Grizzly bear use of whitebark pine habitats in the Washburn Range
by Shannon Rhea Podruzny

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Fish and Wildlife Management
Montana State University

Abstract:
Whitebark pine (Pinus albicaulis) habitats are important to Yellowstone grizzly bears (Ursus arctos) as refuges and sources of food. In 1988, large-scale fires burned 28% of the whitebark pine in Yellowstone National Park. I examined grizzly bear use of whitebark pine habitats in the Washburn Bear Management Unit in north central Yellowstone National Park before (1978-87) and after (1989-97) the fires. Radiocollared grizzly bears were not located in habitat types in proportion to their availability, patterns of habitat selection were similar in both periods, and differences in habitat use and availability were more pronounced in years of good whitebark pine cone crops. Ground investigations revealed that sites used by grizzly bears for feeding on whitebark pine seeds were similar in both periods. I compared sites used by bears to randomly sampled sites within the whitebark pine zone in 1996. Bears selected sites that were generally higher in elevation, steeper, and more densely forested than random sites. White pine blister rust (Cronartium ribicold), a disease which threatens whitebark pine populations across the continent, was present in 9% of the whitebark pines on sampled plots. Grizzly bears obtain whitebark pine seeds mainly by raiding red squirrel (Tamiasciurus hudsonicus) cone caches, or middens. I repeated (1995-97) a study that examined the relationships between whitebark pine, red squirrels, and grizzly bears on Mt. Washburn proper (1984-86). Half of the study transects burned in 1988. Red squirrel midden density increased in unbumed areas, but decreased overall. Midden size's were 51% smaller post-fire, and bear use of middens decreased by 64% post-fire. Whereas the fires did not disrupt grizzly bear use patterns on a large scale, significant local effects were evident. I recommend (1) prevention of further large-scale losses of whitebark pine habitats until burned areas regenerate and (2) investigation of the effects of the fires on grizzly bear use of whitebark pine seeds on an ecosystem-wide scale.

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APPROVAL

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This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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ABSTRACT

Whitebark pine (*Pinus albicaulis*) habitats are important to Yellowstone grizzly bears (*Ursus arctos*) as refuges and sources of food. In 1988, large-scale fires burned 28% of the whitebark pine in Yellowstone National Park. I examined grizzly bear use of whitebark pine habitats in the Washburn Bear Management Unit in north central Yellowstone National Park before (1978-87) and after (1989-97) the fires. Radiocollared grizzly bears were not located in habitat types in proportion to their availability, patterns of habitat selection were similar in both periods, and differences in habitat use and availability were more pronounced in years of good whitebark pine cone crops. Ground investigations revealed that sites used by grizzly bears for feeding on whitebark pine seeds were similar in both periods. I compared sites used by bears to randomly sampled sites within the whitebark pine zone in 1996. Bears selected sites that were generally higher in elevation, steeper, and more densely forested than random sites. White pine blister rust (*Cronartium ribicola*), a disease which threatens whitebark pine populations across the continent, was present in 9% of the whitebark pines on sampled plots. Grizzly bears obtain whitebark pine seeds mainly by raiding red squirrel (*Tamiasciurus hudsonicus*) cone caches, or middens. I repeated (1995-97) a study that examined the relationships between whitebark pine, red squirrels, and grizzly bears on Mt. Washburn proper (1984-86). Half of the study transects burned in 1988. Red squirrel midden density increased in unburned areas, but decreased overall. Midden sizes were 51% smaller post-fire, and bear use of middens decreased by 64% post-fire. Whereas the fires did not disrupt grizzly bear use patterns on a large scale, significant local effects were evident. I recommend (1) prevention of further large-scale losses of whitebark pine habitats until burned areas regenerate and (2) investigation of the effects of the fires on grizzly bear use of whitebark pine seeds on an ecosystem-wide scale.

INTRODUCTION

Whitebark pine (*Pinus albicaulis*) seeds are an important food of Yellowstone grizzly bears (*Ursus arctos*) (Blanchard 1980, Kendall 1983, Mattson and Jonkel 1990, Mattson et al. 1991). The lipid-rich seeds provide a high-calorie food source of particular value when bears are building fat deposits during hyperphagia (Mealey 1980, Mattson and Reinhart 1994). Annual cone crops vary greatly, with little or no cone production occurring between irregular intervals of large crop yields (Arno and Hoff 1989). Yellowstone grizzlies consume whitebark pine seeds almost exclusively when the seeds are available in sufficient quantities (Blanchard 1990, Mattson et al. 1992). Extensive use of pine seeds occurs when cone crops are large, averaging >13-23 cones per tree on monitored transects (Blanchard 1990, Mattson and Reinhart 1994). In years of low cone crops, bears forage closer to human facilities and roads, increasing the number of management actions and bear mortalities (Mattson et al. 1992).

Red squirrels (*Tamiasciurus hudsonicus*) are important intermediaries for grizzly bears foraging on pine seeds. Red squirrels harvest the indehiscent cones after they mature in late summer and fall (Kendall 1983) and cache them in middens within their territories (Smith 1970). Middens are food storage areas identified by the accumulation of cone debris (Finley 1969). A midden may be used by successive generations of red squirrels, and is a central feature of each individual's territory (Finley 1969, Rusch and Reeder 1978). Yellowstone grizzlies obtain whitebark pine seeds mainly by raiding middens and taking cones (Kendall 1983, Reinhart and Mattson 1990, Mattson and

Reinhart 1994). Therefore, consideration of red squirrel populations may be important to effective management of grizzly bear habitat within the whitebark pine zone.

The Interagency Grizzly Bear Study Team (IGBST) studied the relationships among grizzly bears, red squirrels, and whitebark pine on the Mt. Washburn massif from 1984-87 (Reinhart and Mattson 1990, Mattson and Reinhart 1990, 1996, 1997). Vocalizations, sightings, and middens recorded on line transects served as indices of red squirrel abundance. Use of pine seeds by bears was documented with counts of 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% subalpine forests of the Washburn Range and half of the red squirrel study transects. Stand-replacing fires may benefit whitebark pine populations by creating open sites where regeneration is most successful (Morgan et al. 1994). However, as cone production remains relatively low until stands are more than 100 years old (Weaver et al. 1990), a considerable amount of effective whitebark pine habitat for grizzly bears has been removed for much of the next century.

Whitebark pine populations across the northern Rocky Mountains are declining or at risk from the effects of white pine blister rust (*Cronartium ribicola*), mountain pine beetles (*Dendroctonus ponderosae*), and advancing succession due to fire suppression (Keane and Morgan 1994, Kendall and Arno 1990, Kendall 1994). White pine blister rust, a fungus introduced into this continent from Europe in 1910, is considered to be the most damaging factor across the range of whitebark pine (Arno and Hoff 1989, Keane and Morgan 1994, Hoff and Hagle 1990). Whitebark pine mortality rates from blister rust in northwest Montana have been as high as 90%, and mortality rates are increasing southward along the Continental Divide towards Yellowstone (Keane and Morgan 1994). Mortality rates in Yellowstone's colder, drier climate are currently low, about 4% (Kendall, in press).

Reduction of mast crops due to mortality of mature trees and lower productivity of infected trees may hinder the recovery of grizzly bear populations (Kendall and Arno 1990). To assess current grizzly bear use of whitebark pine habitats and the effects of the 1988 fires, I examined data collected by myself and the IGBST in northcentral Yellowstone National Park. The specific study objectives were to:

1. Compare use and availability of whitebark pine habitats in both the pre- and post-fire periods on a coarse scale using radiolocation data and digital vegetation maps;

2. Compare specific physical and vegetative characteristics of sites used by bears before the fires with sites used after the fires;

3. Examine random sites within whitebark pine habitats for specific characteristics (e.g., whitebark pine crown diameter, levels of pathogens) for comparison with whitebark pine sites used in the same year; and

4. More specifically quantify the effects of the fires on red squirrels and bear use of whitebark pine seeds by repeating the original Mt. Washburn transect study.

STUDY AREA

The Washburn Bear Management Unit served as the study area (Figure 1). The 831 km^2 area encompassed the Washburn Range in northcentral Yellowstone National Park. Elevations ranged from 1600 m at the north entrance of the park to 3150 m at Mt. Washburn in the southeast portion of the study area. The climate of the area was characterized by long, cold winters and cool summers (Dirks and Martner 1982). Average temperature for January, the coldest month, was –10.6° C at the Tower Falls climate station (Dirks and Martner 1982). Average maximum temperature for July, the warmest month, was 26.3° C (Dirks and Martner 1982).

The study area contained a wide variety of plant communities. Big sagebrush (*Artemesia tridentata*)/Idaho fescue (*Festuca idahoensis*) communities and Douglas fir (*Pseudotsuga menziesii*) or lodgepole pine (*Pinus contorta*) forests were typical of the northern portion of the study area (Despain 1990). Lodgepole pine forests, mostly in the subalpine fir (*Abies lasiocarpa*)/grouse whortleberry (*Vaccinium scoparium*) climax habitat type, blanketed the rhyolite flows of the Central Plateau in much of the study area (Despain 1990). The Washburn Range, remnants of 40 million-year-old Abasaroka volcanoes (Keefer 1971), remained as islands above the more recent lava flows in the central and eastern portion of the study area. Those mountains supported a wide variety of forested habitat types, including subalpine fir/western meadowrue (*Thalictrum occidentale*) and subalpine fir/grouse whortleberry-whitebark pine climax types, interspersed with smaller patches of non-forested areas (Despain 1990).

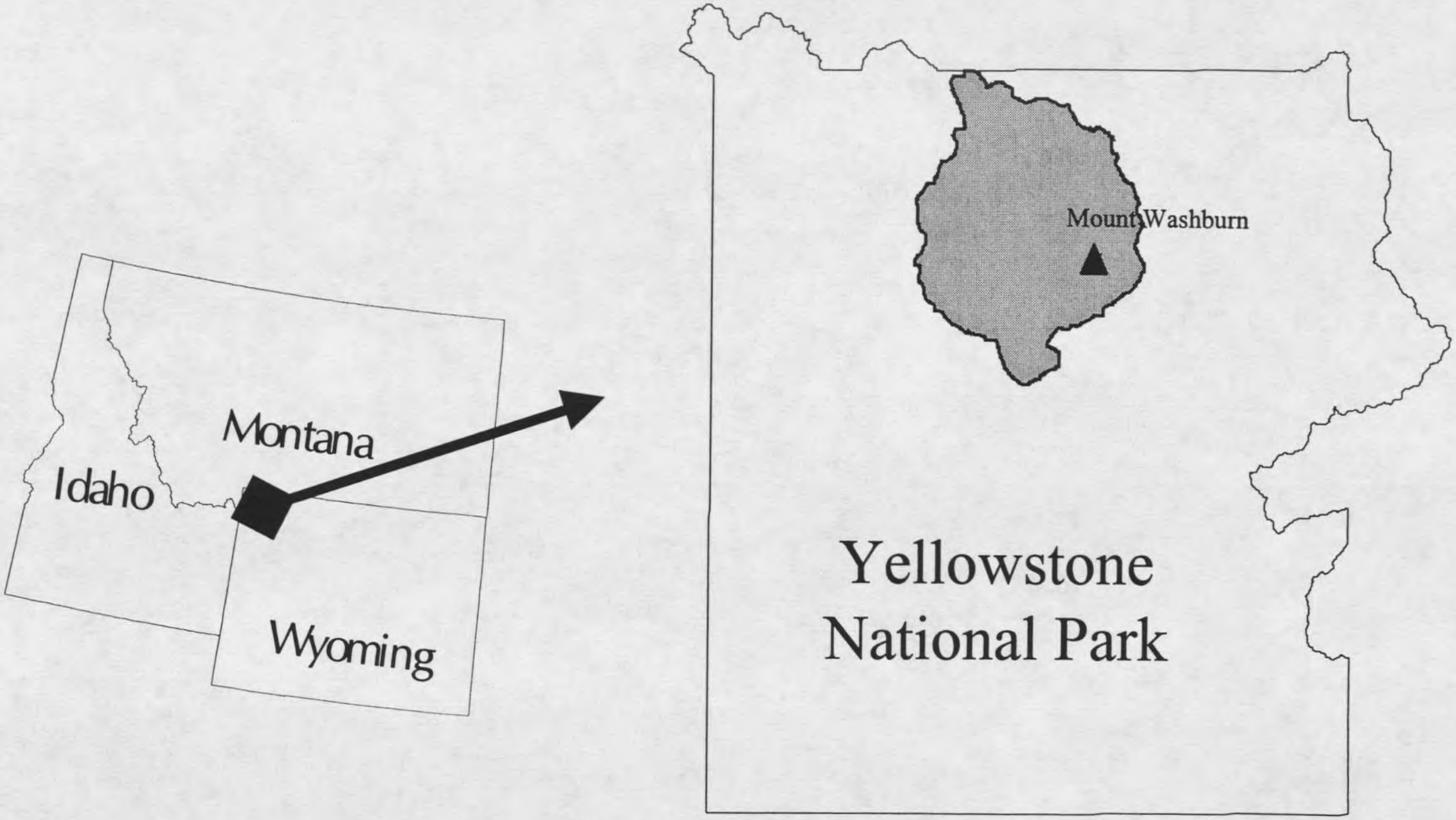


Figure 1. The study area, as delineated by the boundaries of the Washburn Bear Management Unit in northcentral Yellowstone National Park.

