main Ranges of Banff National Park, and is less common in more arid, eastern portions of the Front Ranges (Hamer and Pengelly 2015; Hamer 2016; I. Pengelly and A. Buckingham unpubl. data 2010).

Methods

I conducted fieldwork during 2013–2018 using data from 21 of 26 Grizzly Bears equipped with GPS collars as part of a 2010–2016 study of Grizzly Bear mortality in Banff and Yoho national parks (Whittington *et al.* 2018). Preliminary results from three of these collared bears (Bears 72, 128, 138) were reported by Hamer and Pengelly (2015); I have included these data here, given that my study is an extension of that previous work. I excluded two of the 26 bears (Bears 140, 149) because their collars provided only four GPS fixes from late summer–autumn (when pine seeds are eaten; Kendall 1983), and I was unable to study the GPS fixes of Bear 161 because unseasonal snowfalls in September 2018 prohibited data collection. In addition, based on an aerial survey for five-needle pines (I. Pengelly and A. Buckingham unpubl. data 2010), I judged that home ranges of four bears, located in the arid, eastern slopes of the Front Ranges, likely lacked Whitebark Pine stands; for two of these bears (Bears 135, 155), I found Limber Pine in the home ranges but no Whitebark Pine, and I, therefore, excluded the other two bears (Bears 131, 134) from the study.

For the 21 studied bears, I considered GPS fixes dating from August through November. Of this subset of date-constrained GPS fixes, I selected a smaller subset for field inspection based on knowledge of five-needle pine distribution in Banff National Park (Hamer and Pengelly 2015; Hamer 2016) and on habitat determined from the geographical information system, QGIS (v. 2.14; QGIS Development Team 2018) with topographic and Google Satellite layers. I selected fixes in habitat where Whitebark Pine was likely to occur: forest and open forest at higher elevations (~1800–2300 m) above valley bottoms. Finally, I also attempted to select GPS fixes for field inspection that were within 5 km of motor vehicle access, although three excavated middens and six other sites checked for middens were 5–14 km from the nearest road.

As in a concurrent study (Hamer 2016), I attributed all excavations found in middens to bears, and all excavated middens I observed contained either Whitebark Pine or Limber Pine cones or cone scales; only one of these excavated middens contained both Whitebark Pine and Limber Pine cones (Hamer 2016), and it was not possible to quantify the five-needle pine cones or cone scales in the middens. Bears also excavate middens found at valley-bottom beside the Canadian Pacific Railway in Banff National Park to obtain anthropogenic seeds gathered by Red Squirrels from railway car spillage (Put *et al.* 2017); these excavations, being distant from Whitebark Pine and Limber Pine, are not pertinent to my study. If I found an excavated Red Squirrel midden containing Whitebark Pine cones or cone scales, I classified this location as a putative Whitebark Pine feeding site, and I inferred that bears with GPS fixes (see Table 1) near this site had consumed Whitebark Pine seeds. It is possible that some of the excavated middens were a result of activity by American Black Bears (*Ursus americanus*); however, my study addressed Grizzly Bear proximity to excavated middens with the inference being that a Grizzly Bear near an excavated midden was seeking five-needle pine seeds at the midden.

To reduce the likelihood of obtaining false positives from coincidental overlap of GPS fixes with excavated middens, I attempted to obtain, for each bear, two instances of GPS locations near excavated middens (hereafter referred to as links) indicating possible consumption of Whitebark Pine seeds. Once two links were achieved, I shifted field effort to other bears. To reduce the likelihood of obtaining false negatives when bears lacked evidence of feeding on Whitebark Pine seeds, I spent 5.3 ± 3.6 (SD; range 2–9) field days searching their GPS fixes. This field effort was not quantifiable in terms of GPS fixes investigated on the ground because some bears had low fix rates (e.g., one fix/4 h) whereas other bears had up to one fix/min; the number of fixes at accessed sites varied from one to many, and some sites, when field-checked, proved to lack Whitebark Pine.

