Whitebark Pine (*Pinus albicaulis*) Seeds as Food for Bears (*Ursus* spp.) in Banff National Park, Alberta

David Hamer[1, 3] and Ian Pengelly[2]

[1]300–379 Spring Creek Drive, Canmore, Alberta T1W 0G8 Canada
[2]235 Lady MacDonald Drive, Canmore, Alberta T1W 1H2 Canada
[3]Corresponding author: j.david.hamer@gmail.com

Hamer, David, and Ian Pengelly. 2015. Whitebark Pine (*Pinus albicaulis*) seeds as food for bears (*Ursus* spp.) in Banff National Park, Alberta. Canadian Field-Naturalist 129(1): 8–14.

The large, nutrient-rich seeds of Whitebark Pine (*Pinus albicaulis* Engelmann) are important food for bears (*Ursus* spp.) in Yellowstone National Park. In Banff National Park, studies have shown that American Black Bears (*Ursus americanus*) eat these seeds, but little additional information is available. We studied Whitebark Pine in Banff National Park to address this information gap. Because bears obtain Whitebark Pine seeds from Red Squirrel (*Tamiasciurus hudsonicus*) middens, our objective was to measure the abundance, habitat characteristics, and use by bears of middens in Whitebark Pine forests. A second objective was to determine whether Grizzly Bears (*U. arctos*) in Banff National Park also eat Whitebark Pine seeds. In 2011–2012, we ran 29 ha of 20–50 m wide transects at 10 sites with accessible Whitebark Pine stands and found 0–3.7 middens/ha (mean 1.23, SD 1.17, $n = 10$). Midden density was weakly related to total basal area of all conifers but not to basal area of Whitebark Pine. Middens were located in the upper subalpine at an average elevation of 2110 m (SD 90, $n = 8$) on 41–248° facing slopes with a mean steepness of 28° (SD 5, $n = 8$). Bears had excavated middens at all eight sites where we found middens; at the remaining two sites, middens did not occur within our transects. Overall, 24 (67%) of the 36 middens located in our transects had been dug by bears. In October 2013, we searched areas where three global positioning system (GPS)-collared Grizzly Bears had been located in late September 2013 and found five recently dug middens located less than 6 m from GPS fixes. These observations are, to our knowledge, the first conclusive evidence that Grizzly Bears in Banff National Park eat Whitebark Pine seeds. Because Whitebark Pine occurs at high elevations on steep slopes where human use is low, this resource may be important in keeping bears in habitat where risk of human-caused mortality is lower. Our results may assist managers responsible for conservation of bears in Banff National Park, where both American Black Bears and Grizzly Bears are subject to high levels of human-caused mortality.

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

Introduction

The large, nutrient-rich seeds of Whitebark Pine (*Pinus albicaulis* Engelmann) are a major food for Grizzly Bears (*Ursus arctos*) and American Black Bears (*U. americanus*) in the Greater Yellowstone Ecosystem (GYE; Fortin *et al.* 2013). As stated by Mattson and Reinhart (1997:926): "When whitebark pine seeds are abundant, grizzly bears [in the GYE] eat virtually nothing else." Mattson *et al.* (1992) found that in years of high seed availability, GYE Grizzly Bears were half as likely to use areas within 5 km of roads or within 8 km of other developments because Whitebark Pine's high elevation distribution typically is remote from human facilities. In contrast, in years of small Whitebark Pine seed crops, mortality of adult female Grizzly Bears averaged 2.3 times higher, and mortality of subadult males averaged 3.3 times higher than in years of large seed crops, which the authors attributed to the tendency of bears to range closer to human facilities in years of pine seed scarcity.