Other large carnivores inhabited the study area, including gray wolves (*Canis lupus*), coyotes (*Canis latrans*), bobcats (*Felis rufus*), mountain lions (*Felis concolor*), and black bears (*Ursus americanus*). The area also supported bighorn sheep (*Ovis canadensis*), mule deer (*Odocoileus hemionus*), Shiras moose (*Alces alces*), and abundant elk (*Cervus elaphus*) populations. Other species in the study area were known to use whitebark pine seeds, including Clark's nutcrackers (*Nucifraga columbiana*), Stellar's jays (*Cyanocitta stelleri*), ravens (*Corvus corax*), pine grosbeaks (*Pinicola enucleator*), mountain chickadees (*Parus gambeli*), red-breasted nuthatches (*Sitta canadensis*), red squirrels, and chipmunks (*Eutamias* spp.) (Hutchins 1990).

The red squirrel transect study area (Figure 2) was located on the northwest portion of Mt. Washburn, and was described in detail by Reinhart and Mattson (1990) and Mattson and Reinhart (1996, 1997). This 9.5 km^2 study area ranged in elevation from 2,360 m to 2,870 m. Topography was moderately steep and mainly north- and west-facing. Forest cover in the area was typical of Yellowstone's whitebark pine zone and, aside from burned areas, consisted mostly of mature stands of whitebark pine, lodgepole pine, subalpine fir, and Englemann spruce (*Picea engelmannii*).

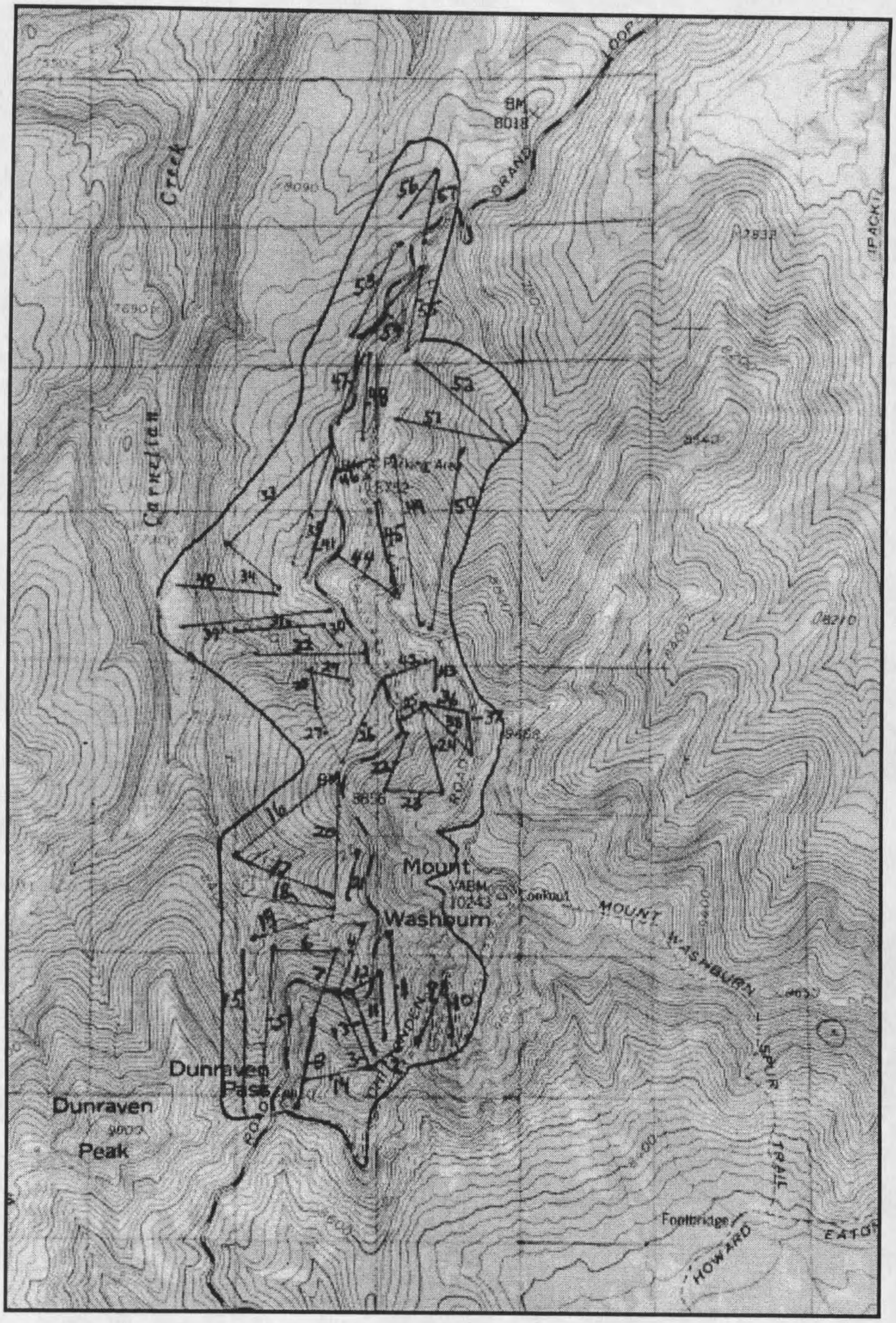


Figure 2. Red squirrel transects, Mt. Washburn, Yellowstone National Park, 1984-86 and 1995-97.

METHODS

Habitat Use and Availability 1978-87 and 1989-97

To evaluate habitat use by grizzlies during autumn of both pre- and post-fire periods, I used aerial radiolocations of grizzly bears and available digital vegetation maps. Digital maps of the study area (Mattson and Despain 1985) were developed by Yellowstone National Park biologists using the vegetation classification system of Despain (1990). Plant communities were identified on 1:20,000 scale aerial photographs and digitized from 1:62,500 scale topographic maps. The minimum community size was 5 acres. Following the 1988 fires, aerial photography and satellite imagery were used to update the vegetation map.

I classified years by fall whitebark pine cone production. As part of an interagency effort, annual whitebark cone production has been monitored on permanent transects across the ecosystem since 1980 (Blanchard 1990). One of the whitebark pine monitoring transects was located on Mt. Washburn (Figure 1). I classified years as "good cone years" when production exceeded 20 cones per tree (n = 10) on that transect. I subjectively classified 1978 and 1979 based on descriptions given by Kendall (1983). Good cone crop years occurred in 1978, 1980, 1982, 1985, 1989, 1991, and 1996 (Figure 3).

Aerial relocations of radiocollared bears were attempted from a fixed-wing aircraft approximately weekly from den emergence to denning (Blanchard and Knight 1991). Telemetry flights typically occurred between 0600 and 1300 hours local time. To

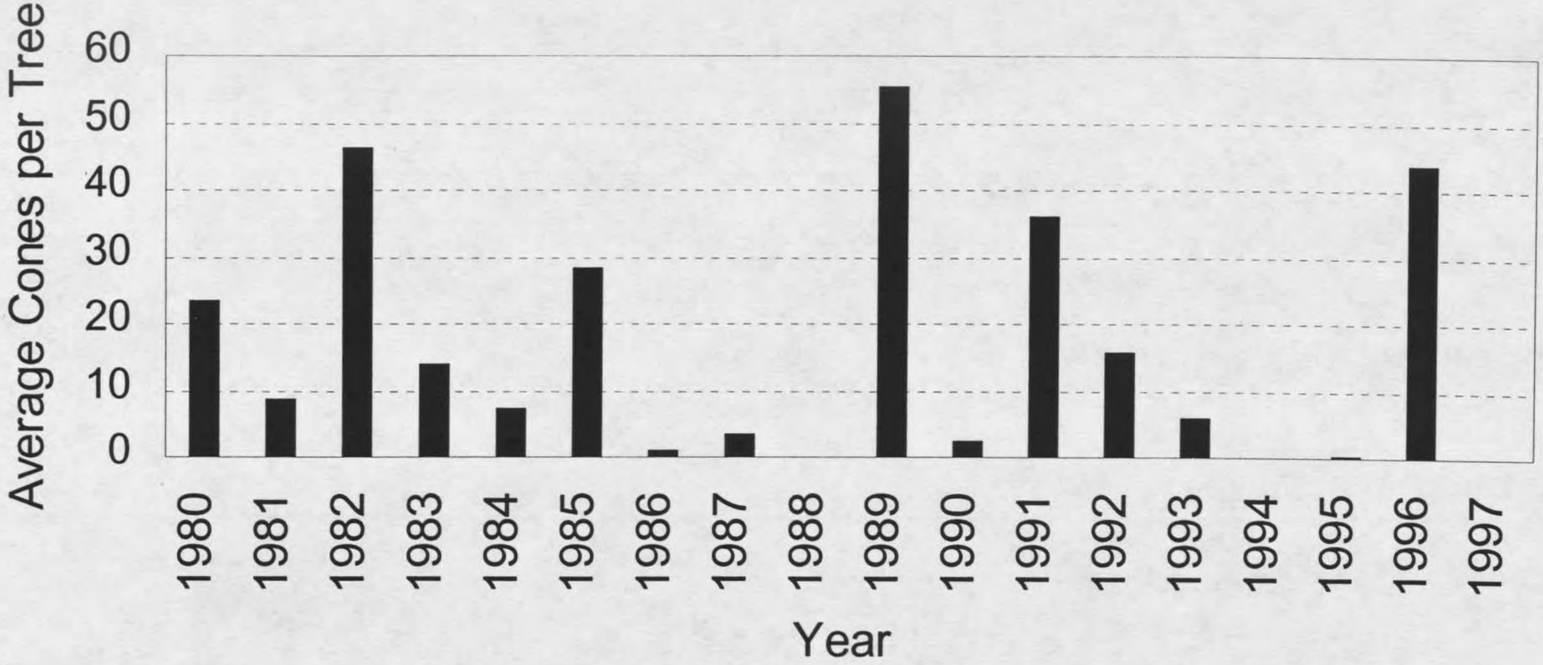


Figure 3. Average cones per whitebark pine tree on a monitoring transect established in 1980 on Mt. Washburn, Yellowstone National Park (IGBST data). Extensive use of whitebark pine seeds by grizzly bears typically occured when cone production exceeded 21 cones per tree (Mattson et al. 1994). Yellowstone National Park biologists counted cones on 10 permanently marked trees each year prior to the onset of heavy cone-use by red squirrels and Clark's nutcrackers. Based on desciptions given by Kendall (1983), I also classified 1978 as an abundant cone crop year.

attribute relocations with standard vegetation classifications, I used Program ArcInfo (ESRI, Inc. 1995) to overlay radiolocations from each period on the corresponding digital map (Despain 1990). Based on the original vegetation classifications, I assigned habitat types (Table 1) to the locations for the following analyses.

