DETERMINING THE RELATIONSHIP BETWEEN WHITEBARK PINE STAND-LEVEL HEALTH AND SEED DISPERSAL BY CLARK'S NUTCRACKER

by

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Thesis directed by Professor Diana F. Tomback

ABSTRACT

Whitebark pine (*Pinus albicaulis*) in the northern Rocky Mountains is declining from infection by the exotic pathogen *Cronartium ribicola*, which causes white pine blister rust, and from outbreaks of mountain pine beetles (*Dendroctonus ponderosae*). Previous studies demonstrated that as whitebark pine stands are progressively damaged or killed by blister rust and beetles, Clark's nutcrackers (*Nucifraga columbiana*), the main seed dispersers for whitebark pine, make fewer stand visits when cones are produced and seeds are ripe. The goal here was to test these observations further by examining relationships between whitebark pine forest health and nutcracker visitation with a different study design. I hypothesized that relatively few nutcrackers visit whitebark pine stands with low live whitebark pine basal area, high blister rust infection rate, and thus lower cone production. If this hypothesis is supported by data, what are the implications for whitebark pine seed dispersal and regeneration? In 2008, I established ten 1 km x 30 m transects and two forest health plots per transect in Yellowstone, Grand Teton, Glacier, and Waterton Lakes National Parks. I gathered data on tree health, cone counts, and nutcracker occurrence in 2008 and 2009 from these transects and plots. MANOVA results indicated that *park* was a significant predictor of variation in health and nutcracker visits. However, logistic regression analysis failed to isolate a single variable or combination of variables associated with nutcracker occurrence; several models were identified as comparable in predictive strength. In comparison to previous findings, we found a somewhat lower cone production threshold predicting the probability of nutcracker occurrence. This finding offers more hope for areas with fewer living trees or heavily damaged trees. Otherwise, if nutcrackers stop visiting whitebark pine stands with high damage and mortality, natural regeneration will diminish greatly. For example, areas burned by wildfire may not regenerate. If nutcrackers are not dispersing seeds from damaged stands, then seed or seedling planting may be highly appropriate restoration strategies for these areas.

This abstract accurately represents the content of the candidate's thesis. I recommend its publication.

Signed______________________
Diana F. Tomback

DEDICATION

I dedicate this thesis to my parents for their support of my graduate education and for instilling me with an appreciation for life-long learning.

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CHAPTER 1

INTRODUCTION AND BACKGROUND

Significance of study

Background and significance

Whitebark pine (*Pinus albicaulis*) is a keystone and foundation species of high elevation ecosystems in the western U.S. and Canada (Tomback et al. 2001a, Ellison et al. 2005). In the northwestern U.S. and throughout much of its Canadian distribution, whitebark pine is declining rapidly from a combination of white pine blister rust infection (caused by the invasive pathogen *Cronartium ribicola*) and mountain pine beetle (*Dendroctonus ponderosae*) outbreaks. Whitebark pine is highly susceptible to blister rust, and only a small percentage of trees (usually <5%) show resistance (Hoff et al. 1980). Mountain pine beetles kill both blister rust-resistant and non-resistant trees, thus reducing the rate of spread of resistant genes for blister rust resistance. Therefore, the combination of an introduced pathogen and native pest infestations poses serious challenges to maintaining healthy whitebark pine ecosystems. Currently, whitebark pine losses are greatest in the northern Rocky Mountains of the U.S., the inter-mountain region, and adjacent regions in southern Canada, where blister rust infection levels are high, and outbreaks of mountain pine beetle have been rapidly expanding (Kendall and Keane 2001, Schwandt 2006, Gibson et al. 2008).

Dispersal of whitebark pine seeds is primarily accomplished by Clark's nutcrackers (*Nucifraga columbiana*), which harvest and cache seeds throughout mountain terrain. The coevolved, mutualistic relationship between whitebark pine and the Clark's nutcracker is an integral part of the natural history of the northern Rocky Mountains (Lanner 1982).

This interaction now appears threatened as whitebark pine succumbs to blister rust and mountain pine beetles. Previous work shows that nutcrackers are sensitive to the number of seeds available within a stand and are efficient foragers (e.g., Tomback 1978, Vander Wall 1988). McKinney and Tomback (2007) and McKinney et al. (2009) show that nutcrackers may be less likely to visit blister rust-diseased whitebark pine trees, which often have fewer cones than healthy trees because of crown damage. With little to no seed dispersal, natural whitebark regeneration is anticipated to decline throughout regions with damaged stands and high mortality. In particular, whitebark pine regeneration in burned areas near these stands may be delayed or greatly reduced. Whitebark pine is typically a post-fire pioneer in the subalpine zone (Arno and Hoff 1990, Tomback et al. 2001b).

Restoration of whitebark pine through planting blister rust resistant seedlings, and protection of potentially blister rust resistant trees against mountain pine beetle, are management strategies advocated by the U.S. Forest Service and supported by several national parks (Tomback et al. 2001a, Schwandt 2006). Given that limited funding is available for restoration, it is critical that restoration be prioritized for areas where whitebark is in the worst shape. Results from this study, which relates nutcracker occurrence to stand health, could provide useful information for the prioritization process used by parks.

Questions addressed in this study

Overall, I am interested in determining whether living whitebark pine stand density and health, and thus cone production capacity, predicts the occurrence of nutcrackers in whitebark pine communities. If so, identifying the variables associated with badly damaged stands which are unlikely to have nutcrackers visit (even if some cones are being produced) has important management applications.

Here, the following specific questions are asked: 1) What are the differences in whitebark pine health, stand composition, and basal area (abundance) within plots at study sites among four national parks? 2) Are there differences in cone numbers among parks and from year to year? 3) Are there differences in observed squirrel numbers (they are influential seed predators on whitebark cones)? 4) Are there differences in observed nutcracker numbers observed from park to park? 5) Are there differences in whitebark pine regeneration (seedlings) from park to park? 6) Is there an overall relationship between cone numbers and nutcracker occurrence? 7) Are there variables that predict nutcracker occurrence within and across parks? 8) How does the relationship between cone production and proportion of observation hours with one or more nutcracker sightings relate to the relationship observed by McKinney et al. (2009)? How did the cone production threshold determined from this study relate to the threshold observed by McKinney et al. (2009)? 9) What cone production threshold can be used to prioritize whitebark pine stands for restoration?

Background information

Natural history and ecosystem function

Whitebark pine is one of five species of bird-dispersed pines in the genus *Pinus* (Family Pinaceae), subgenus *Strobus* (the white pines), section *Strobus,* subsection *Cembrae* (the stone pines). Only whitebark pine is found in North America; the other four stone pines occur in Europe and Asia (Price et al. 1998). Whitebark pine is distributed at treeline and subalpine elevations across eastern and western montane regions in the western U.S. and Canada. In the Rocky Mountains, it ranges from the Wind River and Salt River Ranges of western Wyoming north to about 54 °N in Alberta and British Columbia. It is also distributed from the southern Sierra Nevada and Cascades north through the Coastal Mountains of British Colombia to 55 ° N. Isolated stands occur in the northern Great Basin (Nevada), as well as other areas (Critchfield and Little 1966, McCaughey and Schmidt 2001) (Figure 1).

McCaughey and Tomback (2001) provide an overview of cone development and seed production. As is typical in stone pines, trees grow slowly and the first production of male and female cones begins around age 20 to 30 years, although large cone crops are not produced until age 80 to 120 years. Seed and pollen cone formation occurs from mid-July to mid-September. After overwintering, both male and female cones begin development in April and May. Mature cones produce two large, wingless seeds on each cone scale (on average, 75 seeds per cone). The cones of whitebark pine are indehiscent, which means that cones remain closed even after seeds ripen. Thus, whitebark pine depends on nutcrackers to remove seeds from cones and disperse them. Consequently, whitebark pine occurs completely within the range of the Clark's nutcracker (see Figure 1 below). Cone production in whitebark pine varies from to year to year and is influenced by tree canopy cover and size, and climatic conditions, as well as insect and disease presence. Good cone crops are typically produced every three years (McCaughey and Tomback 2001). Whitebark pine cone production peaks on average at 250 years of age (Arno and Hoff 1990).

Whitebark pine occurs across a continuum of community types (Arno and Hoff 1990, Arno 2001). On favorable sites in the lower upper subalpine, it occurs as a seral species. After disturbance, and particularly wildfire, whitebark pine is one of the first conifers to regenerate, because of rapid seed dispersal by Clark's nutcrackers and seedlings tolerant of harsh conditions (McCaughey and Tomback

2001, Tomback et al. 2001b). Because whitebark pine is a poor competitor and moderately shade-intolerant, it declines in these seral communities over time as faster-growing, shade-tolerant conifers colonize and continue to regenerate. On harsh sites, usually at higher elevations, its competitors are often suppressed by wind and exposure. Whitebark thus can occur as a dominant climax species under these conditions. In treeline communities, whitebark often assumes a krummholz growth form (a stunted, low growing tree) due to exposure (Arno and Hoff 1990).

Historically, whitebark pine has been a prominent subalpine and treeline species in Glacier National Park and adjacent Waterton Lakes National Park, as well as in the Greater Yellowstone Area, including Grand Teton and Yellowstone National Parks (Arno and Hoff 1990). This long-lived conifer plays an important role in the high elevation ecosystem. It is considered a keystone and foundation species for numerous reasons: it stabilizes soil at treeline; pioneers after fire or other disturbance, paving the way for community development; grows in terrain that may otherwise prove inhospitable due to harsh environments; and provides an important, high quality food source for various small granivorous birds and mammals. Thus, whitebark pine both stabilizes high elevation communities, and enhances community biodiversity (Arno and Hoff 1990, Tomback et al. 2001a, Tomback and Kendall 2001, Ellison et al. 2005).

Figure 1. Whitebark (cross-hatched) and nutcracker (grey) distribution range (Ridgely et al. 2005, U.S. Geographical Survey 1999)

Clark's nutcracker

Clark's nutcracker (Family Corvidae) is distributed throughout high elevation forest habitats in the western United States and Canada (Figure 1). Nutcrackers are pale grey birds with black and white markings on wings and tail. They are sexually monomorphic, but males are often larger than females (Mewaldt 1958). Clark's nutcrackers are morphologically adapted to a diet of fresh and stored conifer seeds. Their long, sharp bills are used to dig into unripe, closed cones to extract seeds (VanderWall and Balda 1977, Tomback 1978). They are opportunistic conifer-seed specialists that vary their diet based on cone availability from various conifers from year to year (Tomback 1983, 1998, Lanner 1996). Nutcrackers have a coevolved mutualistic relationship with whitebark pine (e.g., Tomback 1978, 1982, 1983, Lanner 1980, 1996, Tomback and Linhart 1990). The large, wingless seeds of whitebark pine are dependent upon Clark's nutcrackers for dispersal (Hutchins and Lanner 1982, Tomback 1982). In turn, when whitebark pine seeds are available, they comprise an important part of the Clark's nutcracker diet (Giuntoli and Mewaldt 1978, Tomback 1978). Before whitebark pine seeds ripen (in mid to late August), Clark's nutcrackers act as seed predators and shred cones as they remove pieces of seeds. This activity leaves obvious signs of harvest (Tomback 1998). Later, as seeds ripen, Clark's nutcrackers act as seed dispersers. At this time, nutcrackers fill their throat pouch (sublingual pouch) with seeds for transport to cache sites. This behavior is easily observed in the field and is equated with seed dispersal (Tomback 1978, 2001). These birds can differentiate between healthy and unhealthy pine seeds (Vander Wall and Balda 1977), and also move from regions where cone production has failed to regions that produce good cone crops (see review in Tomback 1998).