Use of Whitebark Pine seeds by bears in Canada has not been clearly described. Whitebark Pine seeds were recorded in the diet of American Black Bears in Banff National Park (Kansas *et al.* 1989; Raine and Kansas 1990), although information on habitat use was limited to the general observation that American Black Bears feeding on Common Juniper (*Juniperus communis* L.) cones, Common Bearberry (*Arctostaphylos uva-ursi* [L.] Sprengel) fruits, and Whitebark Pine seeds frequented higher elevations in moderate to steeply sloping, south-facing, sub-xeric pine forests. Seeds of Whitebark Pine were also eaten by a radio-collared Grizzly Bear in Yoho National Park in 1 year of a 3-year study along the Continental Divide immediately west of Banff National Park (Raine and Riddell 1991). No habitat information was provided other than that this feeding occurred on high-elevation slopes.

McLellan and Hovey (1995) noted that Whitebark Pines were common in their southeast British Columbia study area, but they observed only one case of Grizzly Bears apparently feeding on seeds, and Whitebark Pine seeds did not occur in their sample of scats. In southwestern Alberta, Hamer *et al.* (1991) did not record Grizzly Bear use of Whitebark Pine seeds in Waterton Lakes National Park. In central Alberta, Whitebark Pine seeds were not recorded in Grizzly Bear food-habit studies conducted in Jasper National Park, Banff National Park, or the Jasper–Edson area (Russell *et al.*

1979; Hamer and Herrero 1987; Munro *et al.* 2006), although the Banff study area was northeast of the zone of Whitebark Pine abundance in the park. A Grizzly Bear study (Wielgus 1986) and an American Black Bear study (Holcroft and Herrero 1991) in Kananaskis, immediately east of Banff National Park, also did not record bear use of Whitebark Pine seeds.

We studied Whitebark Pine in and near Banff National Park during 2011–2013 to address the lack of specific research regarding use of pine seeds by bears in this area. Because Mattson and Reinhart (1997) found that all Whitebark Pine seeds eaten by bears in the GYE were obtained from Red Squirrel (*Tamiasciurus hudsonicus*) middens, our principal objectives were to record the abundance, habitat characteristics, and evidence of use by bears of Red Squirrel middens in Whitebark Pine forests. Because field evidence of bear use of middens is not species specific, we also checked areas where radio-collared Grizzly Bears had been located to address the specific question: do Grizzly Bears in Banff National Park eat Whitebark Pine seeds?

Study Area

Banff National Park occupies 6641 km^2 in the central Rocky Mountains of Alberta, Canada. The park extends eastward from the Continental Divide to encompass mountainous habitat of both the Main Ranges and the more easterly, more arid Front Ranges. Elevation in Banff National Park ranges from 1330 m to 3610 m with the tree line at roughly 2300 m. The subalpine zone is at approximately 1500–2350 m, with the upper subalpine (generally cooler and wetter, with deeper and longer lasting snow) beginning at about 2000 m (Achuff 1982). Our study sites were between 1900 m and 2300 m where Whitebark Pine occurs.

We worked in Whitebark Pine stands that exhibited little mortality from White-Pine Blister Rust (*Cronartium ribicola*) or Mountain Pine Beetle (*Dendroctonus ponderosae*). Banff National Park currently has a low rate of White-Pine Blister Rust infection compared with locations north and south along the Rocky Mountains (Smith *et al.* 2008, 2013). Because we located study sites in Whitebark Pine stands, Whitebark Pine was often co-dominant in our plots. Based on basal areas recorded during our analyses, the relative abundance of Whitebark Pine was 38%, Interior Spruce (*Picea engelmannii* var. *engelmannii* × *P. glauca*) 32%, Subalpine Fir (*Abies lasiocarpa* [Hooker] Nuttall) 19%, Lodgepole Pine (*Pinus contorta* Douglas ex Loudon) 11%, and Subalpine Larch (*Larix lyallii* Parlatore) 1%. The understory included submesic Soapberry (*Shepherdia canadensis* [L.] Nuttall)–Common Juniper–Common Bearberry communities; mesic Grouseberry (*Vaccinium scoparium* Leiberg ex Coville) and Grouseberry–Soapberry communities; and subhygric Subalpine Fir (saplings)–False Azalea (*Menziesia ferruginea* J. E. Smith syn. *M. glabella*)–feathermoss (e.g., *Hylocomium splendens, Pleurozium schreberi*) communities (Corns and Achuff 1982).

