

FIRE, RED SQUIRRELS, WHITEBARK PINE, AND YELLOWSTONE GRIZZLY BEARS

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Abstract: Whitebark pine (*Pinus albicaulis*) habitats are important to Yellowstone grizzly bears (*Ursus arctos*) as refugia and sources of food. Ecological relationships between whitebark pine, red squirrels (*Tamiasciurus hudsonicus*), and grizzly bear use of pine seeds on Mt. Washburn in Yellowstone National Park, Wyoming, were examined during 1984–86. Following large-scale fires in 1988, we repeated the study in 1995–97 to examine the effects of fire on availability of whitebark pine seed in red squirrel middens and on bear use of middens. Half of the total length of the original line transects burned. We found no red squirrel middens in burned areas. Post-fire linear-abundance (no./km) of active squirrel middens that were pooled from burned and unburned areas decreased 27% compared to pre-fire abundance, but increased in unburned portions of some habitat types. Mean size of active middens decreased 54% post-fire. Use of pine seeds by bears (linear abundance of excavated middens) in pooled burned and unburned habitats decreased by 64%, likely due to the combined effects of reduced midden availability and smaller midden size. We discourage any further large-scale losses of seed producing trees from management-prescribed fires or timber harvesting until the effects of fire on ecological relationships in the whitebark pine zone are better understood.

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Whitebark pine seeds are an important food of Yellowstone grizzly bears; they are high in lipid content and provide a rich source of calories when bears are building fat deposits for winter hibernation (Mattson and Reinhart 1994). During years of abundant whitebark pine cone crops, bears forage almost exclusively on pine seeds, using habitats in the whitebark pine zone, which is typically >2,400 m elevation (Mattson et al. 1992). Conversely, when pine seeds are unavailable, grizzly bears move closer to human facilities and roads, increasing the likelihood of being killed by humans (Blanchard 1990, Mattson et al. 1992).

Red squirrels are important intermediaries for grizzly bears foraging on pine seeds. Red squirrels harvest and cache whitebark pine cones after they mature in late summer and fall (Kendall 1983). A central feature of a red squirrel's territory is the midden, a large, traditionally-used food storage area identified by an accumulation of cone debris (Finley 1969, Rusch and Reeder 1978). In the Yellowstone area, grizzly bears obtain pine seeds mostly by raiding red squirrel middens for cones (Kendall 1983, Reinhart and Mattson 1990, Mattson and Reinhart 1994). Therefore, consideration of red squirrel populations may be very important to effective management of grizzly bear habitat within the whitebark pine zone. Optimum squirrel habitat within the whitebark pine zone consists of habitats with high overstory–basal area and high species diversity on moderate slopes (Reinhart and Mattson 1990, Mattson and Reinhart 1997).

During 1984–89, the Interagency Grizzly Bear Study Team (IGBST) studied the relationships among grizzly bears, red squirrels, and whitebark pine on 2 study areas in the Yellowstone ecosystem (Mattson and Reinhart 1990, 1996, 1997; Reinhart and Mattson 1990). One study area was located on the Mt. Washburn massif in northcentral Yellowstone National Park (Fig. 1). They indexed red squirrel abundance by recording vocalizations, sightings, and middens on line transect surveys. Use of pine seeds by bears was documented by counting excavated middens along the same transects (Reinhart and Mattson 1990).

More than a quarter of Yellowstone's whitebark pine zone burned in 1988 (Renkin and Despain 1992), including approximately 30% of the subalpine forests in the Washburn range and half of the IGBST study area transects. During 1995–97, we replicated the original study to investigate the effects of the habitat changes resulting from the fires. We hypothesized that (1) midden abundance would decline overall in the study area due to loss of suitable red squirrel habitat; (2) midden abundance in unburned stands would either increase due to increased packing of squirrels, or decline if increased area of forest edge degraded the habitat value of remaining forest stands; (3) the ratio of occupied to unoccupied middens would change if squirrel populations changed; (4) the size of active (occupied) middens would be unchanged if squirrel abundance in unburned areas remained the same or declined, but would decrease due to

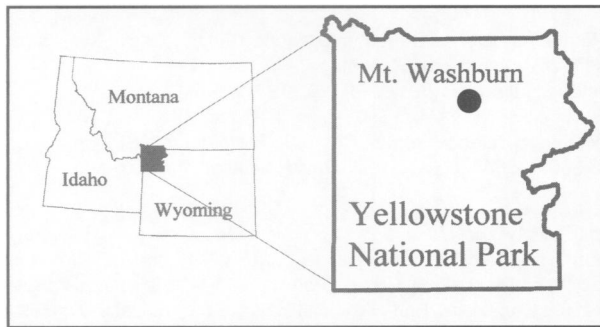


Fig. 1. Study area location on Mt. Washburn, Wyoming, in northcentral Yellowstone National Park, for a study conducted in 1984–86 and 1995–97.

intraspecific competition for available cones if squirrel abundance increased; and (5) use of middens by grizzly bears in the study area would decline compared to pre-fire levels due to an overall decrease in red squirrel midden abundance.

