Clark's Nutcracker Seed Harvest Patterns in Glacier National Park and a Novel Method for Monitoring Whitebark Pine Cones

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Abstract

Clark's Nutcracker (*Nucifraga columbiana*) is the primary seed disperser of whitebark pine (*Pinus albicaulis*), which is in decline throughout its range. There is concern that a decline in whitebark pine will lead to a subsequent decline in local populations of Clark's Nutcracker. Because natural regeneration depends on the presence of Clark's Nutcracker, the process of harvesting whitebark pine seeds needs to be fully understood. In addition, resource managers need a cost-effective method for monitoring nutcracker occurrence in whitebark pine stands during the seed harvest season. I visited eleven study sites in Glacier National Park, Montana, where I searched for Clark's Nutcracker and surveyed whitebark pine cones for seed harvesting scars, the presence of which indicated that nutcrackers harvested seeds. I documented cone use patterns of Clark's Nutcracker and the major cone predator, red squirrel (*Tamiasciurus hudsonicus*), at five sites. To identify factors that influence cone use, I ran a correlation analysis with nutcracker and red squirrel seed harvesting variables with physical, compositional, and whitebark pine-related factors. I found that nutcrackers harvested seed at every site that had cones available. Nutcrackers harvested seed from a greater proportion of whitebark pine cones in stands where they started intensively harvesting seeds earlier. Nutcrackers began intensively harvesting seeds earlier in stands with higher relative dominance of whitebark pine. Red squirrels depleted the cone source more rapidly in stands with greater whitebark pine mortality, and at one site depleted the cone source completely before nutcrackers began intensively harvesting seeds from that site. The results of this study suggest that Clark's Nutcracker will continue to harvest seeds even as whitebark pine declines, but the decline in whitebark pine may lead to decreased seed dispersal due to greater pre-dispersal cone predation by red squirrels. Finally, I evaluated direct and indirect monitoring methods to identify a cost-effective method to accurately monitor Clark's Nutcracker occurrence in whitebark pine stands during the seed harvest season. I found that surveying scars made by seed-harvesting nutcrackers on whitebark pine cones was the most accurate and economical method of monitoring Clark's Nutcracker occurrence in an area with a low population of Clark's Nutcracker.

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Chapter 1
Introduction

Clark's Nutcracker (*Nucifraga columbiana*) was described by its namesake, explorer William Clark, as "a Bird of the woodpecker kind" (Jollie 1953). It is easy to see how Clark confused this gray and black, jay-sized bird with a woodpecker; the nutcracker, actually a member of the family Corvidae, has a very long bill, 37.7 (± 1.9) cm for females and 40.1 (± 1.8) cm for males (Mewaldt 1958). The bill is adapted in size and shape for opening conifer cones, the seeds being a primary source of food for nutcrackers (Giuntoli and Mewaldt 1978, Vander Wall and Balda 1981). Nutcrackers inhabit mountainous areas throughout western North America, where they spend late summer and fall harvesting and caching the seeds of large-seeded pines. Individual nutcrackers can store over 10,000 seeds each year, which they scatter in caches of one to fifteen seeds (Vander Wall and Balda 1977, Hutchins and Lanner 1982, Tomback 1982). The stored seeds serve as an important source of food in winter and spring, when weather in the mountains can be harsh and other sources of food are in low supply (Mewaldt 1956, Giuntoli and Mewaldt 1978).

To ensure an adequate food supply, nutcrackers often store seeds in excess: it is estimated that they cache 1.8 – 5 times the amount of energy that is needed to survive winter (Vander Wall and Balda 1977, Tomback 1982, Vander Wall 1988). The seeds that they do not retrieve germinate if conditions are suitable. A number of pines, including whitebark (*Pinus albicaulis*), limber (*P. flexilis*), Colorado piñon (*P. edulis*), single-leaf piñon (*P. monophylla*), and southwestern white (*P. strobiformis*), have their seeds dispersed by Clark's Nutcracker (Vander Wall and Balda 1977, Tomback 1978, Lanner and Vander Wall 1980, Vander Wall 1988, Tomback and Linhart 1990).

Whitebark pine grows in the subalpine and alpine regions of the northern Rocky Mountains, Cascade Mountains, and Sierra Nevada in western North America (Schmidt 1994). Whitebark pine exhibits a number of adaptations for dispersal by nutcrackers. Whitebark pine cones are often situated at the top of upswept branches, which makes them both visible and easily accessible to nutcrackers flying over (Lanner 1982). The wingless seeds of whitebark pine enable nutcrackers to process seeds quickly (Lanner 1982). In addition, the seeds are large and are a high-calorie, nutritious source of food for nutcrackers (Lanner 1982, Tomback and Linhart 1990).

Whitebark pine cones are indehiscent and must be opened by an animal (Lanner 1982). Nutcrackers use their sturdy bill to chisel through the cone scales and extract seeds. Red squirrel

(*Tamiasciurus hudsonicus*) is the only other species that is known to forage extensively on whitebark pine (Hutchins and Lanner 1982). Although red squirrels also store whitebark pine seeds, they are ineffective seed dispersers because the storage sites—middens that are often located under trees and contain thousands of cones—do not provide suitable conditions for germination (Hutchins and Lanner 1982). Thus, whitebark pine depends on the seed caching behavior of Clark's Nutcracker for effective dissemination of its seeds (Hutchins and Lanner 1982, Tomback 1982).

Clark's Nutcracker exhibits multiple adaptations for feeding on large-seeded pines. Nutcrackers use their long, sturdy bills to open cones and cache seeds (Vander Wall and Balda 1981). When harvesting seeds, nutcrackers store them in a unique sublingual pouch, situated under their tongue, which allows nutcrackers to gather as many as 150 whitebark pine seeds during a foraging bout before flying to a cache site (Bock et al. 1973, Tomback 1978). Nutcrackers are strong flyers; they have been known to transport seeds as far as 32.6 km (Lorenz et al. 2011). Another key adaptation is an enlarged hippocampus, which allows nutcrackers to remember the locations of tens of thousands of seed caches for at least 183 days (Balda and Kamil 1992).

Although Clark's Nutcrackers do not depend exclusively on whitebark pine for their survival range-wide, the status of whitebark pine can influence local populations of nutcrackers (McKinney et al. 2009). Recent declines in whitebark pine populations have raised concerns about the stability of nutcracker populations in areas where whitebark pine is a major food source (Tomback and Kendall 2001, McKinney et al. 2009). Whitebark pine has suffered heavy losses in the past century, due to the combined effects of pine beetle outbreaks and climate change, fire suppression and successional replacement, and the spread of an introduced fungal pathogen, white pine blister rust (*Cronartium ribicola*) (Tomback et al. 2001). These declines have prompted the United States Fish and Wildlife Service to give whitebark pine a "warranted but precluded" status on the endangered species list (U.S. Fish and Wildlife Service 2011), and the Canadian government has declared whitebark pine to be endangered (COSEWIC 2010).

The loss of whitebark pine could have major effects in subalpine ecosystems. Whitebark pine is a keystone species that plays an important role in maintaining biodiversity in western North America's forests (Tomback et al. 2001). It provides food and shelter for several wildlife species, including Clark's Nutcracker, red squirrel, grizzly and black bear, as well as a myriad of other mammals and birds (Tomback and Kendall 2001). At the higher elevations and in recently burned areas, whitebark pine is a pioneer species that inhabits areas unsuitable for other species (Tomback 1986, Lanner 1996, Tomback et al. 2001). Whitebark pine stabilizes the soil and creates microsites that other plants and animals can inhabit (Callaway 1998, Tomback et al. 2001, Ellison et al. 2005). Whitebark pine is also an important component of mountain watersheds; whitebark pine's stabilizing roots, open canopies, and presence at the higher elevations slows the rate of snow melt and reduces soil erosion (Farnes 1990, Tomback et al. 2001).

The Northern Divide Ecosystem (NDE), which includes Glacier National Park and the surrounding national forest land, is known to have the highest amount of whitebark pine mortality due to blister rust infection (Kendall and Keane 2001). In Glacier, 44 percent of whitebark pine trees have been killed by blister rust, and of the remaining live trees 78 percent are infected (Kendall et al. 1996). Park managers have implemented a whitebark pine restoration plan, which in large part consists of collecting seeds from whitebark pine trees that show resistance to blister rust and manually planting seedlings in whitebark pine habitat (Burr et al.

2001, Asebrook et al. 2011). However, successful long-term restoration must also include natural regeneration, which requires the continued presence of Clark's Nutcracker (Hoff et al. 2001). A study conducted by McKinney and colleagues (2009) concluded that the probability of seed dispersal by nutcrackers drops dramatically when whitebark pine cone production falls below a threshold of 1000 cones ha^{-1}, indicating that nutcrackers avoid areas with low cone production. McKinney and colleagues (2009) estimated that whitebark pine live basal area of at least 5.0 m^2 ha^{-1} would support cone production at the level necessary to ensure seed dispersal by nutcrackers, and that NDE had average whitebark pine live basal area of just 1.9 m^2 ha^{-1}. Because of the low abundance of whitebark pine in Glacier National Park, there is danger that, as the whitebark pine forests continue to decline, nutcrackers will eventually fail to harvest and cache seeds and whitebark pine will not propagate naturally.

Because of the threat posed by white pine blister rust, there is an urgent need to understand the factors that influence Clark's Nutcracker seed harvesting in Glacier National Park. In Chapter 2, I evaluate the threshold model proposed by McKinney and colleagues (2009). I also examine the relationships that exist between Clark's Nutcracker and red squirrel seed harvesting patterns and various physical, compositional, whitebark pine health, and cone production characteristics of whitebark pine stands. My results suggest that the mechanisms guiding Clark's Nutcracker seed harvesting in Glacier National Park are more complex than the threshold model, and that red squirrels have a major influence on the number of cones available for nutcrackers, particularly in stands with high whitebark pine mortality.

As resource managers seek information on Clark's Nutcracker use of whitebark pine stands, there is need for an economical monitoring method that can reliably detect nutcrackers. The prevailing techniques for monitoring Clark's Nutcracker are variations of common breeding bird survey methods, including point counts and transects. However, standard breeding bird survey methods are problematic when monitoring nutcrackers in part because nutcrackers are not territorial and can be difficult to detect (Lorenz and Sullivan 2010). These methods are also very time-consuming and must be carried out by well-trained technicians. Indirect monitoring techniques are used to monitor the population status of many bird species that are difficult to survey using standard breeding bird survey techniques (Bibby et al. 1992). A possible indirect method for monitoring Clark's Nutcracker is to conduct cone surveys for whitebark pine cones with Clark's Nutcracker seed harvesting scars. Cones that are harvested by nutcrackers remain on the tree and seed harvesting scars can easily be detected with binoculars.

Chapter 3 is an evaluation of direct and indirect methods of monitoring Clark's Nutcracker occurrence in Glacier National Park during seed harvest season. I examine the reliability of breeding bird surveys (timed surveys), incidental sighting records, and whitebark pine cone surveys in documenting Clark's Nutcracker use of whitebark pine stands. The results suggest that the direct monitoring methods, timed surveys and incidental sighting records, do not provide accurate information on nutcracker occurrence. Cone surveys did reliably document nutcracker occurrence and, with proper planning, could be an economically feasible method for monitoring Clark's Nutcracker, particularly in areas where nutcracker populations are low.

Literature Cited

Asebrook, J., J. Lapp, and T. Carolin. 2011. Whitebark and limber pine restoration and monitoring in Glacier National Park, p. 335–337. *In* R. E. Keane, D. F. Tomback, M. P. Murray, and C. M. Smith [eds.], Proceedings of the high five symposium: the future of high-elevation, five-needle white pines in Western North America, June 28–30, 2010, Missoula, Montana. USDA Forest Service RMRS-P-63.

Balda, R. P., and A. C. Kamil. 1992. Long-term spatial memory in the Clark's Nutcracker, *Nucifraga columbiana*. Animal Behavior 44:761–769.

Bibby, C. J., N. D. Burgess, and D. A. Hill. 1992. Birds census techniques. Academic Press, Limited, London.

Bock, W. J., R. P. Balda, and S. B. Vander Wall. 1973. Morphology of the sublingual pouch and tongue musculature in Clark's Nutcracker. Auk 90:491–519.

Burr, K. E., A. Eramian, and K. Eggleston. 2001. Growing whitebark pine seedlings for restoration, p. 325–345. *In* D. F. Tomback, S. F. Arno, and R. E. Keane [eds.], Whitebark pine communities: ecology and restoration. Island Press, Washington, DC.
Callaway, R. M. 1998. Competition and facilitation on elevation gradients in subalpine forests of the northern Rocky Mountains, USA. Oikos 82:561–573.

COSEWIC. 2010. COSEWIC assessment and status report on the whitebark pine *Pinus albicaulis* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa, Canada.

Ellison, A. M, M. S. Bank, B. D. Clinton, E. A. Colburn, K. Elliott, C. R. Ford, D. R. Foster, B. D. Kloeppel, J. D. Knoepp, G. M. Lovett, J. Mohan, D. A. Orwig, N. L. Rodenhouse, W. V. Sobczak, K. A. Stinson, J. K. Stone, C. M. Swan, J. Thompson, B. Von Holle, and J. R. Webster. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment 3:479–486.

Farnes, P. E. 1990. SNOTEL and snow course data describing the hydrology of whitebark pine ecosystems, p. 302–304. *In* W. C. Schmidt and K. J. McDonald [eds.], Proceedings of the symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource, March 29–31, 1989, Bozeman, Montana. USDA Forest Service General Technical Report INT-GTR-270.

Giuntoli, M., and L. R. Mewaldt. 1978. Stomach contents of Clark's Nutcrackers collected in western Montana. Auk 95:595–598.