When an excavated midden was found near a GPS location fix, I recorded midden size, slope aspect, slope steepness, basal area of trees using a 2 m^2/ha prism, distance to nearest Whitebark Pine tree, and distance between the nearest GPS location fix and midden using a hand-held GPS unit (Garmin GPSMap 60, Olathe, Kansas, USA). I also checked for presence of Whitebark Pine cones and cone scales (Hamer and Pengelly 2015). Middens were recorded only once when calculating summary statistics of site parameters, regardless of the number of linked GPS fixes whether from the same bear on different dates or from different GPS-collared bears.

I established one paired plot with each excavated midden using a hand-held GPS unit to place the plots 50 m map distance from the midden and on the same elevational contour. Comparisons between excavated middens and plots were made using the non-parametric Wilcoxon paired-sample test in R (Wilcox.test, two-sided, v. 3.4.3; R Core Team 2014). Comparisons were not made for either slope aspect (which will usually remain essentially unchanged over 50 m) or elevation (which was identical for midden and matched plot given the methods used).

Results

Fifteen of the 21 studied Grizzly Bears (71%) were linked to excavated middens containing Whitebark Pine seeds. More conservatively, 15 of 23 bears (65%) were linked to these feeding sites when including the two bears (Bears 131, 134) omitted from analyses because their home ranges did not appear to include Whitebark Pine. The field signs linking bears to Whitebark Pine seeds were located a mean distance of 12 ± 14 (SD) m (range 0–49 m) from the associated Grizzly Bears' GPS locations. Observations with substantial (22–49 m) distances between fix and midden were viewed as putative links between collared bears and Whitebark Pine feeding sites when corroborated by additional, supporting field evidence

TABLE 1. Field evidence linking locations of GPS-collared Grizzly Bears (*Ursus arctos*) to 29 excavated Red Squirrel (*Tamiasciurus hudsonicus*) middens in Banff National Park, Alberta, 2013–2018.

Grizzly Bear	Distance from excavated midden,* m	Corroborating field evidence
Bear 122 Bear 122	22 36	Bear 122 had eight fixes within ~0.1 ha; two excavated middens were adjacent, one on contour to the right and one on contour to the left of the 0.1-ha site.
Bear 125	29	Bear 125's GPS fix fell 29 m from a 50 m^2 excavated midden but 4 m from an adjacent, undug, 11 m^2 satellite midden (Hamer and Pengelly 2015); Bear 125 was also located 6 m from an excavated midden at another site.
Bear 160	35	Bear 160 was also located 3–11 m from excavated middens at three other sites.
Bear 64	39	Four excavated middens occurred within 4 ha; Bear 64 was also located 9 m from an excavated midden at another site.
Bear 141	45	Two excavated middens occurred 45 m apart; Bear 141's GPS fix was 12 m from one and 45 m from the other.
Bear 130	49	This excavated midden plus four others occurred along ~300 m linear distance of a forested ridge proximal to Bear 130's GPS fix; Bear 130 was also located 6 m from an excavated midden at another site.

Note: GPS = global positioning system.
*In 22 cases, bears were located <14 m from an excavated midden (mean 5 m, range 1–13 m). A proximity of ≤13 m establishes a strong link between GPS-collared bears and feeding sites where bears obtain Whitebark Pine seeds.

(Table 1). Twelve of the 15 bears were linked to at least two excavated middens. Three bears (Bears 136, 143, 144) were linked to single excavated middens, although Bear 136 was also linked to scats containing >90% pine seeds, found in a bedding site and dating to three GPS fixes made 20 days before my field investigation; this site was 2.2 km from an excavated midden where Bear 136 had been located one day before his presence at the bedding site (D.H. pers. obs.). All excavated middens contained Whitebark Pine cones or cone scales; one midden contained both Limber Pine and Whitebark Pine cones (Bear 130; Hamer 2016). Mean midden size was 76 ± 47 m^2 (range 18–181 m^2, $n = 26$).

Excavated middens occurred on all slope aspects, although only one midden occurred on a slope facing northwest (270–359°); midden locations are determined by Red Squirrels. The observed frequency of slope aspects did not differ from that expected if the four cardinal directions (315–44° north, 45–134° east, 135–224° south, 225–314° west) were equally represented ($\chi^2_3 = 3.8$, $P = 0.28$, $n = 26$). Excavated middens were on steep slopes (mean 26 ± 8°, range 6–38°, $n = 26$) in upper subalpine habitat (elevation mean 2103 ± 101 m, range 1860–2280 m, $n = 28$).