Nutcrackers cache an estimated 35,000 to 98,000 whitebark pine seeds per individual per year, which are later used as food for themselves and their young (Hutchins and Lanner 1982, Tomback 1982). Nutcrackers typically cache seeds within a few hundred meters from their harvesting site, but longer caching distances range from 1-3.5 km (Hutchins and Lanner 1982, Dimmick 1993). Caches are buried 1-3cm deep in soil or gravel substrate. Mean cache size is 3.2-3.7 (Hutchins and Lanner 1982, Tomback 1982). Cache sites can be in a variety of habitats (i.e. burned areas, open and closed forests, meadows, dry slopes) and can even be placed above ground in logs, rocks, or trees. Ground caches are concealed with substrate and smoothed over (Tomback 1978). Nutcrackers have a well-developed spatial memory that allows them to accurately locate caches (in a laboratory setting) for up to 270 days (Kamil and Balda 1985). Whitebark pine seed caches are recovered from February through July (Tomback 1978, Vander Wall and Hutchins 1983). Unrecovered caches often germinate after snowmelt or rain. In whitebark pine communities, Steller's jays (*Cyanocitta stelleri*), mountain chickadees (*Poecile gambeli*), common ravens (*Corvus corax*), pine grosbeaks (*Pinicola enucleator*), red crossbills, deer mice (*Peromyscus maniculatus*), chipmunks (*Tamias* spp.), and pine squirrels (*Tamiasciurus hudsonicus*) also consume whitebark pine seeds (Tomback 1978, Hutchins and Lanner 1982). Pine squirrels (*Tamiasciurus hudsonicus and T. douglasi*) are the dominant predispersal seed predator of whitebark pines. They frequently out-compete nutcrackers for seeds by cutting cones down from trees to store in middens, which further reduces seed dispersal by nutcrackers and results in fewer nutcrackers visiting areas where pine squirrels are present (Tomback 1978, Siepelski and Benkman 2008). Squirrel predation of whitebark seeds has serious consequences. Selection by whitebark pine against squirrel predation weakens the selection by nutcrackers for large seeds and high numbers of seeds per cone. Pine squirrels have also been shown to reduce whitebark stand density (Siepelski and Benkman 2008).

In the Rocky Mountains, both grizzly (*Ursus arctos*) and black bears (*Ursus americanus*) consume whitebark pine seeds taken from cones in squirrel middens (or even from trees); these seeds are an important pre-hibernation food for bears in the Greater Yellowstone Area and Rocky Mountain Front (Mattson et al. 2001).

Blister rust

White pine blister rust is now present nearly rangewide in whitebark pine (Kendall and Keane 2001, McDonald and Hoff 2001). The only regions reporting low to no infection levels in whitebark pine are the interior Great Basin and the southern Sierra Nevada (Schwandt 2006). Blister rust originated in Asia and became established in eastern North American around 1890. It was introduced several times to the Pacific Northwest, U.S. and Canada by 1910. By 1970, blister rust distribution had reached as far south as southern New Mexico (Hawksworth 1990). Blister rust reached northern Colorado by 1998 and had reached southern Colorado by 2003 (Johnson and Jacobi 2000). It was found in the Jarbidge Wilderness of Nevada in 2002 (Vogler and Charlet 2004). Susceptible hosts include five-needled white pines such as eastern white pine (*Pinus strobus*), western white pine (*Pinus monticola*), sugar pine (*Pinus lambertiana*), whitebark pine, limber pine (*Pinus flexilis*), Rocky Mountain bristlecone pine (*Pinus aristata*), Great Basin bristlecone pine (*Pinus longaeva*), foxtail pine

(*Pinus balfouriana*), and southwestern white pine (*Pinus strobiformis*) (McDonald and Hoff 2001).

The rust fungus requires two hosts, a pine and an alternate host plant, to complete its life cycle (McDonald and Hoff 2001). Known hosts include *Ribes* spp. (currants and gooseberries), *Castilleja* sp. (Indian paintbrush), and *Pedicularis* sp. (lousewort) (McDonald et al. 2006). Attempts to control the disease by eradicating the alternate hosts have been unsuccessful (Benedict 1981). The life cycle is summarized in McDonald and Hoff (2001): Basidiospores from an alternate host enter whitebark pine through needle stomata in late summer or early fall. The infection begins as a yellow or red spot on the needles and may progress to a swollen area on a branch or trunk. Two to three years after infection, this swollen area becomes a canker that produces aeciospores. The canker eventually kills cone-bearing branches by girdling them, thus reducing seed production, and kills trees by weakening them or girdling the trunk. Aeciospores are wind-dispersed and can travel up to 500 km (McDonald and Hoff 2001).

Mountain pine beetle

Also threatening whitebark pine forest health are outbreaks of the mountain pine beetle, a native insect that can use any pine species as host. Mountain pine beetles attack live conifers by tunneling into the bark, forming vertical tunnels, and laying approximately 75 eggs per female. When the eggs hatch, the larvae tunnel away from the hatching site and produce characteristic horizontal tunnels visible under the bark. Larvae overwinter under the bark and emerge in early summer as adults (Leatherman et al*.* 2007).

Mountain pine beetle outbreaks have occurred intermittently throughout the 20th century, probably driven by warm, dry weather conditions and host availability (Logan and Powell 2001). Outbreaks occurred from about 1910 to the 1930’s and again throughout the 1970’s and 80’s. Large areas of long dead trees are referred to as “ghost forests.” Whitebark ghost forests are still present in many areas today as a result of past beetle kill (Kendall and Keane 2001). The current outbreak began approximately 10 years ago.

Mountain pine beetle typically attacks whitebark pine that is experiencing stressful growing conditions (Leatherman et al*.* 2007). Stress is currently caused by drought (water stress) from warmer temperatures (Logan and Powell 2001, Gibson et al. 2008). Healthy trees produce pitch tubes (visible on the trunk) in defense against the beetles. These resin tubes are produced in an attempt by the tree to expel the beetles from its bark. However, under drought or other stressful conditions, trees may not be able to produce pitch tubes (Leatherman et al. 2007). Because pine beetles prefer older whitebark trees, which tend to produce a lot of cones, beetle outbreaks can drastically decrease seed production in an area. Trees that are infected with blister rust can be more vulnerable to a successful beetle infestation as well (Six and Adams 2007, Bockino 2008). Mountain pine beetle outbreaks now range from British Columbia to California and east throughout the Rocky Mountains. Infestations of mountain pine beetle are killing great numbers of whitebark pine in the GYA, the northwestern U.S., and western Canada (Gibson et al. 2008).

Ecosystem level

Significance of declines

Fewer than 5% of whitebark pine are genetically resistant to blister rust disease (Hoff et al. 1994). In some forests in the northern Rocky Mountains, especially in Glacier National Park, blister rust infection levels can be as high as 90-100% (Kendall et al. 1996, Kendall and Keane 2001, Smith et al. 2008). The study areas used here, Waterton Lakes and Glacier National Parks in the northern Rocky Mountains and Yellowstone and Grand Teton National Parks in the Central Rocky Mountains, represent two extremes on the whitebark pine blister rust infection continuum. Recent assessments in Glacier and Waterton Lakes National Parks (Smith et al. 2008) and the Greater Yellowstone Area (GYA) (GYWPMWG 2008) indicate mean blister rust infection levels to be 67%, 71.5%, and 26%, respectively. Glacier National Park, the contiguous Waterton Lakes National Park in Canada, and the contiguous Blackfeet Reservation have the highest mean blister rust infection and mortality levels known rangewide for whitebark pine (with mortality from all factors ca. 50%) (Smith et al. 2008). Farther to the south, in Yellowstone and Grand Teton national parks, blister rust infection levels and damage are much lower, but appear to have increased recently, reaching an overall average of about 20% (GYWPMWG 2008).

The rust pathogen has been present in northwest Montana since 1927 and on the continental divide in Glacier National Park since 1939 (Mielke 1943). In contrast, blister rust has been slow to invade the GYA; surveys for blister rust in Yellowstone National Park in 1970 indicated no occurrence in 26 of 29 whitebark pine stands surveyed, and extremely low incidence (1 or 2%) in three stands. A second survey eight years later indicated infections in a few stands previously without blister rust and some increase in two stands to 5-6% (Carlson 1978). Carlson (1978) suggested that both the ecological conditions in the GYA, e.g., less susceptible alternate host species, and climate were unfavorable to the spread of the blister rust pathogen, but blister rust levels are clearly increasing. Thus, blister rust continues to spread into new regions where hosts are present, and intensify in areas where it is already present.

Whitebark is declining nearly rangewide from the combination of blister rust infection and pine beetle infestation. As a result, the nutcracker-whitebark pine relationship may be threatened in areas with high blister rust infection and mountain pine beetle outbreaks. Mountain pine beetles kill both blister rust-resistant and non-resistant trees, thus greatly reducing the possibility that natural selection can spread resistance to blister rust fast enough. Therefore, the combination of introduced pathogen and native pest infestations pose serious challenges to maintaining healthy whitebark pine ecosystems in the future. McKinney and Tomback (2007) and McKinney et al. (2009) have shown that nutcrackers make fewer visits to forest stands with high levels of blister rust damage and mortality. Nutcrackers are energy-sensitive foragers, meaning that they select areas for seed harvest based on rates of energy intake (Tomback 1978, Tomback and Kramer 1980, Vander Wall 1988). Thus, they may be less likely to visit blister rust-diseased or damaged whitebark pine trees, which have fewer cones than healthy trees because of crown damage (McDonald and Hoff 2001, McKinney and Tomback 2007, McKinney et al. 2009). If cone decline continues, seed dispersal by nutcrackers could be reduced, disconnecting the mutualistic relationship between nutcrackers and whitebark pine (McKinney et al. 2009, Tomback and Achuff in press). With little to no seed dispersal, natural whitebark regeneration will decline throughout regions with highly damaged stands; in particular, burned areas near these stands are unlikely to regenerate with whitebark pine, which is typically a post-fire pioneer in the subalpine zone (Arno and Hoff 1990, Tomback et al. 2001b, Tomback and Achuff in press).

Restoration of whitebark pine through planting of rust- resistant seedlings and protection of healthy trees are management strategies advocated by the U.S. Forest Service and supported by different national parks (Schwandt 2006, Tomback and Achuff in press). Glacier National Park and adjacent national forests, and national forests in the Greater Yellowstone Area have implemented some restoration projects (Schwandt 2009). Given that limited funding is available for restoration, it is critical that areas for restoration be prioritized and restoration implemented.

CHAPTER 2

METHODS

Study design

Study areas and transect sites

Research sites. Dates of all fieldwork are as follows: July 4 to August 1 and August 23 to September 3, 2008; July 10 to 24 and August 26 to September 8, 2009. All research took place in study sites in Grand Teton, Yellowstone, Glacier, and Waterton Lakes National Parks. From this point forward, National Park will be abbreviated NP. Research study areas are mapped in Fig. 2 and major characteristics are listed in Table 1.

Grand Teton NP. Grand Teton NP is located entirely in Wyoming, only 30 km south of Yellowstone NP (Figure 2). The park is 1,253.5 sq km in area. Spruce-fir forests are dominant in Grand Teton NP, although lodgepole pine (*Pinus contorta*) is the most common conifer. Whitebark pine grows above 2438 ft. Also present are Douglas-fir (*Pseudotsuga menziesii*), subalpine fir (*Abies lasiocarpa)*, Engelmann spruce (*Picea engelmannii*), and blue spruce (*Picea* *pungens*) (Crandall 1977). Research transects in Grand Teton NP are on Teewinot Mountain and below Amphitheater Lake. Both transects are located in the Teton Mountain Range, and both are accessed from trailheads adjacent to the Lupine Meadows parking area, located in the central part of the park.

The Teewinot transect is placed along the Apex trail (a rough climber's trail), which has steep switchbacks. The transect began approximately 4 km east of the trailhead. The Amphitheater Lake transect is accessed from the more widely used Garnett Canyon trailhead, and placed off a switch-backing trail just below Amphitheater Lake. Elevation ranged from 2738 to 2867 m. The transect began approximately 5 km from the trailhead.

Yellowstone NP. Yellowstone NP comprises 8,992.5 sq km with 96% in northwestern Wyoming, 3% in southern Montana, and 1% in eastern Idaho. Greater than eighty percent of the park is forested. Whereas subalpine forests of Engelmann spruce and subalpine fir) comprise the main climax forest vegetation, representing about 77% of the Park's forest cover, lodgepole pine forms the dominant successional subalpine forest communities, and is the most common tree in the park. The remainder of forest is whitebark pine and Douglas-fir Whitebark pine becomes the dominant canopy species above 2560 m elevation (Renkin and Despain 1992). I set up research transects in upper subalpine forests where whitebark pine ranged in importance from co-dominant to a dominant forest species.

The study sites in Yellowstone NP were located near Craig Pass, Dunraven Pass, and Avalanche Peak (Figure 2). Craig Pass is located in the southwest part of the Park. It is accessed from the road between West Thumb and Old Faithful, adjacent to a parking pullout just at the Craig Pass Divide (2518 m). This area represented a suitable but different whitebark pine community type from anywhere else in this study, but no trails were present in this area. Consequently, the transect was routed through open forest, accessed due south from the pullout area. The transect ran along a slight ridge through open forest (Table 1).