Hoff, R. J., D. E. Ferguson, G. I. McDonald, and R. E. Keane. 2001. Strategies for managing whitebark pine in the presence of white pine blister rust, p. 346–366. *In* D. F. Tomback, S. F. Arno, and R. E. Keane [eds.], Whitebark pine communities: ecology and restoration. Island Press, Washington, DC.

Hutchins, H. E., and R. M. Lanner. 1982. The central role of Clark's Nutcracker in the dispersal and establishment of whitebark pine. Oecologia 55:192–201.

Jollie, M. 1953. The birds observed in Idaho by the Lewis and Clark expedition, 1804–1806. Murrelet 34:1–5.

Kendall, K. C., and R. E. Keane. 2001. Whitebark pine decline: infection, mortality, and population trends, p. 221–242. *In* D. F. Tomback, S. F. Arno, and R. E. Keane [eds.], Whitebark pine communities: ecology and restoration. Island Press, Washington, DC.

Kendall, K., D. Schirokauer, E. Shanahan, R. Watt, D. Reinhart, R. Renkin, S. Cain, and G. Green. 1996. Whitebark pine health in northern Rockies national park ecosystems: a preliminary report. Nutcrackers Notes 7:16.

Lanner, R. M. 1982. Adapations of whitebark pine for seed dispersal by Clark's Nutcracker. Canadian Journal of Forest Research 12:391–402.

Lanner, R. M. 1996. Made for each other: a symbiosis of birds and pines. Oxford University Press, New York.

Lanner, R. M., and S. B. Vander Wall. 1980. Dispersal of limber pine seed by Clark's Nutcracker. Journal of Forestry 78:637–639.

Lorenz, T. J., and K. A. Sullivan. 2010. Comparison of survey methods for monitoring Clark's Nutcrackers and predicting dispersal of whitebark pine seeds. Journal of Field Ornithology 81:430–441.

Lorenz, T. J., K. A. Sullivan, A. V. Bakian, and C. A. Aubry. 2011. Cache-site selection in Clark's Nutcracker (*Nucifraga columbiana*). Auk 128:237–247.

McKinney, S. T., C. E. Fiedler, and D. F. Tomback. 2009. Invasive pathogen threatens bird-pine mutualism: implications for sustaining a high-elevation ecosystem. Ecological Applications 19:597–607.

Mewaldt, L. R. 1956. Nesting behavior of the Clark's Nutcracker. Condor 58:3–23.

Mewaldt, L. R. 1958. Pterylography and natural and experimentally induced molt in Clark's Nutcracker. Condor 60:165–187.

Schmidt, W. C. 1994. Distribution of stone pines, p. 1–6. *In* W. C. Schmidt, and F. K. Holtmeier [eds.], Proceedings of the international workshop on subalpine stone pines and their environment: the status of our knowledge, September 5–11, 1992, St. Moritz, Switzerland. USDA Forest Service General Technical Report INT-GTR-309.

Tomback. D. F. 1978. Foraging strategies of Clark's Nutcracker. Living Bird 16:123–161.

Tomback, D. F. 1982. Dispersal of whitebark pine seeds by Clark's Nutcracker: a mutualism hypothesis. Journal of Animal Ecology 51:451–467.

Tomback, D. F. 1986. Post-fire regeneration of krummholz whitebark pine: a consequence of nutcracker seed caching. Madroño 33:100–110.

Tomback, D. F., S. F. Arno, and R. E. Keane. 2001. The compelling case for management intervention, p. 3–25. *In* D. F. Tomback, S. F. Arno, and R. E. Keane [eds.], Whitebark pine communities: ecology and restoration. Island Press, Washington, DC.

Tomback, D. F., and K. C. Kendall. 2001. Biodiversity losses: the downward spiral, p. 243–262. *In* D. F. Tomback, S. F. Arno, and R. E. Keane [eds.], Whitebark pine communities: ecology and restoration. Island Press, Washington, DC.

Tomback, D. F., and Y. B. Linhart. 1990. The evolution of bird-dispersed pines. Evolutionary Ecology 4:185–219.

U.S. Fish and Wildlife Service. 2011. Endangered and threatened wildlife and plants; 12-month finding on a petition to list *Pinus albicaulis* as endangered or threatened with critical habitat. Federal Register 76:42631–42654.

Vander Wall. S. B. 1988. Foraging of Clark's Nutcrackers on rapidly changing pine seed resources. Condor 90:621–631.

Vander Wall, S. B., and R. P. Balda. 1977. Co-adaptations of Clark's Nutcracker and pinyon pine for efficient seed harvest and dispersal. Ecological Monographs 47:89–111.

Vander Wall, S. B., and R. P. Balda. 1981. Ecology and evolution of food storage behavior in conifer-seed-caching Corvids. Zeitschrift fur Tierpsychologie 56:217–242.

Chapter 2
Patterns of whitebark pine seed harvest among Clark's Nutcrackers and red squirrels in Glacier National Park

Abstract

Whitebark pine (*Pinus albicaulis*), a keystone species, is in decline throughout its range. Restoration efforts include allowing for natural regeneration. To assess the effectiveness of natural regeneration, there must be an understanding of the factors that influence seed harvesting by Clark's Nutcracker, the primary seed disperser of whitebark pine, and the red squirrel, a major whitebark pine seed predator. In Glacier National Park, Montana, where whitebark pine cone density is typically very low, I evaluated a threshold model that states that the probability of seed dispersal by Clark's Nutcracker is small in areas where whitebark pine cone density is low due to decreased visitation by nutcrackers. To test the efficacy of this model and identify other factors that may contribute to nutcracker seed harvesting, I examined relationships between Clark's Nutcracker and red squirrel harvesting patterns on whitebark pine cones and physical, compositional, whitebark pine health, and cone production characteristics at the stand level. I found evidence of Clark's Nutcracker seed harvesting in all sites with available whitebark pine cones, regardless of cone density. Clark's Nutcrackers harvested seeds from a greater proportion

of cones in stands where intensive seed harvesting began earlier. This was driven in part by nutcracker preference to begin intensively harvesting seeds earlier at sites with higher relative dominance of whitebark pine. Red squirrels, in turn, removed a larger proportion of cones at sites nutcrackers harvested later. In addition, red squirrels depleted the cone source more rapidly at sites with greater whitebark pine mortality, indicating that red squirrel populations may be resilient to whitebark pine decline. I reject the hypothesis that nutcrackers do not visit sites with low cone production. However, my data support the implication of the threshold model that the probability of seed dispersal decreases as whitebark pine declines, due to nutcracker preference to begin intensively harvesting earlier at sites with greater relative dominance of whitebark pine and squirrel resilience to the decline in whitebark pine. Whitebark pine restoration plans should include red squirrel population management or focused seed collecting in areas with high pre-dispersal seed predation by red squirrels.

Introduction

Whitebark pine (*Pinus albicaulis*), which grows in subalpine and timberline regions in the mountains of northwestern United States and western Canada (Arno and Weaver 1990, Arno 2001), is a keystone species that stabilizes soils, prevents erosion, regulates runoff, and provides food and habitat for a multitude of organisms (Hutchins and Lanner 1982, Kendall 1983, Arno and Hoff 1990, Farnes 1990, Tomback et al. 2001). Whitebark pine is in decline throughout its range (Tomback et al. 2001). This decline can be attributed to three known threats: massive mountain pine beetle (*Dendroctonus ponderosae*) outbreaks, successional replacement due to fire suppression, and infection by an exotic fungal pathogen, white pine blister rust (*Cronartium ribicola*) (Tomback et al. 2001). Restoration efforts include silvicultural thinning, prescribed fire, planting blister rust-resistant whitebark pine seedlings, attaching verbenone patches to trees to ward off mountain pine beetle infestations, and allowing for natural regeneration of blister rust-resistant cultivars (Hoff et al. 2001, Keane and Parsons 2010, Kegley and Gibson 2011).

Natural regeneration of whitebark pine depends on the presence and foraging behavior of Clark's Nutcracker (*Nucifraga columbiana*), the primary seed disperser of whitebark pine (Hutchins and Lanner 1982). During summer and fall nutcrackers harvest seeds of large-seeded pines, including whitebark pine, and store them in caches, which they retrieve in the winter and spring when other sources of food are rare (Tomback 1982). In one study by Tomback (1982), nutcrackers were estimated to retrieve only 55% of cached seeds. Nutcrackers cache a few seeds in thousands of sites both in the ground and in trees, and excess seeds left in the ground germinate if conditions are suitable (Tomback 1982). Whitebark pine has large, wingless seeds and indehiscent cones, an adaptation for dispersal by Clark's Nutcracker (Lanner 1982). Nutcrackers are among the few animals that can easily open whitebark pine cones to access the seeds, and most other animals that forage on whitebark pine seeds consume the seeds or store them in locations unsuitable for germination (Hutchins and Lanner 1982). Because of this, whitebark pine depends on Clark's Nutcracker for effective seed dispersal (Hutchins and Lanner 1982).

Nutcrackers begin intensively harvesting and caching whitebark pine seeds from mid-August (Hutchins and Lanner 1982) to mid-September (Dimmick 1993), after cones ripen. Before that time, nutcrackers may forage on whitebark pine seeds and eat them in situ, but seed harvest is much slower and they do not cache the seeds (Tomback 1978, 1998, Hutchins and Lanner 1982). Intensive seed harvest continues until the cones are depleted or the nutcrackers' attention is diverted to a ripening, abundant seed source of another conifer species (Hutchins and Lanner 1982, Tomback 1982, Vander Wall 1988). However, Clark's Nutcracker seed harvesting behavior is spatially and temporally variable and likely depends on community structure and whitebark pine cone production, among other ecological variables (McKinney et al. 2009, Lorenz et al. 2011).

One factor that may influence nutcracker seed harvesting is the presence of competitors. A variety of birds and mammals consume whitebark pine seeds, including woodpeckers, grosbeaks, chipmunks, ground squirrels, and bears (Hutchins and Lanner 1982, Tomback and Kendall 2001). However, only one species besides Clark's Nutcracker has a major effect on the whitebark pine cone crop: the red squirrel (*Tamiasciurus hudsonicus*). The red squirrel forages mainly on conifer seeds. Like nutcrackers, red squirrels harvest and store whitebark pine seeds to use as a source of food in the winter (Hutchins and Lanner 1982). However, their method of harvest and storage is quite different: red squirrels remove entire cones from trees and store the cones in mass storage piles called middens, located within heavily defended territories (Smith 1981). Although red squirrels do not consume all of the seeds they store, their storage sites are rarely favorable for germination (Hutchins and Lanner 1982).

Red squirrels can play a major role in the whitebark pine communities they inhabit. In areas where red squirrels are abundant, they exert a strong selective pressure favoring cone defenses over traits that increase nutcracker foraging effectiveness (Siepielski and Benkman 2007). In some areas, red squirrels may remove more than 80 percent of cones before nutcrackers begin harvesting seeds (Hutchins and Lanner 1982, McKinney and Tomback 2007). Despite their affinity for whitebark pine seeds, red squirrels prefer habitat that also contains other conifer species (Mattson and Reinhart 1997, McKinney and Fiedler 2010): high pre-dispersal cone predation by red squirrels typically occurs in mixed-conifer stands where whitebark pine is not the dominant species (Hutchins and Lanner 1982, McKinney and Tomback 2007, McKinney and Fiedler 2010). Whitebark pine, like many pine species, has variable annual cone production and occasionally experiences crop failure (Tomback 1982, Crone et al. 2011). Presumably red squirrels prefer mixed conifer stands because they provide more food security (Mattson and Reinhart 1997, McKinney and Fiedler 2010). Red squirrel populations may remain robust as whitebark pine declines by foraging on seeds of other conifer species (McKinney and Tomback 2007). Consequently, red squirrels have the potential to remove a larger proportion of cones as whitebark pine mortality increases.

To assess the effectiveness of natural regeneration, there needs to be an understanding of nutcracker and red squirrel foraging ecology as well as knowledge of how whitebark pine decline affects nutcracker and red squirrel seed harvesting. In a study on the effect of whitebark pine decline on Clark's Nutcracker seed harvesting, McKinney and his colleagues (2009) proposed a seed dispersal probability threshold based on whitebark pine cone density. They postulated that a cone density of 1000 cones ha^{-1} would have a high likelihood of seed dispersal and that, as cone density declines, the probability of seed dispersal by Clark's Nutcracker drops drastically (McKinney et al. 2009). When cone density dropped to 130 cones ha^{-1}, nutcracker occurrence became "negligible," where the proportion of survey hours with nutcracker detections was about 0 (McKinney et al. 2009). They suggested that nutcrackers are responding to the decline in cone availability with population declines or emigration to areas with greater cone production (McKinney et al. 2009). In effect, their study suggests that nutcrackers avoid sites with low cone density and harvest seeds in areas with more whitebark pine cones. In addition, they estimated that whitebark pine live basal area would need to be at least 5.0 m^2 ha^{-1} to support a cone density of 1000 cones ha^{-1} (McKinney et al. 2009).

I conducted this study in Glacier National Park, Montana, as part of the effort to develop a whitebark pine restoration plan. The decline in whitebark pine at Glacier National Park is largely due to succession caused by fire suppression (Arno 2001) and blister rust infection (Kendall and Keane 2001). Glacier National Park is part of the region hit the hardest by white pine blister rust (Kendall and Keane 2001). In Glacier National Park, 44 percent of whitebark pine has been killed and 78 percent of the living trees are infected with blister rust (Kendall et al. 1996). Whitebark pine is rarely the dominant species in the forests of Glacier National Park and is mainly present in mixed conifer forests with subalpine fir (*Abies lasciocarpa*), lodgepole pine (*Pinus contorta*), and Engelmann spruce (*Picea engelmannii*) (McKinney et al. 2009, McKinney and Fiedler 2010). In the Northern Divide Ecosystem (NDE), which includes Glacier National Park and adjacent National Forests, red squirrels remove a high proportion of whitebark pine cones in mixed-forest stands that contain whitebark pine (McKinney and Fiedler 2010). In addition, nutcrackers are seen less frequently in the NDE than they are in the Greater Yellowstone Ecosystem (GYE) and Bitterroot Mountains Ecosystem (BME) (McKinney et al. 2009). Compared to the GYE and BME, whitebark pine occurs at a relatively low density in the NDE, with an average whitebark pine live basal area of 1.9 m^2 ha^{-1} (McKinney et al. 2009). This value falls well below the 5.0 m^2 ha^{-1} whitebark pine live basal area threshold suggested as necessary for high probability of seed dispersal (McKinney et al. 2009). There is concern that Clark's Nutcrackers will emigrate from areas with low cone production and fail to harvest and cache seeds from sites that contain low levels of whitebark pine, thus impeding the natural regeneration of whitebark pine in Glacier National Park.