Methods

Transects

We established belt transects at 10 sites in Whitebark Pine forests to measure the density, habitat characteristics, and use by bears of Red Squirrel middens (i.e., locations where squirrels cache large numbers of conifer cones, shred these cones to obtain seeds, and thus create conspicuous deposits of organic material). We identified Whitebark Pine stands from aerial survey (I. Pengelly and A. Buckingham, Parks Canada, unpublished data), knowledge of Whitebark Pine stands in the park, and reconnaissance from roads and trails. At 71% of our surveyed areas, Whitebark Pine basal area was greater than 4 m^2/ha. We established six transect sites in the main Bow Valley, two in the North Saskatchewan watershed at the north end of the park, and two 0.3 and 2.4 km west of Banff National Park in Kootenay and Yoho national parks, respectively. The average distance between transect sites was 57 km (range 0.2–157 km). Transect sites were 0.4–3.8 km from road access. Fieldwork was conducted from 7 September to 2 October 2011, except at one partly surveyed site where we completed work in 2012.

We used a transect width that allowed the enclosed area to be accurately surveyed without excessive coursing up and down slope. Most transects (51% of hectares surveyed) were 30 m wide and conducted by two people. We also ran 20-, 40-, and 50-m wide transects with one, three, and four people, respectively. We ran transects on the elevational contour of the start point, with one person maintaining this elevation so that middens near a transect edge could be accurately placed inside or outside of the transect.

Transects were 114–607 m long and ended either at a natural feature, such as an avalanche slope or rock talus, or after a preselected distance, commonly 200 or 400 m. Transect length was measured with a hand-held global positioning system (GPS) unit. At the end point, a new transect was typically run in the reverse direction, starting at a preselected distance up or down slope.

Only middens whose centres were inside a transect were recorded. A midden centre was defined as the centre of the "midden tree" (for those formed around the base of a large-diameter tree) when this was unambiguous; otherwise, it was the intersection of the axes of midden length and width. Only middens with conifer-cone debris more than 20 cm deep and covering more than 10 m^2 (> 6 m^2 if depth > 30 cm) were included. These criteria were used to exclude the numerous smaller deposits of cones and cone debris across the landscape that result from squirrel feeding activity. We also defined a secondary (diffuse) midden (Gurnell 1984) as a smaller midden (but meeting our criteria of minimum depth and area) whose centre was also with-

in the transect and that was less than 25 m from a larger midden (average distance 13.8 m). These secondary middens were assumed to be part of the resident squirrel's caching and feeding activity (Gurnell 1984) and, hence, were not analyzed separately to avoid pseudoreplication.

At each midden, we measured midden length (the longest axis of the midden) and width (the greatest dimension at right angles to the long axis) and multiplied these numbers to obtain midden area (Mattson and Reinhart 1997). We recorded location and elevation using a hand-held GPS unit, slope aspect and steepness using a compass with built-in clinometer, and conifer basal area using a 2 m^2/ha prism. Visible Whitebark Pine cones were counted, but we did not disturb middens to tally buried cones. Excavated middens and middens with nearby bear fecal deposits (scats) containing pine seeds were recorded as used by bears.

We also recorded site characteristics at systematic points along transects (null plots). These null plots were placed 160 m from the last midden or transect starting point when no midden occurred within 200 m. We measured distances with a GPS unit and used these distances to locate null plot centres without bias.

GPS-collared Grizzly Bears

During late October 2013, we searched areas where three GPS-collared Grizzly Bears had been located. These bears were collared by Parks Canada for another study and generated GPS locational fixes every 20 minutes to 4 h. We selected a small subset of fixes from those obtained during 7–29 September 2013 in Banff National Park, 1.9–9.0 km from vehicle access, and in upper subalpine areas where Whitebark Pines are found. Google Maps (satellite view) was used as a layer in the geographic information system, QGIS (open-source software, version 2.0.1), to exclude fixes in non-forested habitat. Fixes were searched for signs of bear activity. Red Squirrel middens, if present near the fix, were examined in the same way as those located on our transects.