Compared with surrounding habitat as measured at paired plots 50 m distant, excavated middens were on slopes that were significantly less steep and in stands with significantly greater basal area of both Subalpine Fir and all coniferous trees (Table 2).

Discussion

The main finding of this study was that most GPS-collared Grizzly Bears (15 of 21, 71%) were linked to excavated middens containing Whitebark Pine seeds. Of the remaining six bears, some may be false negatives because time and difficult access limited ground-checking to a small subset of each bear's GPS fixes. In addition, my conclusion that four bears (Bears 131, 134, 135, 155) did not have Whitebark Pine stands in their home ranges remains to be confirmed with further field observation. The Front Ranges north of the Bow Valley in Banff National Park do not appear to contain Whitebark Pine stands, and feeding on Whitebark Pine seeds was not reported in earlier work along the eastern slopes of this portion of Alberta (Russell *et al.* 1979; Hamer and Herrero 1987; Munro *et al.* 2006).

My study had several limitations and caveats. First, the mean separation between fixes and excavated middens was 12 m but ranged up to 49 m. The larger separations were accepted as valid links to Whitebark Pine when other evidence, as reported in Table 1, supported this conclusion. One bear (Bear 158) was separated by 23 m from an excavated midden, but had no other links. Furthermore, this fix dated to 10 August, a time when bears normally feed on fleshy fruits. For all other bears, fixes linking to Whitebark Pine dated from September (65%), October (28%), and November (7%). I classified Bear 158 as lacking a link to a Whitebark Pine feeding site. Second, some separation between fix and midden may reflect GPS error of both collar and my hand-held unit, especially

TABLE 2. Habitat characteristics at 22 excavated Red Squirrel (*Tamiasciurus hudsonicus*) middens compared with 22 random plots 50 m distant from excavated middens near location fixes from GPS-collared Grizzly Bears (*Ursus arctos*) in Banff National Park, Alberta, 2013–2018.

	Excavated middens			Paired plots			Wilcoxon paired-sample test	
Site variable	Mean	SD	Range	Mean	SD	Range	Wilcoxon *V*	*P*
Distance to GPS fix, m	10	11	1–36	—	—	—	—	—
Elevation, m*	2102	105	1861–2281	—	—	—	—	—
Slope steepness, °	26	7	6–38	32	6	23–48	19.5	< 0.01
Distance to nearest Whitebark Pine, m	8	12	1–42	12	19	1–80	55.5	0.20
Basal area, m^2/ha								
Whitebark Pine (*Pinus albicaulis*)	9	13	0–54	7	7	0–24	83	0.45
Interior Spruce (*Picea engelmannii* var. *engelmannii* × *Picea glauca*)	17	13	0–24	11	10	0–30	185.5	0.06
Subalpine Fir (*Abies lasiocarpa*)	19	16	0–52	9	11	0–44	126.5	0.02
All conifer species	47	11	28–68	29	17	0–78	201	< 0.01

Note: GPS = global positioning system, SD = standard deviation.
*Plots have the same elevation as paired middens; see Methods.

in narrow, steep-walled, or heavily-forested valleys. Even in flat and relatively open terrain, mean location errors of 8–12 m are found from GPS collars (D'Eon and Delparte 2005). Finally, for the two bears that had only single links to Whitebark Pine, there is an increased chance that I obtained a false positive result, compared with the 13 bears with two or more links. Weighing against this possible error is the chance of failing to detect seed use because of the intermittent fixes obtained by GPS collars. The collars used on Banff Grizzly Bears typically obtained fixes every four hours and thus could have obtained locations before and after, but not while, a bear was at a midden.

I did not find evidence that Grizzly Bears in Banff National Park harvested pine cones directly from trees in this or a related Limber Pine study (Hamer 2016). A similar conclusion was reached in the Yellowstone ecosystem where claw marks on tree trunks or broken branches were not observed (Kendall 1983). However, bears do climb for cones (Kuhn and Vander Wall 2007), including Grizzly Bears (D. McIntyre pers. comm. 31 March 2014; C.R. McLellan pers. comm. 18 September 2018). My study also did not address the extent of annual use of Whitebark Pine seeds by GPS-collared bears.