In this study, I assess the efficacy of McKinney and his colleagues' (2009) threshold model in Glacier National Park. The threshold model states that seed dispersal probability declines sharply as cone density drops below 1000 cones ha^{-1} or whitebark pine live basal area is below 5.0 m^2 ha^{-1} (McKinney et al. 2009). To determine if the threshold model is applicable in Glacier National Park, I test the hypothesis that Clark's Nutcrackers do not harvest seeds from stands with low cone density and low whitebark pine live basal area. If this hypothesis is correct, sites with very low cone densities (below 130 cones ha^{-1}) and low whitebark pine live basal area should show no evidence of Clark's Nutcracker seed harvesting. I also consider additional factors that may influence the proportion of cones harvested by nutcrackers. To do this, I examine patterns of cone use by Clark's Nutcrackers and red squirrels in whitebark pine communities and evaluate how they are affected by specific physical, compositional, cone, and forest health factors.

Methods

Study area. I studied Clark's Nutcrackers and red squirrel use of whitebark pine cones during the summers of 2010 and 2011 in Glacier National Park, Montana (48.2–48.9˚N, 113.2–114.1˚W), at eleven study sites throughout the park (Fig. 2-1). I selected sites based on the presence of whitebark pine and accessibility. Elevation ranged from 1739 meters to 2198 meters. Each site was composed of one or two 1-ha plots (100 x 100 m) where I conducted whitebark pine tree monitoring, cone counts, and forest community sampling.

Cone production, cone predation, and seed harvesting by Clark's Nutcracker. I measured cone production at ten sites in 2010 and five sites in 2011, adapting the methods described by

McKinney and colleagues (2009). Upon arrival at a site, a member of my research team walked a random number of paces (between 1 and 100) in a random direction and identified the nearest cone-bearing whitebark pine tree. I marked the location on a global positioning system (GPS) and took notes on location and tree characteristics for future identification. I repeated this step for subsequent trees with the previously selected cone tree as the starting location. Cone trees were at least 20 meters apart. If a randomly selected tree was less than 20 meters from a previously selected cone tree, I skipped that tree and randomly selected another tree following the method described above. In 2010, some sites (Cutbank, Dawson Pass, Highline, and Numa) had few cone-bearing whitebark pine trees, and randomly selecting trees was not possible. At these sites I conducted a thorough search of the area and selected every cone-bearing whitebark pine tree that I could identify. In 2010 I selected a minimum of two and a maximum of seven cone trees (mean = 4.6) at each site, depending on the prevalence of cone-producing whitebark pine trees. In 2011, I selected a minimum of five and a maximum of ten (mean = 8.8) cone trees at each site. At one site, Atlantic, the maximum number of trees that I could conduct weekly cone counts on, accounting for travel time, was five cone trees. Because there were no cones produced at Atlantic in 2010, I selected the five cone trees in 2011 following the same methods as in 2010. At the remaining four study sites in 2011, I used the same cone trees that I selected in 2010 and randomly selected four to five additional cone trees, starting at the final cone tree from the previous year.

In 2010 I conducted two cone counts. The initial cone counts were 15 July to 25 August. A second cone count was conducted for each site between 10 August and 30 September. In 2011 I conducted weekly cone counts, beginning 25 July to 4 August and repeated each week until over 90 percent of the cones at a site had evidence of seed harvesting by nutcrackers or had been removed. Final cone count dates ranged from 29 August to 18 September. During each visit, an assistant and I used binoculars to count all the visible cones on each of the cone trees from multiple vantage points. At each vantage point the assistant and I counted cones separately and then repeated the count together. We kept track of cones that we counted at previous vantage points to avoid counting individual cones more than once. To estimate cone production, I calculated the average number of cones per tree during the initial cone count for each site. In 2011, the difference in total number of cones from week to week was attributed to removal by red squirrel.

I also took note of any cones that showed evidence of seed harvesting by Clark's Nutcracker. Nutcrackers harvest seeds from cones that are still attached to the tree by drilling on the cones to remove scales and expose the seeds (Tomback 1978). Nutcrackers do not remove cones as they harvest seeds (Tomback 1978, Hutchins and Lanner 1982) except occasionally late in the season when the cone source is nearly depleted (pers. obs.). Because nutcrackers will often extract many seeds from the same cone during a seed harvest bout, nutcracker seed harvest scars give the cone a dished out or shredded look that is very visible (Fig. 2-2). During each count, I recorded the number of cones with nutcracker seed harvesting scars. The presence of nutcracker seed harvesting scars at a site indicated that nutcrackers harvested seeds in that stand.

In 2011, I determined the week when nutcrackers started harvesting whitebark pine seeds for caching (intensive harvest start week) by plotting the percent of cones harvested by nutcrackers against the week the count was taken for each site. Because nutcrackers increase their foraging intensity once they start caching seeds (Tomback 1978, 1998, Hutchins and Lanner 1982), the point at which the slope of the line rapidly increased was deemed the intensive harvest start week. The designation was confirmed by observations of a nutcracker placing seeds in its sublingual pouch at one of the sites (Atlantic) during the following week. I also used the weekly cone counts to determine the total proportion of cones that had been harvested by Clark's Nutcracker by dividing the number of cones with nutcracker seed harvesting scars by the initial number of cones.

To determine the rate at which red squirrels removed whitebark pine cones (removal rate), I conducted simple linear regression analyses on mean cones per tree as a function of count week for each site (R Development Core Team 2011). I also calculated relative removal rate for red squirrels as the removal rate divided by the cone density estimate for each stand in 2011. This is a measurement of the rate at which red squirrels deplete the cone source.

Forest characteristics and whitebark pine health. I adapted the methods described by McKinney and his colleagues (2009) to measure forest composition and physical forest stand characteristics for the five sites where we conducted weekly cone counts in 2011. Each site was composed of one or two 1-ha plots, depending on the size of the stand and cone tree density. Starting at an arbitrary corner of the plot, I walked a random number of paces in a random direction (while staying within the plot), to the starting point. At the starting point, I recorded the UTM coordinates and elevation, and then I set up a 10 x 50 meter (500 m^2) belt transect along a random azimuth. Each 1-ha plot had two 10 x 50 meter belt transects, which were at least 20 meters apart. Within each transect an assistant and I measured the diameter at breast height (DBH; 1.4 m above the ground) of every tree with a diameter greater than or equal to 7.0 cm. At the mid-point of each transect, I measured slope with a clinometer and aspect using a compass. I used DBH to calculate basal area of each tree species as well as total basal area for each site. Basal area was used to calculate relative dominance of each tree species (% of total basal area). I also calculated tree diversity using Simpson's diversity index.

The remaining sites, those not included in the 2011 weekly cone count, were composed of one to three 1-ha plots, each of which contained two 10 x 50 meter belt transects, set up using the method described above. However, I only measured DBH of whitebark pine trees (DBH $\geq$ 7.0 cm). I used that number to calculate basal area of whitebark pine at each of the sites. I also carried out detailed whitebark pine health analyses on every transect at all eleven sites (Tomback et al. 2005).

I assessed the health of every whitebark pine tree in each transect at all eleven sites by recording the presence or absence of blister rust cankers or canker scars and the percent of the crown (extending from the top of the tree down to the lowest branches) that was dead. Every whitebark pine tree was inspected for the presence of cones. In addition to live trees, I measured and recorded the DBH of all whitebark pine snags. I used DBH to calculate the basal area of snags at each site. For each site I estimated percent of living whitebark pine trees infected with blister rust, percent crown kill on living whitebark pine trees, number of cone-producing whitebark pine trees per hectare, and proportion of total whitebark pine basal area (living trees and snags) that was dead. Additionally, I estimated the cone density (number of cones ha^{-1}) at each site as the product of the number of cone-bearing trees per hectare and cone production (average number of cones per tree in initial cone count).

Clark's Nutcracker and red squirrel detections. Each site was visited at least twice during August and September 2010 and 2011, the time period when whitebark pine cones become ripe and seed harvesting by both Clark's Nutcracker and red squirrel commences (Hutchins and Lanner 1982, McKinney and Tomback 2007). Once I arrived on site I noted the time, and while a field assistant and I were conducting work (either counting cones or measuring site characteristics) we actively searched for Clark's Nutcrackers. I recorded all detections, either seen or heard, and kept note of the time, number of birds, UTM coordinates, and behavioral observations. I calculated the mean time to first sighting for each site. I also used nutcracker sightings to calculate the sighting frequency for each site, which is the total number sightings at a site divided by the total time (minutes) spent at a site for 2010 and 2011 combined.

In 2011, I actively searched for red squirrels at each of the five sites where I conducted weekly cone counts. A field assistant and I looked and listened for red squirrels while we conducting other work. I recorded the time of the detection, location, and behavioral observations. I used red squirrel detections to calculate sighting frequency for red squirrels at each site by dividing total number of detections by total time (minutes) spent on site.

Statistical analyses. I used Microsoft Excel (Microsoft Corporation 2001) and R (R Development Core Team 2011) for all computations and analyses. I conduced all analyses at the site level, using transect and cone tree means as estimates of the site values. To examine whether Clark's Nutcracker responds to density of whitebark pine trees, I conducted a simple linear regression analysis of nutcracker sighting frequency, 2010 and 2011 combined, as a function of whitebark pine live basal area (n = 11 sites). I conducted a simple linear regression analysis of nutcracker sighting frequency each year as a function of cone density to examine nutcracker response to cone density (n = 15 site-years). However, 2010 cone densities are rough estimates because they are based the number of cone-producing trees present in 2011 and the number of cone-producing trees varies annually (Weaver and Forcella 1986). I used a correlation analysis (Pearson's simple correlation analysis; n = 5 sites in 2011) to investigate the presence and strength of relationships between Clark's Nutcracker seed harvesting and occurrence (intensive harvest start week, sighting frequency, time to first sighting), red squirrel predation and occurrence (removal rate, relative removal rate, sighting frequency), physical site characteristics (elevation, northing, aspect, slope), forest characteristics (total basal area, tree diversity), whitebark pine composition (live basal area, relative dominance, mean DBH), whitebark pine health (% infected, % crown kill, % dead), and whitebark pine cone characteristics (cones per tree, cone trees ha^{-1}, cones ha^{-1}). Intensive harvest start week was analyzed separately (n = 4 sites) because one of the sites (Scenic) had to be omitted due to the complete removal of cones before nutcrackers started intensively harvesting seeds. I conducted a simple linear regression analysis to determine whether there was a relationship between intensive harvest start week and the proportion of cones harvested by nutcrackers. I examined relationships that had a significance value of at least P = 0.1 because the small sample size might have led to some relationships being masked if the significance value was lower. Mean values are reported with standard deviation following in parentheses, unless otherwise noted.

Results

Do Clark's Nutcrackers harvest seeds from stands with low levels of whitebark pine? The amount of whitebark pine at each of the eleven sites varied, with live basal area ranging from < 0.1 m^2 ha^{-1} to 12.8 m^2 ha^{-1} (Table 2-1). Overall, whitebark pine was sparse, with an average live basal area of whitebark pine of 2.5 m^2 ha^{-1} and a median of 1.4 m^2 ha^{-1}. Cone density estimates varied among the sites and between years, with 10 to 4186 cones ha^{-1} in 2010 and 366 to 2000 cones ha^{-1} in 2011 (Table 2-1). In 2010, seven study sites had cone densities below 130 cones ha^{-1} (Table 2-1). I located cones with nutcracker seed harvesting scars at all ten cone-producing stands in 2010 and at all five stands in 2011, regardless of the prominence of whitebark pine or cone density. Though nutcracker sighting data was limited by as few as two visits to some sites, there was no relationship between nutcracker sighting frequency and whitebark pine live basal area (R = 0.045, P = 0.6; Fig. 2-3a), nor was there any relationship between nutcracker sighting frequency and cone density (R = 0.13, P = 0.2; Fig. 2-3b). These findings compel me to reject the hypothesis that Clark's Nutcrackers do not harvest seeds from stands with low cone density and low whitebark pine live basal area.

Clark's Nutcracker use of whitebark pine stands. Analysis revealed a number of relationships between nutcracker response variables—sighting frequency, time to first sighting, and intensive harvest start week—and whitebark pine relative dominance and cone production. I found nutcrackers more quickly at the sites where whitebark pine is more dominant: mean time to first sighting and whitebark pine relative dominance were negatively correlated (R = -0.83, P = 0.09; Fig. 2-4). Whitebark pine relative dominance was also significantly correlated with the week when nutcrackers started intensively harvesting whitebark pine seeds, such that nutcrackers started intensive harvesting earlier in the sites where whitebark pine was more dominant (R = -0.96, P = 0.04; Fig. 2-4). I saw nutcrackers more frequently in stands with higher cone production: there was a significant positive correlation between sighting frequency and the average number of cones per tree (R = 0.952, P = 0.01; Fig. 2-4). These results suggest that nutcrackers focus their harvesting efforts in stands where whitebark pine is more dominant and where the trees carry more cones.