STUDY AREA

The study area was located on the Mt. Washburn massif in northcentral Yellowstone National Park (Fig. 1) and was described in detail by Reinhart and Mattson (1990) and Mattson and Reinhart (1996, 1997). The 9.5-km² study area encompassed the elevational range of mature whitebark pine, from 2,360 m to the upper limits of erect tree growth at 2,870 m. Topography was moderately steep and mainly north- and west-facing. Forest cover on the site was typical of Yellowstone's whitebark pine zone and, aside from burned areas, consisted mostly of mature stands of whitebark pine, lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*). Biomass of whitebark pine varied considerably with site and stand conditions (Mattson and Reinhart 1990).

METHODS

Data collection

We placed 57 line transects throughout the study area (Reinhart and Mattson 1990; Mattson and Reinhart 1996, 1997) and we used 1:20,000-scale aerial photographs and ground truthing to delineate 84 forest stands. We classified stands by standard climax habitat type (Steele et al. 1983) and cover type (Despain 1986). Climax habitat type indicated physical site conditions and potential climax vegetation, whereas cover type indicated current overstory composition and successional stand structure.

Because one objective of the pre-fire study was to examine the main effects of habitat and cover types, transects were situated originally to maximize the length of transects in stand interiors and minimize the length near stand edges by crossing stand boundaries at mostly right angles. Each stand contained portions of 1–6 transects. Total length and the length of burned and unburned portions of transects were measured on aerial photographs and corrected for slope. Transects varied in length from 200 to 1000 m.

We surveyed 29 km of transects each year of the study except 1984, when we surveyed only 17 km. Data collection was consistent between pre- (1984–86) and post-fire (1995–97) study periods. A pair of observers walked each transect, sampling them in the same order each year during 10 August–28 September. The second author sampled all pre-fire years and the senior author sampled all post-fire years. Because red squirrels exhibit fidelity to single middens within their territories (Finley 1969, Smith 1970), we assumed that midden abundance directly reflected squirrel population density. We recorded all red squirrel middens visible from the transect line and referenced them to the closest point along the line. We classified middens as active if currently occupied by a red squirrel (Finley 1969; i.e., we observed a squirrel at the midden or fresh cone clippings) and as used if excavated by a bear. We estimated the age of bear excavations based on the condition of remaining cone cores and weathering of excavated pockets, which clearly distinguished recent (<2 months) from older activity. We measured midden length (longest distance) and width (perpendicular to length) in meters. Midden depth was not recorded.

Analyses

We determined linear abundance (no./km) of squirrel middens and bear-excavated middens. We used linear abundance rather than area density to avoid introducing error associated with estimating probability detection functions (Burnham et al. 1980) and because area densities were not necessary for testing our hypotheses. However, we had to assume that probability of detection did not differ between pre- and post-fire periods or by habitat type. We believe this assumption was reasonable because we used the same sampling procedures in both periods and, based on our observations, changes in vegetative composition of unburned stands were probably small. Due to the high elevation and harsh climate, understory plant communities in the study area change slowly (D.G. Despain, U.S. Geological Survey [USGS], personal communication, Bozeman, Montana, USA, 1998)

Red Squirrel Activity.—We calculated linear abundance of middens by habitat type each year by summing the number of middens encountered in all stands of each habitat type and dividing by the length of transect in each habitat type. We pooled data by habitat type due to the large number of transect segments with no middens observed. We condensed 27 combinations of climax habitat (Steele et al. 1983) and cover (Despain 1986) type classifications into 5 habitat types (Table 1) to increase sample sizes. We used 2-way analysis-of-variance (ANOVA) to test for differences in linear abundance of middens by habitat type and study period for (1) burned and unburned areas, pooled and (2) unburned habitats only. We used 1-tailed *t*-tests to test for post-fire reduction in linear abundance of middens by habitat type (burned and unburned, pooled) and 2-tailed *t*-tests to test

for post-fire change in linear abundance within unburned habitats. A single linear abundance for each habitat type each year constituted the separate observations for these analyses. We tested for differences in average size (length x width) of active middens, by period and habitat type, using 2-way ANOVA. Because the distribution of midden size was skewed, we normalized the data using a natural log transformation prior to testing.