Dunraven Pass is located on Mt. Washburn (Washburn Range) in the north central part of the Park (Figure 2), accessed either from the Canyon or Roosevelt Junctions. The transect begins approximately 0.4 km up a trail from the parking area. The transect heads cross-country along a ridge. It was not placed on trail, which was an old, wide road not trending through much whitebark pine habitat initially. The transect ranged in elevation from 2805 m to 2838 m.

Avalanche Peak is located in the east central part of the park in the Absaroka Mountain Range (Figure 2). The transect followed the Avalanche Peak hiking trail. There were many dead and downed trees around the transect.

Glacier NP. Glacier NP, located in the northwest corner of Montana, is 4,100 sq km in area, and extends to the Canadian-U.S. border (Figure 2). Fifty-five percent of Glacier National Park is forested, but with a diversity of forest types, including several Pacific Northwest forest communities west of the continental divide. Spruce-fir forests consist of lodgepole and whitebark pine, subalpine fir, Engelmann spruce, and western larch (*Larix occidentalis*). Above 1,829 ft in elevation, krummholz conifer growth forms become common. The west side of the park is mixed conifer forest (Gadd 1995, Rockwell 2007).

Transect placement in Glacier NP is below Siyeh Pass, above Scenic Point, and on Elk Mountain (Figure 2). All transects are located within the Lewis Range. Siyeh Bend trailhead is located east of Logan Pass in the central part of the park, accessed from Going to the Sun Road. The transect begins approximately 4 km from the trailhead at the Siyeh Pass/Piegan Pass trail junction within an extensive forested area below Mount Siyeh.

The Scenic Point Trail starts from a small parking area in the southwestern Two Medicine area, on the east slope of Glacier NP. The transect, which is generally straight, begins approximately 6.4 km from the trailhead, on the southwest aspect of Scenic Point peak within a treeline community.

The Elk Mountain transect was located in the Livingston Range in Glacier NP. Elk Mountain (2388 m) lies along the southernmost edge of the park and is accessed by US Highway 2. The transect upper end was approximately 5 km from the trailhead and approximately 1 km from the summit.

Waterton Lakes NP. Waterton Lakes NP, which is contiguous with Glacier N P, begins at the Canadian border in southern Alberta (Figure 2). Together, both parks comprise part of a single ecosystem. Administered by Parks Canada, Waterton Lakes NP is 505 sq km in area. Spruce-fir forest and pine/aspen (*Populus tremuloides*) forests comprise the majority of the forested area (Gadd 1995, Rockwell 2007).

Transects in Waterton Lakes NP were established near Summit Lake and below Rowe Lake. Transects were located within the Lewis Range. The Carthew-Alderson Trial led from the trailhead at Cameron Lake to Summit Lake. The trailhead lies at the end of the Akamina

Parkway, on the north side of Cameron Lake. The transect’s upper end was approximately 4.3 km from the Cameron Lake parking lot. It was established beyond Summit Lake and just off a gradually sloping trail.

The Rowe Lake trail was accessed from the Rowe Lake trailhead, on the west side of the Akamina Parkway. The upper end of the transect was approximately 5.4 km from the trailhead, and was established below Rowe Lake just off the hiking trail.

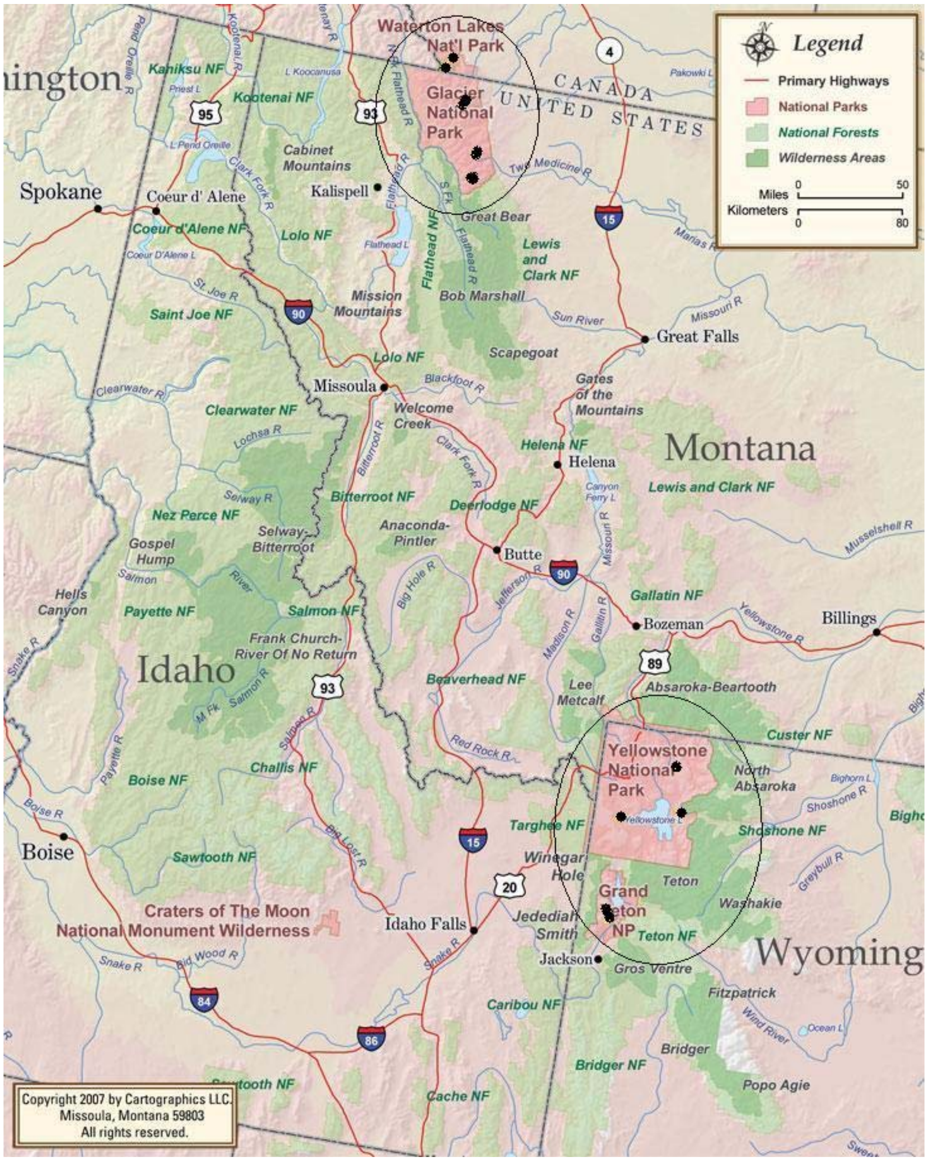


Figure 2. Study sites (reproduced with permission from Cartographics LLC, www.rockymountainmaps.com)

Table 1. Transect description. Elevation is the high point of each transect, and latitude/longitude is from GPS readings at the upper end of the transect. TH=trailhead

Transects	Elevation	Latitude/Longitude	Habitat	Access
Grand Teton National Park				
Amphitheater Lake (AL)	2867	43° 43.738, 110° 46.330	Subalpine forest	Garnet Canyon TH
Teewinot Mountain (TM)	2837	43° 44.569, 110° 45.050	Subalpine forest	Apex TH
Yellowstone National Park				
Craig Pass (CP)	2626	44° 25. 564,110° 40.060	Subalpine forest	Road
Dunraven Pass (DP)	2838	44° 47.327, 110° 26.992	Mixed subalpine meadow and open forest	Mt. Washburn TH
Avalanche Peak (AP)	2900	44° 28.697, 110° 08.070	Subalpine forest	Avalanche Peak TH
Glacier National Park				
Siyeh Pass (SP)	2185	48° 42.819, 113°38.813	Subalpine forest	Siyeh Pass TH
Scenic Point (SCP)	2216	48° 29.112, 113° 19.074	Subalpine/treeline	Scenic Point TH
Elk Mountain (EM)	2182	48° 18.137, 113° 26.566	Subalpine/treeline	Elk Mountain TH
Waterton Lakes National Park				
Summit Lake (SL)	1945	49° 00.478, 114° 01.493	Subalpine/open canopy forest	Summit Lake TH
Rowe Lake (RL)	2170	49° 03.159, 110° 03.547	subalpine/open canopy forest	Rowe Lake TH

Table 2. Health plot characteristics. Elevation and aspect are at center of plot (25 m point on plot).

Transects	**Elevation (m)**	**Aspect(°)**	**Mean DBH (cm)**	**Percent whitebark pine overstory**
Grand Teton National Park				
Amphitheater Lake (AL)	2823	20	33.9	39.3
	2738	185	24.9	37.5
Teewinot Mountain (TM)	2836	5	38.9	56.7
	2783	5	37.1	40
Yellowstone National Park				
Craig Pass (CP)	2612	38	14.1	90
	2626	24	8.3	30
Dunraven Pass (DP)	2868	155	16.9	55.9
	2801	210	19.3	71.4
Avalanche Peak (AP)	2728	190	36.4	28.2
	2740	165	23.9	9.1
Glacier National Park				
Siyeh Pass (SP)	2167	232	33.5	0
	2145	210	25.5	4
Scenic Point (SCP)	2089	210	11.4	29
	2183	210	4.4	73
Elk Mountain (EM)	2182	220	20.3	25
	2123	219	7.3	21
Waterton Lakes National Park				
Summit Lake (SL)	1945	190	1.8	0
	1923	155	15.9	5
Rowe Lake (RL)	2182	200	17.4	5
	2196	160	22.7	10

Transects and health plots

Transect establishment. Two 1 km x 30 m belt transects were established through forest communities with mature whitebark pine in Grand Teton NP, three in nearby Yellowstone NP, three in Glacier NP, and two in nearby Waterton Lakes NP during July 2008, with the help of field assistants (D. F. Tomback and Katie Chipman).

One transect (Dunraven Pass) in Yellowstone NP was accessed from the Dunraven Pass Mt. Washburn trailhead, but started off trail and headed cross-country upslope. A second transect, Craig Pass, also in Yellowstone NP started 25 m from one of the main roads in Yellowstone. The other eight transects were established parallel to existing trails.

Transect placements were dependent on the following constraints: transects were placed in areas with at least 1 km of continuous whitebark habitat and accessible (round trip) in one day, on foot. The field team worked in conjunction with park staff and scouted possible areas in which to place transects. In all cases, placement of transects was coordinated with park resource managers, to make certain that the transects were not readily apparent to park visitors but accessible enough to facilitate efficient sampling by park staff in subsequent years.

These constraints limited areas where transects could potentially be placed. Once a transect area with suitable whitebark habitat was chosen, the transects were measured out with a 50 m transect tape. The field team would measure out 100 m, and then move 5 m to 10 m off trail to mark each 100 m section, for the entire total 1 km distance. The start, finish, and pathway of each transect were georeferenced using a Garmin GPS 12 XL unit and marked on topographical maps. Because existing trails and roads were used for access and because of the scattered locations of continuous whitebark habitat, transects were not placed at random, but the starting points were randomized. Each 100 m section was numbered (1 through 11).

Health plot set up. Two 50 m x 10 m plots were established within each transect. The locations of the two plots along a given transect were randomized as follows: a random numbers table was used to select two consecutive numbers, from 0 to 9, representing specific 100 m sections along the transect. Once the 100 m section points were identified, the field team would randomly choose a start point and establish the health plot parallel to the transect line (when slope steepness or habitat did not preclude this option). From that point, 50 m would be measured out using a meter tape. A second meter tape was used to measure a 5 m on each side of the 50 m tape. Pin flags in open ground and surveyor's tape in trees were used to demarcate the belts. Once the health plot was created, data (as described below) were gathered within the plot limits. The start and end points of each plot were georeferenced and marked by tree tags and/or rebar. Notes were taken to ensure that the health plot could be recreated on later visits. Once data were gathered, transect tapes and pin flags were removed. Occasionally, randomly selected section numbers placed the plots on very steep terrain or in unsuitable habitat. When this occurred, we chose the next number on the random number table. Survey methods followed Tomback et al. (2005) and GYWPMWG (2008).

Point count station set up. Each transect had six point count stations, one every 200 m (every other section point, starting at 0 m) along the 1 km. Point count stations were georeferenced. They were also marked with tree tags and, temporarily, by surveyor's tape.