I used the Neu et al. (1974) method to compare use and availability of habitat types. Use was defined by the number of relocations in each habitat type during autumn. Availability of each habitat type (percent of total area) was calculated using ArcInfo (ESRI, Inc. 1995). I compared use and availability in both the pre- and post-fire periods for the population in (1) all years, (2) good cone crop years, (3) poor cone crop years. Following the overall chi-square test, I used Bonferroni simultaneous confidence intervals (Neu et al. 1974) to evaluate use of each habitat type relative to its availability. Because the Neu et al. method does not identify which habitats are more preferred than others, I used the Friedman test (Conover 1980) to rank habitat types in order of relative preference.

Whitebark Pine Seed Feeding Sites 1978-87 and 1989-97

A subsample of the aerial relocations described above was visited by field crews each year. Field crews described each activity site in detail according to the procedures reported by Blanchard (1985) and Mattson (1997). I participated in data collection on a majority of these sites during 1994-97. Information recorded on a standard form (Appendix A) at each plot included detailed descriptions of the physical site, the vegetation, and bear activity. Activity site descriptions were also recorded at sites with

Table 1. Habitat types of the Washburn Bear Management Unit, Yellowstone National Park, 1978-87 and 1989-97. Vegetative communities were originally mapped (Despain 1990, Mattson and Reinhart 1996, 1997) by standard climax habitat type (Steele et al. 1983) and cover type (Despain 1990), and then grouped into these 8 categories.

Pure Whitebark	*P. albicaulis* series habitat types with whitebark pine cover types. Typically higher elevation, exposed sites with open mature canopies and sparse understories.
Whitebark/Fir	*Abies lasiocarpa/Vaccinium scoparium–P. albicaulis* climax habitat type with lodgepole, whitebark, and spruce/fir cover types. Milder sites typically with whitebark pine and other species co-dominant in the canopy, with grouse-whortleberry prominent in the understory.
Vaccinium	*A. lasiocarpa/V. scoparium–V. scoparium* habitat type with lodgepole or spruce/fir cover types. Drier sites typically dominated by lodgepole pine with grouse-whortleberry dominant in the understory.
Mesic	Moist sites with *A. lasiocarpa* as the climax dominant tree and *V. globulare* or *Thalictrum occidentale* abundant in the understory. Cover types include whitebark pine, lodgepole pine, and spruce/fir.
Wet	Typically *A. lasiocarpa/Calamagrostis canadensis* with spruce/fir or whitebark cover types. Lush sites with saturated soils.
Burned	Canopy burned forest.
Mosaic Burn[ab]	Partially burned mature forest.
Other[a]	Habitats not containing mature whitebark pine, including non-forested and lower elevation habitats.

[a]Not used for analyses of red squirrel transect data.

[b]Not present in the pre-fire period (1978-87)

evidence of bear activity encountered en route to radiolocations. I evaluated these data together with data collected at aerial relocations.

I examined activity site data collected at whitebark pine-seed feeding sites in the study area from 1978-87 and from 1989-97. Based on other studies (Mattson et al. 1994, Mattson and Reinhart 1997), I characterized pine seed feeding sites using 14 variables. Aspect, slope, elevation, and distance to forest edge described physical site characteristics. Habitat type (Table 1), total basal area of all conifers, percent forest cover, and percent deadfall cover described vegetative composition and structure. Structure of whitebark pine on each site was described by average diameter-at-breast-height (dbh), relative abundance category, percent cover category, and percent of total basal area. Size of middens used and the percent of each midden excavated were recorded for most sites.

I used a 2-sample approach to test for differences between periods in each variable (Zar 1984). For categorical variables (i.e., habitat type, relative abundance of whitebark pine, percent whitebark pine cover), I used Pearson's chi-squared tests of independence (StatSoft 1994). I used Watkin's *F*-test for two circular means (Program ORIANA 1.0, Kovach 1994) to test for differences in aspect. I used Mann-Whitney *U*-tests for the continuous variables (StatSoft 1994) because the samples from many variables were not normally distributed.

Random and Bear-Used Sites 1996

Sampling Design for Random Sites

To survey characteristics of currently available whitebark pine habitats, I collected standard activity site data (as above) at randomly located sites in the study area. Sample size was limited due to time available and remoteness of the study area. I attempted to survey 48 plots during the sample period, August-October 1996. Placement of each sample plot involved two random selections. From an existing digital map of post-fire vegetation (Despain 1990), I used ArcView (ESRI, Inc. 1992) to produce a color map of the unit (Appendix B) with the vegetation grouped into 8 habitat types (Table 1). The 48 sites were partitioned among the 5 habitat types that should support mature whitebark pine using proportional allocation. I excluded mosaic burns, canopy burns, and "other" habitat types from these plots.

The study area was subdivided into logical units for partitioning placement of the sites. The eastern portion of the study area was accessible from a road, while the western area was further divided into 3 sub-areas that each involved backcountry trips. Because information on area of each habitat type was not available for these backcountry units, sample sites were partitioned among them according to visual estimates of area of available habitats. Plots were placed along line transects within each area.

For the eastern region, 4 transects appeared to adequately cover the area and habitat types, given the geographic layout of the region. The first transect was randomly placed across the eastern region parallel to and 400 m south from northing UTM 4961000. The remaining 3 transects were placed at 2 km intervals south of the first transect. The same method was used to place 2 transects in one sub-area of the western region. In the remaining 2 sub-areas of the western region, possible transect lines were drawn and then randomly selected. Plots were placed at distances along the transects using a random number table. The minimum distance between plot centers was 125 m.

Data Collection and Analyses

In addition to the standard information collected at activity sites (Blanchard 1985, Mattson 1997), I collected additional data at these plots, including: (1) age, height, crown diameter, cone production, and sources of mortality for whitebark pine on each plot; (2) observations of red squirrels at the site; (3) number and size of middens; (4) degree of burn intensity; and (5) percentage of infestation by white pine blister rust and mountain pine beetles. I also collected this information at whitebark pine feeding sites in the study area during 1996.

I compared whitebark pine feeding sites used by grizzly bears in the autumn of 1996 with the random sites using the same 2-sample approach as in the previous section. Pearson's chi-squared test of independence was used to compare categorical variables between random and used sites. I used Program Oriana 1.0 (Kovach 1994) to compare topographic aspects. I used Mann-Whitney *U*-tests to compare the continuous variables, including the additional variables collected at these sites.

Red Squirrel Transects (1984-86 and 1995-97)

Data Collection

For the original study (Reinhart and Mattson 1990, Mattson and Reinhart 1996, 1997), 57 line transects were placed throughout the whitebark pine zone on the northwest portion of Mt. Washburn (Figure 2). Forest stands on the study area were delineated using aerial photographs (1:20,000 scale) and ground truthing. Transects were placed to maximize the length traversing stand interiors and to minimize edge effect between habitat types by crossing stand boundaries at mostly right angles. Stands were classified using the system described by Despain (1990). Eighty-four stands were each sampled by 1-6 transects. I used the same transects post-fire. I determined transect lengths and the proportion burned from aerial photographs and corrected the lengths for slope. Transects varied in length from 200 m to 1000 m.

Field data collection was consistent between the pre-fire (1984-86) and post-fire study periods (1995-97). Twenty-nine km of transect were surveyed during each of the study years, except for 1984, when only 17 km were surveyed. A pair of observers walked the transects in the same order each year between 10 August and 28 September. One observer sampled all pre-fire years (Mattson and Reinhart 1997), and I sampled all post-fire years using the same methods. Following the original procedures, I recorded all red squirrel middens visible from the transect line and referenced them to the closest point along the line. I classified middens as "active" if currently occupied by a red squirrel and "used" if excavated by a bear. Occupancy of middens was determined by the observation of a squirrel at the midden or the presence of fresh cone clippings (Finley 1969). I estimated age of excavations based on condition of remaining cone cores and weathering of excavated pockets. Recent and older excavations were clearly distinguishable. I measured midden length (longest distance) and width (perpendicular to the length measurement) in meters.

Analyses

I used linear density (No./km) as my measure of abundance of squirrel middens and bear-excavated middens. I used linear density rather than area density to avoid introducing additional error due to calculation of probability-detection-function estimates from line transect data (Burnham et al. 1980). However, to use linear densities, I had to assume that probability detection functions did not differ between pre- and post-fire periods and by individual habitat types. This is a plausible assumption because I used the same procedures as in the pre-fire period and changes in the vegetative composition of unburned stands were minute. Deviations from this assumption could introduce some degree of error into my analysis.

Red Squirrel Activity. I calculated linear density of middens by habitat type each year. I consolidated the original 27 standard vegetation classifications into 5 habitat types (Table 1), to help accommodate small sample sizes. I used ANOVAs to test for differences in linear density of middens by habitat type and study period for (1) burned and unburned areas, pooled, and for (2) unburned habitats alone. I used 1-tailed *t*-tests to test for post-fire reduction in linear density of middens in each habitat type, pooling burned and unburned areas. I used 2-tailed t-tests to test for post-fire change in mean annual linear densities within unburned habitats. Individual years constituted the observations for these analyses.

I used 2x2 contingency tables to compare the proportions of active middens between the 2 periods (1) in different habitat types and (2) with different levels of cone abundance. Based on previous studies (Blanchard 1990, Kendall 1983), I identified 3 cone abundance levels: (1) low cone crop year following a low-to-moderate cone crop, (2) high cone crop year following a low cone crop, and (3) low cone crop following a high cone crop. One year of each type occurred during the pre- and post-fire study periods, in the above order (Figure 3).

I compared the average size (length * width) of active middens by period and habitat type, using ANOVA. Because the distributions of midden size were skewed right, I used a natural-log transformation to normalize them for the tests.

<u>Bear Use</u>. I examined linear densities of excavated middens by period for all habitat types combined. I calculated post-fire linear densities for both the unburned portions of transects and all (burned and unburned) habitats. I used linear densities of excavations associated with abundant cone years (1985 and 1996) to represent bear use in each period. Because bears may have excavated middens after we walked the transects each year, I calculated linear densities of dug middens using excavations found in 1986 and 1997. Previous studies documented bear use of middens to be closely associated

with the cone production year (Kendall 1983, Blanchard 1990). In both studies, bears began using middens as soon as cones are available in the fall and, depending upon cone crop size, continued feeding on pine nuts into the following spring/summer, until the supplies were exhausted. I attributed excavations of middens within the previous 2 months to the current year's cone crop. Excavations that occurred within the previous year but before the preceding 2 months were attributed to the previous year's cone crop (Mattson and Reinhart 1997).

RESULTS

Habitat Use and Availability 1978-87 and 1989-97

Thirty-five percent of the 831 km^2 study area burned in 1988. The 5 habitat types that contained mature whitebark comprised 57.3% of the study area in the pre-fire period and 26.7% of the study area in the post-fire period (Figure 4). The post-fire area of whitebark pine habitats was 47% of the pre-fire area. Considering only those 5 habitat types, relative proportions of area of habitat types did not differ between periods ($\chi^2 = 0.04$, df = 4, $P = 0.99$). Considering all 8 habitat types, composition of habitat types was also not different between periods ($\chi^2 = 9.62$, df = 7, $P = 0.211$).

Two hundred and eighty-eight relocations were observed in the study area during autumns of the pre-fire period and 144 relocations were made during autumns of the post-fire period (Table 2). Proportions of locations in each habitat type were different between the pre- and post-fire periods in all years ($\chi^2 = 83.5$, df = 7, $P < 0.001$), in good cone crop years ($\chi^2 = 12.5$, df = 7, $P = 0.084$), and in poor cone crop years ($\chi^2 = 80.7$, df = 7, $P < 0.001$). Considering only the 5 habitats which contained mature whitebark pine, proportions of locations in each habitat type were **not** different between periods in all years ($\chi^2 = 4.3$, df = 4, $P = 0.363$), in good cone crop years ($\chi^2 = 5.5$, df = 4, $P = 0.243$), and in poor cone crop years ($\chi^2 = 4.1$, df = 4, $P = 0.399$).