The Clark's Nutcracker response variables were also correlated with a variety of other factors. Intensive harvest start week was negatively correlated with the percent of dead whitebark pine in the stand (R = -0.95, P = 0.05; Fig. 2-4). This may be because the percentage of whitebark pine that is dead is correlated with relative dominance of whitebark pine (R = 0.96, P = 0.01; Fig. 2-4), which, as noted above, is also correlated with intensive harvest start week. Sighting frequency was negatively correlated with elevation (R = -0.93, P = 0.02; Fig. 2-4). This is probably due to the strong negative correlation between elevation and mean cones per tree (R = -0.974, P = 0.005; Fig. 2-4), which is also correlated with sighting frequency. Intensive harvest start week was negatively correlated with slope (R = -0.91, P = 0.09; Fig. 2-4), and slope is negatively correlated with the number cone trees per hectare (R = -0.86, P = 0.06; Fig. 2-4). This means that as the slope becomes steeper, the number of cone trees declines but nutcrackers start intensive harvesting sooner. However, no relationships are evident between intensive harvest start week and any of the cone variables.

Nutcrackers harvested seeds from a greater percentage of the whitebark pine cones in the stands with earlier intensive harvest start weeks (R = -0.985, P = 0.015; Fig. 2-5). Presumably this is because nutcrackers started intensively harvesting seeds before the red squirrels removed many of the cones, and a greater proportion of cones were still available for nutcracker harvesting. There was a higher percentage of cones remaining on the trees at the start of nutcracker harvest in the stands where nutcrackers started intensive harvesting sooner (R = -0.96, P = 0.04).

Red squirrel impact on whitebark pine cone availability. Clark's Nutcrackers' major competitor for whitebark pine seeds, the red squirrel, removed whitebark pine cones at a linear rate. Removal rate, which is the slope of the linear regression line for cone removal, is defined as the average number of cones per tree removed per week. Red squirrels removed cones at a faster rate in stands were whitebark pine was more dominant: removal rate was positively correlated with the relative dominance of whitebark pine (R = 0.85, P = 0.07; Fig. 2-4). Red squirrels also removed cones more quickly in stands with larger whitebark pine trees: removal rate was positively correlated to mean diameter at breast height (DBH) of the whitebark pine trees (R = 0.92, P = 0.03; Fig. 2-4). The stands with bigger trees also had higher cone production: DBH was positively correlated to the average number of cones per tree (R = 0.84, P = 0.08; Fig. 2-4).

The relative removal rate measures how rapidly red squirrels deplete the cone source. Relative removal rate was positively correlated with the percentage of dead whitebark pine trees in a stand (R = 0.98, P = 0.004; Fig. 2-4) as well as the percentage of dead branches in the crown (crown kill) of live trees (R = 0.83, P = 0.08; Fig. 2-4), indicating that red squirrels depleted the cone source more rapidly in stands where blister rust infection had greater impact. Red squirrels also depleted the cone source more rapidly in stands where whitebark pine was more dominant: relative removal rate and relative dominance of whitebark pine were positively correlated (R = 0.88, P = 0.05; Fig. 2-4). Relative dominance of whitebark pine was also positively correlated with percentage of whitebark pine trees that are dead (R = 0.96, P = 0.01; Fig. 2-4). Finally, relative removal rate was positively correlated with aspect (R = 0.85, P = 0.07; Fig. 2-4), with red squirrels depleting the cone source more rapidly at sites with more southwest-facing aspects (all the sites had a southerly aspect, ranging from SE to SW). Red squirrels were detected more frequently in stands that had a greater proportion of dead whitebark (R = 0.85, P = 0.07; Fig. 2-4) as well as stands with higher crown kill (R = 0.96, P = 0.008; Fig. 2-4). There were no relationships between red squirrel detection frequency and any whitebark pine-related factors, including relative dominance of whitebark pine and cone production.

Other relationships. Analysis revealed relationships between the various physical, compositional, and whitebark pine-related variables. Most of these relationships have been described above. The few that remain highlight relationships between composition and the number of cone-producing whitebark pine trees. Total basal area was positively correlated with number of cone-bearing whitebark pine trees per hectare (R = 0.96, P = 0.008; Fig. 2-4). Tree diversity was positively correlated with total basal area (R = 0.86, P = 0.06; Fig. 2-4) as well as the number of cone-bearing whitebark pine trees per hectare (R = 0.83, P = 0.08; Fig. 2-4). As the amount of trees in the stand (total basal area) increased, tree diversity and the number of cone-bearing whitebark pine trees also increased. Neither of the composition-related variables nor the number of cone-bearing whitebark pine trees were related to Clark's Nutcracker or red squirrel responses.

Discussion

A previous study of Clark's Nutcracker seed harvesting in whitebark pine ecosystems proposed that nutcrackers respond to whitebark pine cone availability via a threshold effect: forest stands with whitebark pine cone densities of less than 1000 cones ha^{-1} have an increasingly smaller probability of seed dispersal as cone density declines, and that stands with 130 cones ha^{-1} are very unlikely to be visited by nutcrackers (McKinney et al. 2009). My research indicates that, in Glacier National Park, the ecological processes guiding nutcracker seed harvesting do not follow the threshold model, which describes a relationship between seed dispersal probability and whitebark pine cone density. The results of this study dispute the threshold model because I found nutcracker seed harvesting scars on whitebark pine cones at every site with cone-producing whitebark pine trees, including seven of the ten sites in 2010 that had estimated cone production of less than 130 cones ha^{-1}. This indicates that nutcrackers foraged on whitebark pine cones at sites that had very low cone density, and likely harvested and cached seeds from those sites.

The discrepancy in these two studies exists in part because of differences in sampling methodology. McKinney and his colleagues (2009) searched a 1-ha block for nutcrackers for one hour each time they visited a site. They defined seed dispersal as an observation of nutcrackers harvesting seeds and storing them in their sublingual pouch for transport. They calculated seed dispersal probability by completing a logistic regression, comparing whether or not they observed seed dispersal at a site to the estimated cone density (number of cones per hectare) at that site. Nutcrackers are extremely mobile and fly over large areas to harvest and cache seeds (Lorenz and Sullivan 2009). The probability of detecting a nutcracker and observing sublingual pouching within a one-hour period in a single stand is low when nutcrackers are in low abundance. In this study, the proportion of visits with nutcracker detections was 71% during the seed harvest season and yet all sites with cones showed evidence of nutcracker harvesting. When nutcrackers were detected, it took an average of 42.7 (± 45.7) minutes to detect a nutcracker, by either sight or sound, and 49.8 (± 58.6) minutes to observe a nutcracker. Thus, a 1-hour survey may take place at a time when nutcrackers are not visiting that particular stand, and there is no opportunity for viewing seed pouching. In an area like Glacier National Park with few nutcrackers and sparse whitebark pine, it is likely that McKinney missed many seed pouching events and miscalculated seed dispersal probability.

My results suggest that, in Glacier National Park, nutcrackers are not a limiting factor in the natural regeneration of whitebark pine. Nutcrackers will visit stands containing cones even when whitebark pine trees and cones are at low densities. However, nutcrackers did not harvest from whitebark pine stands randomly and some stands have a greater proportion of seeds harvested by nutcrackers. Nutcrackers initiated intensive seed harvest earlier in stands where whitebark pine was more dominant and spent more time in stands with greater cone production. Although nutcrackers eventually seem to visit every stand containing whitebark pine cones, stands visited late in the harvest season were often stripped of cones by red squirrels. In 2011, the two sites that nutcrackers started harvesting later in the season had over 75 percent of the cones removed by red squirrels before nutcrackers started intensively harvesting seeds in those stands. Thus, stands where nutcrackers start intensive harvesting earlier are more likely to have a greater proportion of the seed source harvested and cached by nutcrackers, while sites where nutcrackers start intensive harvesting later are likely to have more cones removed by red squirrels and fewer seeds cached by nutcrackers.

This study revealed that red squirrels removed a greater proportion of cones more quickly at sites where there was greater whitebark pine mortality and a higher percentage of crown kill on the live trees. This result is consistent with findings from earlier studies in the Bitterrott Mountains Ecosystem (McKinney and Tomback 2007) and the Northern Divide Ecosystem (McKinney and Fiedler 2010), which suggest that red squirrel populations may not decline as whitebark pine abundance and cone density declines. Though red squirrels may prefer the large, high-calorie whitebark pine seeds (Smith 1970, Hutchins and Lanner1982), other conifers in the mixed-conifer forests where red squirrel densities are greatest (Mattson and Reinhart 1997) provide a more dependable supply of food. Thus, red squirrels may not rely on whitebark pine, but use it opportunistically when cones are available. As whitebark pine declines, red squirrels can deplete the available cone source very rapidly.

My research supports the implication of McKinney and his colleagues (2009) that the probability of seed dispersal drops as whitebark pine declines. There are two reasons for this: (1) nutcrackers started intensively harvesting seeds earlier in stands where whitebark pine was more dominant and spent more time in areas where whitebark pine trees were more productive; and (2) red squirrels removed a larger proportion of the cones in the stands where nutcrackers started intensively harvesting seeds later. The forest stands that are most vulnerable to having few cones harvested by Clark's Nutcracker are the ones with high whitebark pine mortality and low relative dominance of whitebark pine. Even stands where whitebark pine is more prominent have the potential for red squirrels to remove most cones before nutcrackers begin intensively harvesting seeds. In 2011, one site, Scenic Point, which had the highest relative dominance of whitebark pine and as well as the greatest whitebark pine mortality, experienced 100 percent cone removal by red squirrels before nutcrackers started intensively harvesting seeds. The problem posed by red squirrels is substantial and will likely be a major threat to natural regeneration as whitebark pine continues to decline.

Restoration efforts that utilize natural regeneration should focus on maintaining stands where Clark's Nutcrackers can efficiently harvest seeds from a high proportion of the total cone source. In areas of decline, this can be achieved by halting the loss of whitebark pine and limiting red squirrel access to whitebark pine cones. Steps to limit mountain pine beetle attacks, such as the attachment of verbenone patches, should focus on healthy cone-producing trees, particularly trees planted as part of the restoration process or in the stands where whitebark pine is more prominent. In areas with high whitebark pine mortality, seedling-planting efforts may be needed to supplement the declining cone source. While the effects will not be immediate, this will help ensure that nutcrackers will have future access to whitebark pine seeds, once the trees begin producing cones. In addition, there may be a need to manage squirrel populations. To limit red squirrel access to whitebark pine cones, selective thinning of other late-successional tree species and controlled burns that mimic historically suppressed natural processes should be carried out in stands experiencing advanced succession and high whitebark pine mortality (Keane and Arno 2001, Keane and Parsons 2010). An alternative to squirrel population management is to manually collect the seeds from whitebark pine cones in stands that experience high pre-dispersal seed predation by red squirrels, particularly from trees that show signs of resistance to blister rust, then grow and plant the seedlings (Hoff et al. 2001). Although these steps do not directly support the natural regeneration process, they may help increase the incidence of blister rust resistance, and maintain whitebark pine genetic diversity (Dekker-Robertson and Bruederle 2001).

Literature Cited

Arno, S. F. 2001. Community types and natural disturbance processes, p. 74–88. *In* D. F. Tomback, S. F. Arno, and R. E. Keane [eds.], Whitebark pine communities: ecology and restoration. Island Press, Washington, DC.

Arno, S. F., and R. J. Hoff. 1990. *Pinus albicaulis* Engelm. Whitebark pine, p. 268–279. *In* R. M. Burns and B. H. Honkala [eds.], Silvics of North America. USDA Forest Service, Agriculture Handbook 654.

Arno, S. F., and T. Weaver. 1990. Whitebark pine community types and their patterns on the landscape, p. 97–105. *In* W. C. Schmidt and K. J. McDonald [eds.], Proceedings of the symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource, March 29–31, 1989, Bozeman, Montana. USDA Forest Service General Technical Report INT-GTR-270.

Crone, E. E., E. J. B. McIntire, and J. Brodie. 2011. What defines mast seeding? Spatio-temporal patterns of cone production by whitebark pine. Journal of Ecology 99:438–444.

Dekker-Robertson, D., and L. P. Bruederle. 2001. Management implications of genetic structure, p. 310–324. *In* D. F. Tomback, S. F. Arno, and R. E. Keane [eds.], Whitebark pine communities: ecology and restoration. Island Press, Washington, DC.

Dimmick, C. R. 1993. Life history and the development of cache-recovery behaviors in Clark's Nutcracker. Ph.D. dissertation, Northern Arizona University, Flagstaff, AZ.

Farnes, P. E. 1990. SNOTEL and snow course data describing the hydrology of whitebark pine ecosystems, p. 302–304. *In* W. C. Schmidt and K. J. McDonald [eds.], Proceedings of the symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource, March 29–31, 1989, Bozeman, Montana. USDA Forest Service General Technical Report INT-GTR-270.

Hoff, R. J., D. E. Ferguson, G. I. McDonald, and R. E. Keane. 2001. Strategies for managing whitebark pine in the presence of white pine blister rust, p. 346–366. *In* D.F. Tomback, S.F. Arno, and R.E. Keane [eds.], Whitebark pine communities: ecology and restoration. Island Press, Washington, DC.

Hutchins, H. E., and R. M. Lanner. 1982. The central role of Clark's Nutcracker in the dispersal and establishment of whitebark pine. Oecologia 55:192–201.

Keane, R. E., and S. F. Arno. 2001. Restoration Concepts and Techniques, p. 367–400. *In* D. F. Tomback, S. F. Arno, and R. E. Keane [eds.], Whitebark pine communities: ecology and restoration. Island Press, Washington, DC.

Keane, R. E., and R. A. Parsons. 2010. Restoring whitebark pine forests of the northern Rocky Mountains, USA. Ecological Restoration 28:56–70.

Kegley, S., and K. Gibson. 2011. The use of verbenone to protect whitebark pine from mountain pine beetle, p. 96. *In* R. E. Keane, D. F. Tomback, M. P. Murray, and C. M. Smith [eds.], Proceedings of the high five symposium: the future of high-elevation, five-needle white pines in Western North America, June 28–30, 2010, Missoula, Montana. USDA Forest Service RMRS-P-63.