Data Collection

Health plot and nutcracker data

Whitebark pine stand data. The health plots were created in July, 2008, to survey stand structure and composition, whitebark pine diameters at breast height or 1.4 m (dbh), blister rust infection level and canopy damage, mountain pine beetle symptoms, tree mortality and cause, whitebark pine regeneration, and cone numbers. All canopy level trees were counted to determine stand composition by species. For all whitebark pine greater than 1 cm at dhb on the plot, dbh was taken using metal dbh tapes. Diameter was used to calculate live basal area (LBA). LBA was converted to a measure of tree basal area density, here based on the 500 sq m of the health plot.

Whitebark pine canopy damage was classified into categories based on a percentage scale. Canopy kill was first assessed by an observer as an approximate percentage of the entire canopy with branches devoid of foliage, and then placed in one of the following categories: 1 (0-5% dead), 2 (6-15% dead), 3 (16-25% dead), 4 (26-35% dead), 5 (36-45% dead), 6 (46-55% dead), 7 (56-65% dead), 8 (66-75% dead), 9 (76-85% dead), 10 (86-95% dead), and 11 (96-100% dead) (Tomback et al. 2005). This set of categories recognizes that small amounts of canopy kill or living canopy are easier to quantify than larger. Blister rust infection was classified by location (branch vs. trunk) and presence of aecia/cankers (active or inactive), as well as the presence of secondary symptoms (sap oozing, rodent gnawing, and stripped bark). Only trees with active cankers were classified as being infected with blister rust. Mountain pine beetle symptoms were classified as new attacks on trees, older attacked tree, or as beetle galleries present on dead trees.

All whitebark mortality was noted. If the cause of mortality was discernable, it was recorded. Dead trees were counted and dbh measured even if the cause of death could not be determined. Whitebark pine regeneration, defined here as seedlings <50 cm in height, was counted by walking methodically through the health plot and counting using hand held counters. Mountain pine beetle attacks were updated in late summer, 2008, and again during early and late summer in 2009.

Cone count and nutcracker point count data

Cone counts. Cone count data were taken on the health plots during each visit. Early and late season whitebark pine cone counts were performed from the ground using binoculars with an objective of at least 10 x 42. All whitebark pine trees larger than saplings were examined for cone production. Counts were done by at least 2 people from different vantage points. From multiple cone observations, counts were averaged. Data collection took place twice per year: in mid to late July 2008, before seed dispersal began, and again between late August and early September, once seed dispersal was underway. This protocol was repeated for 2009. From cone count data, an estimate of al cones per hectare was later calculated, using the larger of the two values. To do this, I took the total cone counts (per 1000 m^2) and multiplied them by 10 to estimate number of cones per hectare.

Nutcracker point counts. The point count techniques employed in this study are based on survey methods outlined in Ralph et al. (1993). Because the point counts here were primarily for inventory, point count duration was ten minutes. Counts occurred four times per summer for 10 minutes each point on six points per transect. Transects were surveyed by stopping every 200 m at the designated point count stations for 10 minutes of data collection and slowly walking between point count stations. Data collected during each point count included start time and end time, number of nutcracker sightings, nutcracker activities per observation (e.g., flying over, perching, breaking into cones, caching, etc), nutcracker vocalizations without sightings, and squirrel sightings.

Nutcrackers heard, but not seen, on point counts were classified as an observation. I attempted to avoid counting the same nutcrackers twice by trying to view nutcrackers counted when possible. When nutcrackers could only be heard, I did my best to auditorily follow their call directions and only count them once. The transects were 1 km x 30 m officially, but we did not mark 15 m on both sides of the midline. When I observed or heard a nutcracker, I had to decide whether it was counted as “on transect” or off. This was much easier for visual observations than for vocalization-based counts. By mistake I may have occasionally counted birds that were beyond the 30 m transect width. Squirrel count data were also taken during nutcracker point counts. Two point counts (am and pm) took place on each visit for a total of 4 point counts per year per point, or a total of 240 min of time spent gathering observations per transect. Morning point counts took place before noon (generally before 10am). Afternoon point counts occurred between 1 and 6 pm. There was always at least a 2.5 hour window between counts.

Nutcracker point counts may have been hampered by snowy weather on the Rowe Lake transect (Waterton Lakes NP) in late summer of 2008. Visibility was poor. But given the fact that even during fair weather, I never observed more than 1 nutcracker on this transect, it is unlikely that data were significantly affected.

Data analysis

Statistical analysis.

Software used in analysis. I used R version 2.10.1 and Microsoft Excel to perform all statistical analysis and create figures. Significance level established was alpha = 0.05. Data were log transformed (ln) to account for skew. Not all data was tested for normality.

Multiple analysis of variance (MANOVA). I used one-way MANOVA to test for differences among means for each variable. Variables tested are as follows: mean of total healthy trees for each park and each year, mean of total whitebark with blister rust infection (for each park and year), mean of total whitebark with recent pine beetle infestation (for each park and year), mean of total number of dead whitebark (for each park and year), mean cone count (for each park and year), mean LBA (for each park and year), total squirrel observations (for each park and year), total nutcracker observation counts (for each park and year), and mean regeneration (for each park and year). MANOVA was performed to identify interactions among explanatory and response variables. The focus of this analysis was on forest health and the differences among variables among parks. Due to skewed data distributions, MANOVA was performed with log transformed (ln) data. Explanatory variables were park, year, and interaction (simultaneous influence of both park and year). Response variables were total healthy whitebark, total sick whitebark (blister rust and pine beetle), total number of dead whitebark, total number of cones, LBA, squirrel observations, and regeneration. Box plots were constructed for data distributions by park.

Simple linear regression. Simple regression and correlation analysis were used to determine whether there was a relationship between the number of cones (independent variable) and number of nutcrackers observed per year (dependent variable) (Hill and Lewicki 2005).

Logistic regression and AIC analysis. Logistic regression and AIC (Akaike's Information Criterion) analyses were used to look at the relationship between multiple independent variables and one dependent variable. Independent variables (total healthy whitebark, total sick whitebark (blister rust and pine beetle), total number of dead whitebark, total number of cones, LBA, and squirrel presence) were used to model the dependent variable of nutcracker occurrence (presence or absence). I wanted to identify the most parsimonious independent explanatory variable and/or model to predict nutcracker occurrence. By definition, logistic regression predicts the probability of occurrence of an event (here, the presence/absence of nutcrackers) by fitting data to a logistic curve or line. AIC values were used to rank models and variables. Low AIC values identified the most parsimonious variables and models. Among seven independent variables, there were 128 possible model combinations. Logistic regression was performed on each of these models individually. From the regression output, AIC value was calculated and recorded for each model. All models were then ranked by AIC value (from smallest to largest). Δ AIC was computed by subtracting the range of AIC values for the one in question (Akaike 1987). Δ AIC is the measure of a given model relative to the best model in the set. Any model with a Δ AIC of less than 2 is considered competitive and more parsimonious. The weight of each variable (from each model) was summed to try to isolate the most influential variable. The entire process was repeated on different data sets: data from early 2008, late 2008, 2008 combined, early 2009, late 2009, 2009 combined, and 2008 and 2009 combined.

Cone threshold comparison. McKinney et al. (2009) made predictions about nutcracker presence based on cone densities. Their model indicated that a threshold value of ~130 cones/ha was required for reliable nutcracker occurrence. Figure 3 in McKinney et al. (2009) shows their simple linear-regression model for the proportion of total observation hours vs. nutcracker occurrence ($y= -0.449 + 0.019x$). To compare my data to McKinney et al (2009), I first had to transform the data from number of nutcracker observations per point count to proportion of total point count observation hours with at least one nutcracker observed. I divided the counts into early and late 2008 and early and late 2009 to obtain proportion of observation hours with nutcracker occurrence, which was the unit of comparison for McKinney et al. (2009). I graphed the observed data versus the expected values from the model in McKinney et al. (2009). I also did a simple linear regression of ln cones/ha^2 (y) vs. bird presence/absence per observation hour (x) to compare with their model of cone threshold data. For this regression analysis as well, the original count data (in form of number of nutcracker observations per point count) was transformed to proportion of total point count observation hours with nutcrackers observed.

CHAPTER 3

RESULTS

Transect Site Characteristics

Site Characteristics

General characteristics. Transects in the two southern parks (Grand Teton and Yellowstone NPs) had similar site characteristics, as did transects in the two northern parks (Glacier and Waterton Lakes NPs) (See Table 1). As expected from park history, Grand Teton and Yellowstone NP had relatively healthy whitebark pine and low infection levels of blister rust, but higher recent whitebark pine mortality from mountain pine beetles. Blister rust levels were much higher in Glacier and Waterton Lakes, but recent mountain pine beetle-related mortality was lower. In general, the northern parks had lower densities of living whitebark pine. Due to past blister rust infections and pine beetle outbreaks in this region, whitebark pine was comprised of high numbers of dead trees interspersed with an occasional healthy tree.

Grand Teton NP. The Teewinot Mountain transect was within upper subalpine forest. It increased in elevation throughout. The forest was open and composed of 57% whitebark and 43% subalpine fir. Plot one was in a climax successional stage. Plot three was similar to plot one, but slightly steeper. Canopy was co-dominated by 60% subalpine fir and 40% whitebark pine. Undergrowth dominants for both plots include *Vaccinium scoparium, Vaccinium globulare,* and *Arnica* sp.

The Amphitheater Lake transect was placed off a widely switch-backing trail with gradual elevational gain just below Amphitheater Lake. Plots were placed at points four and eleven. The forest at point four was open, but undergrowth was shrubby and dense. Canopy consisted of 61% subalpine fir and 39% whitebark pine. Undergrowth dominants included *Vaccinium scoparium, Vacciniumn globulare, Carex* sp., and *Arnica* sp. The plot was in a climax successional stage. Plot eleven was similar to plot four in forest composition (63% subalpine fir, 37% whitebark pine). Undergrowth was comprised primarily of *Vaccinium scoparium* and *Vaccinium globulare*. Forests on both plots appeared to be climax communities.

Yellowstone NP. The Craig Pass area has little elevation change with whitebark pine dominating the forest overstory; the stand was in a mid to late successional stage. Health plots were at points seven and nine. The habitat at point seven was open forest and consisted of 90% whitebark pine, 6.7% lodgepole pine (*Pinus contorta*), and 3.3% subalpine fir (*Abies lasiocarpa*) (Table 1). Dominant undergrowth species for both plots included *Vaccinium scoparium* and *Poa* sp. Craig Pass had high whitebark regeneration (399 total seedlings). Plot nine was similar to plot seven. The habitat was open, but consisted of 69% lodgepole pine and 31% whitebark pine.

The Dunraven Pass transect increased in elevation and crossed both meadow and small stands of trees. The tree stands appeared to be either late successional or, at higher elevations, climax communities. Plots were located at points three and ten. At point three, Canopy was dominated by 54% whitebark pine, 41% Engelmann spruce, and 5% subalpine fir (Table 1). Dominant undergrowth included A*rnica* sp., *Lupinus* sp, and G*entiana* sp. Plot ten was more open and in a climax successional stage. Canopy was composed of 71% whitebark and 29% subalpine fir. Undergrowth dominants were A*rnica* sp., *Poa* sp., *Vaccinium scoparium*, *Achillea millefolium,* and *Epilobium angustifolium.*

The Avalanche Peak transect also increased in elevation. The forest type here is successionally advanced with dense trees and closed canopy. Plots were located at points eight and nine. The canopy was composed of 82% subalpine fir, 9% whitebark pine, and 9% Engelmann spruce, with an understory of*Vaccinium scoparium, Vaccinium globulare, Carex* sp., and *Erythronium montanum*. Plot nine was contiguous with plot eight and thus similar in habitat. The canopy was composed of 60% subalpine fir, 28% whitebark pine, and 12% lodgepole pine (Table 1). Undergrowth dominants included *Vaccinium scoparium, Vaccinium globulare, Epilobium angustifolium,* and *Erythronium montanum.*

Glacier NP. The Siyeh Pass transect was located below Siyeh Pass in a relatively flat (mean slope of 5°), open, forested area. Plots were placed at points six and ten. Forests in both plots were in a late successional stage. The living canopy of plot six consisted entire of subalpine fir. Whitebark present was dead or too young to be at canopy level. Undergrowth dominants included *Claytonia* sp., *Erythronium grandiflorum, Luzula* sp., *Phyllodoce empetriformis,* and *Arnica* sp.