Some middens were thoroughly excavated and, in some cases, an animal trail was visible on the forest floor, leading into the midden. Learned behaviour may contribute to habitual use: one excavated midden had GPS fixes from a female Grizzly Bear (Bear 64) dating to 25 September 2012, as well as fixes from three of her offspring on 6 September 2014 (Bear 144), 20 September 2014 (Bear 148), and 10 September 2015 (Bear 160). Conversely, a second female Grizzly Bear (Bear 72) and two of her offspring (Bears 142, 143) had just one link to Whitebark Pine (Bear 143). These bears focussed on fruits of *Vaccinium* spp. and Black Crowberry (*Empetrum nigrum* L.) and roots of Yellow Hedysarum (*Hedysarum sulphurescens* Rydberg) during late summer and early autumn at the GPS fixes I investigated. Dietary differences among individual Grizzly Bears have been documented in other populations (Christensen *et al.* 2005; Edwards *et al.* 2011).

Grizzly Bears in the Yellowstone ecosystem tend to experience lower mortality rates in years when Whitebark Pine cones are abundant, a result attributed to at least two factors. First, Whitebark Pine feeding sites typically occur in high-elevation sites remote from high levels of human activity. Second, human–bear conflicts (which predictably occur in less-secure habitat) are a common cause of Grizzly Bear mortality (Mattson *et al.* 1992). Whitebark Pine cone abundance was the highest-ranked habitat covariate in models explaining the survival of Grizzly Bears in the Yellowstone ecosystem for 1993–2001 (Haroldson *et al.* 2006). In Banff National Park, Grizzly Bear mortality is largely human caused: 75% for females and 86% for males (Garshelis *et al.* 2005). Thus, Grizzly Bears that feed on Whitebark Pine seeds, if they occupy habitat that is remote from the Bow Valley transportation corridor and other foci of human activity, may experience lower risk of mortality. Further, the results of my study—where roughly two-thirds of the 21 studied Grizzly Bears were linked to Whitebark Pine feeding sites—suggest that a substantial portion of the Banff Grizzly Bear population may so benefit.

In Yellowstone, Whitebark Pine has been subject to high mortality, and use of this secure habitat by Yellowstone Grizzly Bears may be diminishing (Costello *et al.* 2014). Whitebark Pine surveys in the Canadian Rocky Mountains during 1996–2004 found high levels of infection (60–73%) by White Pine Blister Rust (*Cronartium ribicola*) both south (Waterton Lakes National Park) and north (Jasper National Park) of Banff National Park, but Banff had relatively low levels of infection (16%; Smith *et al.* 2008). Reassessment in 2009 found that infection and mortality were increasing, but, again, levels remained lower in Banff National Park (Smith *et al.* 2013). The predicted loss of Whitebark Pine from the effects of White Pine Blister Rust was one of the reasons for the Committee on the Status of Endangered Wildlife in Canada to assess the species as Endangered (COSEWIC 2010), which led to its listing as Endangered under the Canadian *Species at Risk Act* (SARA Registry 2019). Hence, managers may be able to provide for two at-risk species by conserving Whitebark Pine in a region that currently experiences lower than expected mortality from White Pine Blister Rust, at the same time providing secure feeding habitat for, according to my results, a substantial portion of Banff National Park's Grizzly Bear population.

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Literature Cited

Achuff, P.L. 1982. Vegetation: introduction and methods. Pages 71–75 *in* Ecological (Biophysical) Land Classification of Banff and Jasper National Parks. Volume II: Soil and Vegetation Resources. Publication SS-82-44. *Edited by* W.D. Holland and G.M. Coen. Alberta Institute of Pedology, Edmonton, Alberta, Canada.

Christensen, J.R., M. MacDuffee, R.W. Macdonald, M. Whiticar, and P.S. Ross. 2005. Persistent organic pollutants in British Columbia Grizzly Bears: consequence of divergent diets. Environmental Science and Technology 39: 6952–6960. https://doi.org/10.1021/es050749f

Ciarniello, L.M. 2018. A review of food security for grizzly bears in British Columbia. Grizzly Bear Foundation, Vancouver, British Columbia, Canada.