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

Kendall, K. C., and R. E. Keane. 2001. Whitebark pine decline: infection, mortality, and population trends, p. 221–242. *In* D. F. Tomback, S. F. Arno, and R. E. Keane [eds.], Whitebark pine communities: ecology and restoration. Island Press, Washington, DC.

Kendall, K., D. Schirokauer, E. Shanahan, R. Watt, D. Reinhart, R. Renkin, S. Cain, and G. Green. 1996. Whitebark pine health in northern Rockies national park ecosystems: A preliminary report. Nutcrackers Notes 7:16.

Lanner, R. M. 1982. Adapations of whitebark pine for seed dispersal by Clark's Nutcracker. Canadian Journal of Forest Research 12:391–402.

Lorenz, T. J., and K. A. Sullivan. 2009. Seasonal differences in space use by Clark's Nutcrackers in the Cascade Range. Condor 111:326–340.

Lorenz, T. J., K. A. Sullivan, A. V. Bakian, and C. A. Aubry. 2011. Cache-site selection in Clark's Nutcracker (*Nucifraga columbiana*). Auk 128:237–247.

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.

McKinney, S. T., and C. E. Fiedler. 2010. Tree squirrel habitat selection and predispersal seed predation in a declining subalpine conifer. Oecologia 162:697–707.

McKinney, S. T., C. E. Fiedler, and D. F. Tomback. 2009. Invasive pathogen threatens bird-pine mutualism: implications for sustaining a high-elevation ecosystem. Ecological Applications 19:597–607.

McKinney, S. T., and D. F. Tomback. 2007. The influence of white pine blister rust on seed dispersal in whitebark pine. Canadian Journal of Forest Research 37:1044–1057.

Microsoft Corporation. 2001. Microsoft Office Excel 2001. Microsoft Corporation, Redmond, WA.

R Development Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Siepielski, A. M. and C. W. Benkman. 2007. Selection by a predispersal seed predator constrains the evolution of avian seed dispersal in pines. Functional Ecology 21:611–618.

Smith, C. C. 1970. The coevolution of *Tamiasciurus* and conifers. Ecological Monographs 40: 349–371.

Smith, C. C. 1981. The indivisible niche of *Tamiasciurus*: an example of non-partitioning of resources. Ecological Monographs. 51:343–363.

Tomback. D. F. 1978. Foraging strategies of Clark's Nutcracker. Living Bird 16:123–161.

Tomback, D. F. 1982. Dispersal of whitebark pine seeds by Clark's Nutcracker: a mutualism hypothesis. Journal of Animal Ecology 51:451–467.

Tomback, D. F. 1998. Clark's Nutcracker (*Nucifraga columbiana*). *In* A. Poole and F. Gill [eds.], The birds of North America, no. 331. Birds of North America, Inc., Philadelphia.

Tomback, D. F., S. F. Arno, and R. E. Keane. 2001. The compelling case for management intervention, p. 3–25. *In* D. F. Tomback, S. F. Arno, and R. E. Keane [eds.], Whitebark pine communities: ecology and restoration. Island Press, Washington, DC.

Tomback, D. F., R. E. Keane, W. W. McCaughey, and C. Smith. 2005. Methods for surveying and monitoring whitebark pine for blister rust infection and damage. Whitebark Pine Ecosystem Foundation, Missoula, Montana.

Tomback, D. F., and K. C. Kendall. 2001. Biodiversity losses: The downward spiral, p. 243–262. *In* D. F. Tomback, S. F. Arno, and R. E. Keane [eds.], Whitebark pine communities: ecology and restoration. Island Press, Washington, DC.

Vander Wall, S. B. 1988. Foraging of Clark's Nutcrackers on rapidly changing pine seed resources. Condor 90:621–631.

Weaver, T., and F. Forcella. 1986. Cone production in *Pinus albicaulis* forests, p. 68–76. *In* R. C. Shearer, [ed.], Proceedings of the symposium on conifer tree seed in the Inland Mountain West. August 5–6, 1985, Missoula, Montana. USDA Forest Service, General Technical Report INT-GTR-203.

Chapter 3

Comparison of direct and indirect methods for monitoring small populations of Clark's Nutcracker

Abstract

Clark's Nutcracker (*Nucifraga columbiana*) is the primary seed disperser for whitebark pine (*Pinus albicaulis*), which is in decline throughout the western United States and Canada. Consequently, local population declines in Clark's Nutcracker could hinder the natural regeneration process and recovery of whitebark pine populations. Researchers and resource managers are in need of a low-cost method that can reliably detect Clark's Nutcracker occurrence in whitebark pine stands during seed harvest season. Direct methods for monitoring nutcrackers include variations on breeding bird surveys and analyses of incidental sightings. In addition, nutcracker occurrence can be indirectly monitored by documenting the presence of seed harvesting scars on whitebark pine cones. I compared these monitoring methods at 11 sites in Glacier National Park, Montana. To determine the effectiveness of timed surveys, I recorded nutcracker detections and calculated average time to detection and detection frequency. Using incidental sighting records I compared differences in nutcracker detection and whitebark pine factors between sites with perceived high nutcracker occurrence (hotspots) and low nutcracker occurrence (coldspots). I also completed cone surveys at each site and searched for whitebark pine cones with nutcracker seed harvesting scars. It took an average of 42.7 (± 45.7) minutes to detect a nutcracker and overall detection frequency during the seed harvest season was 0.5 detections per hour. There were no differences between hotspots and coldspots in any of the factors analyzed, including average time to detection and detection frequency. Whitebark pine seed harvesting scars were observed at every survey site, even though one site had no nutcracker detections. Neither timed surveys nor incidental sighting records proved to be a reliable method of detecting nutcracker occurrence. Cone surveys, if they are planned to account for variations in nutcracker seed harvesting patterns, can reliably and economically detect nutcracker occurrence during the seed harvest season.

Introduction

Clark's Nutcracker (*Nucifraga columbiana*), a bird of the Corvidae family that occurs in mountainous regions of western North America, is an important seed disperser for multiple pine species, including whitebark pine (*Pinus albicaulis*) (Hutchins and Lanner 1982, Tomback 1982). In late summer and fall, nutcrackers harvest whitebark pine seeds and store them in thousands of small caches, which they retrieve in winter and spring, when other sources of food are scarce (Tomback 1982, 1998). Nutcrackers cache an excess of seeds and those not retrieved may germinate if conditions are suitable (Vander Wall and Balda 1977, Tomback 1982, Vander Wall 1988). Whitebark pine has evolved adaptations that facilitate seed dispersal by Clark's Nutcracker (Lanner 1982) and depends on this bird for future propagation. Clark's Nutcracker is the only species believed to be an effective seed disperser of whitebark pine (Hutchins and Lanner 1982).

Whitebark pine is in decline throughout its range in western North America's mountain forests. This decline is due to a variety of natural and human-caused threats, including forest succession due to fire suppression, massive outbreaks of the native mountain pine beetle

(*Dendroctonus ponderosae*), and infection by the exotic fungal pathogen white pine blister rust (*Cronartium ribicola*) (Tomback et al. 2001). Whitebark pine is a keystone species and its loss would affect snowmelt patterns, erosion, forest succession, and biodiversity in subalpine communities (Tomback et al. 2001). Restoration efforts are in progress, and resource managers are seeking to maintain the natural regeneration process, which is necessary for the long-term survival of whitebark pine (Hoff et al. 2001). However, there is concern that the decline in whitebark pine will lead to a subsequent declines in local Clark's Nutcracker populations, thus hindering seed dispersal (Tomback and Kendall 2001, McKinney et al. 2009). Efforts to monitor Clark's Nutcracker are underway in a variety of locations using several methodologies (e.g. McKinney et al. 2009, Barringer 2010, Lorenz and Sullivan 2010, Schaming 2011, Scott et al. 2011, this study).

There is no specific monitoring method available for Clark's Nutcracker. Researchers typically monitor nutcracker populations using breeding bird survey methods, including point counts and line transects (collectively referred to as "timed surveys" hereafter). However, these types of surveys, which are designed for territorial breeding songbirds, pose problems when surveying nutcrackers (Lorenz and Sullivan 2010). Nutcracker monitoring usually occurs during the seed harvest season, when nutcrackers are not breeding, and nutcrackers are not territorial (Tomback 1998). In addition, nutcrackers are highly mobile, particularly during seed harvest season when they have been observed transporting seeds as far as 32.6 km to cache sites (Lorenz et al. 2011). Finally, while nutcrackers are easy to locate when harvesting and caching seeds in groups, individual birds are often inconspicuous: in a study on the efficacy of traditional survey methods in Washington State, radio-tagged birds known to be in the area were never detected during thirty-minute timed surveys (Lorenz and Sullivan 2010). Researchers have adapted timed survey techniques to account for the unpredictability in nutcracker behavior by extending the length of time at point counts (Siepielski and Benkman 2007, Barringer 2010) or walking transects twice per visit (Scott et al. 2011). McKinney and colleagues (2009) extended both the area under question and the length of time of the survey: they recorded all nutcracker observations inside a 1-ha block over the course of an hour. The effectiveness of these adapted methods remains untested.

Resource managers often do not have the means to monitor nutcrackers using timed surveys. Nutcracker habitat, subalpine forest, is often accessible only on foot, and the methods currently in use are very time-intensive and require highly skilled observers. There is a need for a monitoring technique for Clark's Nutcracker that is low in cost and can be carried out in conjunction with other field data collection by agency employees or by citizen scientists and volunteers. Keeping track of incidental Clark's Nutcracker sightings may be a low-cost monitoring method, as the agency only needs to alert staff and volunteers to report nutcracker sightings and then record sightings in a database. Indirect monitoring may also be an economical approach to collecting information on nutcracker occurrence in whitebark pine stands (Bibby et al. 1992, MacKenzie et al. 2002). The highly visible seed harvesting scars left by nutcrackers on whitebark pine cones provide an opportunity for indirect monitoring (Lorenz and Sullivan 2010).

In this study, I evaluated the efficacy of using direct monitoring (timed surveys and incidental sighting records) and indirect monitoring (whitebark pine cone surveys) for documenting Clark's Nutcrackers occurrence in whitebark pine stands during seed harvest season. To do this, I examined the incidence of nutcracker detections, patterns in apparent nutcracker occurrence, and presence or absence of nutcracker seed harvesting scars on whitebark pine cones. A reliable method should consistently detect nutcrackers at every monitored site they use; otherwise characteristics of sites that falsely appear unused may be misinterpreted as unfavorable to nutcrackers.

Methods

*Study sites***.** This study was conducted in Glacier National Park, Montana (48.2–48.9˚N, 113.2–114.1˚W) in July – September 2010 and 2011. I identified study sites by examining historical sighting records with ArcGIS version 9.3 (ESRI, Inc., Redlands, CA). Using a projected vegetation map (Hop et al. 2007) and a map of the trail system, I located 100-ha zones where whitebark pine forest occurred within 400 meters of a trail (hereafter whitebark pine zone). I examined nutcracker sightings using NPS R-10 records dating from 1961 to 2009, Glacier National Park's High Country Citizen Science reports from 2008 and 2009, and personal sighting records from 2009. Whitebark pine zones that contained at least five Clark's Nutcracker sightings within a ten-year period were deemed "hotspots." Zones that contained one or zero Clark's Nutcracker sightings were deemed "coldspots." I excluded sites that took longer than a day to visit as well as those where stands containing whitebark pine were inaccessible by foot. I identified eleven study sites: six hotspots (with 11, 9, 6, 10, 27, and 5 sightings in whitebark pine zone) and five coldspots (with 0, 0, 1, 1, and 0 sightings in whitebark pine zones; Fig. 3-1).

Field study. I collected data at the study sites from mid-July through September 2010 and 2011. During each visit I actively searched for Clark's Nutcracker. I began my search upon arrival to a study site. A field assistant and I actively scanned the sky and listened for Clark's Nutcracker vocalizations while collecting forest composition and whitebark pine cone data (see below). I recorded all detections, either seen or heard, and took note of the time, number of birds, location, and behavioral observations. I calculated time to detection for the first detection at each site. I also calculated the proportion of visits with nutcracker sightings as well as detection frequency, which is the total number of sightings divided by time (hours) spent on site. For analyses, I used detection data from the harvest period, 15 August to 30 September. Each site was visited at least once per year during that period.

Each study site was composed of one to three adjacent 1-ha blocks within a contiguous forest stand, depending on the size of the stand and whitebark pine tree density. Each 1-ha block had two randomly placed 10 x 50 meter belt transects, which were at least 20 meters apart. For each transect, an assistant and I measured the diameter at breast height (DBH; 1.4 m above the ground) of every whitebark pine tree with a diameter greater than or equal to 7.0 cm. I used DBH measurements to estimate live basal area of whitebark pine in each stand.

At each study site, I counted cones on randomly selected whitebark pine cone trees. Cone trees were at least 20 meters apart and occurred within the established 1-ha block. In 2010 I counted whitebark pine cones at ten sites, each containing a minimum of 2 and a maximum of 7 cone trees (mean = 4.6), depending on the abundance of cone-producing whitebark pine trees. In 2011, I revisited four sites and added a fifth site that did not produce cones in 2010. For the new site, I randomly selected 5 cone trees. For the four study sites in that were used in the 2010 study, I used the same cone trees that I selected in 2010 and randomly selected 4 to 5 additional cone trees. Cone tree locations were recorded in a global positioning system (GPS) and tree characteristics were noted so cone trees were easy to relocate.