We used 2 x 2 contingency tables to test for differences in the proportion of middens that were active pre- and post-fire by habitat type and for years of different cone abundance. Whitebark pine cone production had been monitored annually in the study area since 1980 (Blanchard 1990). Whitebark pine seed production followed a similar multi-annual pattern during pre- and post-fire study periods (Fig. 2). In each study period, the cone

Table 1. Habitat types used for analysis of line transect data on Mt. Washburn, Yellowstone National Park, 1984–85 and 1995–97. Forest stands were classified by standard climax habitat type and cover type and grouped into 5 categories.

Type	Description
Pure whitebark	<i>P. albicaulis</i> series habitat types with whitebark pine cover types. Typically higher elevation exposed sites with open, mature canopies and sparse understories.
Whitebark–fir	<i>Abies lasiocarpa/Vaccinium scoparium–P. albicaulis</i> habitat type with lodgepole, whitebark, and spruce–fir cover types. Milder sites typically with whitebark pine and other species co-dominant in the canopy, and grouse whortleberry (<i>v. scoparium</i>) prominent in the understory.
Vaccinium	<i>A. lasiocarpa/V. scoparium–V. scoparium</i> habitat type with lodgepole or spruce–fir cover types. Drier sites typically dominated by lodgepole pine with grouse whortleberry dominant in the understory.
Mesic	Typically <i>A. lasiocarpa/V. globulare</i> or <i>A. lasiocarpa/Thalictrum occidentale</i> habitat types. Moist sites with cover types including whitebark pine, lodgepole pine, and spruce–fir.
Wet	Typically <i>A. lasiocarpa/Calamagrostis canadensis</i> habitat types with spruce–fir or whitebark cover types. Lush sites with saturated soils.

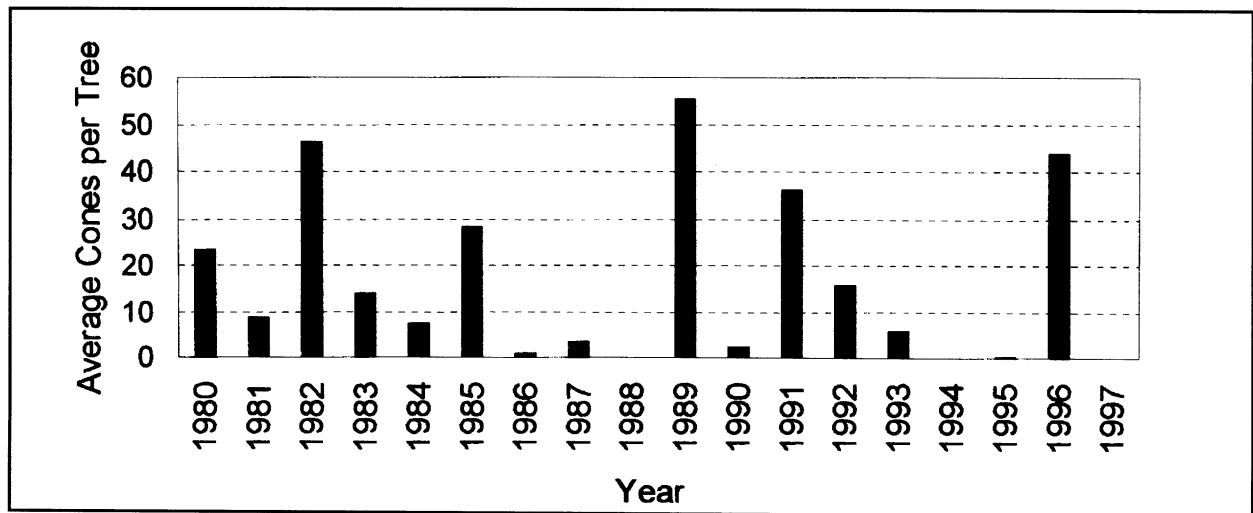


Fig. 2. Annual cone production by whitebark pine along a permanently marked 10-tree transect on Mt. Washburn, Yellowstone National Park (National Park Service, Yellowstone National Park, Wyoming, USA, and USGS Interagency Grizzly Bear Study Team, Bozeman, Montana, USA, unpublished data).

crop was small the first year (following a small–medium crop in the year prior to the study), large the second year, and small the third year. Although cone production was substantially higher in 1996 than in 1985, both were considered high cone production years and we expected bear response to these patterns of crop levels to be similar (Mattson et al. 1994).

Bear Use.—We calculated linear abundance of excavated middens across all habitat types combined for the pre- and post-fire periods. Post-fire, we calculated linear abundance separately for unburned portions of transects and for burned and unburned portions combined. For estimates of bear use, we used only linear abundance of middens excavated during 1985 and 1996, when cone crops were large. Because bears may have excavated middens after we walked the transects and excavations were visible during the following year, we calculated linear abundance of dug middens using excavations found in 1986 and 1997 that were associated with the previous years' cone crops.