The Scenic Point transect is located in the Two Medicine area of Glacier (Figure 2). Plots were located at points one and seven. Both plots were in lower treeline climax communities. The trees here were dwarfed or flagged by harsh environmental conditions. Canopy for plot 1 consisted of 71% subalpine fir and 29% whitebark pine. Undergrowth was comprised of *Arctostaphylos uva-ursi, Juniperis communis, Astragalus* sp., *Sedum* sp., and *Potentilla* sp. Canopy for plot seven was composed of 73% whitebark pine, and 26% subalpine fir. Undergrowth consisted of *Juniperis communis, Sedum* sp., *Potentilla* sp, *Eriogonum* sp., *Lupinus* sp, *Arctostaphylos uva-ursi, Achillea millefolium, Carex* sp., and *Campanula rotundifolia*.

Both plots on the Elk Mountain transect were in climax communities within a transitional ecotone between subalpine forest and treeline, and located at points one and six. Flagged and dwarfed trees indicated that this plot was very wind-blown. For plot one, the canopy was composed of 50% Engelmann spruce, 25% whitebark pine, and 25% Douglas-fir. Undergrowth was comprised of *Vaccinium globulare, Carex* sp., *Campanula rotundifolia*, *Sedum* sp., *Arctostaphylos uva-ursi, Eriogonum* sp., *Juniperis communis,* and *Silene* sp. The canopy of plot six consisted of 58% subalpine fir, 21% Engelmann spruce, and 21% lodgepole pine. Undergrowth dominants were *Vaccinium globulare, Vaccinium scoparium, Carex* sp., *Sedum* sp., *Arctostaphylos uva-ursi, Lupinus* sp., *Potentilla* sp., *Xerophllum tenax, Oxytropis* sp., and *Erigeron* sp.

Waterton Lakes NP. Both plots on the Summit Lake transect were in late seral successional stages. Plots were located at points four and seven. At plot 4 four, canopy was 100% subalpine fir. Whitebark here was either dead or too young to be at canopy level. Undergrowth was comprised of *Menzesia ferruginea* sp., *Xerophllum tenax, Vaccinium globulare, Vaccinium scoparium,* and *Sorbus americana*. Plot seven was similar to four, yet slightly steeper. At plot seven, canopy was 95% subalpine fir and 5% whitebark pine. Undergrowth dominants were *Menzesia* sp., *Xerophllum tenax, Vaccinium globulare, Vaccinium scoparium,* and *Sorbus americana.*

The Rowe Lake transect plots were located at points one and two. Both were in climax communities. Plot one ran parallel to Rowe Lake. Canopy was comprised of 86% alpine larch, 9% subalpine fir, and 5% whitebark pine. Plot two was slightly steeper than plot one. Canopy was comprised of 83% subalpine fir, 10% whitebark pine, and 7% alpine larch. Undergrowth for both plots was similar comprised of *Xerophllum tenax, Vaccinium globulare, Vaccinium scoparium, Luzula* sp., and *Arnica* sp.

Health plot variables

Individual variables

Live basal area. LBA measurements were similar among the two southern parks (Grand Teton and Yellowstone) and the two northern parks (GNP and WLNP) (Table 3). In Grand Teton NP, Teewinot Mountain had a mean of 0.12 m^2 (0.082 SD), and Amphitheater Lake mean LBA was 0.065 m^2 (0.06 SD). In Yellowstone NP, health plot means were as follows: Craig Pass-- 0.022m^2 (0.047 SD), Dunraven Pass-- 0.031 m^2 (0.038 SD), Avalanche Peak -- 0.038 m^2 (0.032 SD). In Glacier NP, individual transects means as follows: Siyeh Pass--- 0.041 m^2 (0.028 SD), Scenic Point--- 0.006 m^2 (0.009 SD), and Elk Mountain--- 0.010 m^2 (0.014 SD). Waterton Lakes transects are as follows: Summit Lake had a mean LBA of 0.011 m^2 (0.017 SD), and Rowe Lake had a mean LBA of 0.035 m^2 (0.038 SD).

Healthy trees. In Grand Teton NP in 2008, Amphitheater Lake had 15 healthy trees, and Teewinot had 12. In 2009, Amphitheater Lake had 2, and Teewinot had 3. In 2008 and 2009, on Yellowstone NP plots, Craig Pass had 111 total healthy trees, Dunraven Pass had 45, and Avalanche Peak had 6. In Glacier NP in 2008 and 2009, Siyeh Pass had 2, Scenic Point had 3, and Elk Mountain had 2. In Waterton Lakes in 2008 and 2009, Summit Lake had 1 and Rowe Lake had 3.

Blister rust. Blister rust infection levels and mortality varied within and among parks (Table 3). In Grand Teton National Park, the Amphitheater Lake and Teewinot Mountain plots had no mortality from rust, but blister rust infection levels were around 20%. In Yellowstone NP, blister rust infection levels were very low on all transects. Plots on Craig Pass and Dunraven Pass had no mortality from rust. Avalanche Peak had no blister rust present on plots. Health plots in Glacier NP varied greatly in percentage of trees with blister rust, from 0% at Siyeh Pass to over 60% at Scenic Point. The Siyeh Pass and Elk Mountain plots had no discernible mortality from blister rust; however, Scenic Point plots had 13% mortality from rust. In Waterton Lakes NP, blister rust levels were high on both transects—and about 50% on the health plots (Table 2). On the Summit Lake health plots, mean whitebark mortality from blister rust was 16.7%. On the Rowe Lake plots, there was no discernible recent mortality from rust, but very few living trees.

Mountain pine beetle. Much like blister rust, mountain pine beetle infestation differed between and within parks (Table 3). Grand Teton NP health plots had new beetle infestations between 2008 and 2009. This was the only park to have an increase in pine beetle attacks between transect visits (Table 2). On the Teewinot Mountain plots, pine beetle infestation increased 11.4% between the two years, whereas Amphitheater Lake increased 17.1%. In Yellowstone National Park, mountain pine beetle infestation was not found on the Craig Pass health plots, although there were a few scattered recently killed trees off transect. Dunraven Pass had serious pine beetle infestation in 2008 and 2009, but the highest infestation levels of all health plots occurred on Avalanche Peak. There, in both 2008 and 2009, 79% of the whitebark on plots was infested with mountain pine beetle.

None of the three Glacier NP transects had pine beetle infestation in 2008 or 2009. Waterton Lakes transects had some pine beetle infestation, but numbers were low (Table 4).

Cone counts. Cone counts varied within and between parks and years (Table 4 and Figure 3). In 2008 in Grand Teton NP, health plots on Teewinot Mountain had a mean of 0.16 cones per whitebark (0.56 SD), and Amphitheater Lake plots had a mean of 0.32 cones per tree (0.9 SD). In 2009, health plots on Teewinot Mountain had a mean of 1.71 cones per tree (6.4 SD) and Amphitheater Lake plots had a mean of 0.59 cones per tree (3.29 SD). In 2008, health plots on Craig Pass in Yellowstone NP had a mean of 0.4 cones per tree (1.3 SD), Dunraven Pass plots had a mean of 1.1 cones per tree (4.7 SD), and Avalanche Peak plots had a mean of 0.08 cones per tree (0.4 SD). In 2009, Craig Pass plots had a mean of 3.4 cones per tree (11.5 SD), Dunraven

Pass plots had a mean of 2.3 cones per tree (8.21 SD), and Avalanche Peak plots had a mean of 0.33 cones per tree (1.6 SD). In Glacier NP in 2008, health plots on Siyeh Pass had a mean of 1.43 cones per tree (3.78 SD), Scenic Point had a mean of 0.13 cones per tree (0.63 SD), and Elk Mountain plots had no cones. In 2009, health plots on Siyeh Pass health plots had a mean of 1.57 cones per tree (4.16 SD). Neither Scenic Point nor Elk Mountain plots had any cones in 2009. Health plots in Waterton Lakes NP had no cones in 2008 or 2009.

Dead trees. Grand Teton and Yellowstone NP had the highest numbers of dead trees from all causes, but that is simply because they had more total trees (Table 4). The Teewinot Mountain plots in Grand Teton NP had 43% dead trees combined, as of 2009, and the Amphitheater Lake plots had 29% dead whitebark. In Yellowstone NP, on both Craig Pass plots combined, 4% of all whitebark pine were dead, and on Dunraven Pass health plots, 21% of all whitebark were dead. The Avalanche Peak plots had a combined 70.8% of dead trees because of low numbers of whitebark pines and higher levels of pine beetle mortality. In Glacier and Waterton Lakes NP, actual numbers of dead trees were much lower on the plots, but because of low total numbers of whitebark pine, percentages were deceptively high. On the Siyeh Pass transect in Glacier NP, 71.5% of all whitebark pine were dead. On Scenic Point, 17.3% of whitebark pine was dead. The Elk Mountain plots had 60% dead whitebark pine. In Waterton Lakes NP, the Summit Lake transect had 1 dead tree that represented16.7% total dead whitebark pine. On the Rowe Lake transect, 33.3% of whitebark pine was dead.

Whitebark pine regeneration. I summed regeneration numbers for the two health plots to t calculate the following densities. In Grand Teton NP, Teewinot Mountain health plots had 0.26 seedlings per m^2, and Amphitheater Lake plots had 0.09 seedlings per m^2. In Yellowstone NP, regeneration on Craig Pass and Dunraven Pass plots was the highest of all study sites (Table 3). Densities of regeneration follow: Craig Pass-- 6.45 seedlings per m^2, Dunraven Pass--1.6 seedlings per m^2, and Avalanche Peak -- 0.11 seedlings per m^2. In Glacier NP, regeneration numbers were much lower, as follows: Siyeh Pass-- 0.03 seedlings per m^2, Scenic Point-- 0.17 seedlings per m^2, and Elk Mountain-- 0.04 seedlings per m^2. Waterton Lakes NP transects had the lowest total regeneration of all study sites: Summit Lake plots had 0.02 seedlings per m^2, and Rowe Lake plots had 0.06 seedlings per m^2.

Nutcracker counts and observation. Nutcracker observation counts were summed across visits (4 per year). Nutcrackers were frequently viewed on the two transects in Grand Teton NP. In Yellowstone, nutcracker counts were highest overall on the Craig Pass and Dunraven Pass transects during point counts (the two Yellowstone NP transects with the highest cone counts) (Table 3 and Figure 4). On the Craig Pass transect, nutcrackers were frequently observed breaking into cones and placing seeds in their sublingual pouches after seeds had ripened in late summer. On these visits, nutcrackers were observed caching seeds during point counts throughout the Craig Pass transect. The Avalanche Peak point counts were lower, but birds were still fairly common in both years. In Glacier NP, nutcrackers were only observed on the Scenic Point transect point counts. No nutcrackers were ever observed during Siyeh Pass or Elk Mountain point counts. Nutcracker observations also were rare in Waterton Lakes NP.

Squirrel observations. Pine squirrel presence on each transect was variable. Squirrel observation numbers by transect point counts are found in Table 4. Squirrels were not always highest in areas with the highest numbers of cones. Squirrel cone cutting could potentially exert a significant effect on whitebark pine seed availability. In early summer 2009, a single tree on the Siyeh Pass transect had cones. By late summer, squirrels had cut down all 11 cones from that tree.