Data analysis

Sites were our sampling units. For each transect site, we assessed the relation between midden density and conifer basal area and between midden density and the proportion of Whitebark Pines using the linear model in R (open-source software, version 3.0.2). Because of our small sample size, we present differences in characteristics among middens obtained by transecting, middens located at GPS sites, and plots located at null sites visually using box-and-whisker diagrams in R. Secondary middens were excluded from all analyses except for calculation of total middens per hectare.

Results

Middens located by transecting

The mean density of Red Squirrel middens in our 10 transect sites was 1.23 middens/ha (SD 1.17, Table 1) and 1.81 middens/ha (SD 1.84) if secondary middens were included. Mean midden size was 97 m^2 (SD 64, range 30–218 m^2, $n = 8$).

All middens contained Whitebark Pine cone scales, but we found few cached Whitebark Pine cones in 2011 compared with the hundreds we found in several middens during a 1-day pilot project in 2010. In 2011, the three largest caches of Whitebark Pine cones held 195, 67, and 7 cones. No cached Whitebark Pine cones were found in the three middens located at the site completed in 2012.

TABLE 1. Results of transect survey of Red Squirrel (*Tamiasciurus hudsonicus*) middens conducted in Whitebark Pine (*Pinus albicaulis*) stands in and adjacent to Banff National Park, Alberta, 2011–2012.

Transect site	Area surveyed (ha)	No. middens	Mean slope aspect* (°)	Mean slope steepness * (°)	Mean elevation * (m)	Mean basal area of Whitebark Pine* (m^2/ha)	Mean basal area of other conifers* (m^2/ha)	Midden density (no./ha)	Mean midden area (m^2)	Evidence of use by bears
A	4.17	2	41	20	2000	7.0	26.0	0.48	137	Dug, scat
B	3.01	3	240	31	2150	6.0	32.0	1.00	96	Dug, scat
C	2.52	0	265	31	2020	9.0	20.0	0	—	—
D	2.06	4	189	33	2210	27.0	7.2	1.95	39	Dug
E	2.99	11	176	30	2210	11.6	24.7	3.68	51	Dug, scat
F	4.43	6	190	30	2100	10.3	32.7	1.36	68	Dug
G	1.84	0	240	33	1990	6.7	8.0	0	—	—
H	2.44	6	248	22	1960	22.0	27.0	2.46	218	Dug, scat
I	2.05	1	230	34	2150	10.0	24.0	0.49	135	Dug
J	3.61	3	185	23	2070	18.7	8.9	0.83	30	Dug, scat
Total	29.12	36	—	—	—	—	—	—	—	—
Mean	—	—	200	29	2090	12.8	21.1	1.23	97	—
SD	—	—	64	5	90	7.2	9.7	1.17	64	—

*At null plots if no middens occurred at that transect site.