Previous studies documented a close association between bear use of pine seeds and crop size (Kendall 1983, Blanchard 1990, Mattson and Reinhart 1994, Mattson et al. 1994). Bears begin using middens as soon as cones are available in the fall and, depending on the size of the crop, may continue feeding on pine seeds into the following year until the seeds are totally consumed (Mattson

et al. 1994). Thus, we attributed excavations of middens estimated to be ≤ 2 months old to the current year's cone crop, and we attributed those estimated at 2–12 months old to the previous year's crop (Mattson and Reinhart 1997).

RESULTS

In 1988, 15 km (49%) of the established transects burned, including portions of all habitat types except the pure whitebark type (Fig. 3). After the fires, the relative abundance (km of transect) of the 5 habitat types remaining in unburned portions of the transects did not differ from their pre-fire relative abundance (Pearson's $\chi^2_4 = 0.93$, $P = 0.92$).

Red Squirrel Activity

We observed no red squirrels or middens in burned areas. Linear abundance of active middens varied before and after the fires (period) ($F_1 = 8.35$, $n = 30$, $P < 0.01$) and by habitat type ($F_4 = 9.84$, $n = 30$, $P < 0.01$), with significant interaction between period and habitat type ($F_4 = 2.86$, $n = 30$, $P = 0.05$; Table 2). Overall, linear abundance of active middens in burned and unburned areas, pooled, decreased 27% post-fire; specifically, abundances decreased in the wet ($t_4 = 2.57$, $P = 0.03$) and *vaccinium* ($t_4 = 4.48$, $P < 0.01$) types, but

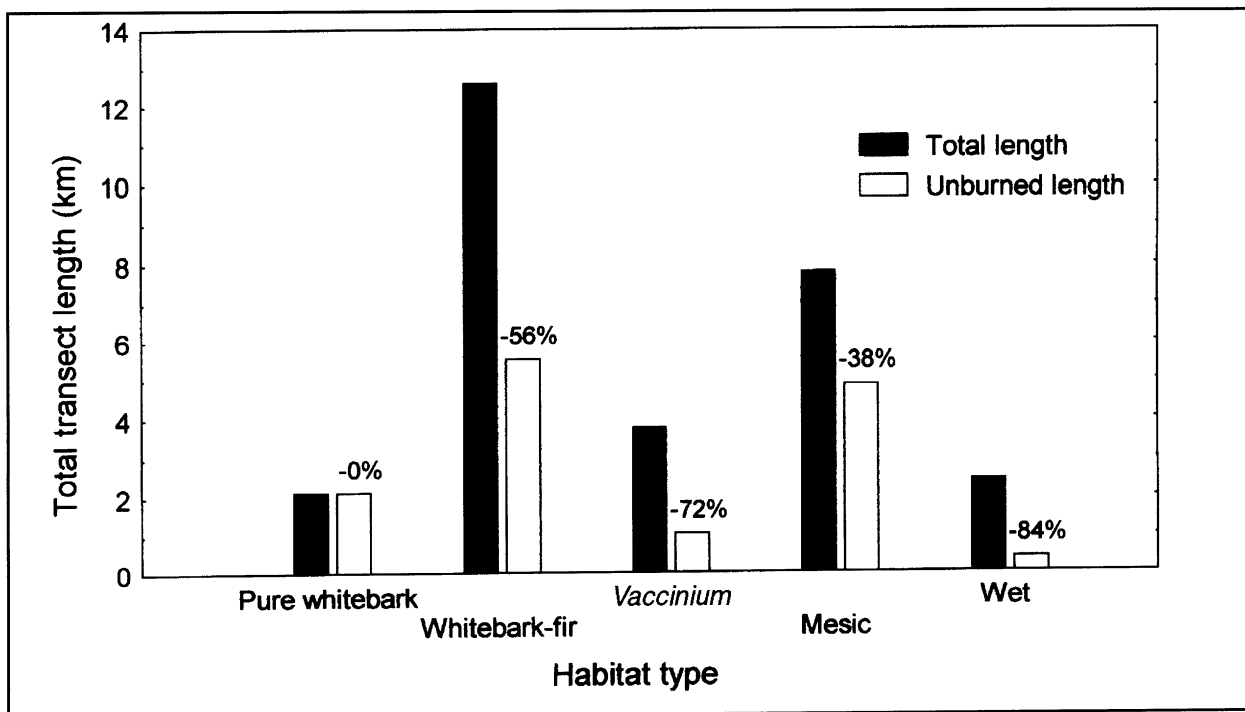


Fig. 3. Total transect length (km) in 5 habitat types on Mt. Washburn, Yellowstone National Park, Wyoming, before (1984–86) and after (1995–97) catastrophic fires in 1988. Percent reduction in unburned transect length after the 1988 fires is noted.