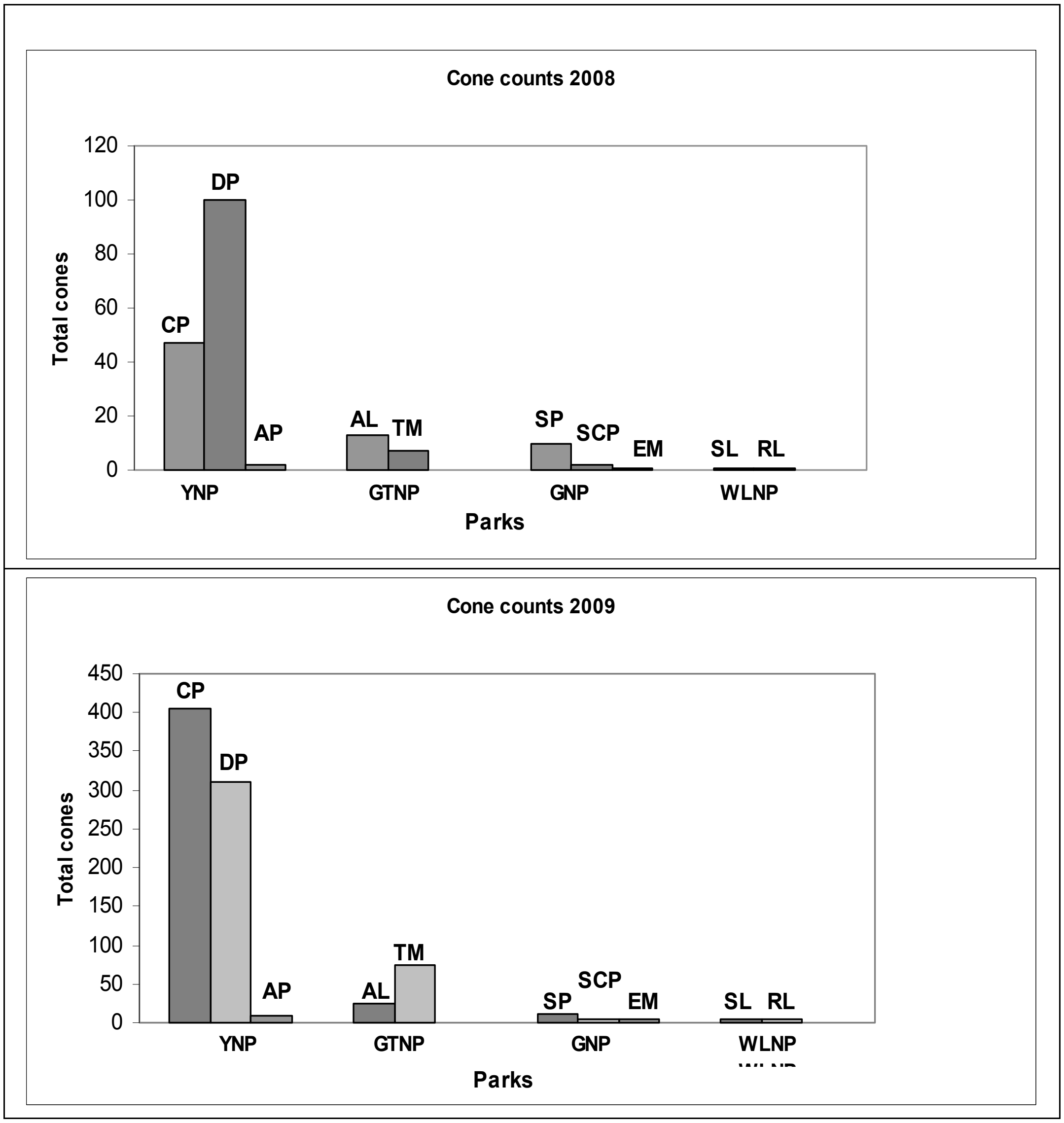


Figure 3. Cones counts from 2008 and 2009 (scales differ between years). Each bar represents a different transect. Cone numbers are summed from the two health plots per transect.

Table 3. Transect health plot variables. Percentages and LBA measurements were based on sums of both health plots per transect.

Park	**YNP**			**GTNP**		**GNP**			**WLNP**	
Transect	**CP**	**DP**	**AP**	**AL**	**TM**	**SP**	**SCP**	**EM**	**SL**	**RL**
DBH (cm) (min/max/avg/ median)	1/64/11.5/ 5.7	1/47/18/17	8/82/33.2 /32	2/51/27.6 /29.4	3/63/37.9 /38.3	17/45/30 /32.1	2/23/17 /6.5	5/20/8.6 /7.6	2/32/13 /8.2	1/50/22.1 /21.9
% Blister rust	0.8	2.2	0	21.9	18.2	0	60.8	30	50	52.3
% Pine beetle (2008/2009)*	0	22.6	79.2	26.8 43.9	40.9 52.3	0	0	0	16.7	14.3
Canopy kill class (avg)	1.13	1.29	1.57	3.69	3.62	2	5.47	2.5	8.6	4.14
Total LBA (m^2/ha)	2.029/ 20.29	3.029/ 30.29	0.2289/ 2.29	1.826/ 18.26	3.153/ 31.53	0.0821/ 0.821	0.1118/ 1.118	0.0436/ 0.436	0.0421/ 0.421	0.3327/ 3.327
Total dead whitebark	5	29	17	12	19	5	4	6	1	7
Regeneration ***	645	160	11	9	26	3	17	4	2	6

*Due to the nature of pine beetle infestation, infection levels increased in Grand Teton NP from 2008 to 2009. It was consistent in all other parks.

** Canopy kill classes: 1(0-5%), 2(6-15%), 3(16-25%), 4(26-35%), 5(36-45%), 6(46-55%), 7(56-65%), 8(66-75%), 9(76-85%), 10(86-95%), 11(96-100%)

***Regeneration was summed across both health subplots

Table 4. Transect cone count, and nutcracker, and squirrel observations.

Park		**YNP**			**GTNP**		**GNP**			**WLNP**	
Transect		**CP**	**DP**	**AP**	**AL**	**TM**	**SP**	**SCP**	**EM**	**SL**	**RL**
Cones counted	2008	47	100	2	13	7	10	2	0	0	0
	2009	405	311	8	24	75	11	0	0	0	0
Nutcracker* Observations	2008	26	30	7	10	31	0	6	0	2	1
	2009	44	13	13	18	18	0	8	0	0	0
Squirrel** observations	2008	6	2	2	17	6	1	2	0	4	2
	2009	4	4	1	14	10	0	1	0	2	0

* Nutcracker observations are summed for all point counts per year

** Squirrels observations are summed for all point counts per year

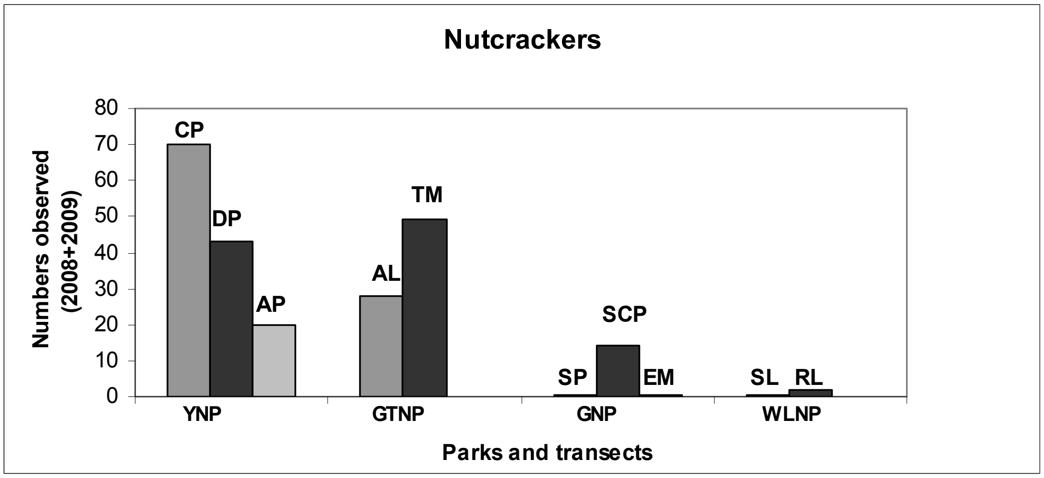


Figure 4. Observed nutcracker numbers by park. 2008 and 2009 nutcracker counts were combined.

Data analysis results

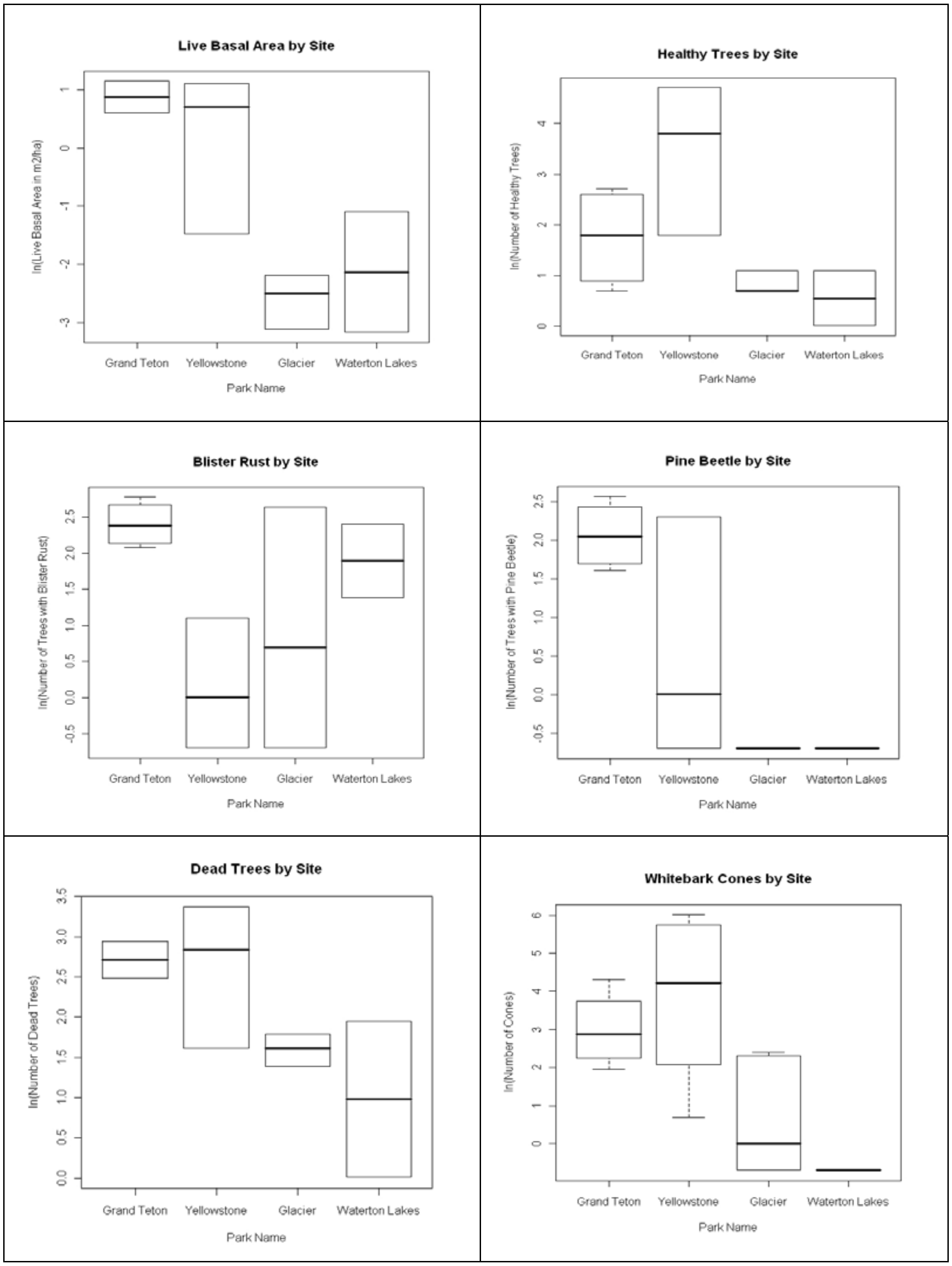
MANOVA

I used MANOVA to compare variables across transects and parks to see if there were differences in the p-values associated with each variable. MANOVA results, which combined transect plot data for each park, showed no interaction effect (P=0.26). Univariate analysis showed no difference by *year*. Multivariate analysis showed a significant interaction effect by *park* (P= 0.000016, df = 6). Unfortunately, sample sizes were inadequate to analyze at the transect level. Table 5 shows how all variables differed significantly at the *park* level. This indicates that variable values within each park were unique. All P-values were statistically significant.

Table 5. MANOVA P-values.

Variable	**P-value by park**
Total healthy whitebark	0.00105
Total blister rust	0.0376
Total pine beetle	0.00198
Total dead whitebark	0.0168
Total cones	0.00252
Live basal area	0.000482
Squirrel counts	0.000416
Regeneration	0.0758
Nutcracker counts	0.000985

Figure 5 shows boxplots of the variable distribution for LBA, total healthy trees, blister rust, total mountain trees affected by pine beetle, total dead trees, whitebark cones by study site, regeneration numbers by site, and nutcracker counts by park. Medians vary greatly among parks for all variables.