Radiocollared grizzly bears did not use habitats in proportion to their availability (Table 3). The whitebark/fir type was the most preferred habitat type during autumns of

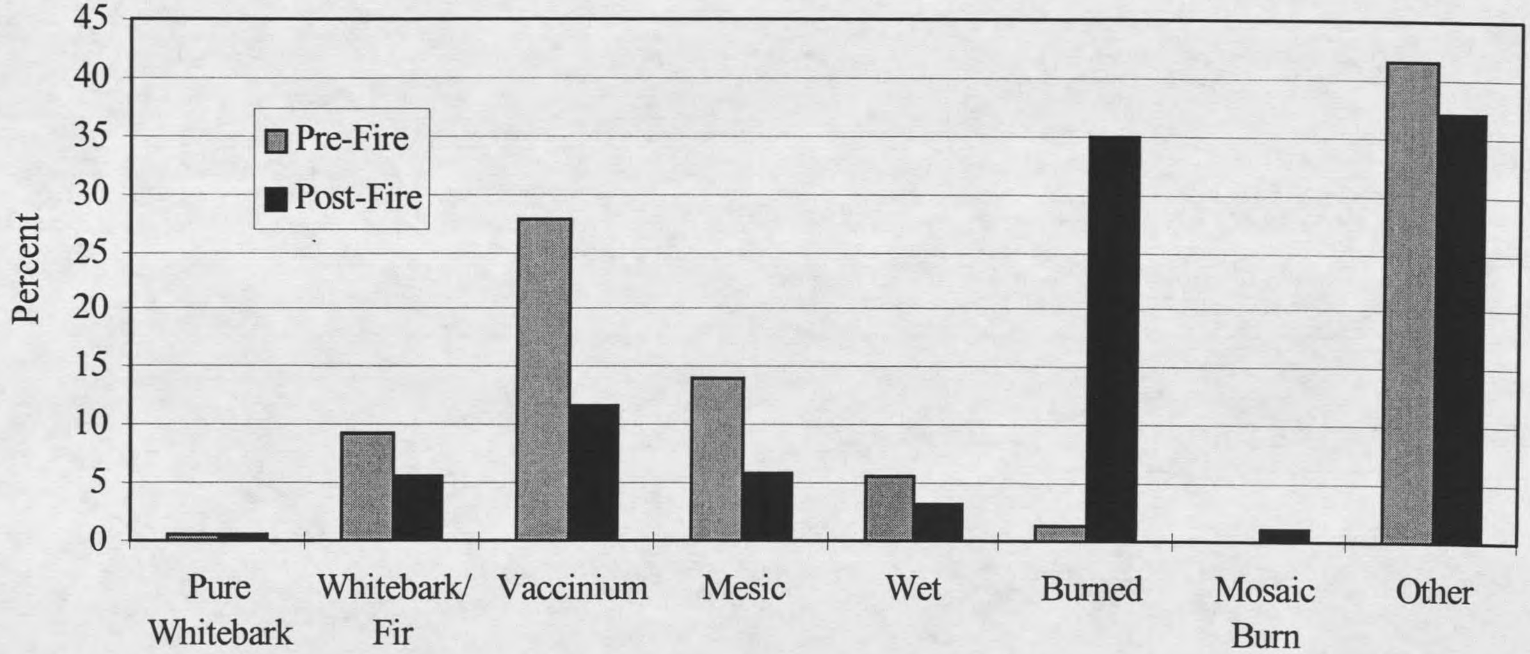


Figure 4. Percent coverage by habitat type in the Washburn Bear Management Unit, Yellowstone National Park, before and after the 1988 fires.

Table 2. Number of aerial relocations of grizzly bears by habitat type and percent availability of habitat types in the Washburn Bear Management Unit, Yellowstone National Park, during autumns of the pre- (1978-87) and post-fire (1989-97) periods. Percentages of total relocations are given in parentheses following actual counts.

	Pure Whitebark	Whitebark/ Fir	Vaccinium	Mesic	Wet	Burned	Partial Burn	Other	Total
Pre-Fire									
All years	6 (2%)	64 (22%)	31 (11%)	59 (21%)	30 (10%)	3 (1%)	0 (0%)	95 (33%)	288
Cone years[a]	2 (2.5%)	32 (38%)	13 (16%)	7 (8%)	12 (14%)	2 (2.5%)	0 (0%)	16 (19%)	84
Poor cone years	4 (2%)	32 (16%)	18 (9%)	52 (25%)	18 (9%)	1 (0%)	0 (0%)	79 (39%)	204
Availability	1%	9%	28%	14%	6%	1%	0%	41%	
Post-fire									
All years	0 (0%)	23 (16%)	14 (10%)	28 (19%)	8 (6%)	38 (26%)	3 (2%)	30 (21%)	144
Cone years[a]	0 (0%)	16 (36%)	5 (11%)	9 (20%)	4 (9%)	5 (11%)	1 (2%)	5 (11%)	45
Poor cone years[b]	0 (0%)	7 (7%)	9 (9%)	19 (19%)	4 (4%)	33 (33%)	2 (2%)	25 (25%)	99
Availability	1%	6%	11%	6%	3%	35%	1%	37%	

[a]Cone years occurred when whitebark pine cone production exceeded 20 cones per tree on the Mt. Washburn monitoring transect (IGBST data), Yellowstone National Park. Cone years included 1978, 1980, 1982, and 1985 in the pre-fire period and 1989, 1991, and 1996 in the post-fire period.

[b]Percentages do not sum to 100% due to rounding error.

Table 3. Test statistics for hypotheses of no difference between proportions of used and available habitats[a] in the Washburn Bear Management Unit, Yellowstone National Park, during autumn 1978-87 and 1989-97.

	Autumns including:					
	Good whitebark pine cone years		Poor whitebark pine cone years		All years	
Analysis method MCP	Pre-fire	Post-fire	Pre-fire	Post-fire	Pre-fire	Post-fire
Neu[b]	$\chi^2 = 109.3$ $P < 0.001$	$\chi^2 = 107.5$ $P < 0.001$	$\chi^2 = 66.9$ $P < 0.001$	$\chi^2 = 37.2$ $P < 0.001$	$\chi^2 = 119.9$ $P < 0.001$	$\chi^2 = 92.1$ $P < 0.001$
Bonferroni CI's						
Used More	C	C	E	E	C E F	C E
No Difference	A B E F	D E F H	A B C F G	A C D F G H	A B	A D F H
Used Less	D G	A B G	D	B	D G	B G
Friedman[c]	$T_2 = 5.769$ $P < 0.001$	$T_2 = 6.217$ $P < 0.005$	$T_2 = 5.520$ $P < 0.001$	$T_2 = 1.375$ $P < 0.600$	$T_2 = 7.938$ $P < 0.001$	$T_2 = 3.500$ $P = 0.017$
Studentized MCP[d]	G D E A B F C	G A H B D F E C	D A G F B C E		D G A F B C E	G A B F H E D C

[a]Habitat types: A = burn B = pure whitebark C = whitebark/fir D = vaccinium E = mesic F = wet G = other H = mosaic

[b]Tests were conducted following the procedures of Neu et al. (1974).

[c]Tests were conducted following the procedures described by Conover (1980).

[d]Habitat types arranged left to right in order of increasing rank. Ranks of underlined types were not significantly different ($\alpha = 0.1$).

good cone crop years in both periods, while the "other" habitat type was least preferred in the same years. The mesic type ranked higher in good cone crop years of the post-fire period. The mesic type was also the preferred habitat type in autumns of poor cone crop years. During the post-fire period, burned habitats were used more often in poor cone years. One-third of the relocations in those years were in burned habitats, compared to 11% in good cone crop years. The mesic and whitebark/fir types were the most preferred in both periods considering all years.

Whitebark Pine Seed Feeding Sites 1978-87 and 1989-97

Data were collected at 45 and 33 whitebark pine seed feeding sites in the pre- and post-fire periods, respectively. One incidence of feeding activity occurred in the spring following a large cone crop in the pre-fire period. Proportions of feeding sites among habitat types differed between the two periods ($\chi^2 = 9.305$, df = 4, $P = 0.054$) (Table 4). In the pre-fire period, 67% of the sites were in the whitebark/fir type and 24% were in the mesic type. In the post-fire period, 33% of the sites were in the whitebark/fir type and 48% were in the mesic type.

Table 4. Number of sites used by grizzly bears for feeding on whitebark pine seeds, by habitat type and study period, found in the Washburn Bear Management Unit, Yellowstone National Park, 1978-87 and 1989-97. Percentages of total sites used in each period are given in parentheses following actual counts.

	Pure Whitebark	Whitebark/ Fir	Vaccinium	Mesic	Wet	Mosaic Burn
Pre-fire	0 (0%)	30 (67%)	2 (4%)	11 (24%)	2 (4%)	0 (0%)
Post-fire	0 (0%)	11 (33%)	2 (2%)	16 (49%)	3 (9%)	1 (3%)

Pre- and post-fire feeding sites differed in 5 of the variables recorded at each site. The directions of aspects (Figure 5) recorded at pre-fire feeding sites were uniformly distributed (Kovach 1994, Rayleigh test of uniformity, $P = 0.32$), whereas post-fire sites were more concentrated (Rayleigh test of uniformity, $P = 0.01$) on east- and south-facing slopes (mean = 117.82°, SE = 17.35°). Post-fire feeding sites also had greater degree of slope ($Z = -1.957$, $P = 0.050$), percent forest cover ($Z = -2.665$, $P = 0.008$), and distance to forest edge ($Z = -3.597$, $P = 0.0003$). Post-fire sites also had less deadfall, measured in percent of ground cover, than pre-fire sites ($Z = -2.114$, $P = 0.035$). Other continuous variables recorded at whitebark pine feeding sites did not differ between periods (Table 5). Pre- and post-fire sites were also not different by whitebark pine abundance category ($\chi^2 = 3.325$, df = 3, $P = 0.344$) and cover category ($\chi^2 = 6.961$, df = 4, $P = 0.138$).

Random and Bear-Used Sites 1996

I sampled 46 random sites and 22 bear-used sites in the study area during 1996 (Table 6). The proportions of feeding sites by habitat type differed from random sites ($\chi^2 = 13.855$, df = 5, $P = 0.017$). No whitebark pine feeding sites were found in the pure whitebark and vaccinium types. Used sites also differed from random sites in 10 continuous variables (Table 7). Used sites were generally higher than random sites in slope, elevation, percent forest cover, total basal area, whitebark pine basal area, percent of total basal area in whitebark pine, whitebark pine dbh, age of whitebark pine, midden size, and percent of midden surface excavated.