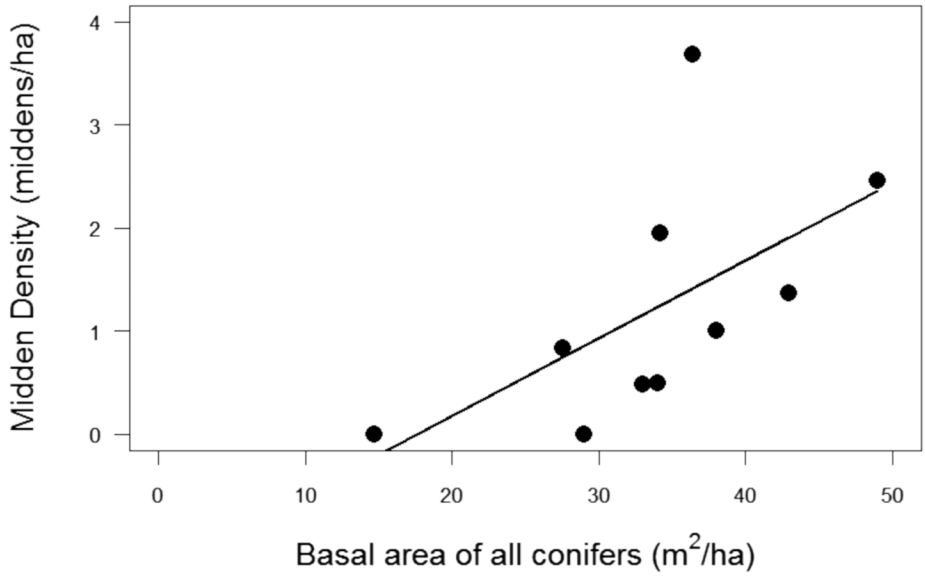

FIGURE 1. Relation between density of Red Squirrel (*Tamiasciurus hudsonicus*) middens and conifer basal area in 10 Whitebark Pine (*Pinus albicaulis*) belt transect sites in and adjacent to Banff National Park, Alberta, 2011– 2012.

We found a weak positive relation between midden density and forest basal area, with total basal area of conifers explaining 27% of the variation in the data (adjusted $r^2 = 0.272$; $F = 4.36$; 1, 8 df; $P = 0.07$; Figure 1). We did not find a relation between midden density and basal area of either Whitebark Pines ($P = 0.2$) or other species of conifer ($P \geq 0.3$) or between midden density and the proportion of total conifer basal area accounted for by Whitebark Pine ($P = 0.7$).

Middens had been excavated by bears at eight of the 10 transect sites; at the two remaining sites, we did not record any middens within the transects (Table 1). Overall, 24 (67%) of the 36 middens found in our transect sites had been dug by bears. Eight (33%) of the 24 dug middens had been excavated recently (i.e., late summer or early autumn 2011). We also found bear scats containing Whitebark Pine seeds at five of the 10 transect sites (Table 1).

Null plots had similar elevation, slope aspect, slope steepness, and basal area of Interior Spruce compared with midden plots (Figure 2a, b, c, and g). However, the basal areas of all conifers, Whitebark Pine, and Subalpine Fir were, respectively, about 1.3, 1.5, and 2.0 times greater at middens than at null plots (Figure 2e, f, and h). Middens tended to occur on less-steep slopes (mean 27.7° [SD 5.5, $n = 8$] than null plots (mean 31.7° [SD 3.4, $n = 8$]).

Use of middens by GPS-collared Grizzly Bears

We located recently dug middens at three GPS fixes of an adult female Grizzly Bear and at two fixes of a subadult male Grizzly Bear. All five dug middens were less than 6 m from GPS fixes and, thus, were linked to Grizzly Bear activity. Bear scats containing Whitebark Pine seeds occurred at three of these GPS sites. The central axes of Whitebark Pine cones, some with attached cone scales, numbered > 100, > 100, 30, 1, and 0 at the five sites. The midden with no identified cone axes contained Whitebark Pine cone scales.

We searched more than 15 satellite fixes from a third GPS-collared Grizzly Bear, at four locations occurring over 8 km linear distance in the park. We did not find Whitebark Pine feeding signs or Whitebark Pine stands at or near any of the fixes from this adult female.

The five middens found at fixes of GPS-collared Grizzly Bears had habitat characteristics notably similar to those of the middens we recorded from transects, including mean elevation (2150 m vs. 2110 m), aspect (210° vs. 190°), and slope steepness (29° vs. 28°). Mean midden size (94 m^2 vs. 97 m^2) and total conifer basal area (35 m^2/ha vs. 37 m^2/ha) were also similar. However, mean Whitebark Pine basal area was 7 m^2/ha at GPS-located middens but 14 m^2/ha at transect middens. Contributing to this difference was one GPS-located midden on a bench with a 16° slope, with no Whitebark Pines at the site (although Whitebark Pine trees were abundant on a steep, 37° slope 35 m away). These comparisons are displayed non-parametrically (i.e., using medians and quartiles) in box-and-whisker diagrams (Figure 2). Our GPS sample is small, but the notable overall similarity between the GPS data and the transect data supports the validity of our midden sampling by transect.