Table 2. Three-year mean^a linear abundance (middens/km) of red squirrel middens by habitat type along transects on Mt. Washburn, Yellowstone National Park, Wyoming, USA, during pre- (1984–86) and post-fire (1995–97) sampling periods.

Habitat types	1984–86		1995–97			
	Active	Total	Burned and unburned, pooled		Unburned	
			Active	Total	Active	Total
Pure whitebark	0.16	0.63	0.00	0.31	0.00	0.31
Whitebark–fir	1.98	5.42	1.53	2.64b	3.49	6.02
<i>Vaccinium</i>	1.62	2.84	0.36c	0.36c	1.28	1.28
Mesic	3.73	6.10	3.63	5.00	5.82	8.01
Wet	3.10	6.37	0.00b	0.14b	0.00d	0.86d
All types	2.35	4.93	1.71	2.60 b	3.51	5.35

^a Individual observations consisted of a singular linear abundance for each habitat type (i.e., number of observations in a habitat type divided by total length of transects in that type) each year, thus $n = 3$ for each mean.

^b Means were significantly lower in the later period; 1-tailed t -test, $P \leq 0.05$.

^c Means were significantly lower in the later period; 1-tailed t -test, $P \leq 0.01$.

^d Means were significantly different between the 2 periods; 2-tailed t -test, $P \leq 0.10$.

Table 3. Counts of middens and χ^2 of homogeneity for proportions of active middens pre- and post-fire, by habitat type along transects on Mt. Washburn, Yellowstone National Park, Wyoming, USA, 1984–86 and 1995–97.

Habitat type	1984–86		1995–97		n	χ^2	df	P
	Active	Inactive	Active	Inactive				
Pure whitebark ^a	1	3	0	2	6	0.60	1	0.439
Whitebark–fir	64	108	58	42	272	11.05	1	0.001
<i>Vaccinium</i> ^a	16	12	4	0	32	2.74	1	0.098
Mesic	77	49	85	32	243	3.63	1	0.057
Wet ^a	18	19	0	1	38	0.92	1	0.336
All types	176	191	147	77	591	17.52	1	0.000

^a Low expected cell frequency (i.e., <5) occurred due to small sample in 1 or both periods.

not in the pure whitebark, whitebark–fir, and mesic types.

Considering only unburned areas post-fire and all areas pre-fire, linear abundance of active red squirrel middens also varied by habitat type ($F_4 = 6.64$, $n = 30$, $P = 0.01$; Table 2), with a significant interaction between the effects of period and habitat type ($F_4 = 2.61$, $n = 30$, $P = 0.07$). Whereas abundance of active middens in the wet type decreased post-fire ($t_4 = 2.57$, $P = 0.06$), other habitat types showed no significant change.

Although the overall linear abundance of active middens declined, the ratio of active to inactive middens increased post-fire; across all habitat types, 48% of middens observed in the pre-fire period were active versus 66% post-fire ($\chi^2_1 = 17.52$, $n = 591$, $P < 0.01$; Table 3). This was due primarily to an increase in the proportion of active middens in the whitebark–fir type ($\chi^2_1 = 11.05$, $n = 272$, $P < 0.01$). Considering only the years with large cone crops (1985 and 1996), results were the same; a greater proportion of middens was active in 1996 than in 1985 ($\chi^2_1 = 47.94$, $n = 266$, $P < 0.01$). In other years, the proportions of active middens did not differ between periods.

The size of active red squirrel middens differed by study period ($F_1 = 13.16$, $n = 466$, $P < 0.01$) and habitat type ($F_4 = 7.07$, $n = 466$, $P < 0.01$). However, there was no interaction between the effects of period and habitat type

($F_4 = 0.76$, $n = 466$, $P = 0.56$). Mean midden size decreased 54% post-fire (Table 4).

Bear Use

Use of whitebark pine seeds by bears reflected cone abundance; more bear-excavated middens were found during and immediately following years with abundant cone crops (e.g., during the 2nd and 3rd year of each sampling period; Table 5) than during the first year of each period, when cone production had been poor for 2 years. Most middens excavated by bears were observed the year following a large cone crop (i.e., bears continued to excavate middens either in the fall after we sampled or the following spring). Pooling burned and unburned areas, linear abundance of excavated middens during the post-fire study period was 64% less than during the pre-fire period. In the unburned portion of the post-fire study area, linear abundance of excavated middens decreased 25% from the pre-fire period. The average size of middens excavated in 1996 was 40% smaller than in 1985 (1-sided $t_{56} = 3.32$, $P = 0.002$).