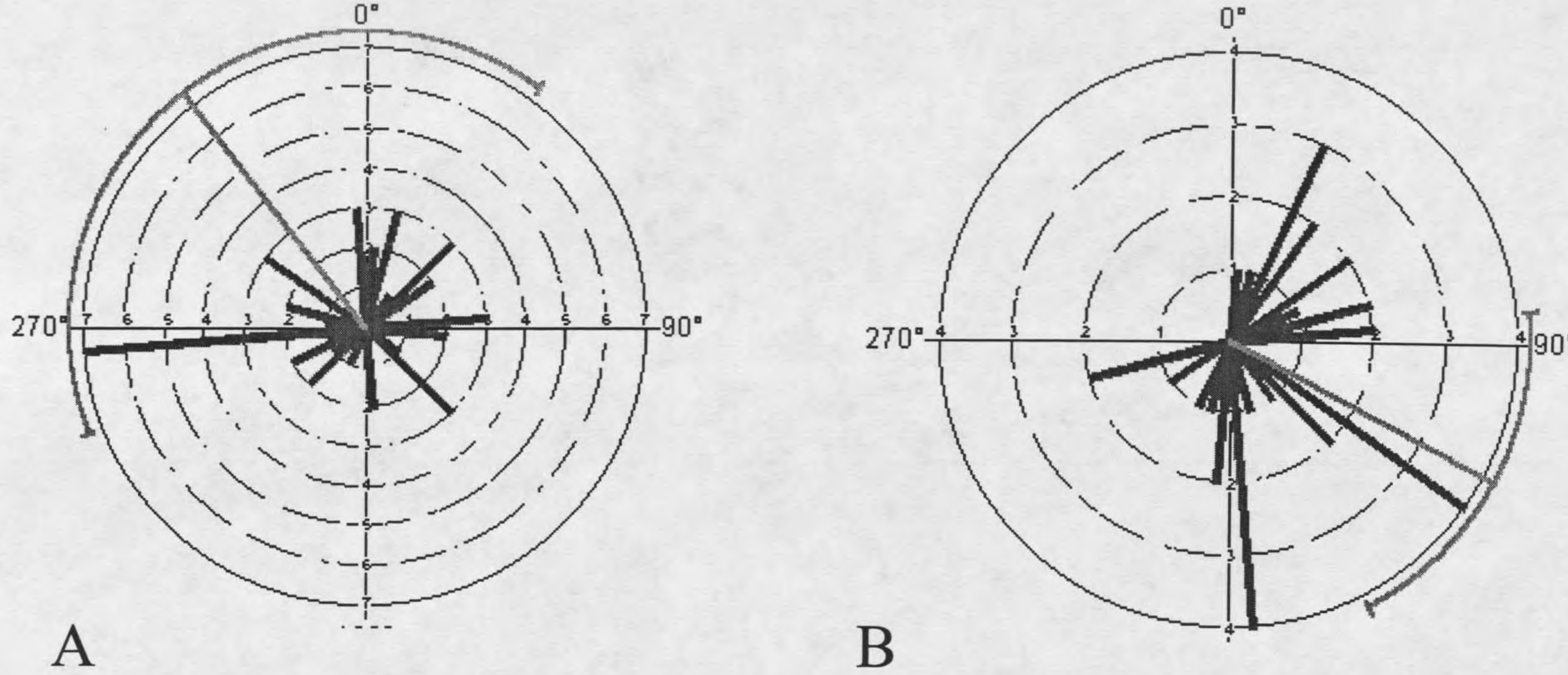


Figure 5. Circular plots of directions of aspects observed at whitebark pine feeding sites during the (A) pre- and (B) post-fire study periods in the Washburn Bear Management Unit, Yellowstone National Park, 1978-87 and 1989-97. The length of the dark bars indicates frequency. The lighter gray lines and arcs show the mean aspects and 95% confidence intervals around the means. Tests for differences between the two periods were unreliable due to the uniform distribution of directions observed in the pre-fire period.

Table 5. Values of continuous variables recorded at 78 whitebark-pine feeding sites in the Washburn Bear Managment Unit, Yellowstone National Park, 1978-87 and 1989-97. *P* values were derived from Mann-Whitney *U*-tests for differences between the pre- and post-fire periods. Differences in *n* values within each period were due to missing data or absences of that feature.

	Pre-Fire Sites (1978-87)				Post-Fire Sites (1989-97)				
Variable	*n*	$\bar{x}$	SE	median	*n*	$\bar{x}$	SE	median	*P*
Slope (°)	45	12.5	1.2	11	33	14.9	1.1	16	0.008
Elevation (m)	45	2655	16.3	2682	33	2667	12.1	2652	0.667
Distance to forest edge (m)	38	70.6	28.6	30	33	254.2	53.7	150	0.0003
Forest cover (%)	29	37.7	3.0	30	32	27.7	2.0	23.5	0.008
Deadfall cover (%)	11	15.3	2.7	20	33	8.3	0.96	7	0.035
Total basal area (m^2/ha)	27	49.8	4.6	41.3	33	47.7	4.2	41.3	0.727
Whitebark pine basal area (m^2/ha)	27	15.99	3.5	9.2	33	14.6	2.7	9.2	0.976
Basal area in whitebark pine (%)	27	30.8	0.1	22.2	33	30.8	0.04	30	0.870
Mean whitebark pine dbh (cm)	18	39.4	3.5	32.6	24	42.4	1.9	40.75	0.137
Midden surface area (m^2)	26	166.0	22.7	120	30	227.3	47	175.5	0.774
Midden surface excavated (%)	26	41.7	5.5	40	29	44.1	6.6	28	0.996

Table 6. Number of random sites and sites used by grizzly bears, by habitat type, in the Washburn Bear Management Unit, Yellowstone National Park, 1996. Percentages of total random or used sites are given in parentheses following the actual counts. Random sites were allocated among habitat types according to the proportion of the study area occupied by each habitat type.

	Pure Whitebark	Whitebark/Fir	Vaccinium	Mesic	Wet	Mosaic Burn
Random	2 (4%)	18 (39%)	13 (28%)	4 (9%)	9 (20%)	0 (0%)
Used Sites	0 (0%)	12 (55%)	0 (0%)	6 (27%)	3 (14%)	1 (4%)

Table 7. Values of continuous variables recorded at 22 grizzly-bear used sites and 46 random sites in the Washburn Bear Management Unit, Yellowstone National Park, 1996. *P* values were derived from Mann-Whitney U-tests for differences between random and used sites. Differences in *n* values were due to missing data or absences of that feature.

	Random Sites				Bear-Used Sites				
Variable	n	$\bar{x}$	SE	median	n	$\bar{x}$	SE	median	P
Slope (°)	46	12.6	1.3	10.5	22	17	1.4	18	0.015
Elevation (m)	46	2603	18.7	2621	22	2668	20.3	2652	0.042
Distance to forest edge (m)	46	194.5	31.5	100	22	130.2	26.5	100	0.394
Forest cover (%)	45	17.8	1.4	17.0	22	26.9	2.8	22	0.001
Deadfall cover (%)	46	5.1	0.3	4.5	22	4.9	0.4	5.0	0.458
Total basal area (m^2/ha)	46	30.4	2.7	27.5	22	47.2	4.9	45.9	0.003
Whitebark pine basal area (m^2/ha)	46	7.3	1.6	0	22	15.2	3.5	9.2	0.021
Basal area in whitebark pine (%)	46	25	5.1	0	22	34.4	6.5	29.3	0.088
Mean whitebark pine dbh (cm)	38	29.4	2.5	32.6	17	39.8	2.3	40.3	0.049
Height of whitebark pine (m)	38	15.9	1.2	16.3	17	12.4	1.3	12.3	0.126

Table 7. Continued

Variable	Random Sites n	$\bar{x}$	SE	median	Bear-Used Sites n	$\bar{x}$	SE	median	P
Whitebark crown diameter (cm)	38	432.4	34.1	390	17	504.8	50.9	440	0.287
Age of whitebark pine (annuli at 1.5 m)	33	146.7	12.9	130	17	181.5	16.8	162	0.067
Number of red squirrel calls	46	0.8	0.1	1	22	0.6	0.2	0	0.206
Number of red squirrel sightings	46	0.13	0.05	0	22	0.2	0.1	0	0.937
Midden surface area (m^2)	8	48.2	36.3	5	12	68.5	22.6	50.5	0.034
Midden surface excavated (%)	8	22.5	14.7	0	12	79.2	5	85	0.017
Whitebark pine burned (%)	46	2.2	1.4	0	22	4.5	3.14	0	0.844
Whitebark with mountain pine beetle (%)	46	0.3	0.2	0	22	3.2	1.8	0	0.595
Whitebark w/ white pine blister rust (%)	46	9.2	1.8	2	22	8.9	2.1	5	0.854

Random and used sites were not significantly different in the other continuous variables (Table 7) and in categories of whitebark pine abundance ($\chi^2 = 3.886$, df = 2, P = 0.143) and cover ($\chi^2 = 3.819$, df = 2, $P = 0.148$). The mean directions of aspects observed on random and bear-used sites were 137° and 85°, respectively (Figure 6). Watson's test of means of aspects was not reliable due to the uniform distribution of directions (Kovach 1994).

Red Squirrel Transects 1984-86 and 1995-97

In 1988, 15 km or 49% of the established transects burned, including portions of all habitat types except the pure whitebark type (Figure 7). After the fires, the relative composition of unburned habitat types (derived from total unburned transect length) did not differ from the pre-fire habitat composition (total transect length) (Pearson's χ^2 = 0.93, 4 df, $P = 0.92$).

Whitebark pine seed production followed a similar pattern during pre- (1984-84) and post-fire (1995-97) study periods (Figure 3). In each study period, a large cone crop was preceded and followed by small cone crops. Although cone production was substantially higher in 1996 than in 1985, I expected bear response to crop levels to be similar based on other studies (Mattson et al. 1994).

Red Squirrel Activity

No red squirrels or middens were observed in burned areas. Mean linear density of active middens varied by period ($F = 8.35$, $n = 30$, 1 df, $P < 0.01$) and by habitat type

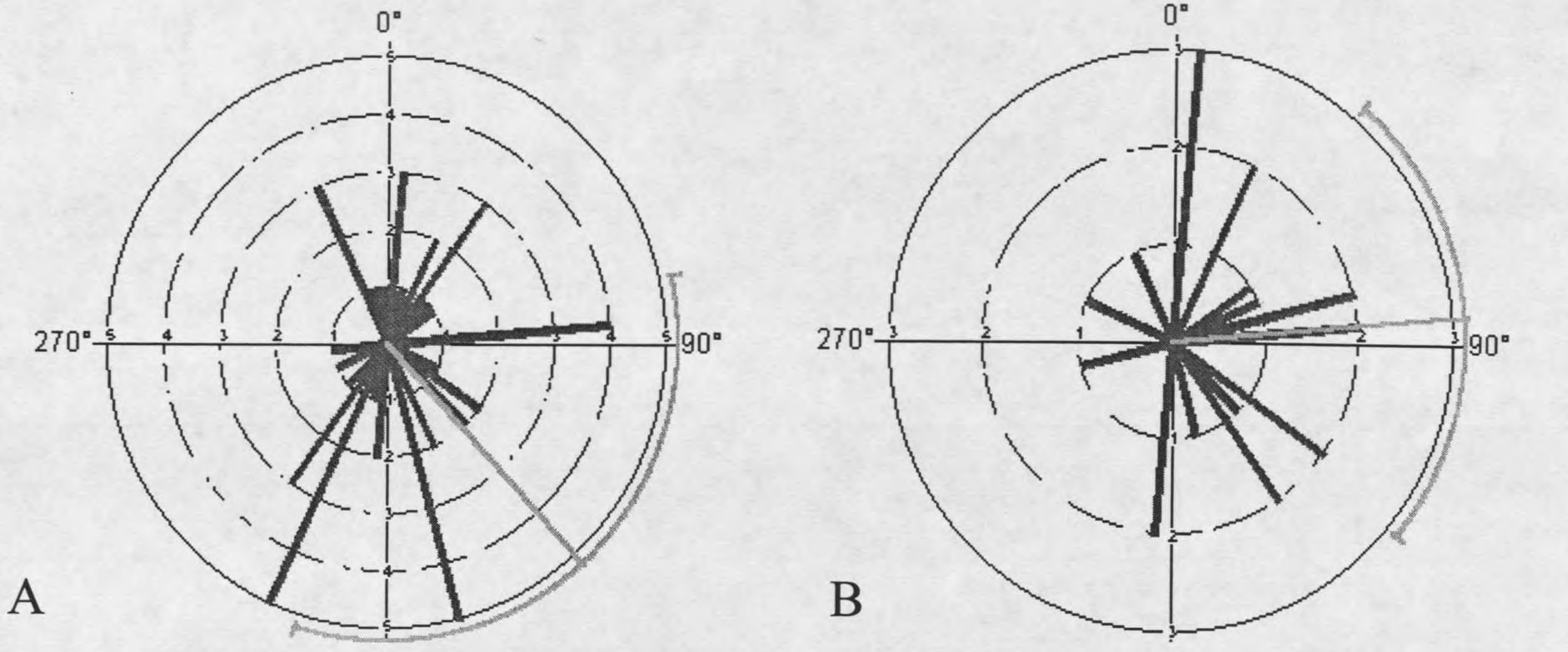


Figure 6. Circular plots of topographical aspects observed at (A) random locations and (B) bear-used sites in the Washburn Bear Management Unit, Yellowstone National Park, 1996. The length of the dark bars indicates frequency. The lighter gray lines and arcs show the mean aspects and 95% confidence intervals around the means. Tests for differences between used and random sites were unreliable due to the uniform distribution of aspects (Kovach 1994).