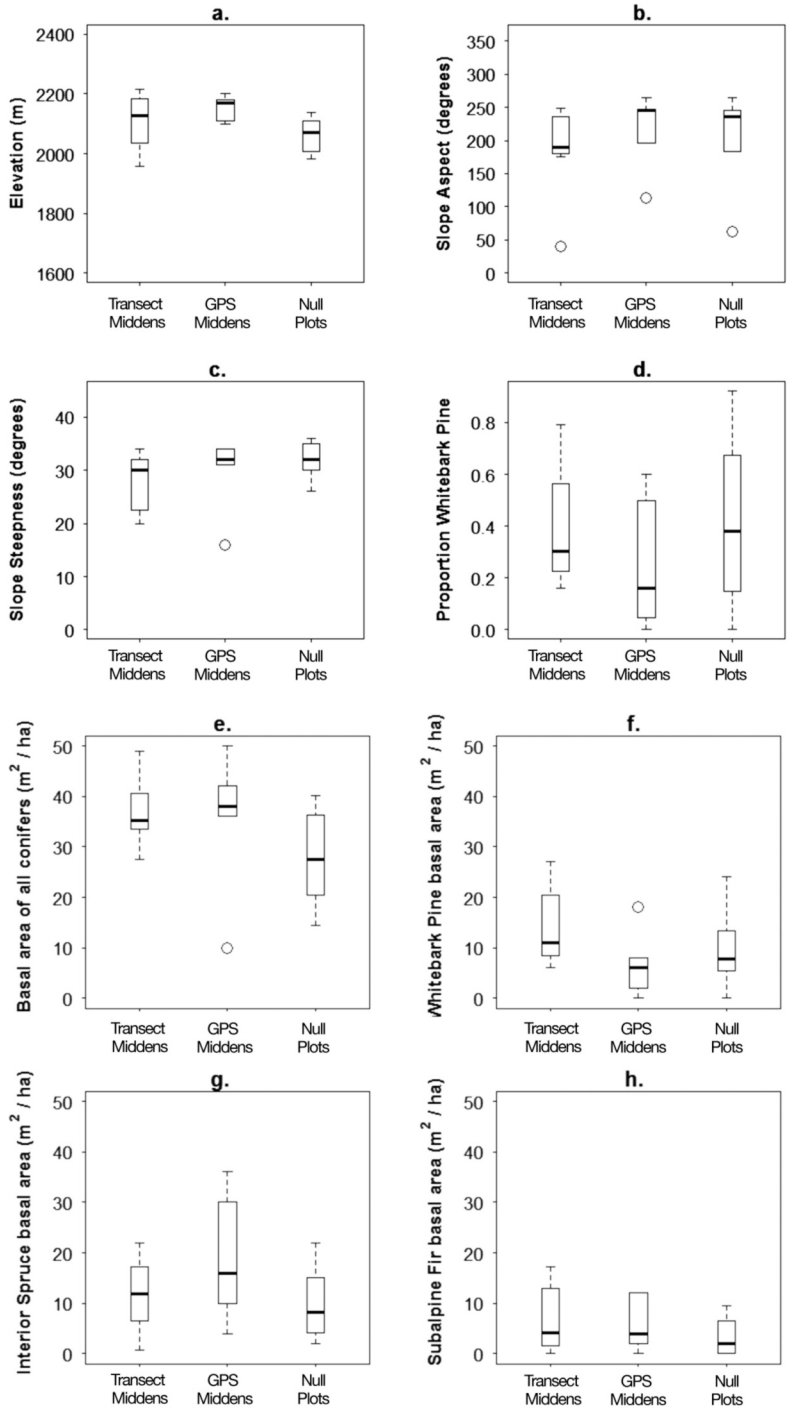

FIGURE 2. Comparison of habitat characteristics at 36 Red Squirrel (*Tamiasciurus hudsonicus*) middens located in eight belt transect sites, five middens within 6 m of satellite fixes of two GPS-collared Grizzly Bears (*Ursus arctos*), and 27 null plots established systematically at 200-m intervals when no midden occurred within a transect for that 200-m distance (8 sites) in Whitebark Pine (*Pinus albicaulis*) stands in and adjacent to Banff National Park, Alberta, 2011–2013. (a) elevation; (b) slope aspect; (c) slope steepness; (d) ratio of Whitebark Pine basal area to total conifer basal area; and basal area of; (e) all conifers; (f) Whitebark Pine; (g) Interior Spruce (*Picea engelmannii* × *P. glauca*); and (h) Subalpine Fir (*Abies lasiocarpa*). Diagrams show median (band inside box), first and third quartiles (top and bottom of box), 1.5 times the interquartile range (ends of whiskers); and outliers beyond the 1.5 interquartile range limits (circles).

Discussion

Our observations of five recently dug Red Squirrel middens within 6 m of fixes obtained from two GPS-collared Grizzly Bears during September 2013, plus the associated scats containing Whitebark Pine seeds, are, to our knowledge, the first conclusive evidence that Grizzly Bears in Banff National Park eat Whitebark Pine seeds.

We found that 67% of the middens located by transecting had been excavated by bears. All eight transect sites where middens were recorded contained excavated middens; however, we did not identify the species of bear involved in these excavations. In 2011, when we ran most transects, middens contained few cached Whitebark Pine cones, and we did not find recently deposited bear scats containing Whitebark Pine seeds as required for DNA sampling. Hence, we were unable to differentiate American Black Bear use from Grizzly Bear use in our transect sites. These results contrast with our 1-day pilot project in 2010 when we found four fresh scats containing pine seeds within 2 ha at a site where we established transects in 2011.

At our transect sites, Whitebark Pine basal area ranged from 0 to 27 m^2/ha, which is higher than the range of 0.2–7 m^2/ha reported for a study area in the nearby Willmore Wilderness Park (McKay and Graham 2010). The greater abundance of Whitebark Pine at our transect sites may partly explain why our mean midden density was greater than the 0.46 middens/ha reported by McKay and Graham (2010). Results from the GYE (Mattson and Reinhart 1997) were more comparable to ours, with Whitebark Pine basal areas of 2–23 m^2/ha and midden densities of 0.2 to 1.1/ha, although only active middens were tallied in that study. Our midden densities were 0–3.7/ha (Table 1). We did not differentiate between active and inactive middens because we judged that such categorization would be subjective and likely unreliable.