Corns, I.G.W., and P.L. Achuff. 1982. Vegetation type descriptions. Pages 75–142 *in* Ecological (Biophysical) Land Classification of Banff and Jasper National Parks. Volume II: Soil and Vegetation Resources. Publication SS-82-44. *Edited by* W.D. Holland and G.M. Coen. Alberta Institute of Pedology, Edmonton, Alberta, Canada.

Costello, C.M., S.L. Cain, S. Pils, L. Frattaroli, M.A. Haroldson, and F.T. van Manen. 2016. Diet and macronutrient optimization in wild ursids: a comparison of grizzly bears with sympatric and allopatric black bears. PLoS ONE 11(5): e0153702. https://doi.org/10.1371/journal.pone.0153702

Costello, C.M., F.T. van Manen, M.A. Haroldson, M.R. Ebinger, S.L. Cain, K.A. Gunther, and D.D. Bjornlie. 2014. Influence of whitebark pine decline on fall habitat use and movements of grizzly bears in the Greater Yellowstone Ecosystem. Ecology and Evolution 4: 2004–2018. https://doi.org/10.1002/ece3.1082

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2010. COSEWIC assessment and status report on the Whitebark Pine *Pinus albicaulis* in Canada. COSEWIC, Ottawa, Ontario, Canada.

D'Eon, R.G., and D. Delparte. 2005. Effects of radio-collar position and orientation on GPS radio-collar performance, and the implications of PDOP in data screening. Journal of Applied Ecology 42: 383–388. https://doi.org/10.1111/j.1365-2664.2005.01010.x

Edwards, M.A., A.E. Derocher, K.A. Hobson, M. Branigan, and J.A. Nagy. 2011. Fast carnivores and slow herbivores: differential foraging strategies among grizzly bears in the Canadian Arctic. Oecologia 165: 877–889. https://doi.org/10.1007/s00442-010-1869-9

Erlenbach, J.A., K.D. Rode, D. Raubenheimer, and C.T. Robbins. 2014. Macronutrient optimization and energy maximization determine diets of brown bears. Journal of Mammalogy 95: 160–168. https://doi.org/10.1644/13-mamm-a-161

Garshelis, D.L., M.L. Gibeau, and S. Herrero. 2005. Grizzly bear demographics in and around Banff National Park and Kananaskis Country, Alberta. Journal of Wildlife Management 69: 277–297. https://doi.org/10.2193/0022-541x(2005)069<0277:gbdiaa>2.0.co;2

Hamer, D. 2016. Excavation of Red Squirrel (*Tamiasciurus hudsonicus*) middens by bears (*Ursus* spp.) in Limber Pine (*Pinus flexilis*) habitat in Banff National Park, Alberta. Canadian Field-Naturalist 130: 281–288. https://doi.org/10.22621/cfn.v130i4.1918

Hamer, D., and S. Herrero. 1987. Grizzly bear food and habitat in the Front Ranges of Banff National Park, Alberta. International Conference on Bear Research and Management 7: 199–213. https://doi.org/10.2307/3872626

Hamer, D., and I. Pengelly. 2015. Whitebark Pine (*Pinus albicaulis*) seeds as food for bears (*Ursus* spp.) in Banff National Park, Alberta. Canadian Field-Naturalist 129: 8–14. https://doi.org/10.22621/cfn.v129i1.1662

Haroldson, M.A., C.C. Schwartz, and G.C. White. 2006. Survival of independent grizzly bears in the greater Yellowstone ecosystem, 1983–2001. Pages 33–42 *in* Temporal, Spatial, and Environmental Influences on the Demographics of Grizzly Bears in the Greater Yellowstone Ecosystem. *Edited by* C.C. Schwartz, M.A. Haroldson, G.C. White, R.B. Harris, S. Cherry, K.A. Keating, D. Moody, and C. Servheen. Wildlife Monograph 161.