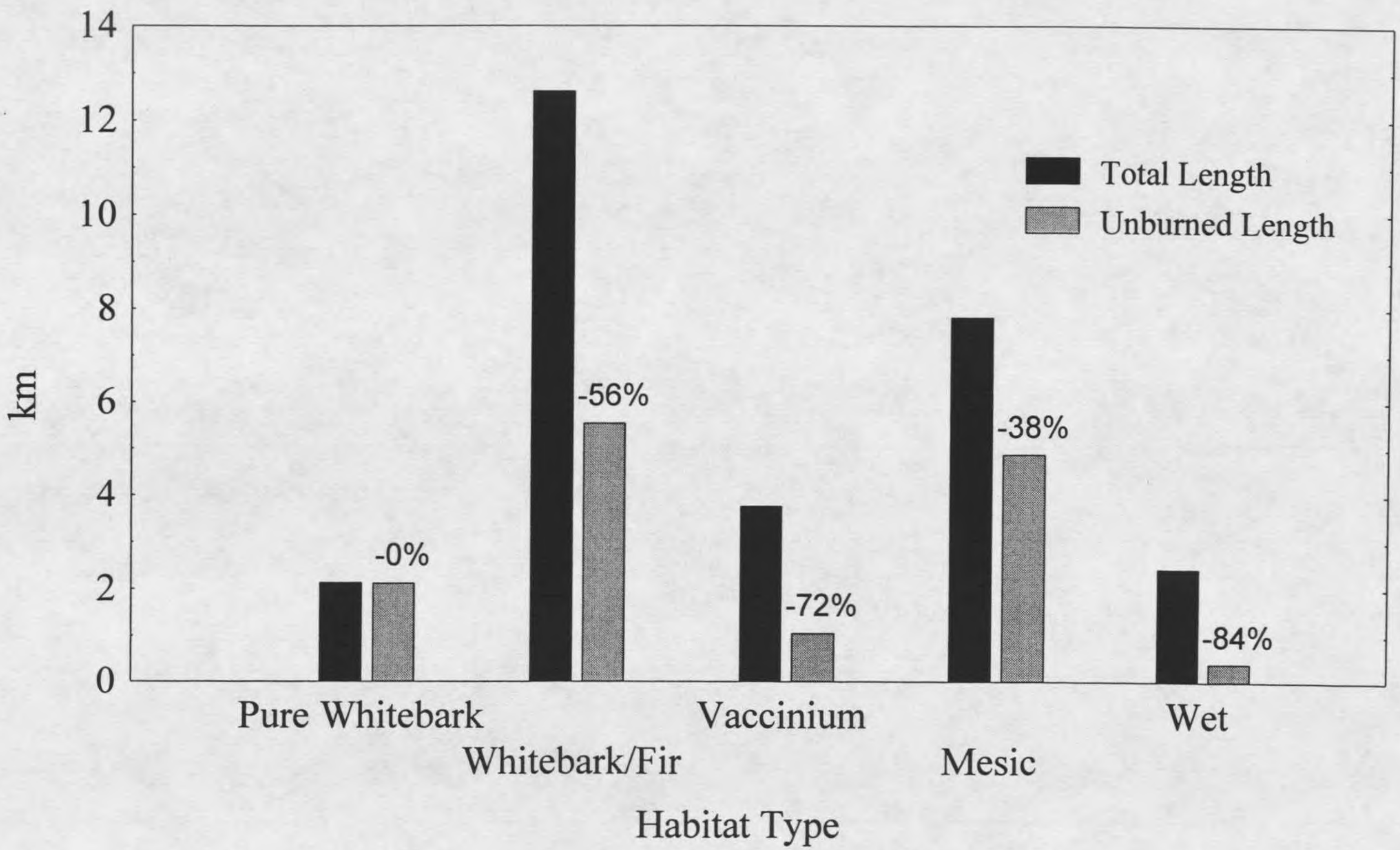


Figure 7. Total length (km) of each habitat type along red squirrel transects on Mt. Washburn, Yellowstone National Park, 1984-86 and 1995-97. Total length (black bars) was used to calculate linear densities for the pre-fire period and for the pooled burned and unburned habitats in the post-fire period. Total unburned length (gray bars) was used to calculate linear densities within unburned portions of each habitat type post-fire. The unburned lengths are labeled with the percent of total length burned.

($F = 9.84$, $n = 30$, 4 df, $P < 0.01$), with significant interaction between period and habitat type ($F = 2.86$, $n = 30$, 4 df, $P = 0.051$) (Table 8). Post-fire linear density of active middens in burned and unburned areas, pooled, decreased by 27% from pre-fire linear densities of active middens. Densities decreased in the wet ($t = 2.57$, 4 df, $P = 0.03$) and vaccinium ($t = 4.48$, 4 df, $P < 0.01$) types and did not decrease in the pure whitebark, whitebark/fir, and mesic types.

Table 8. Mean linear densities (No./km) of red squirrel middens by habitat type on 57 transects, Mt. Washburn, Yellowstone National Park, averaged among years, by period, 1984-86 and 1995-97.

	1984-86		1995-97		1995-97 unburned	
Habitat types	Active	Total	Active	Total	Active	Total
Pure whitebark	0.16	0.63	0.00	0.31	0.00	0.31
Whitebark/fir	1.98	5.42 [a]	1.53	2.64 [a]	3.49	6.02
Vaccinium	1.62 [b]	2.84 [b]	0.36 [b]	0.36 [b]	1.28	1.28
Mesic	3.73	6.10	3.63	5.00	5.82	8.01
Wet	3.10 [a c]	6.37 [a c]	0.00 [a]	0.14 [a]	0.00 [c]	0.86 [c]
All types	2.35	4.93	1.71	2.60	3.51	5.35

[a] Means significantly lower post-fire (1-tailed t-test, $P \leq 0.05$)
[b] Means significantly lower post-fire (1-tailed t-test, $P \leq 0.01$)
[c] Means significantly different (2-tailed t-test, $P \leq 0.10$)

Considering only unburned areas, mean linear density of active red squirrel middens areas varied by habitat type ($F = 6.64$, $n = 30$, 4 df, $P = 0.01$) (Table 8), with a significant interaction between the effects of period and habitat type ($F = 2.61$, $n = 30$, 4 df, $P =$

0.07). Whereas linear density of active middens in the wet type decreased ($t = 2.57$, 4 df, $P = 0.06$), other habitat types showed no significant change.

Combining all habitat types, 48% of the middens observed in the pre-fire period were active compared to 66% of post-fire middens ($\chi^2 = 17.52$, $n = 591$, 1 df, $P < 0.00$) (Table 9). This was primarily due to an increase in the proportion of active middens in the whitebark/fir type ($\chi^2 = 11.05$, $n = 272$, 1 df, $P < 0.01$). No other individual types exhibited a proportional change. Considering the years when the 2 largest crops were produced (year type 2), the proportion of active middens was greater in 1996 than in 1985 ($\chi^2 = 47.94$, $n = 266$, 1 df, $P < 0.01$). In the years before and after these large cone crops, the proportions of active middens did not differ between periods.

Table 9. Counts of red-squirrel middens and chi-square tests of homogeneity for proportions of active middens pre-fire and post-fire, by habitat type along red squirrel transects on Mt. Washburn, Yellowstone National Park, 1984-86 and 1995-97.

	1984-86		1995-97					
Habitat type	Active	Inactive	Active	Inactive	n	χ^2	df	P
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
Vaccinium[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 one or both periods.

The size of active red squirrel middens differed by study period ($F = 13.16$, $n = 466$, 1 df, $P < 0.01$) and habitat type ($F = 7.07$, $n = 466$, 4 df, $P < 0.01$). However, there was no interaction between the effects of period and habitat type ($F = 0.76$, $n = 466$, 4 df, $P = 0.56$). Midden size decreased in the post-fire study period. The average size of active middens was 51% smaller post-fire compared to pre-fire (Table 10).

Table 10. Mean area (m^2) of active red squirrel middens by habitat on transects on Mt. Washburn, Yellowstone National Park, 1984-86 and 1995-97.

	Pre-Fire		Post-Fire	
Habitat type	$\bar{x}$	n	$\bar{x}$	n
Pure whitebark	3.00	1	n/a	0
Whitebark/fir	86.2	50	44.0	56
Vaccinium	64.7	15	4.5	3
Mesic	46.9	68	18.8	81
Wet	46.7	14	n/a	0
All types	61.5	109	29.9	141

Bear Use

Levels of whitebark pine seed use by bears corresponded positively to cone crop size. More bear-excavated middens were found during and following each year that a large cone crop was produced (Table 11) than during the first year of each period. The majority of middens excavated by bears were documented the year following a large cone crop. Pooling burned and unburned areas, the linear density of excavated middens during the post-fire study period was 64% less than during the pre-fire period. Linear density of excavated middens in the unburned portion of the post-fire study area decreased 25% from the pre-fire period. The average size of middens excavated in 1996 was 40% smaller compared to 1985 (1-sided $t = 3.32$, df = 56, $P = 0.002$).

Table 11. Yearly counts of bear-excavated red-squirrel middens on transects on Mt. Washburn, Yellowstone National Park, 1984-86 and 1995-97, and linear-densities of excavations associated with abundant whitebark pine cone crops in 1985 and 1996.

	Current crop	Previous crop	No./km	No./km unburned
Pre-fire				
1984	2	13	n/a	n/a
1985[ab]	40	18	1.53	1.53
1986	0	44	n/a	n/a
Post-fire				
1995	0	0	n/a	n/a
1996[ab]	5	1	0.56	1.15
1997	0	16	n/a	n/a

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

DISCUSSION

Habitat Use and Availability 1978-87 and 1989-97

The 1988 fires reduced the area of whitebark pine-producing habitats by 53%, and these 5 types were available in similar proportions post-fire. Although the number of relocations observed during autumns of the post-fire period was half of the pre-fire number, I believe that this reflects sampling effort rather than a reduction in the bear population. During the pre-fire period, 22 bears were each relocated an average of 13.1 times. The average number of relocations per bear (n = 18) post-fire was 7.6.

Patterns of habitat use by grizzly bears were not greatly different between the two periods. The population exhibited stronger habitat selection (i.e., greater differences between proportions of habitats used and available) in abundant cone crop years. Bears may have employed a more generalist foraging strategy during years of poor cone crops as they searched for alternative foods (Stephens and Krebs 1986). Mattson et al. (1991) found that the diets of individual bears became more similar as high-quality foods became more abundant. Occupancy of preferred sites by adult males may hinder the ability of subadult males and adult females to use those areas (Blanchard and Knight 1991, Mattson 1990, Wielgus and Bunnell 1995). Effects of the loss of whitebark pine habitats would likely first be evident in patterns of habitat selection by subadult males and adult females. Unfortunately, the small sample of this study did not allow comparisons among sex/age classes. Changes in patterns of habitat selection due to loss of whitebark pine habitats might also be evident in habitat use in the spring following good cone crops as bears may have used over-wintered seeds.

In the post-fire period, grizzly bears used burned habitats in proportion to their availability in poor cone years. Bears selected against burned and "other" habitats during good cone crop years. Blanchard and Knight (1996) found that grizzly bear locations throughout Yellowstone National Park (1989-92) occurred in burned and unburned habitats in proportion to their availability except during 1989, a year of abundant whitebark pine seeds. Grazing, primarily on forbs, was the most common feeding activity observed in burned forests (Blanchard and Knight 1996). Mattson (1997) concluded that Yellowstone bears used lodgepole pine forests in early seral stages primarily for traveling and grazing.

Research from other regions indicated that fires benefited grizzly bears by enhancing production of soft mast crops (Hamer and Herrero 1987, Zager et al. 1983). However, berry production in much of the Yellowstone ecosystem is sparse and unreliable, and berries constitute only a small portion of the bears' diets (Mealey 1980, Mattson et al. 1991, Mattson 1997). If bears were selecting habitats based on available foods (as in Costello and Sage, Jr. 1994), bears monitored in this study preferred whitebark pine seeds to alternative foods available in burned areas (Mattson 1997, Blanchard and Knight 1996).