The mean basal areas of Whitebark Pine and Subalpine Fir were greater at midden plots than at null plots, but Interior Spruce basal area did not differ substantially. Because squirrels often establish middens at the bases of large trees, our midden basal areas may be high compared with those for the stand where they were located.

Null plots tended to occur on steeper slopes (26–36°) than middens (20–34°). Flatter microsites, including small benches interrupting the main slope, were locations for some middens. These microsites appeared to provide for the accumulation of midden material, allowing Red Squirrels to store cones in the organic debris. In contrast, on many steep slopes, it appeared that cones and conifer debris would readily disperse downhill from gravity and surface water flow.

Whitebark Pine seeds are a valued resource for bears in the GYE (Kendall 1983; Mattson *et al.* 1991; Fortin *et al.* 2013). Whitebark Pine cone abundance was the highest-ranked habitat covariate (along with year, season, sampling regime, and sex of Grizzly Bear) in six best models that explained Grizzly Bear survival in the GYE for 1983–2001 (Schwartz *et al.* 2006). Raine and Kansas (1990) identified Whitebark Pine seeds as part of the diet of American Black Bears in Banff National Park, and we have shown that Grizzly Bears in Banff National Park also eat these seeds.

American Black Bears in Banff National Park appear to be in decline because of high human-caused mortality (Hebblewhite *et al.* 2003). Grizzly Bears in Banff National Park are at the eastern limit of their range, inhabit one of the most intensively developed landscapes in the world where Grizzly Bears still occur, have the slowest reproductive rate of any Grizzly Bear population yet studied, and also experience high levels of human-caused mortality (Garshelis *et al.* 2005). Our study provides managers with information on a potentially important, nutrient-rich food that may give some bears the energy necessary for reproduction (Rogers 1976), and that, when abundant, can move bears into remote, steep habitat where risk of human-caused mortality is lower.