Hopkins, III, J.B., J. Whittington, A.P. Clevenger, M.A. Sawaya, and C. Cassady St. Clair. 2014. Stable isotopes reveal rail-associated behavior in a threatened carnivore. Isotopes in Environmental and Health Studies 50: 322–331. https://doi.org/10.1080/10256016.2014.922555

Kendall, K.C. 1983. Use of pine nuts by grizzly and black bears in the Yellowstone area. International Conference on Bear Research and Management 5: 166–173. https://doi.org/10.2307/3872534

Kuhn, K.M., and S.B. Vander Wall. 2007. Black bears (*Ursus americanus*) harvest Jeffrey pine (*Pinus jeffreyi*) seeds from tree canopies. Western North American Naturalist 67: 384–388. https://doi.org/10.3398/1527-0904(2007)67[384:bbuahj]2.0.co;2

Lanner, R.M., and B.K. Gilbert. 1994. Nutritive value of whitebark pine seeds and the question of their variable dormancy. Pages 206–211 *in* Proceedings: International Workshop on Subalpine Stone Pines and their Environment: The Status of Our Knowledge. General technical report INT-GTR-309. *Compiled by* W.C. Schmidt and F.K. Holtmeier. United States Department of Agriculture, Forest Service, Ogden, Utah, USA.

Mattson, D.J., B.M. Blanchard, and R.R. Knight. 1991. Food habits of Yellowstone grizzly bears, 1977–1987. Canadian Journal of Zoology 69: 1619–1629. https://doi.org/10.1139/z91-226

Mattson, D.J., B.M. Blanchard, and R.R. Knight. 1992. Yellowstone grizzly bear mortality, human habituation, and whitebark pine seed crops. Journal of Wildlife Management 56: 432–442. https://doi.org/10.2307/3808855

Mattson, D.J., and D.P. Reinhart. 1997. Excavation of red squirrel middens by grizzly bears in the whitebark pine zone. Journal of Applied Ecology 34: 926–940. https://doi.org/10.2307/2405283

Munro, R.H.M., S.E. Nielsen, M.H. Price, G.B. Stenhouse, and M.S. Boyce. 2006. Seasonal and diel patterns of grizzly bear diet and activity in west-central Alberta. Journal of Mammalogy 87: 1112–1121. https://doi.org/10.1644/05-mamm-a-410R3.1

Put, J.E., L. Put, and C. Cassady St. Clair. 2017. Caching behaviour by red squirrels may contribute to food conditioning of grizzly bears. Nature Conservation 21: 1–14. https://doi.org/10.3897/natureconservation.21.12429

QGIS Development Team. 2018. QGIS Geographic Information System. Open Source Geospatial Foundation Project. Accessed 16 June 2020. http://qgis.osgeo.org.

R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Raine, R.M., and R.N. Riddell. 1991. Grizzly bear research in Yoho and Kootenay national parks, 1988–1990. Canadian Parks Service, Western Region, Calgary, Alberta, Canada.

Russell, R.H., J.W. Nolan, N.G. Woody, and G.H. Anderson. 1979. A study of the grizzly bear in Jasper National Park 1975–1978. Canadian Wildlife Service, Edmonton, Alberta, Canada.

SARA (*Species at Risk Act*) Registry. 2019. Species summary: Whitebark Pine (*Pinus albicaulis*). Government of Canada, Ottawa, Ontario, Canada. Accessed 20 July 2020. https://species-registry.canada.ca/index-en.html#/species/1086-748.

Smith, C.M., B. Shepherd, C. Gillies, and J. Stuart-Smith. 2013. Changes in blister rust infection and mortality in whitebark pine over time. Canadian Journal of Forest Research 43: 90–96. https://doi.org/10.1139/cjfr-2012-0127

Smith, C.M., B. Wilson, S. Rasheed, R.C. Walker, T. Carolin, and B. Shepherd. 2008. Whitebark pine and white pine blister rust in the Rocky Mountains of Canada and northern Montana. Canadian Journal of Forest Research 38: 982–995. https://doi.org/10.1139/x07-182

Whittington, J., M. Hebblewhite, and R.B. Chandler. 2018. Generalized spatial mark–resight models with an application to grizzly bears. Journal of Applied Ecology 55: 157–168. https://doi.org/10.1111/1365-2664.12954

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