I conducted two cone counts in 2010 and weekly cone counts in 2011. The first cone count each year was used to estimate average cone production at the stand level. I conducted subsequent cone counts to document evidence of cone use by Clark's Nutcracker. Using binoculars, an assistant and I counted all the visible cones on each of the cone trees from multiple vantage points, and verified the count together to avoid over- or under-counting. We searched for and recorded the number of cones that showed evidence of seed harvesting by nutcrackers (Fig. 3-2). Cones that have been harvested by nutcrackers remain attached to the tree branch and, because nutcrackers drill on cones to remove scales and expose the seeds, appear "shredded" (Tomback 1978; Fig 3-2b). If at least one whitebark pine cone had visible nutcracker seed harvesting scars, that site was considered used by Clark's Nutcracker.

Statistical analysis. I used Welch's t-test to determine if there were differences between hotspots and coldspots in the following variables: whitebark pine live basal area, cones per tree (2010 only), time to first detection (2010 and 2011 combined), and detection frequency (2010 and 2011 combined). Analyses were completed using R statistical software (R Development Core Team 2011). I considered statistical results significant at $\alpha = 0.05$. Means are reported with standard deviation following in parentheses.

Results

Clark's Nutcrackers were detected during 71% of visits in the cone harvest season and at 91% of the study sites. When nutcrackers were detected, it took an average of 42.7 (± 45.7) minutes to detect at least one nutcracker ($n = 32$), with a range of 0.0 to 129.0 minutes. Overall detection frequency was 0.5 detections per hour. Because of the time it took to detect nutcrackers, the variability of time to detection, and low detection frequency, I conclude that timed surveys are not a cost effective method to obtain accurate information on Clark's Nutcracker occurrence in areas with relatively low populations of nutcrackers.

Nutcracker detection frequency ($t_6 = 1.06$, $P = 0.3$), and average time to detection ($t_{29} = 1.39$, $P = 0.2$) did not differ significantly between hotspots and coldspots (Table 3-1). Average whitebark pine live basal area did not differ significantly between hotspots and coldspots ($t_5 = 0.47$, $P = 0.7$; Table 3-1). Cone production in 2010 ($t_5 = 0.85$, $P = 0.4$) and in 2011 ($t_1 = 0.85$, $P = 0.6$) were not significantly different between hotspots and coldspots (Table 3-1). Nutcrackers were never detected at one site, Highline, even though seed harvesting scars were apparent. Incidental sighting records do not provide a reliable documentation of nutcracker activity during the seed harvest season, because there is seemingly no difference between hotspots and coldspots despite the lack of incidental sightings in coldspots.

In both years of the study I identified nutcracker seed harvesting scars on whitebark pine cones at every survey site with available cones (Table 3-2). Seed harvesting scars became more evident late August through September (Fig. 3-3a) and weekly surveys revealed differences in the starting date of intensive seed harvesting by nutcrackers (Fig. 3-3b).

Discussion

Direct observation methods. I found that the use of timed surveys (typically 1-hour surveys, one to three times a year per site; Siepielski and Benkman 2007, McKinney et al. 2009, Barringer 2010) is not likely to produce cost effective, reliable data on the presence or absence of nutcrackers in areas where nutcrackers are not abundant. Although the average time to detection, 42.7 (± 45.7) minutes, fell within the 1-hour survey time, nearly a quarter of the sightings occurred more than 90 minutes after arrival to a site. Additionally, 29% of visits to sites with nutcracker seed harvesting scars on whitebark pine cones had no nutcracker detections, even though I spent an average of 148.9 (± 65.1) minutes at those sites. Nutcrackers favor stands that provide them with the greatest energy gain (Tomback and Kramer 1980, Vander Wall 1988, Chapter 2). In an area like Glacier National Park, where nutcrackers are relatively scarce (McKinney et al. 2009), less favorable stands may go for days without any visits from nutcrackers and may not be visited until later in the harvest season (Chapter 2). Depending on when timed surveys occur, nutcrackers may not be detected at sites that they actually use.

Although incidental sighting records are low-cost and require minimal training, they do not accurately reflect Clark's Nutcracker use of whitebark pine stands in Glacier National Park. Nutcracker occurrence in perceived coldspots was no different than nutcracker occurrence in perceived hotspots, and nutcracker seed harvesting scars were present at every site regardless of hotspot or coldspot designation. Sighting records appeared to reflect trail usage by park volunteers and employees rather than nutcracker occurrence. Citizen science sightings often came from volunteers who were traveling to or at mountain goat survey sites, which were visited repeatedly. Other sighting records came from park employees or visitors who were hiking popular trails. Clark's Nutcracker use of less visited whitebark pine stands was probably underrepresented.

Indirect monitoring. For researchers or resource managers with limited funds and personnel, the best option may be to indirectly monitor nutcrackers by surveying harvested whitebark pine cones. This method will give accurate results for relatively low effort. Nutcracker seed harvesting scars are highly visible and whitebark pine cones often remain attached to the tree after nutcrackers harvest seeds (Tomback 1978, Siepielski and Benkman 2007). Once in an area where whitebark pine occurs, locating a cone-producing tree and inspecting cones for seed harvest scars would take very little time. Cone surveys can be incorporated into standard data collection protocols by field crews or citizen scientists conducting other work in or near whitebark pine stands. Nutcracker non-use of whitebark pine stands can be identified when whitebark pine cones remain unopened through the seed harvest season. One complication with this technique is that at a few sites red squirrels remove all cones before seed harvesting scars are detected. In this situation, the presence of nutcrackers cannot be assessed and absence cannot be confirmed (MacKenzie 2005).

Methods can range from low-effort, searching an area once until a cone with seed harvesting scars is identified, to high-effort, counting cones of multiple cone trees at a site on several occasions. If the goal is to simply detect nutcracker occurrence, the easiest method of doing so would be for a field crew that is already doing work in or around a whitebark pine zone to look for seed harvesting scars on whitebark pine cones. Cone surveys will be most effective if they are planned to account for variation in annual cone production, nutcracker seed harvest patterns, and cone removal by red squirrels. Whitebark pine cone production varies annually, and some stands do not produce any cones in some years (Crone et al. 2011, Chapter 2). Thus, higher-effort methods will give more accurate results. Ideally, study sites should be visited before cones are fully mature and begin to be harvested by nutcrackers and red squirrels, around mid-July, to identify sites with cone trees and estimate cone production. Nutcrackers may forage on trees with fewer cones later in the seed harvest season (Christensen et al. 1991). To increase the likelihood of detecting a cone with seed harvesting scars on the first visit, at least one tree with greater than average cone production should be counted. Nutcrackers appear to begin harvesting seeds earlier in stands where whitebark pine is relatively more dominant (Chapter 2). Stands with lower relative dominance of whitebark pine should be visited later in the seed harvest season. Red squirrels have the potential to completely deplete the whitebark pine cone source, and they deplete the cone source more rapidly in stands with higher whitebark pine mortality (Chapter 2). Stands with high whitebark pine mortality therefore should be visited earlier in the seed harvest season to determine if nutcrackers are harvesting seeds before cone removal by red squirrels.

The advantage of using cone surveys, apart from being economically viable, is that the scars provide absolute proof that nutcrackers are harvesting seeds and that there is the potential for natural regeneration of whitebark pine from that stand. For land managers working on whitebark pine regeneration, this is the critical information they need about Clark's Nutcracker populations in their area.

Literature Cited

Barringer, L. E. 2010. Determining the relationship between whitebark pine stand-level health and seed dispersal by Clark's Nutcracker. M.S. thesis, University of Colorado, Denver, CO.

Bibby, C. J., N. D. Burgess, and D. A. Hill. 1992. Birds census techniques. Academic Press, Limited, London.

Christensen, K. M., T. G. Whitham, and R. P. Balda. 1991. Discrimination among pinyon pine trees by Clark's Nutcracker: effects of cone crop size and cone characters. Oecologia 86:402–407.

Crone, E. E., E. J. B. McIntire, and J. Brodie. 2011. What defines mast seeding? Spatio-temporal patterns of cone production by whitebark pine. Journal of Ecology 99:438–444.

Hoff, R. J., D. E. Ferguson, G. I. McDonald, and R. E. Keane. 2001. Strategies for managing whitebark pine in the presence of white pine blister rust, p. 346–366. *In* D. F. Tomback, S. F. Arno, and R. E. Keane [eds.], Whitebark pine communities: ecology and restoration. Island Press, Washington, DC.

Hop, K., M. Reid, J. Dieck, S. Lubrinski, and S. Cooper. 2007. U.S. Geological Survey-National Park Service vegetation mapping program: Waterton-Glacier International Peace Park. U.S. Geological Survey, Upper Midwest Environmental Sciences Center, La Crosse, WI.

Hutchins, H. E., and R. M. Lanner. 1982. The central role of Clark's Nutcracker in the dispersal and establishment of whitebark pine. Oecologia 55:192–201.

Lanner, R. M. 1982. Adapations of whitebark pine for seed dispersal by Clark's Nutcracker. Canadian Journal of Forest Research 12:391–402.

Lorenz, T. J., and K. A. Sullivan. 2010. Comparison of survey methods for monitoring Clark's Nutcrackers and predicting dispersal of whitebark pine seeds. Journal of Field Ornithology 81:430–441.

Lorenz, T. J., K. A. Sullivan, A. V. Bakian, and C. A. Aubry. 2011. Cache-site selection in Clark's Nutcracker (*Nucifraga columbiana*). Auk 128:237–247.

MacKenzie, D. I. 2005. What are the issues with presence-absence data for wildlife managers? Journal of Wildlife Management 69:849–860.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droegie, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248–2255.

McKinney, S. T., C. E. Fiedler, and D. F. Tomback. 2009. Invasive pathogen threatens bird-pine mutualism: implications for sustaining a high-elevation ecosystem. Ecological Applications 19:597–607.

R Development Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Schaming, T. 2011. Clark's Nutcracker demography and habitat use in Bridger-Teton National Forest—preliminary analyses, p. 75. *In* R. E. Keane, D. F. Tomback, M. P. Murray, and C. M. Smith [eds.], Proceedings of the high five symposium: the future of high-elevation, five-needle white pines in Western North America, June 28–30, 2010, Missoula, Montana. USDA Forest Service RMRS-P-63.

Scott, J. D., D. F. Tomback, and M. B. Wunder. 2011. Determining Clark's Nutcracker use of whitebark pine communities in regard to stand health in Waterton-Glacier International Peace Park, p. 61–62. *In* R. E. Keane, D. F. Tomback, M. P. Murray, and C. M. Smith [eds.], Proceedings of the high five symposium: the future of high-elevation, five-needle white pines in Western North America, June 28–30, 2010, Missoula, Montana. USDA Forest Service RMRS-P-63.

Siepielski, A. M., and C. W. Benkman. 2007. Convergent patterns in the selection mosaic for two North American bird-dispersed pines. Ecological Monographs 77:203–220.

Tomback. D. F. 1978. Foraging strategies of Clark's Nutcracker. Living Bird 16:123–161.

Tomback, D. F. 1982. Dispersal of whitebark pine seeds by Clark's Nutcracker: A mutualism hypothesis. Journal of Animal Ecology 51:451–467.

Tomback, D. F. 1998. Clark's Nutcracker (*Nucifraga columbiana*). *In* A. Poole and F. Gill [eds.], The birds of North America, no. 331. Birds of North America, Inc., Philadelphia.

Tomback, D. F., S. F. Arno, and R. E. Keane. 2001. The compelling case for management intervention, p. 3–25. *In* D. F. Tomback, S. F. Arno, and R. E. Keane [eds.], Whitebark pine communities: ecology and restoration. Island Press, Washington, DC.

Tomback, D. F., and K. C. Kendall. 2001. Biodiversity losses: the downward spiral, p. 243–262. *In* D. F. Tomback, S. F. Arno, and R. E. Keane [eds.], Whitebark pine communities: ecology and restoration. Island Press, Washington, DC.

Tomback, D. F., and K. A. Kramer. 1980. Limber pine seed harvest by Clark's Nutcracker in the Sierra Nevada: timing and foraging behavior. Condor 82:467–468.

Vander Wall. S. B. 1988. Foraging of Clark's Nutcrackers on rapidly changing pine seed resources. Condor 90:621–631.

Vander Wall, S. B., and R. P. Balda. 1977. Coadaptations of the Clark's Nutcrackers and the pinyon pine for efficient seed harvest and dispersal. Ecological Monographs 47:89–111.

Chapter 4
Conclusion

The culmination of this study is that Clark's Nutcracker is a complex character in whitebark pine ecosystems. Across Glacier National Park it is difficult to predict nutcracker occurrence, given low detection frequencies and variable time to detection, even in whitebark pine stands during seed harvest season. Despite unpredictable nutcracker occurrence, the results of this study offer explanations for some of the inherent complexities of Clark's Nutcracker and whitebark pine ecosystems during seed harvest season.

By utilizing whitebark pine cone surveys, this study confirmed that nutcrackers harvest seeds from whitebark pine cones in stands with minimal whitebark pine live basal area and low cone density. This is particularly important in stands that have high mortality from blister rust because the trees nutcrackers are harvesting seeds from may have genetic resistance to blister rust. In addition, this study identified that nutcrackers do not begin intensively harvesting seeds at the same time at every site, but instead seem to have a preference for beginning intensive seed harvest in areas where whitebark pine is more dominant. Until now it was assumed that intensive harvest start time was more or less ubiquitous within an ecosystem. This preference is notable because the timing of intensive seed harvest affects the proportion of seeds harvested and cached by nutcrackers. Stands harvested later have a lower proportion of cones available because red squirrels, which prefer whitebark pine cones to those of other conifer species, have more time to deplete the cone source. These findings demonstrate the incredibly important role red squirrels play in reducing whitebark pine cone availability. This study also corroborated previous studies that suggest red squirrels are not affected by whitebark pine mortality and will be an increasing threat in whitebark pine ecosystems as the tree continues to decline.