Acknowledgements

Financial support and GPS fixes were provided by Parks Canada. We are also grateful for the contributions of A. Buckingham, M. Didkowsky, A. Forshner, B. Fyten, S. Herrero, T. Jung, B. Low, J. Park, D. Verhulst, J. Whittington, L. Wiggins, N. Woode, and anonymous reviewers. Publication costs for this article were supported by the Thomas H. Manning Fund of The Ottawa Field-Naturalists' Club.

Literature Cited

Achuff, P. L. 1982. Key to vegetation types. Pages 142–145 *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, University of Alberta., Edmonton, Alberta, Canada.

Corns, I. G. W., and **Achuff, P. L.** 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, University of Alberta., Edmonton, Alberta, Canada..

Fortin, J. K., C. C. Schwartz, K. A. Gunther, J. E. Teisberg, M. A. Haroldson, M. A. Evans, and **C. T. Robbins.** 2013. Dietary adjustability of grizzly bears and American black bears in Yellowstone National Park. Journal of Wildlife Management 77: 270–281.

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.

Gurnell, J. 1984. Home range, territoriality, caching behaviour and food supply of the red squirrel (*Tamiasciurus hudsonicus fremonti*) in a subalpine lodgepole pine forest. Animal Behavior 32: 1119–1131.

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.

Hamer, D., S. Herrero, and **K. Brady.** 1991. Food and habitat used by grizzly bears, *Ursus arctos*, along the continental divide in Waterton Lakes National Park, Alberta. Canadian Field-Naturalist 105: 325-329.

Hebblewhite, M., M. Percy, and **R. Serrouya.** 2003. Black bear (*Ursus americanus*) survival and demography in the Bow Valley of Banff National Park, Alberta. Biological Conservation 112:415-425.

Holcroft, A. C., and **S. Herrero.** 1991. Black bear, *Ursus americanus*, food habits in southwestern Alberta. Canadian Field-Naturalist 105:335-345.

Kansas, J. L., R. M. Raine, and **M. L. Gibeau.** 1989. Ecological studies of the black bear in Banff National Park, Alberta, 1986–1988. Final report. Canadian Parks Service, Calgary, Alberta.

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.

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.

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.

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.

McKay, T., and **K. Graham.** 2010. Whitebark pine seeds as a food source for grizzly bears in west central Alberta. 2008/2009 pilot study. Pages 30–47 *in* Foothills Research Institute Grizzly Bear Program, 2009 Annual Report. *Edited by* G. B. Stenhouse and K. Graham. Hinton, Alberta, Canada. Accessed January 2012. https://foothillsri.ca/sites/default/files/null/GBP_2010_04_AnnRpt_2009.pdf

McLellan, B. N., and **F. W. Hovey.** 1995. The diet of grizzly bears in the Flathead River drainage of southeastern British Columbia. Canadian Journal of Zoology 73: 704–712.

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.

Raine, R. M., and **J. L. Kansas.** 1990. Black bear seasonal food habits and distribution by elevation in Banff National Park, Alberta. International Conference on Bear Research and Management 8: 297–304.

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 (*Ursus arctos* L.) in Jasper National Park, 1975–1978. Final report. Canadian Wildlife Service, Edmonton, Alberta, Canada. 136 pages.

Rogers, L. L. 1976. Effects of mast and berry crop failures on survival, growth, and reproductive success of black bears. Transactions of the North American Wildlife and Natural Resources Conference 41: 431–438.

Schwartz, C. C., M. A. Haroldson, G. C. White, R. B. Harris, S. Cherry, D. Moody, and **C. Servheen.** 2006. Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. Wildlife Monograph 161: 33-42.

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 Forestry Research 38: 982–995.

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 Forestry Research 43:90-96.

Wielgus, R. B. 1986. Habitat ecology of the grizzly bear in the southern Rocky Mountains of Canada. Master's thesis, University of Idaho, Moscow, Idaho, USA.

Received 8 April 2014
Accepted 1 December 2014