Use of whitebark pine seeds undoubtedly occurred during years I classified as "poor cone" years. Mattson et al. (1994) suggested 20 cones per tree on Yellowstone's monitoring transects as a threshold value above which heavy use of whitebark pine seeds by grizzly bears was likely and below which little use occurred. I adopted that value as an objective means to classify year types. However, bears do use whitebark pine seeds to some degree when cone crops are smaller (Mattson et al. 1994). I also assumed that results of the Mt. Washburn cone transect were representative of the whitebark pine crop throughout the study area. This assumption may have been false in 1987, which was classified as a poor cone year. As evident by observed feeding activity and scat contents (IGBST data), bears used whitebark pine seeds to a large extent during that year.

Whereas the relocations indicated use of habitats, presence does not necessarily imply that bears were foraging in those habitats. Bears also use various habitat types for security cover, bedding, and travel (Mattson 1997, Blanchard and Knight 1996). These remotely-sensed data were insufficient to entirely distinguish between pine seed feeding and other types of use occurring in these habitat types.

Whitebark Pine Seed Feeding Sites 1978-87 and 1989-97

The primary differences between whitebark pine feeding sites used by grizzly bears pre- and post-fire were in the habitat types used. As the area of whitebark/fir and mesic types were reduced similarly, differences in use of each type for feeding could likely be attributed to differences in cone productivity and squirrel populations in each habitat type. While Weaver and Forcella (1986) found little variation in whitebark cone production among stands of the whitebark/fir type, Mattson et al. (1994) found that cone production varied by location within a region. I lacked the data to test for variation in cone production by habitat type within the study area.

The lack of use of sites with northwesterly aspects may have been related to direction of fire spread. The fires generally spread northeastward (Rothermel et al. 1994), in the direction of the prevailing winds. This brought them across the northwest-facing slopes of the study area. The observed decreases in canopy and deadfall cover may be related to the topographical aspects of sites used.

Pre- and post-fire feeding sites were similar in many respects. While the fires affected whitebark pine availability on a landscape scale, it seems reasonable that microsite characteristics conducive to whitebark pine feeding by bears would remain similar. Forest structure of sites used, in terms of stem density and percent composition by whitebark pine, was similar for both periods. Elevation and slope also did not vary between periods. The sizes of middens used in each period were not different.

Total numbers of feeding sites found may not be representative of levels of use by bears because sampling effort varied annually. Relative importance of whitebark pine seeds might be demonstrated by food habits, as determined by analyzing contents of scats collected during activity site investigations during both periods (Mattson et al. 1991, Mattson 1997). Across the ecosystem, whitebark pine seeds composed a smaller percentage of grizzly bears' annual diets in the post-fire period (IGBST data). Whitebark pine seeds occurred in an average of 18% of scats collected annually in the pre-fire period, and 15% of scats collected in the post-fire period. However, the percent volume of whitebark pine seeds decreased post-fire. Whitebark pine seeds averaged 37% of the annual scat volume pre-fire, and 13% post-fire. This data was not available for my study area alone.

Random and Bear-Used Sites 1996

Bears appeared to select patches within whitebark pine habitats that balanced productivity for red squirrels and whitebark pine cones. The denser stands selected by bears likely supported large red squirrel populations. Vahle and Patton (1983) found that red squirrels in Arizona cached cones on sites that had higher-than-average basal area (i.e., dense groups of trees). Sullivan and Moses (1986) found that thinning timber stands reduced red squirrel densities. They also concluded that squirrel populations in mature stands were more stable than in juvenile stands. Factors which positively correlated with red squirrel abundance in Reinhart and Mattson's (1990) study included basal area, overstory species diversity, and "site favorability". Site favorability was an index that positively weighted direct solar radiation and negatively weighted wind exposure and elevation. The steeper slopes and higher elevations used were likely related to the distribution of whitebark pines. Whitebark pine is more dominant on harsh sites and its lower altitudinal limit may be set by competition from other conifer species (Arno and Weaver 1990).

Red Squirrel Transects 1984-86 and 1995-97

Fire played an important role in red squirrel use of habitats along the Mt. Washburn transects. I found no red squirrels or middens in the burned portion of that study area, 7-9 years after the 1988 fires. Despite increases in squirrel midden abundance in unburned portions of 2 common habitat types, overall density of middens still decreased by 27%. This significantly reduced the amount of whitebark pine cones available to bears within the transect 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 positively related to midden size (Mattson and Reinhart 1997). Bears are likely less inclined to excavate smaller middens which offer less energetic profit. Based on Mattson and Reinhart's (1997) model and the size of middens measured in the post-fire years, one would expect a 50% decrease in the likelihood of use by bears (D. J. Mattson, personal communication.). Combined with the 27% decrease in density of active middens, post-fire, the model predicted a 64% reduction in density of bear-excavated middens due to the 1988 fires. In fact, I found a 63% reduction. Thus, bear feeding activity in the whitebark pine zone decreased disproportionately more than midden density. Moreover, bears likely obtained less food from each excavation as they were using smaller middens. Although I 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 number of cones obtained by bears in the study area declined a total of 79% due to local effects of the fires on midden density and size (D. J. Mattson, personal communication).

Red squirrel middens were more abundant in the unburned parts of the transects post-fire compared to pre-fire. Potential explanations for these higher densities include (1) red squirrel population densities increased due to large crops of seeds from other conifers such as lodgepole pine, subalpine fir, and Engelmann spruce (Smith 1970, Kemp and Keith 1970, Mattson and Reinhart 1997), or (2) red squirrel densities increased due to potentially favorable changes in annual climatic conditions (Smith 1968, Rusch and Reeder 1978). I did not collect data on other cone crops or local climate by which to test the latter 2 hypotheses. Larsen et al. (1997) found that female red squirrel life history parameters and reproductive success in the northern boreal forest were unaffected by the experimental addition of supplemental food. However, the smaller average sizes of middens during the post-fire study period suggests that squirrels adjusted to changes in habitats by using smaller, and possibly newer (Finely 1969), territories (Reinhart and Mattson 1990).

The diversity of overstory species in stands of the whitebark/fir and mesic types was higher than in other types (Mattson and Reinhart 1990). Increases in midden density in unburned areas of these more diverse types may be due to an annually less variable supply of food from a greater variety of seed-producing tree species. Lower red squirrel densities in the pure whitebark type may have been caused by the lack of large 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 densities in the wet and vaccinium types may have been an artifact 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 between areas and time-periods. The use of line transects was appropriate for this study because I compared patterns of red squirrel abundance and bear use of whitebark pine seeds in the same area following significant habitat change. Differences in results from the pre- and post-fire periods can likely be attributed to habitat changes because sampling 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), I concluded that, on a per tree basis, whitebark pine cone crops were functionally the same between periods. However, as cone production could not be controlled, the two scenarios were not precisely identical. Fluctuations in whitebark pine crop size were somewhat greater in the post-fire period. I also lacked empirical data on cone production by other species (i.e., Englemann spruce, subalpine fir, and lodgepole pine), which could have been used to test the hypothesis that squirrel populations increased due to abundant alternate foods.

CONCLUSIONS

The 1988 fires burned approximately 53% of forests containing whitebark pine in the study area. Radiocollared grizzly bears exhibited similar patterns of habitat use within whitebark pine habitats during autumns before and after the fires. Following the fires, burned habitats were used in proportion to their availability in poor whitebark pine cone years and less than their availability in abundant cone years. Whitebark pine/subalpine fir communities were most preferred in abundant cone years of both periods, while mesic and whitebark/fir communities were most preferred in all years.

Sites used by bears for feeding on whitebark pine seeds were similar in pre- and post-fire periods. A higher proportion of pre-fire sites were located in whitebark/fir communities, whereas more whitebark pine feeding sites were found in the mesic habitat type post-fire. This was probably a result of local variation in the amounts of pine seeds available through red squirrel middens because the area of both habitat types was reduced in similar proportions. Analysis of scats collected across the ecosystem suggested that whitebark pine seeds constituted a smaller portion of the bears' diets post-fire.

Comparing bear-used sites with randomly sampled sites in 1996 showed that bears were selecting microsites within habitats for feeding on whitebark pine seeds. These sites were typically denser, higher in elevation, and had higher percentage of whitebark pine than sites randomly located in each habitat type. Levels of whitebark pine pathogens (i.e., white pine blister rust and mountain pine beetles) affected a low percentage of trees in sampled plots.

Repeating the original red squirrel transect study on Mt. Washburn offered a more objective comparison between periods and showed a significant impact of the fires on bear use of whitebark pine seeds. While red squirrel density increased in unburned areas, the overall density of red squirrel middens declined by 27% within the transect study area. Grizzly bear use of middens along the transects decreased by 63% overall. Middens were smaller in the post-fire period, and this likely contributed to the decline in bear use of pine seeds.

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 the amount of whitebark pine seeds available to Yellowstone grizzly bears. This loss will likely 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 site for Clark's nutcrackers (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 predictably do not provide bears with as much energy and fat as do 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, a fungus introduced from Europe in 1910 (Kendall and

Arno 1990). In northwestern Montana, the mortality rate of whitebark pine from this disease is estimated at 42%, and infestation rates range from 50-80%. In the colder, drier climate of the Yellowstone area, whitebark pine mortality from this disease is low, about 4% (Kendall, in press). However, stands, which now contain low levels of blister rust infestation, may become imperiled under a global warming scenario (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. I 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, particularly on an ecosystem-wide scale, I encourage caution in the management of whitebark pine habitats. I would discourage any further large-scale losses of whitebark pine habitat and seed-producing trees from management-prescribed fires or timber harvesting. Management of whitebark pine forests for grizzly bears should emphasize maintaining large, secure areas of diverse habitat types that support stable whitebark pine stands and red squirrel populations.

LITERATURE CITED

Arno, S. F. and R. J. Hoff. 1989. Silvics of whitebark pine (*Pinus albicaulis*). U. S. Forest Service Intermountain Research Station General Technical Report INT-253. 11 pp.

Arno, S. F. and T. Weaver. 1990. Whitebark pine community types and their pattern on the landscape. Pages 97-105 *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.

Blanchard, B. M. 1980. Grizzly bear-habitat relationships in the Yellowstone area. International Conference on Bear Research and Management 5:118-123.

Blanchard, B. M. 1985. Field techniques used in the study of grizzly bears. Interagency Grizzly Bear Study Team Report. 24 pp.

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.

Blanchard, B. M. and R. R. Knight. 1991. Movements of Yellowstone grizzly bears. Biological Conservation 58:41-67.

Blanchard, B. M. and R. K. Knight. 1996. Effects of wildfire on grizzly bear movements and food habits. Pages 117-122 *in* Ecological implications of fire in Greater Yellowstone: proceedings of the second biennial scientific conference on the Greater Yellowstone Ecosystem. International Association of Wildland Fire.

Burnham, K. P., D. R. Anderson, and J. L. Laake. 1980. Estimation of density from line transect sampling of biological populations. Wildlife Monographs 72:1-202.

Conover, D. 1980. Practical nonparametric statistics, second edition. Wiley, New York. 493 pp.

Costello, C. M. and R. W. Sage, Jr. 1994. Predicting black bear habitat selection from food abundance under 3 forest management systems. International Conference on Bear Research and Management 9:375-387.

Despain, D. G. 1990. Yellowstone vegetation. Roberts Rinehart Publishers, Boulder, Colorado, USA. 239 pp.

Dirks, R. A. and B. E. Martner. 1982. The climate of Yellowstone and Grand Teton National Parks. U. S. National Park Service Occasional Paper No. 6. 26 pp.

Eberhardt, L. L. 1978. Transect methods for population studies. Journal of Wildlife Management 42:1-31.

ESRI, Inc. 1992. ArcView 2.1b. Environmental Systems Research Institute. Redlands, California.

ESRI, Inc. 1995. ARC/INFO 7.1.4. Environmental Research Institute. Redlands, California.

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.

Hamer, D. and S. Herrero. 1987. Wildfire's influence on grizzly bear feeding ecology in Banff National Park, Alberta. International Conference on Bear Research and Management 7:179-186.

Hoff, R. and S. Hagle. 1990. Diseases of whitebark pine with special emphasis on white pine blister rust. Pages 179-190 *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.

Hutchins, H. E. 1990. Whitebark pine seed dispersal and establishment: who's responsible? Pages 245-255 *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.

Keane, R. E. and P. Morgan. 1994. Decline of whitebark pine in the Bob Marshall Wilderness complex of Montana, U.S.A. Pages 245-253 *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.