This study supported conclusions from recent research that standard breeding bird survey methods are not suitable for monitoring Clark's Nutcracker and offers a novel method of monitoring cone use that can more accurately detect nutcracker use of whitebark pine stands. In addition, this study used cone-monitoring methods to investigate patterns of cone use by nutcrackers and red squirrels. As whitebark pine continues to decline, there is increasing need to understand how nutcrackers and other aspects of whitebark pine ecosystems influence seed dispersal. Acknowledging the inefficiency in standard breeding bird survey methods and utilizing indirect monitoring could bring researchers and resource managers a step closer to understanding the major factors affecting seed dispersal.

As a whole, this study, along with supporting previous research, offers new insights into whitebark pine ecology during the seed harvesting season and details new methods to efficiently and accurately monitor Clark's Nutcracker use of whitebark pine stands. To bring further understanding to various factors influencing seed dispersal during the seed-harvesting step, future research should focus more on red squirrels, which are demonstrably influential in whitebark pine ecosystems yet poorly understood in that setting. Studies should focus on determining local habitat preferences of red squirrels and landscape-level factors that may influence red squirrel occurrence in whitebark pine habitat. It is also important to continue studying Clark's Nutcracker and all aspects of its life history that affect the seed dispersal process. This includes but is not limited to nutcracker breeding, population dynamics (e.g. proportion of residents versus migrants and the role of each), habitat use and foraging habits during the non-harvest season, cache-site preference, and how each of these are affected by whitebark pine abundance, cone availability, and decline. Research in other whitebark pine ecosystems may benefit from carrying out studies similar to the ones presented here, particularly to evaluate the threshold model, determine whether there are differences among stands in intensive harvest start time, and quantify the effect of red squirrels on cone availability.

Tables and Figures

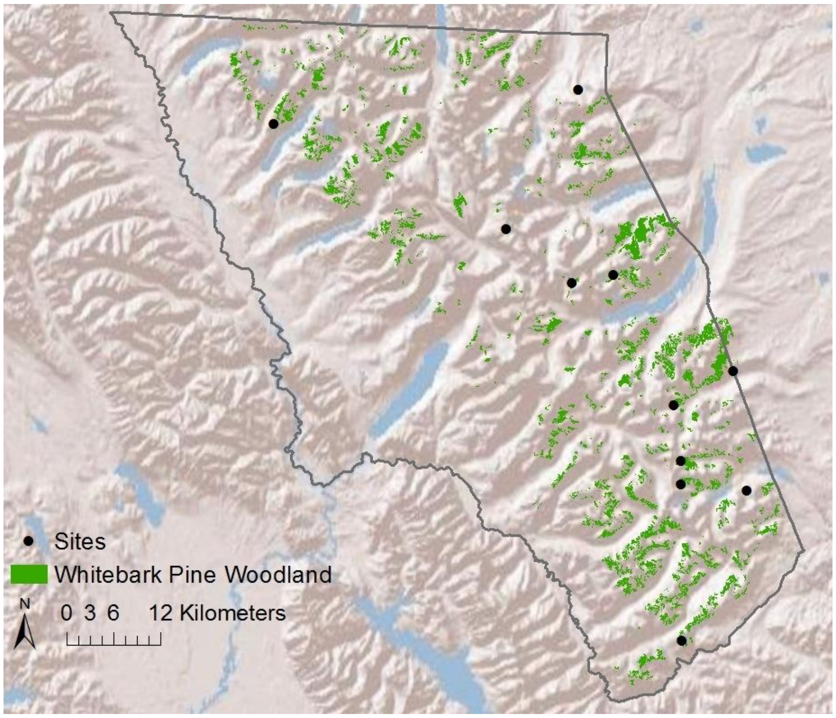
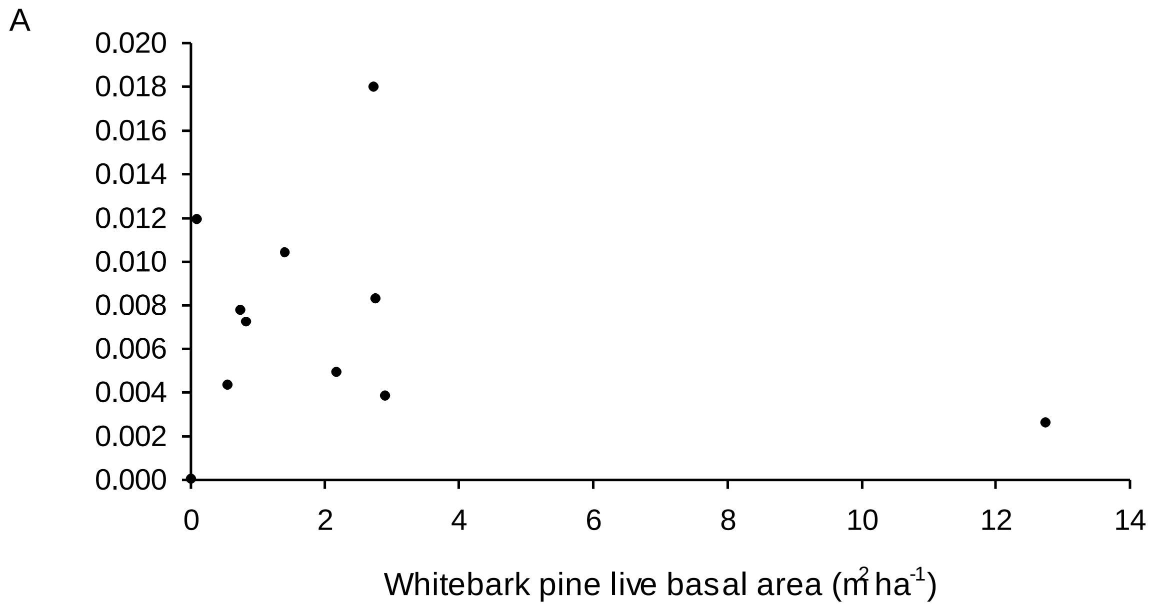


Figure 2-1. Glacier National Park, Montana, study site locations and whitebark pine forest.

Figure 2-2. Whitebark pine cone with Clark’s Nutcracker seed harvesting scars.

Table 2-1. Live basal area (m^2 ha^{-1}) of whitebark pine, 2010 and 2011 cone density (cones ha^{-1}), and Clark's Nutcracker sighting frequency (sightings min^{-1}) in August and September (2010 and 2011 combined) at11 sites in Glacier National Park.

Site	Whitebark pine live basal area (m^2 ha^{-1})	Cone density, 2010 (no. ha^{-1})	Cone density, 2011 (no. ha^{-1})	Sighting frequency (no. min^{-1})
Atlantic	2.7		2000	0.0179
Cutbank	0.8	50		0.0072
Dawson Pass	0.6	15		0.0043
Elk	0.7	648	444	0.0078
Highline	< 0.1	87		0.0000
Lee Ridge	0.1	10		0.0119
Numa	1.4	104	366	0.0104
Oldman	12.8	375		0.0026
Otokomi	2.2	70		0.0049
Preston	2.9	4186	777	0.0038
Scenic	2.8	88	440	0.0083
Mean (±SE)	2.5 (0.2)	563 (407)	605 (307)	0.0079 (0.0068)



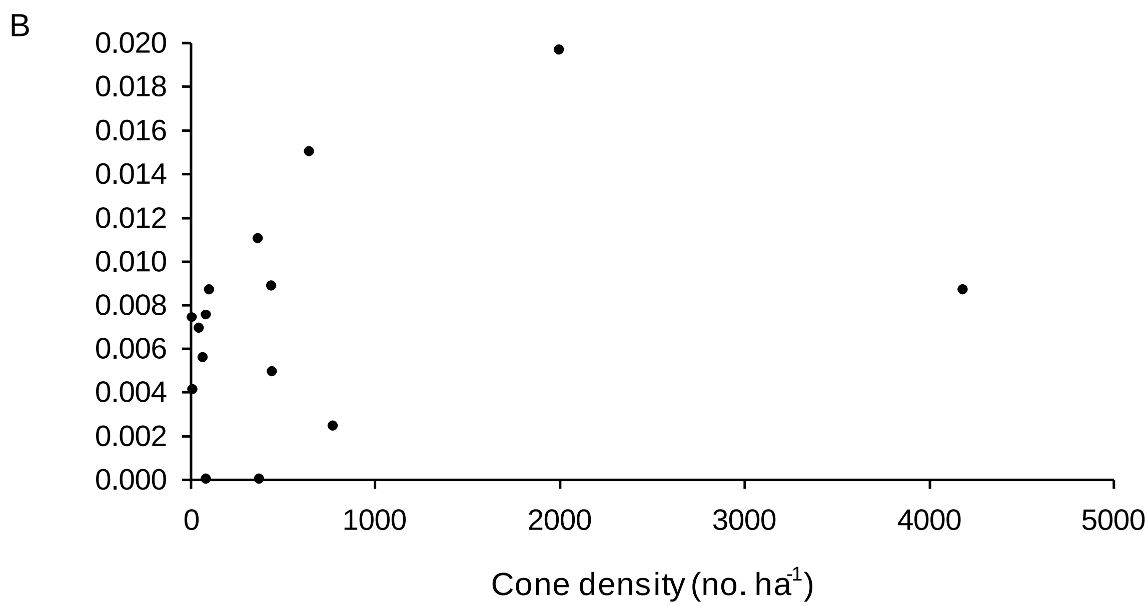


Figure 2-3. Scatter-plots of Clark's Nutcracker sighting frequency (number of sightings min^{-1}) in August and September and (A) whitebark pine live basal area (m^2 ha^{-1}) and (B) whitebark pine cone density (number of cones ha^{-1}). (A) Sighting frequency was calculated 2010 and 2011 combined (n = 11). (B) Comparison of sighting frequency and cone density for each site-year. Sighting frequency was calculated for 2010 and 2011 separately (n = 15).

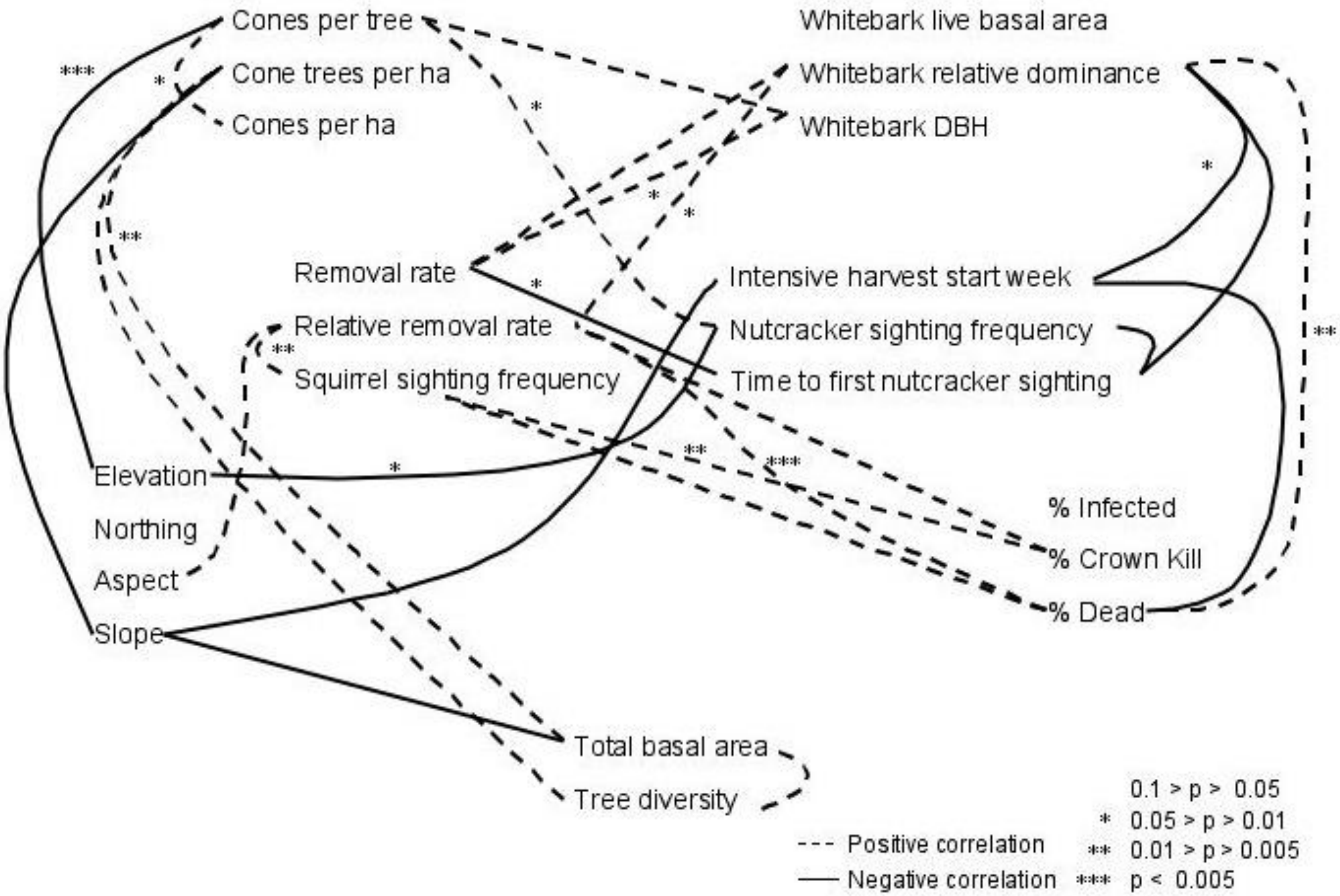


Figure 2-4. Bivariate correlations (Pearson's) among whitebark pine site characteristics and the responses of Clark's Nutcracker and red squirrel. Solid lines represent negative correlations and dashed lines represent positive correlations.