Live Basal Area by Site

Healthy Trees by Site

Blister Rust by Site

Pine Beetle by Site

Dead Trees by Site

Whitebark Cones by Site

Figure 5a. Distribution of health variables as boxplots. Data is summed from two health plots per transect. Plots represent median values and ranges.

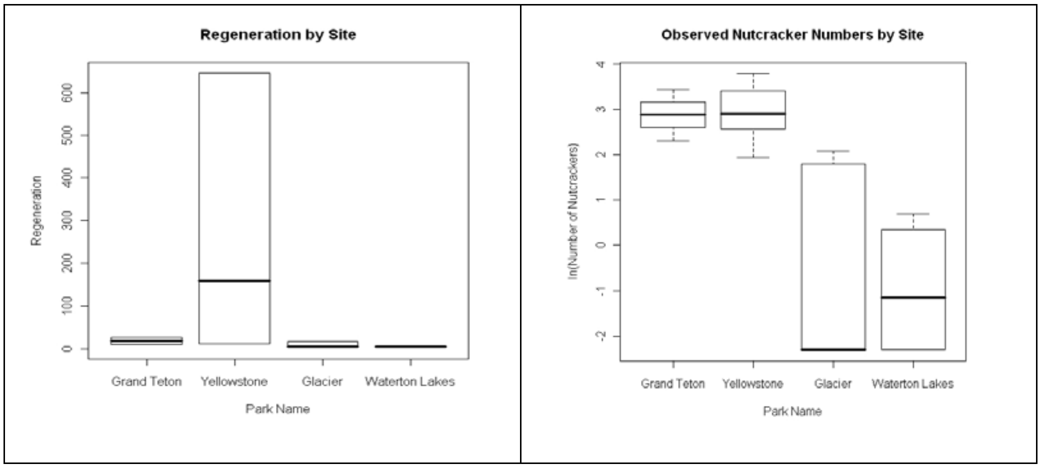


Figure 5b. Distribution results of regeneration (two health plots per transect combined) and nutcracker observation (summed across 2008 and 2009).

Simple Linear Regression.

Simple regression of log transformed (ln) data was used to determine the correlation between numbers of nutcrackers observed and cones counted (per year). Both 2008 and 2009 results showed a significant correlation between the number of cones and the number of nutcracker numbers (Figure 6). For 2008 data, $P = 0.02558$, $R^2 = 0.3992$, and df= 8. For 2009, $P = 9.43*10^{-7}$, $R^2 = 0.4294$, and df= 8.

Logistic Regression and AIC analysis.

Logistic regression was used to determine the most parsimonious variable and model for predicting nutcracker presence vs. absence. However, logistic regression and AIC analysis resulted in model and variable uncertainty. The models consisted of all possible variable combinations. No single model or variable came out to be the most simple or most parsimonious. This could have been the result of too few samples within parks. Alternatively, it is possible that unidentified variables were affecting the results. There was a lack of variation in values for variables among transects within parks, which might be the result of inadequate spatial replication. Parks in the south were very similar in data distribution to each other, as were parks in the north. There were differences between south and north parks, but not between the two individual southern parks and two individual northern parks. Nutcracker occurrence could not be explained by any one variable or model. As Table 6 shows, the weights of individual variables were nearly identical. Table 7 shows the best models, based on variable combination. The most competitive models are those with a Δ AIC ≤ 2, with a Δ AIC of zero being the best model. Total healthy trees, total dead trees, and squirrel presence appear in all of the top models.

Table 6. Proportion of variable weights from MANOVA. Individual weights were very similar (no single variable sufficiently explained nutcracker occurrence).

Variables	**Proportion of weights among variables**
total healthy (TH)	0.146
total sick blister rust (TSBR)	0.141
total sick pine beetle (TSPB)	0.148
total dead (TD)	0.147
total cones (TC)	0.138
total squirrels (squirrels)	0.139
live basal area (LBA)	0.141

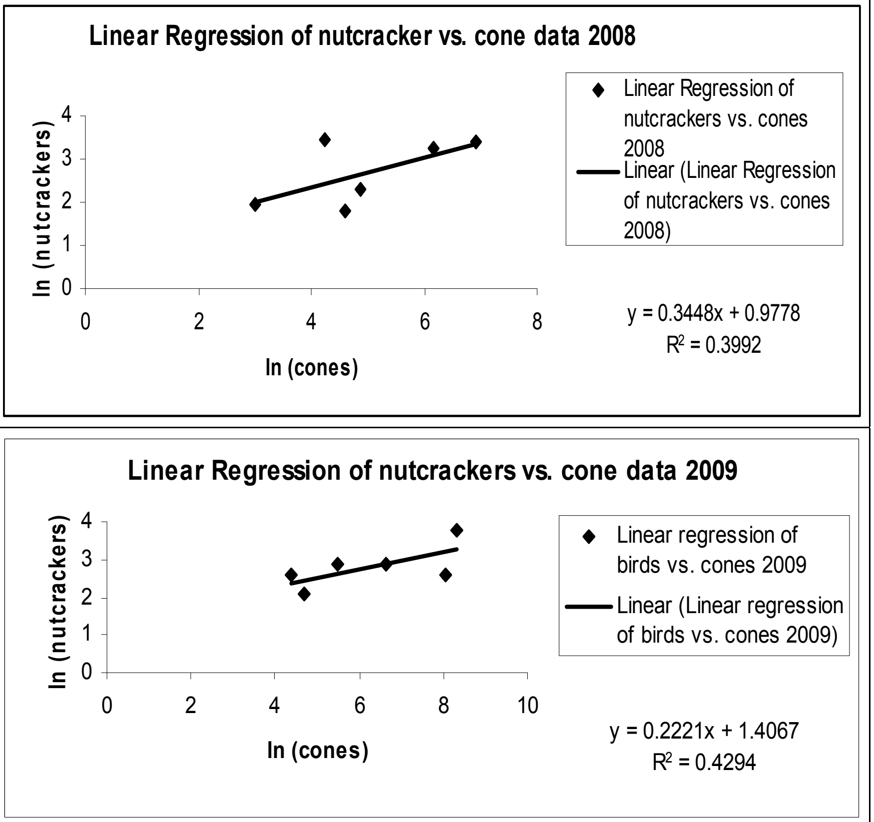
Table 7. Top models as determined from AIC analysis. For the best models, ∆ AIC ≤ 2 (models with the most parsimonious fit are within two AIC values from the top model (∆ AIC = 0).

Top variable combinations	**∆AIC**
TH+TSBR+TD+squirrels	0
TH+TSBR+TSPB+TD+squirrels	2
TH+TSPB+TD+TC+squirrels	2
TH+TSPB+TD+LBA+squirrels	2

TH: total healthy whitebark, TSBR: whitebark sick with blister rust, TSPB: whitebark infested with pine beetle, TD: total dead whitebark, TC: total cones, LBA: live basal area, Squirrels: total squirrels

Cone threshold comparison

With regression analysis, I plotted the proportion of total observation hours with at least one nutcracker vs. transformed number of cones (Figure 7 b) and compared this graph to Figure 3 in McKinney et al. (2009) which is based on the same transformations of data (Figure 7 a). I obtained a different regression model than McKinney et al. (2009): y= 0.1786 + 0.012x vs. y= -0.449 + 0.019x from McKinney et al. (2009) (Figure 7). In relation to my data, the model in McKinney et al. (2009) consistently under-predicted bird occurrence as a function of cone density. In other words, for a given value of cone production, I had a higher probability of seeing nutcrackers than the McKinney et al. (2009) model suggested (Figure 8). Where McKinney et al. (2009) estimated a threshold of ~130 cones/ha for regular nutcracker occurrence, I had observed nutcrackers consistently at ~70 cones/ha, a lower threshold value (see Figures 7). Also, the slope of the line in my graph (Fig. 7 b) was not as steep as McKinney et al.'s (2009), which suggests that as cone numbers decline, the decline in probability of nutcracker occurrence is less rapid. Linear regression analysis between log transformed (ln) cone data and proportion of nutcracker occurrence on number of cones was highly statistically significant, with a P-value of 0.002768 (df = 18, r =0.58). Proportion of observation hours with nutcracker occurrence increases as cone number increases. The adjusted R^2 is 0.3367, meaning that 33.67% of the variation in nutcracker occurrence is explained by cone density (Figure 7).


Linear Regression of nutcracker vs. cone data 2008

Linear Regression of nutcrackers vs. cone data 2009

Figure 6. Simple linear regression of nutcrackers observed and cone numbers (per 1000 m^2).

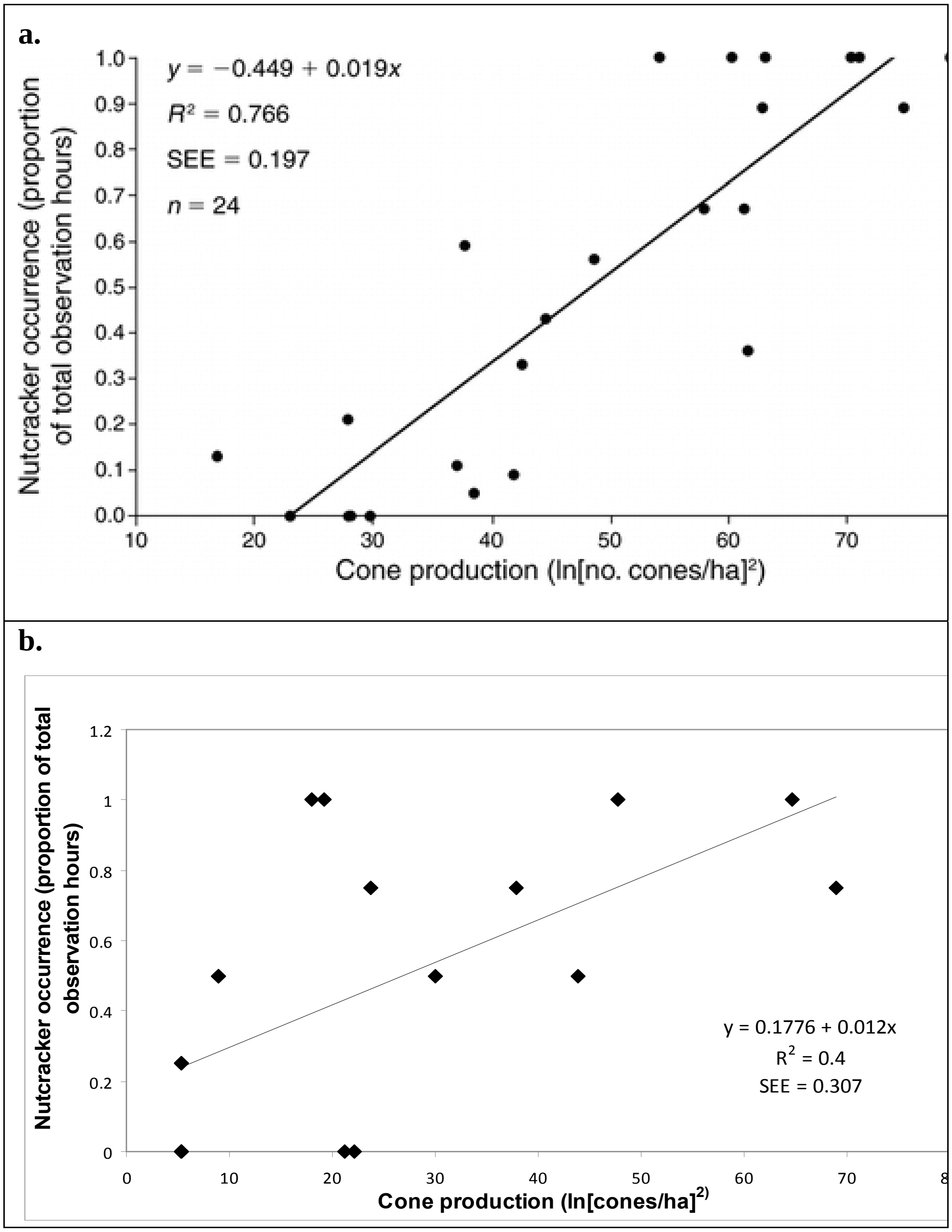


Figure 7. Simple linear regression analysis of a. McKinney et al (2009), top and data from this study, bottom (b.). Probability of observing nutcrackers (y axis) vs. a given value of transformed cone production (x axis). Based on the McKinney et al. (2009), I had a higher probability of observing nutcrackers with fewer cones present per hectare.