DISCUSSION

Fire had a major influence on red squirrel midden numbers on Mt. Washburn. We found no red squirrels or

Table 4. Mean size (m²) of active red squirrel middens by habitat type along transects on Mt. Washburn, Yellowstone National Park, Wyoming, before (1984–86) and after (1995–97) catastrophic fires in 1988.

	1984–86			1995–97		
	\bar{x}	SE	<i>n</i>	\bar{x}	SE	<i>n</i>
Pure whitebark	3.0					0
Whitebark–fir	86.2	16.1		44.0	11.10	56
<i>Vaccinium</i>	64.7	14.4	15	4.5	1.30	3
Mesic	46.9	5.3	68	18.8	3.40	81
Wet	46.7	11.5	14			0
All types	61.7	6.3	148	28.6	4.96	1.4

Table 5. Yearly counts of red squirrel middens excavated by bears along transects on Mt. Washburn, Yellowstone National Park, Wyoming, USA, 1984–86 and 1995–97, and linear abundances of excavations associated with abundant whitebark pine cone crops in 1985 and 1996.

	Current crop	Previous crop	Middens/km	Middens/km unburned
Pre-fire				
1984	2	13		
1985 ^{a,b}	40	18	1.53	1.53
1986	0	44		
Post-fire				
1995	0	0		
1986 ^{a,b}	5	1	0.56	1.15
1997	0	16		

^a Year of abundant cone crop.

^b Because excavations may have occurred after sampling dates, linear abundances of excavated middens for each abundant cone crop were calculated using digs found in the following year.

middens in the burned portion of the study area 7–9 years after the 1988 fires. Despite increases in squirrel abundance in unburned portions of the 2 most common habitat types, overall linear abundance of active middens still decreased by 27%. This significantly reduced the number of whitebark pine cones available to bears within the study area. Moreover, active midden size decreased, and Mattson and Reinhart (1997) showed that grizzly bears obtain fewer cones from smaller middens.

The probability that a bear will excavate a midden is strongly related to midden size (Mattson and Reinhart 1997). Bears could be less inclined to excavate small versus large middens, as they offer less energetic profit. Small middens are less likely to be occupied by a red squirrel and may be less detectable by bears (Mattson and Reinhart 1997). Based on Mattson and Reinhart's (1997) model and the size of middens we measured in post-fire years, we expected a 50% decrease in the likelihood of use by bears. Combined with the 27% decrease in the number of active middens post-fire, the model predicted a 64% reduction in abundance of middens excavated by bears, very close to the actual 63% decline that we observed. Thus, bear feeding activity in the whitebark pine zone decreased disproportionately more than midden abundance. Moreover, bears likely obtained less food

from each excavation, as they were using smaller middens. Although we could not test such a prediction, the non-linear relation between midden size and number of excavated cones presented by Mattson and Reinhart (1997) suggests that the actual number of cones obtained by bears in the study area may have declined by about 79% due to local effects of the fires on midden abundance and size.

Our data suggested that red squirrels may have been more abundant post-fire than pre-fire in unburned parts of the study area, specifically in the whitebark–fir and mesic habitat types. However, due to the high variability among habitat types and our small sample size for each type (3 pre- and 3 post-fire years), we were not able to demonstrate this statistically. For example, depending upon habitat type, an additional change of 0.3–4.3 middens/km would have been required to detect differences at our sample size of 3 years for each period ($P < 0.1$, Power > 0.8 ; USGS Interagency Grizzly Bear Study Team, Bozeman, Montana, USA, unpublished data). Potential explanations for higher linear abundances could include (1) red squirrels adjusted to the loss of habitat initially by packing into smaller territories; (2) abundance increased due to large crops of seeds from other conifers such as lodgepole pine, subalpine fir, and Engelmann spruce (Kemp and Keith 1970, Smith 1970, Mattson and Reinhart 1997); and (3) abundance increased due to potentially favorable changes in annual climatic conditions (Smith 1968, Rusch and Reeder 1978). We did not collect data on other cone crops or local climate by which to test the latter 2 hypotheses. However, the smaller average sizes of middens during the post-fire study, despite similar or greater abundance of whitebark pine cones, supports the hypothesis that squirrels adjusted to change in habitats by using smaller territories (Reinhart and Mattson 1990).

Additionally, the higher diversity of overstory species in the whitebark–fir and mesic types (Mattson and Reinhart 1990) may have provided, year-to-year, a more diverse, and hence more stable, food supply relative to other habitat types, allowing disproportionate increases in midden abundance within unburned areas of those

types. Lower red squirrel abundance in the pure whitebark type may have been related to the small whitebark pine cone crops in the years preceding the post-fire study and the lack of alternative conifer seed sources (Reinhart and Mattson 1990). Lower abundances in the wet and vaccinium types may have been artifacts of error introduced by a much smaller sample size (Halvorson 1984).