Keefer, W. R. 1971. The geologic story of Yellowstone National Park. U. S. Geological Survey Bulletin No. 1347. 92 pp.

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.

Kendall, K. C. 1994. Whitebark pine conservation in North American National Parks. Pages 302-307 *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.

Kendall, K. C. In press. Whitebark pine. *In* M. J. Mack, P. A. Opler, C. E. Haeker-Puckett, P. D. Doran, and L. S. Huckaby, editors. Our living resources: status and trends of the nation's biological resources. U. S. Department of the Interior, Washington, DC.

Kendall, K. C. 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.

Kovach, W. L. 1994. Oriana for Windows 1.0. Kovach Computing Services. Wales, United Kingdom.

Larsen, K. W., C. D. Becker, S. Boutin, and M. Blower. 1997. Effects of hoard manipulations on life history and reproductive success of female red squirrels (Tamiasciurus hudsonicus). Journal of Mammalogy 78:192-203.

Mattson, D. J. 1990. Human impacts on bear habitat use. International Conference on Bear Research and Management 8:35-56.

Mattson, D. J. 1997. Use of lodgepole pine cover types by Yellowstone grizzly bears. Journal of Wildlife Management 61:480-496.

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. G. Despain. 1985. Grizzly bear habitat component mapping handbook for the Yellowstone ecosystem. Unpublished U. S. National Park Service Report.

Mattson, D. J. and C. Jonkel. 1990. Stone pines and bears. Pages 223-226 *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. 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.

Mattson, D. J. and D. P. Reinhart. 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.

Mattson, D. J. and D. P. Reinhart. 1996. Indicators of red squirrel (*Tamiasciurus hudsonicus*) abundance in the whitebark pine zone. Great Basin Naturalist 56:272-309.

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.

Mattson, D. J., D. P. Reinhart, 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 white bark 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.

Mealey, S. P. 1980. The natural food habits of grizzly bears in Yellowstone National Park. International Conference on Bear Research and Management 3: 281-292.

Morgan, P., S. C. Bunting, R. E. Keane, and S. F. Arno. 1994. Fire ecology of whitebark pine forests of the northern Rocky Mountains. Pages 136-141 *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.

Neu, C. W., C. R. Byers, J. M. Peek, and V. Boy. 1974. A technique for analysis of utilization-availability data. Journal of Wildlife Management 38:541-545.

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.

Rothermel, R. C., R. A. Hartford, and C. H. Chase. 1994. Fire growth maps for the 1988 Greater Yellowstone Area fires. USDA Forest Service General Technical Report INT-304. 65 pp.

Rusch, D. A. and W. G. Reeder. 1978. Population ecology of Alberta red squirrels. Ecology 59:400-420.

Smith, M. C. 1968. Red squirrel response to spruce cone failure in interior Alaska. Journal of Wildlife Management 32:305-317.

Smith, C. C. 1970. The coevolution of pine squirrels and conifers. Ecological Monographs 40:349-371.

StatSoft, Inc. 1994. STATISTICA for Windows (volume 1): general conventions and statistics I. StatSoft, Inc..Tulsa, Oklahoma.

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. 122 pp.

Stephens, D. W. and J. R. Krebs. 1986. Foraging theory. Princeton: Princeton University Press.

Sullivan, T. P. and R. A. Moses. 1986. Red squirrel populations in natural and managed stands of lodgepole pine. Journal of Wildlife Management 50: 595-601.

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.

Vahle, J. R. and D. R. Patton. 1983. Red squirrel cover requirements in Arizona mixed conifer forests. Journal of Forestry 81:14-15, 22.

Weaver, T. and F. Forcella. 1986. Cone production in *Pinus albicaulis* forests. Pages 68-76 in R. C. Shearer, compiler. Proceedings – conifer tree seed in the Inland Mountain West Symposium. U. S. Forest Service General Technical Report INT-203.

Weaver, T., F. Forcella, and D. Dale. 1990. Stand development in whitebark pine woodlands. Pages 151-155 *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.

Wielgus, R. B. and F. L. Bunnell. 1995. Test of hypothesis for sexual segregation in grizzly bears. Journal of Wildlife Management 59:552-560.

Zager, P., C. Jonkel, and J. Habeck. 1983. Logging and wildfire influence on grizzly bear habitat in north-western Montana. International Conference on Bear Research and Management 5:124-132.

Zar, J. H. 1984. Biostatistical analaysis. Second ed. Prentice-Hall, Inc., Englewood Cliffs, New Jersey. 718 pp.

APPENDIX A

STANDARD IGBST FORM FOR RECORDING DATA AT GRIZZLY BEAR ACTIVITY SITES

FRONT SIDE

Mattson--5/89

BMU |_ _ _ _ _ _ _|

REVIST ID |_ _ _ _|

HABITAT FIELD FORM

KEY # (ID/ JUL) |_ _ _|_ _ _| UTM |_ _ _ _|_ _ _ _ _| DATE (MO/ DY/ YR) |_ _|_ _|_ _| OBS |_ _|_ _|

LOCATION |_ _ _ _ _ _ _ _ _ _| SIGN AGE |_ _ _ _| DAYBED: Y N SCAT: Y N (NUM: _ _)

ASPECT |_ _ _| SLOPE |_ _| ELEV |_ _ _ _| LNDFRM |_ _ _| DIST FOR/NF |_ _ _ _|

VEGETATION	MICROPLOT 1	2	3	4	5	6	7	8	9	10	USE	SUMMARY FQ	CVR	C
Shrubs														
ARUV														
CRDO														
FRAG														
RHAL														
RIBS														
SHCA														
VACA														
VAGL														
VASC														
Forbs														
ANGL														
CIRS														
CLYT														
EPLB														
EQUI														
HELA														
LOMT														
MECI														
OSCH														
PEGA														
PLYG														
POTA														
STAM														
TARX														
TRAG														
TRFL														
Graminoids														
AGPY														
BRMS														
CALA														
CARX														
DESH														
ELYM														
FEST														
MELC														
PHLM														
POA														
SCRP														
Other														
RDNT														
PGRP1														
PGRP2														
% CVR GRAM														
HEIGHT GRAM														
% CVR FORB														
HEIGHT FORB														

TIMBER VARIABLE PLOT

BAF |_ _| cm/inch

TREE	SPECIES	DBH	DD
1			
2			
3			
4			
5			
6			
7			
8			
9			
10			

SUMMARY

	FQ	DIA	DD
LP			
SF			
SP			
DF			
AS			
WB			

DAYBED 1

LENGTH |_ _ _|
WIDTH |_ _ _|
DEPTH |_ _ _|
DIST TREE |_ _ _|
TREE ID |_ _|
DIST DDFLL |_ _ _|

DAYBED 2

LENGTH |_ _ _|
WIDTH |_ _ _|
DEPTH |_ _ _|
*DIST DAYBED 1 |_ _ _|
DIST TREE |_ _ _|
TREE ID |_ _|
DIST DDFLL |_ _ _|

HT |_ _ _ _ _| CT |_ _ _ _| HGT FOL |_ _| HGT SHRUB |_ _|

TTL GRAM CVR |_ _ _| TTL FORB CVR |_ _ _| TTL SHRUB CVR |_ _ _| TTL FOREST CVR |_ _ _|

DEADFALL CVR |_ _ _| Description:

PHYSIOGNOMY: Burned: Y N Intensity |_ _ _|

Distance to burn/nonburn edge |_ _ _|

BACK SIDE

CARCASS

Species	Sex	Age-class	Carcass age	% consumed: Bear	% consumed: Other scav.	Bear pred: Y N

DESCRIPTION OF FEEDING ACTIVITY:

	Species used	Intensity	Remarks
1			
2			
3			
4			
5			

MEASUREMENTS AND DESCRIPTION:

SPECIES LIST

GRAMINOIDS

Species	Ab	Cvr	P

FORBS

Species	Ab	Cvr	P

SHRUBS

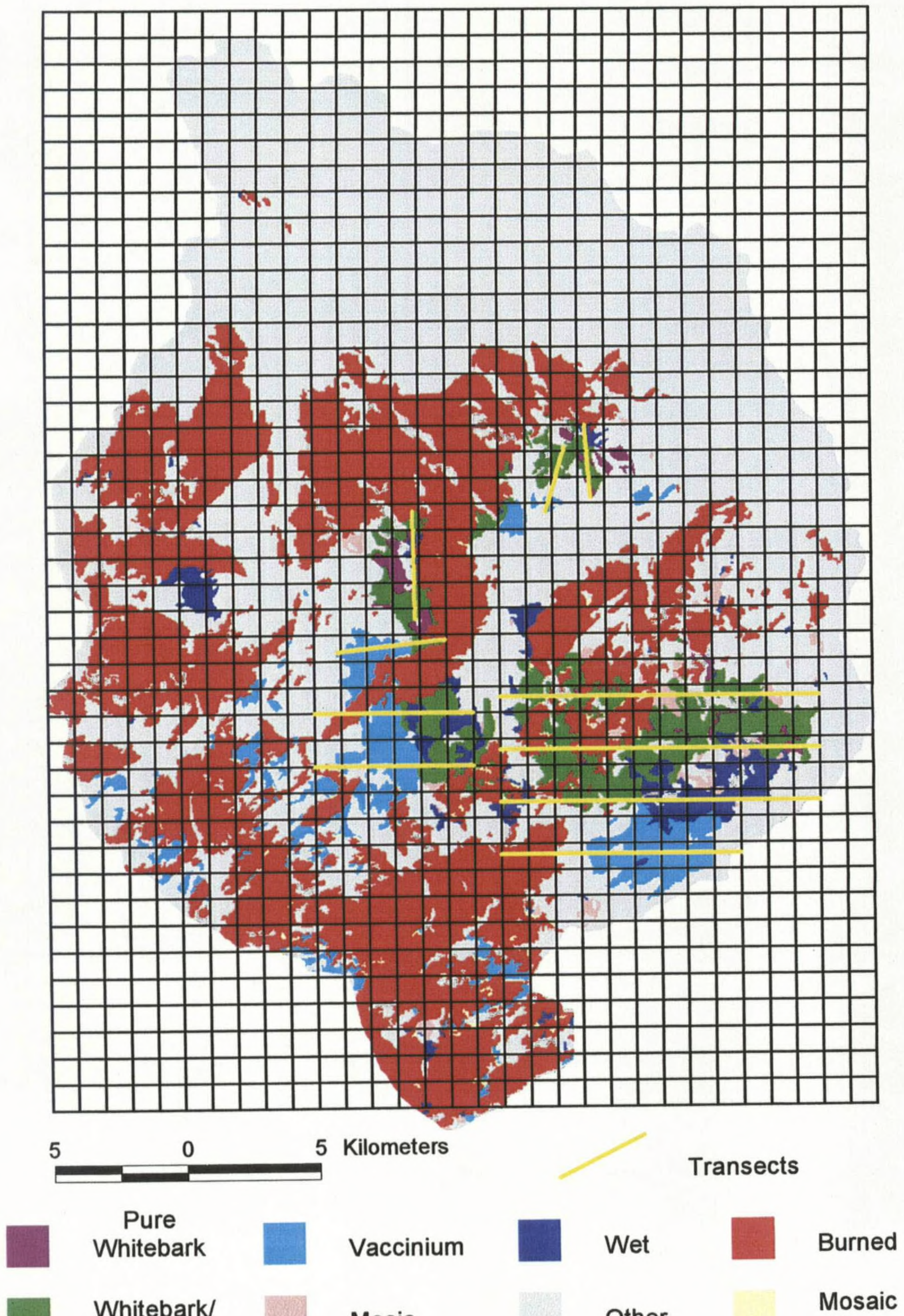
Species	Ab	Cvr	P

TREES

Species	Ab	Cvr	Comp

APPENDIX B

COLOR MAP OF HABITAT TYPES IN THE WASHBURN BEAR MANAGEMENT UNIT AND TRANSECTS USED TO RANDOMLY PLACE SAMPLE PLOTS, 1996


5
0
5 Kilometers
Transects
Pure Whitebark
Vaccinium
Wet
Burned
Whitebark/ Fir
Mesic
Other
Mosaic Burn