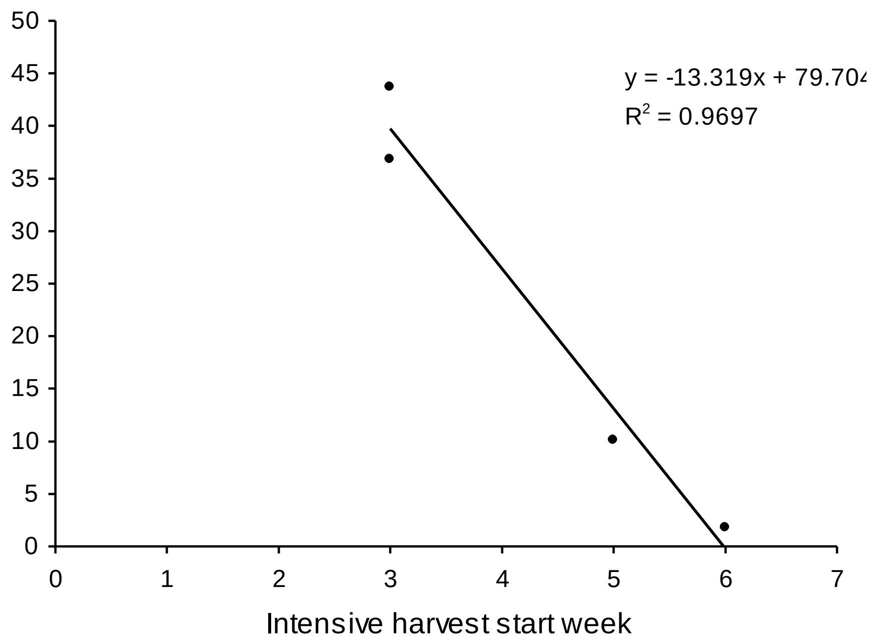


Figure 2-5. Simple linear regression analysis of the percentage of total cones with Clark's Nutcracker seed harvesting scars as a function of the week that Clark's Nutcrackers started intensively harvesting whitebark pine seeds for caches. Omits one site (Scenic) because all cones were removed before Clark's Nutcracker began intensively harvesting seeds.

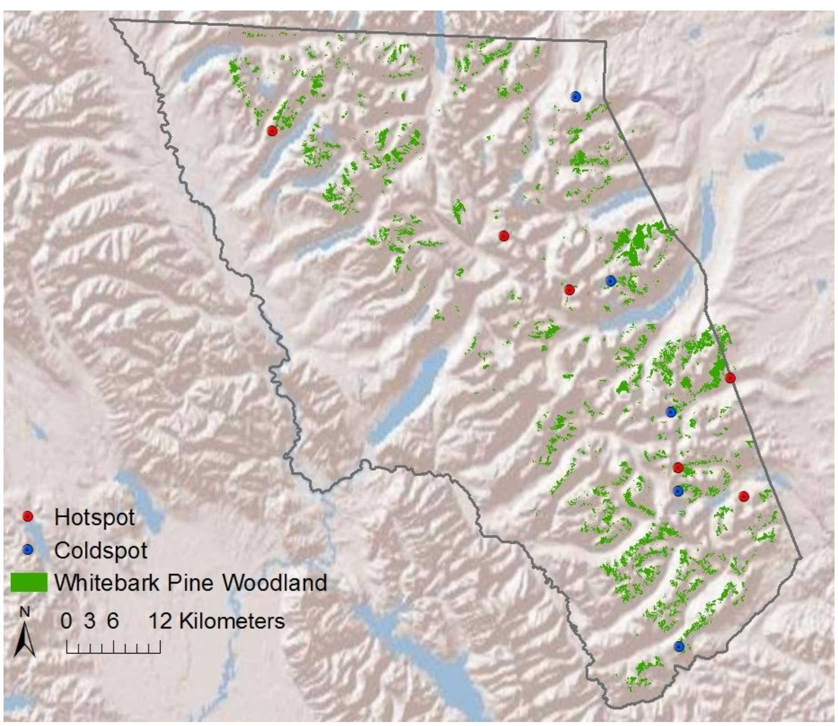


Figure. 3-1. Study sites and whitebark pine forest in Glacier National Park, Montana.

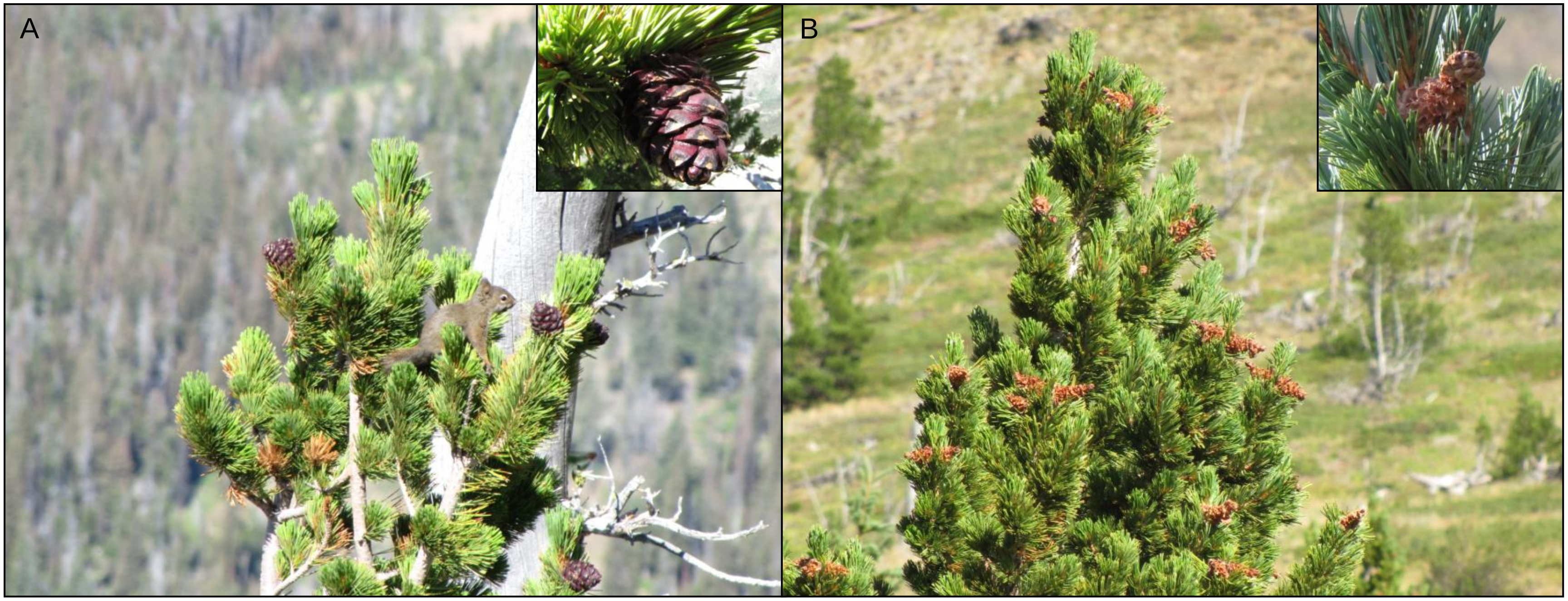


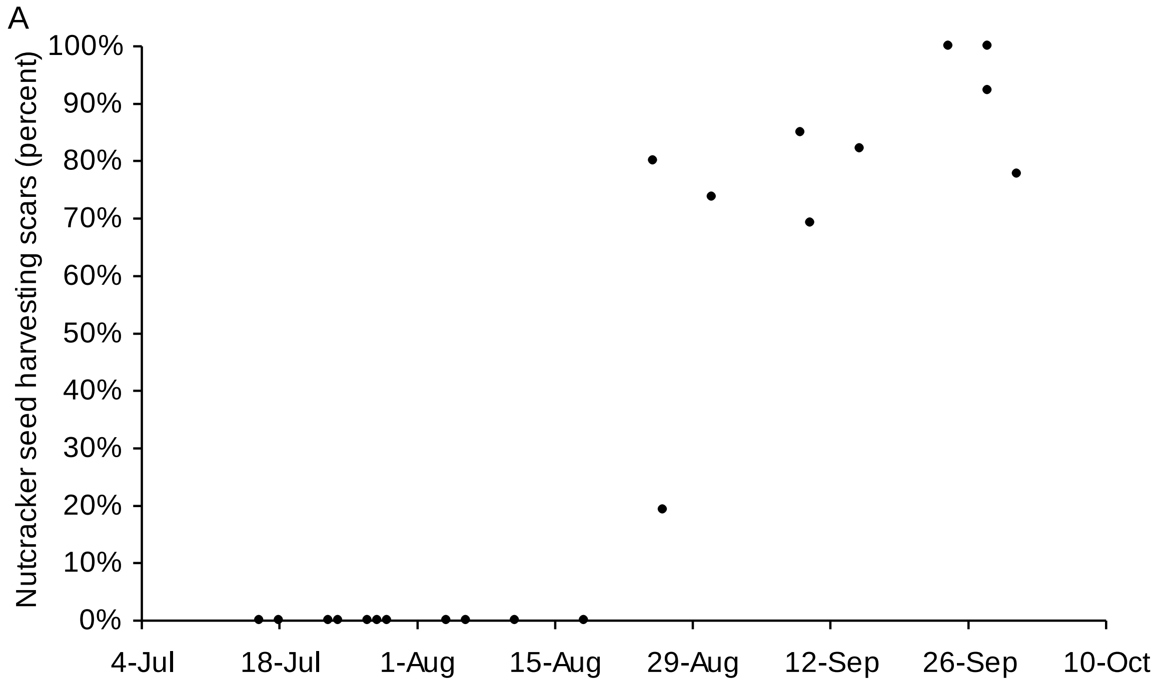
Figure 3-2. Whitebark pine cones (A) without and (B) with Clark's Nutcracker seed harvesting scars. Insets are close-up pictures of the cones.

Table 3-1. Hotspot and coldspot values for nutcracker detection and whitebark pine factors. Standard deviations are in parentheses following the value. There were no significant differences between hotspots and coldspots for any of the factors.

Type	N	Time to first detection (min)	Detection frequency (no. hr^{-1})	Whitebark pine live basal area (m^2 ha^{-1})	Cones per tree (2010)	Cones per tree (2011)
Hotspot	6	52.3 (47.5)	0.4 (0.3)	3.5 (4.7)	15.9 (21.9)	17.1 (5.5)
Coldspot	5	30.3 (41.6)	0.6 (0.4)	1.3 (1.1)	7.0 (8.5)	32.4 (24.9)

Table 3-2. Number of cone trees monitored and the year that nutcracker seed foraging scars where found on whitebark pine cones at each of the sites. Every site but Atlantic was monitored in 2010 and Numa, Preston, Scenic, Elk, and Atlantic were monitored in 2011.

Site	Cone trees 2010	Cone trees 2011	Nutcracker seed harvesting scars
Cutbank	2		2010
Highline	3		2010
Numa	5	10	2010, 2011
Oldman	5		2010
Preston	5	10	2010, 2011
Scenic	5	9	2010, 2011
Dawson Pass	7		2010
Elk	5	10	2010, 2011
Lee Ridge	4		2010
Otokomi	5		2010
Atlantic	0	5	2011



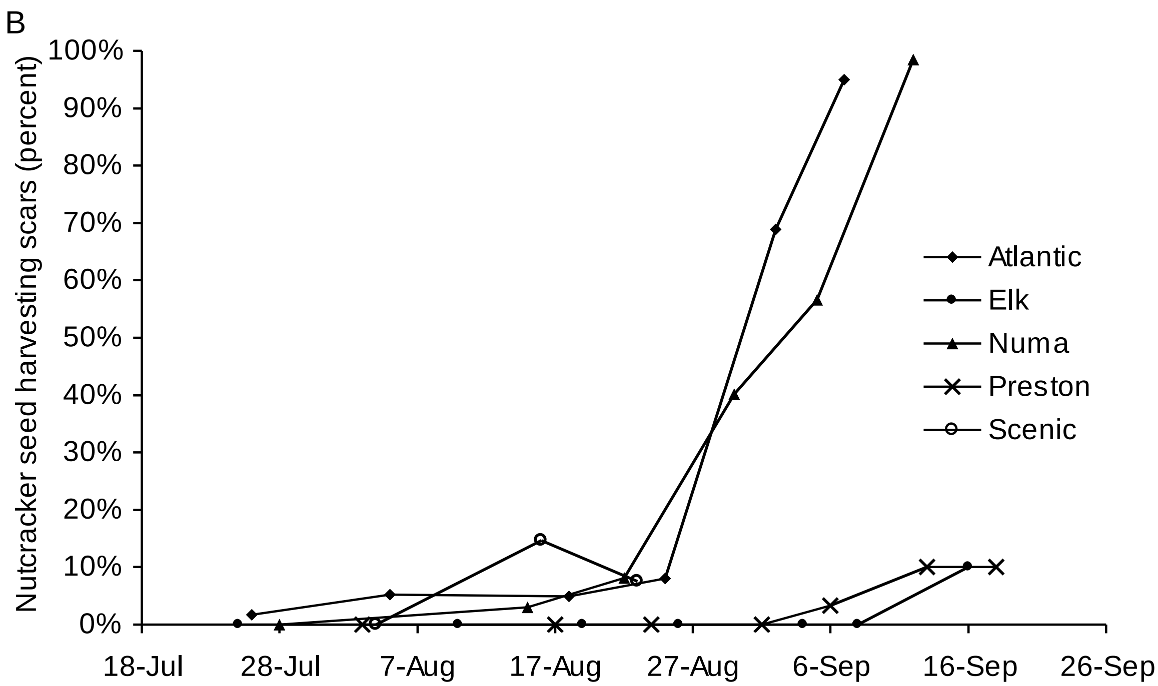


Figure 3-3. Percent of cones opened in (A) 2010 and (B) 2011 over the seed harvest season. (A) Based on percent of seed harvesting cones at each of two visits for eleven study sites (n = 22 visits). (B) Based on percent of seed harvesting cones during weekly cone counts at five study sites.