Line transects have been used to describe the relative abundance and habitat use of wildlife populations (Eberhardt 1978, Halvorson 1984, Mattson and Reinhart 1996) and are useful for comparing data among areas and periods. The use of line transects was appropriate for this study because we compared patterns of red squirrel abundance and bear use of whitebark pine seeds in the same area following significant habitat change. Differences between the pre- and post-fire periods can likely be attributed to habitat changes because census techniques for the 2 study periods were identical and the pattern and size of cone crops were similar.

Based on previous analyses of grizzly bear use of whitebark pine seeds (Blanchard 1990, Mattson and Reinhart 1994, Mattson et al. 1994), we concluded that whitebark pine cone crops were functionally the same between periods. Mattson et al. (1994) found an acutely sigmoidal relationship between bear use of pine seeds and cone crop levels; substantial use began when mean cones/tree exceeded 21 and peaked when mean cones/tree exceeded 27. However, as cone production could not be controlled, the 2 scenarios were not precisely identical. Fluctuations in size of the whitebark pine crop were somewhat greater in the post-fire period. We also lacked empirical data on cone production by other species (i.e., Engelmann spruce, subalpine fir, and lodgepole pine), that could have influenced squirrel populations.

MANAGEMENT IMPLICATIONS

The fires of 1988 burned an estimated 27.5% of the whitebark pine in Yellowstone National Park (Renkin and Despain 1992). This amounted to a sizable decrease in whitebark pine seeds available to Yellowstone grizzly bears. This loss will not be recovered for some time, given the slow rate of whitebark pine maturation and length of time before the trees produce seeds (70–100 years; McCaughey and Schmidt 1990). However, burned habitats facilitate whitebark pine regeneration by providing more seed-caching sites for Clark's nutcrackers (*Nucifraga columbiana*; Tomback 1994) and may produce other foods used by bears (Blanchard and Knight 1996). Even so, the roots and grazed foods used more

commonly in burns after the fires do not provide as concentrated an energy source for bears as pine seeds (Pritchard and Robbins 1990).

Whitebark pine is at risk throughout much of the species' range in North America due to white pine blister rust (*Cronartium ribicola*), a fungus introduced from Europe in 1910 (Kendall and Arno 1990). Mortality rates of whitebark pine from this disease have been as high as 90% in the northwestern portion of the species range (Kendall and Arno 1990). In the colder, drier climate of the Yellowstone area, whitebark pine mortality from blister rust is low, about 4% (Kendall 1998). However, stands that now contain low levels of infection may become imperiled under a global warming scenario (Reinhart and Mattson 1990, Romme and Turner 1991).

Whitebark pine habitat is extremely important to grizzly bears in the Yellowstone ecosystem, as both a refuge and a food source. We recommend more study on the ecological effects of fire and fire management on the long-term health of whitebark pine and its associations with wildlife species. Until these relationships are better understood, we encourage caution in the management of whitebark pine habitats. To prevent further loss of whitebark pine habitat and seed-producing trees in the Yellowstone grizzly bear's range, we discourage timber harvesting or use of management-prescribed fires in the whitebark pine zone. Management of whitebark pine forests for grizzly bears should emphasize maintaining large, secure areas of diverse habitat types supporting stable numbers of whitebark pine trees and red squirrels.

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LITERATURE CITED

- BLANCHARD, B.M. 1990. Relationships between whitebark pine cone production and fall grizzly bear movements. Pages 362–363 in W.C. Schmidt and K.J. McDonald, editors. Proceedings of a symposium on whitebark pine ecosystems: ecology and management of a high mountain resource. U.S. Forest Service General Technical Report INT-270.