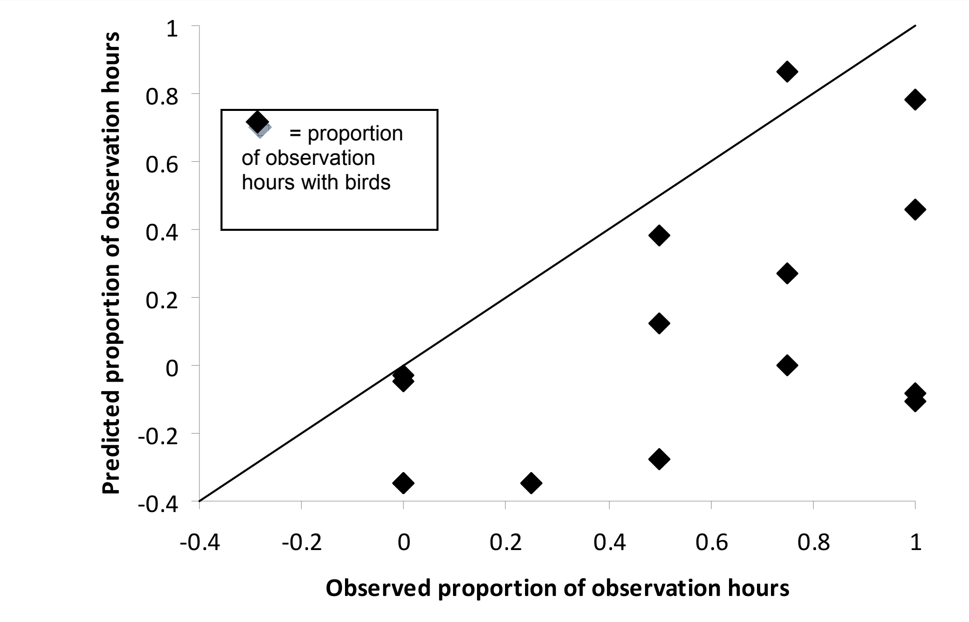


Figure 8 Observed data versus expected values from the model in McKinney et al. (2009). Observed data are scaled identically to that presented by McKinney et al. (2009); they are the proportion of observation hours where a nutcracker was observed. The y axis is the expected value from the model, and the x axis shows the observed values. The diagonal is the 1:1 line that represents perfect prediction from the model. Notice that most observations occur below the 1:1 line indicating that the observed cone density values were lower than expected when assuming the model presented by McKinney et al. (2009).

CHAPTER 4

DISCUSSION

The research goals of this study were to answer a series of questions concerning whitebark pine health and cone production in relation to the likelihood of Clark's nutcracker occurrence and seed dispersal across four national parks in the Central and Northern Rocky Mountains. Since Clark's nutcrackers are essential for seed dispersal services for whitebark pine, this question pertains to whether new generations of whitebark pine will be available in the future in regions widely impacted by *Cronartium ribicola* and mountain pine beetle outbreaks. Each question presented in the introduction under "Questions addressed in this study" is answered below in relation to the data and analyses previously presented.

What are the differences in whitebark pine health stand composition, and basal area (abundance) among study sites within and among four national parks?

Blister rust infection levels were highest in Grand Teton NP and Waterton Lakes NP and in some areas of Glacier NP, whereas the number of pine beetle infested trees were greatest in the two southern parks. The greatest basal area of whitebark was found on health plots in Yellowstone NP. Yellowstone NP also had the greatest percent whitebark pine in the overstory of health plots. The MANOVA data indicated differences in whitebark pine health, stand composition, and basal area (abundance) among the four parks. It was not possible to measure differences between or among specific study sites within each park due to small sample sizes and, perhaps, the need for greater replication. All explanatory variables (number of healthy trees, number of sick trees, number of dead trees, total cone numbers, live basal area, squirrel numbers, and regeneration numbers) were significantly different by park but not from year to year.

Are there differences in cone numbers within plots among sites within parks, between parks, and from year to year?

Cone numbers on health plots were highest on two transects in Yellowstone NP (Craig Pass and Dunraven Pass). There was marked variation in cone counts between 2008 and 2009 in the southern parks, but not in the northern parks. Whitebark in the northern parks was in all around worse condition than whitebark in southern parks. Trees were fewer in number and more affected by blister rust in Glacier and Waterton Lakes NPs. This low mean cone production could be due to long-term rust infection or other unidentified environmental drivers. The MANOVA data indicated differences in cone numbers among the four parks, but not from year to year.

Are there differences in observed squirrel numbers (they are influential seed predators on whitebark cones)?

Squirrel numbers were highest on Grand Teton NP transects and lowest in Glacier and Waterton Lakes NPs. In relation to cone production, squirrels were most abundant in some areas with higher cone numbers, but this was not always the case. The Yellowstone transects with the highest cone counts had relatively few squirrels. MANOVA results showed a significant difference in censused numbers squirrels between parks, but not between years.

Are there differences in observed nutcracker numbers observed from study site to study site and park to park?

Observed nutcrackers were highest in Yellowstone NP on the Craig Pass and Dunraven Pass transects. Lowest observed nutcrackers were on the two Waterton Lakes NP transects. The highest nutcracker observations correlate with the health plots with the highest cone production numbers, as did the lowest nutcracker observation and lowest cone production areas. MANOVA results showed a significant difference in censused numbers of nutcrackers between parks, but not between years.

Are there differences in whitebark pine regeneration (seedlings) from study site to study site and park to park?

Regeneration numbers were highest in the areas with the most cones counted (Yellowstone NP transects) and lowest in areas with few to no cones and unhealthy whitebark (Waterton Lakes NP). The areas with the highest regeneration had some of the highest nutcracker counts. The health plot with the most regeneration was an area (Craig Pass in Yellowstone NP) where I observed nutcrackers actively caching seeds. Regeneration results (from MANOVA) show a difference between parks in regeneration numbers (totals), but not between years. Regeneration density varied from park to park. It was highest on Craig Pass and Dunraven (Yellowstone NP) transects.

Is there an overall relationship between cone numbers within plots and nutcracker occurrence?

Based on linear regression and correlation analyses, I did find a significant relationship between cone numbers and nutcracker occurrence. This correlation supports previous studies that show nutcrackers to be sensitive to food availability. As expected, LBA was highest were cone production was highest (Craig Pass and Dunraven Pass in Yellowstone NP).

Are there variables that predict nutcracker occurrence within and across parks?

The models with the highest Δ AIC numbers included variables such as total healthy whitebark numbers, total amount of whitebark with pine beetle infestation, total dead whitebark numbers, and total numbers of squirrels counted. Although these variables could not be considered predictors of nutcracker occurrence, they were still important. The role of squirrels as a nutcracker predictor is difficult to interpret unless squirrels happen to attracted to the same whitebark attributes as are nutcrackers. However, I was unable to isolate variables (through logistic regression and AIC analysis) that would accurately predict nutcracker occurrence within parks. This may have been because of too few data samples gathered. It could also have been because there were other variables affecting the results that we did not identify and test. There was little variation among transects within parks and possibly inadequate spatial replication overall.

How does the relationship between cone production and proportion of observation hours with one or more nutcracker sightings relate to the relationship observed by McKinney et al. (2009)? How did the cone production threshold determined from this study relate to the threshold observed by McKinney et al. (2009)?

Based on the linear regression results and comparison to McKinney et al. (2009), I found a higher proportion of hours observed with nutcrackers relative to cone production than observed by McKinney et al. (2009). Whereas, McKinney et al. (2009) found a cone threshold of ~130 cones/ha for bird occurrence, my study had nutcrackers consistently at ~70 cones/ha. The slope of McKinney et al.'s figure was 0.019, while the slope from my figure was 0.012. The two figures had similar slopes, but McKinney el al.'s had more data points at the extremes of the scatterplot. These thresholds can be applied to management in that they can be used to aid park management in prioritizing areas most in need of restoration and protection.

What cone production threshold can be used to prioritize whitebark pine stands for restoration?

Based on my data, stands that are producing less than 70 cones per hectare have a low probability of nutcracker visits and may be considered as candidates for restoration, depending on the forest community type. However, McKinney et al. (2009) show a higher threshold value. In the absence of additional data, my threshold would be the more conservative value to use. It would be useful if the parks could further test to refine the cone production threshold to decide how to prioritize whitebark pine stands for restoration by continuing to obtain data on cone counts from plots and nutcracker occurrence from the transects.

The discrepancy between the threshold cone values that I found and what McKinney et al. (2009) found, may indicate that the threshold may only hold true for the geographical areas of each study. Reasons for the discrepancies could also lie in sampling methods (McKinney's 1 ha square vs. my belt transects), nutcracker observation and cone count methods (McKinney's spotting scope vs. my binoculars), or with different years of field sampling (McKinney's 2004-2006 vs. my study's 2008-2009). The threshold values could differ over time depending on the size of the regional nutcracker population in relation to cone production, with more pressure (and lower threshold values) in years with a higher population.

Regeneration was higher in the parks with higher total whitebark pine LBA. Areas with the highest regeneration (Craig Pass and Dunraven Pass in Yellowstone NP) were also the areas of highest cone production. Nutcrackers were also observed harvesting and caching seeds on the Craig Pass transect. The southern parks would most likely benefit more from proactive protective measures, particularly to protect healthy trees against mountain pine beetles (Verbenone placement to protect against mountain pine beetles) while the northern parks may fare better from thinning or burning forests to open up successionally advanced stands for whitebark establishment followed by seedling planting to replace lost nutcracker seed dispersal service (Tomback et al. 2001, Keane and Arno 2001, Schwandt 2006)

Summary of conclusions

Although I can only speak to the two year time period during which I gathered data, and base my comments on a small portion of whitebark pine habitat in each park, the areas where nutcrackers were often seen caching seeds also had the highest numbers of cones. This was the case for 1 out of 3 of the Yellowstone NP transects. Cone numbers on health plots were also high on the two Grand Teton NP transects. These two parks had the healthiest and most abundant whitebark pine. The northern parks (Glacier and Waterton Lakes NPs) had much fewer live whitebark pines, few cones, and few observed nutcrackers. Overall, transects with high numbers of damaged whitebark pine had few to no observed nutcrackers. Southern park transect plots had the most whitebark pine. Even though blister rust and mountain pine beetle were present here, and trees were dying, forests were healthier overall, at least in terms of available LBA. These areas also had the highest numbers of observed nutcrackers. Because northern transects (in Glacier, Waterton Lakes NPs) had little living mature whitebark pine, there were few cones present and few nutcrackers observed. The simple relationship between numbers of cones and numbers of birds would predict this outcome.

The threshold level for nutcracker occurrence was ~70 cones/ha. This threshold value could be applied to whitebark pine management by using the threshold to identify areas with fewer than 70 cones/ha. Those areas should be prioritized for restoration. Areas in Glacier and Waterton Lakes NPs would fall into that category. In those areas, protection of remaining mature whitebark from pine beetle (which was low in these areas), thinning or burning areas in preparation for planting, and planting rust-resistant seedlings would be most effective in starting a new generation of whitebark pine more likely to survive in the presence of blister rust. In parks with a high proportion of live basal area and high nutcracker occurrence (Grand Teton and Yellowstone NPs), restoration by means of protecting large, healthy trees from pine beetle infestation (with Verbenone or other pesticides) and caging cones from nutcracker and squirrel predation may be more effective than planting seedlings.

Although the threshold data are less pessimistic than McKinney et al.'s (2009) findings, whitebark is still in trouble in many areas. In the study sites in Glacier and Waterton Lakes NP, cone production fell well below the threshold of 70 cones/ha. Nutcracker occurrence was also the lowest there when compared to the southern transects. If restoration plantings are not conducted on these study sites (and elsewhere in whitebark pine habitat), the nutcracker-whitebark pine mutualism could be disrupted. This could lead to further geographical isolation and increased risk of extirpation of whitebark pine (Soule 1980, Tomback and Kendall 2001, Tomback and Achuff in press). More long term monitoring across various geographical areas is needed to better determine restoration priorities.

Within the time frame and funding available, I gathered all the data possible on the transects that were established. However, more visits to the transects each year would have provided more data to analyze, and, to identify single influential variables and variable combinations or to tease out within-park differences, more transects would need to be installed and more time would be required to gather data. All parks within the study have expressed interest in continued monitoring of the transects, although none have expressly committed themselves. With more data and further analysis, perhaps the parks involved could better prioritize areas for restoration action.

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