- _____, AND R.K. KNIGHT. 1996. Effects of wildfire on grizzly bear movements and food habits. Pages 117–122 in J.M. Greenlee, editor. Ecological implications of fire in Greater Yellowstone: proceedings of the second biennial scientific conference on the Greater Yellowstone Ecosystem. International Association of Wildland Fire, Fairfield, Washington, USA.
- BURNHAM, K.P., D.R. ANDERSON, AND J.L. LAAKE. 1980. Estimation of density from line transect sampling of biological populations. *Wildlife Monographs* 72.
- DESPAIN, D.G. 1986. Habitat type and cover type as a base for grizzly bear mapping and evaluation. Pages 230–233 in Proceedings—grizzly bear habitat symposium. U.S. Forest Service General Technical Report INT-207.
- EBERHARDT, L.L. 1978. Transect methods for population studies. *Journal of Wildlife Management* 42:1–31.
- FINLEY, R.B., JR. 1969. Cone caches and middens of *Tamiasciurus* in the Rocky Mountain region. University of Kansas Museum of Natural History Miscellaneous Publications 51:233–273.
- HALVORSON, C.H. 1984. Long term monitoring of small vertebrates: a review with suggestions. Pages 11–25 in J.L. Johnson, J.F. Franklin, and R.G. Krebill, editors. Proceedings—research in natural areas: baseline monitoring and management. U.S. Forest Service General Technical Report INT-173.
- KEMP, G.A., AND L.B. KEITH. 1970. Dynamics and regulation of red squirrel (*Tamiasciurus hudsonicus*) populations. *Ecology* 51:763–779.
- 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.
- _____. 1998. Whitebark pine. Pages 483–485 in M.J. Mack, P.A. Opler, C.E. Puckett Haeker, and P.D. Doran, editors. Status and trends of the nation's biological resources. Volume 2. U.S. Department of the Interior, U.S. Geological Survey, Reston, Virginia, USA.
- _____, AND S.F. ARNO. 1990. Whitebark pine—an important but endangered wildlife resource. Pages 264–273 in W.C. Schmidt and K.J. McDonald, editors. Proceedings of a symposium on whitebark pine ecosystems: ecology and management of a high mountain resource. U.S. Forest Service General Technical Report INT-270.
- 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.
- _____, AND D.P. REINHART. 1990. Whitebark pine on the Mount Washburn massif, Yellowstone National Park. Pages 106–117 in W.C. Schmidt and K.J. McDonald, editors. Proceedings of a symposium on whitebark pine ecosystems: ecology and management of a high mountain resource. U.S. Forest Service General Technical Report INT-270.
- _____, AND _____. 1994. Bear use of whitebark pine seeds in North America. Pages 212–220 in W.C. Schmidt and F.K. Holtmeier, editors. Proceedings of an international workshop on subalpine stone pines and their environments: the status of our knowledge. U.S. Forest Service General Technical Report INT-GTR-309.
- _____, AND _____. 1996. Indicators of red squirrel (*Tamiasciurus hudsonicus*) abundance in the whitebark pine zone. *Great Basin Naturalist* 56:272–309.
- _____, AND _____. 1997. Excavation of red squirrel middens by grizzly bears in the whitebark pine zone. *Journal of Applied Ecology* 34:926–940.
- _____, _____, AND B.M. BLANCHARD. 1994. Variation in production and bear use of whitebark pine seeds in the Yellowstone area. Pages 205–220 in D.G. Despain, editor. Plants and their environments: proceedings of the first biennial scientific conference on the Greater Yellowstone Ecosystem. U.S. National Park Service Technical Report NPS/NRYELL/NRTR.
- MCCAUGHEY, W.W., AND W.C. SCHMIDT. 1990. Autecology of whitebark pine. Pages 85–96 in W.C. Schmidt and K.J. McDonald, editors. Proceedings of a symposium on whitebark pine ecosystems: ecology and management of a high mountain resource. U.S. Forest Service General Technical Report INT-270.
- PRITCHARD, G.T., AND C.T. ROBBINS. 1990. Digestive and metabolic efficiencies of grizzly and black bears. *Canadian Journal of Zoology* 68:1645–1651.
- REINHART, D.P., AND D.J. MATTSON. 1990. Red squirrels in the whitebark pine zone. Pages 256–263 in W.C. Schmidt and K.J. McDonald, editors. Proceedings of a symposium on whitebark pine ecosystems: ecology and management of a high mountain resource. U.S. Forest Service General Technical Report INT-270.
- RENKIN, R.R., AND D.G. DESPAIN. 1992. Fuel moisture, forest type, and lightning-caused fire in Yellowstone National Park. *Canadian Journal of Forestry Research* 22:27–45.
- ROMME, W.H., AND M.G. TURNER. 1991. Implications of global climate change for biogeographical patterns in the greater Yellowstone ecosystem. *Conservation Biology* 5:373–386.
- RUSCH, D.A., AND W.G. REEDER. 1978. Population ecology of Alberta red squirrels. *Ecology* 59:400–420.
- SMITH, C.C. 1970. The coevolution of pine squirrels and conifers. *Ecological Monographs* 40:349–371.
- SMITH, M.C. 1968. Red squirrel response to spruce cone failure in interior Alaska. *Journal of Wildlife Management* 32:305–317.
- STEELE, R., S. COOPER, D. ONDOV, D. ROBERTS, AND R. PFISTER. 1983. Forest habitat types of eastern Idaho—western Wyoming. U.S. Forest Service General Technical Report INT-144.
- TOMBACK, D.F. 1994. Effects of seed dispersal by Clark's nutcracker on early postfire regeneration of whitebark pine. Pages 193–198 in W.C. Schmidt and F.K. Holtmeier, editors. Proceedings of an international workshop on subalpine stone pines and their environments: the status of our knowledge. U.S. Forest Service General Technical Report INT-GTR-309.