

## SEED PREDATION AND SELECTION EXERTED BY A SEED PREDATOR INFLUENCE SUBALPINE TREE DENSITIES

ADAM M. SIEPIELSKI<sup>1</sup> AND CRAIG W. BENKMAN

Department of Zoology and Physiology, Department 3166, University of Wyoming, Laramie, Wyoming 82071 USA

**Abstract.** Strongly interacting species often have pronounced direct and indirect effects on other species. Here we focus on the effects of pine squirrels (*Tamiasciurus* spp.), which are a dominant pre-dispersal seed predator of many conifers including limber pines (*Pinus flexilis*) and whitebark pines (*P. albicaulis*). Pine squirrels depress seed abundance by harvesting most limber and whitebark pine cones on their territories. Pine squirrels further reduce seed availability for Clark's Nutcrackers (*Nucifraga columbiana*), the primary seed disperser of these pines, because selection exerted by pine squirrels has reduced the number of seeds per cone and causes seeds to be less accessible. We predicted that, if fewer seeds were available for dispersal by nutcrackers, pine recruitment should be suppressed in areas with pine squirrels. In support of this prediction, stand densities were about two times greater in areas where pine squirrels are absent than in areas where they are present. Alternative explanations that we considered do not account for these differences; however, precipitation may limit stand densities in the absence of seed limitation by pine squirrels. In sum, pine squirrels apparently depress limber and whitebark pine stand densities, with the potential for ecosystem impacts because these pines are foundation species within Western subalpine ecosystems.

**Key words:** ecosystems; natural selection; *Nucifraga columbiana*; *Pinus albicaulis*; *Pinus flexilis*; plant density; plant recruitment; seed dispersal; seed predation; *Tamiasciurus*.

### INTRODUCTION

There has been considerable interest in the effects of certain influential species on community structure and ecosystem processes, including keystone species (Paine 1969) and ecosystem engineers (Jones et al. 1994). Beavers (*Castor canadensis*), for instance, are a classic example of an ecosystem engineer. By cutting trees and damming streams, beavers transform forested habitat into wetlands with subsequent effects on community structure and biodiversity (Jones et al. 1994). Most studies concerning such species have focused on the cascading effects of a particular species' ecology at the ecosystem level. However, in the case of keystone species or strongly interacting species the evolutionary effects of natural selection exerted by these species can be considerable and warrant consideration (Benkman et al. 2008). Yet, few studies have examined whether and how selection exerted by these species directly or indirectly alter community structure and ecosystem processes (Holt 1994, Bailey et al. 2004, Benkman and Siepielski 2004, Whitham et al. 2006, Benkman et al. 2008).

Manuscript received 11 January 2008; accepted 22 February 2008. Corresponding Editor: B. J. Danielson.

<sup>1</sup> Present address: Department of Biological Sciences, Dartmouth College, Hanover, New Hampshire 03755 USA. E-mail: Adam.M.Siepielski@Dartmouth.edu

One example of the cascading effects of selection on ecosystem processes comes from comparisons of the frequency of serotiny, the retention of seeds in cones for extended periods, in lodgepole pine (*Pinus contorta latifolia*; Benkman and Siepielski 2004). The main advantage of serotiny is the accumulation of a canopy seed bank to be released after a stand-replacing fire (Lamont et al. 1991). However, pre-dispersal seed predation by pine squirrels (*Tamiasciurus* spp.), the main predator of seeds in lodgepole pine cones, reduces the benefits of serotiny in pines by greatly diminishing the canopy seed bank and thereby favoring a reduction in the frequency of serotiny. The evolutionary consequences include a large reduction in the average frequency of serotiny in areas where pine squirrels occur compared to areas where they are absent (Benkman and Siepielski 2004). Variation in the frequency of serotiny is important because it influences the density of seedlings following stand-replacing fires and can therefore have major effects on plant and animal communities, and on biogeochemistry during succession (Tinker et al. 1994, Turner et al. 2003, Benkman et al. 2008). Thus, selection exerted by pine squirrels on a heritable life history trait in one species affects the entire ecosystem. We refer to such species as "keystone selective agents" (Benkman and Siepielski 2004). This terminology is meant to highlight the often-overlooked evolutionary conse-

quences of strongly interacting species by explicitly considering the effects of microevolutionary processes (i.e., natural selection) at the community and ecosystem level.

Pine squirrels are strongly interacting species in many other systems as well (e.g., Steele et al. 2005), and thus may act as keystone species and selective agents more widely via their ecological and evolutionary effects as seed predators. The repeated evolution of increased seed defenses in six species of conifers in areas with pine squirrels compared to areas without pine squirrels (Benkman 1999, Benkman et al. 2001, Parchman and Benkman 2002, Siepielski and Benkman 2007a, b; T. L. Parchman and C. W. Benkman, *unpublished data*) strongly implies that pine squirrels act consistently as an important seed predator and selective agent and may have widespread effects. For example, in both limber (*P. flexilis*) and whitebark pines (*P. albicaulis*), selection exerted by pine squirrels has led to an approximate 30% reduction in the number of seeds per cone compared to regions without pine squirrels (Benkman 1995, Siepielski and Benkman 2007a). Seed predation from pine squirrels might thus affect seed dispersal and recruitment in these conifers by directly (i.e., because of seed consumption) and indirectly (i.e., because of evolutionary responses by pines to selection) limiting seed abundance. Indeed, seed addition experiments demonstrate that many plant species are seed limited rather than site limited, with recruitment increasing in response to seed addition (Turnbull et al. 2000). This is particularly the case for large-seeded species that are often animal dispersed (Moles and Westoby 2002, Clark et al. 2007).

Clark's Nutcrackers (*Aves: Nucifraga columbiana*) are the main seed dispersal agent for limber and whitebark pines (Lanner 1996, Tomback 2001). Their interaction is an example of a keystone mutualism, because the formation of subalpine ecosystems dominated by these pines is largely dependent on the dispersal of seeds by nutcrackers (Lanner 1996, Tomback 2001). Thus, factors that affect the abundance and availability of seeds for dispersal by nutcrackers should impact these ecosystems.

The availability of seeds for dispersal by nutcrackers is partly determined by variation in cone structure. Throughout the Rocky Mountains and Sierra Nevada, selection exerted by pine squirrels on limber and whitebark pines has led to fewer seeds per cone and more massive cones that reduce nutcracker seed harvesting and seed dispersal efficiency (Benkman 1995, Siepielski and Benkman 2007a). Pine squirrels are also intense preemptive competitors because they begin removing seeds before nutcrackers, and can remove 80% or more of the seed crop (Benkman et al. 1984). Because pine squirrels bury closed cones not individual seeds (Smith 1970, Benkman et al. 1984) and

conditions in caches generally do not favor germination or seedling survival (Hutchins and Lanner 1982, Tomback 1982), pine squirrels are not considered seed dispersers. In the Great Basin, where pine squirrels have likely been absent for  $\geq 10\,000$  years (e.g., Grayson 1987, Heaton 1990), limber and whitebark pines have lost seed defenses against pine squirrels and have further evolved in response to selection by nutcrackers. Many of the traits under selection by pine squirrels (i.e., number of seeds per cone) are the same traits under selection by nutcrackers, but in opposing directions. Thus, the evolution of seed defenses against pine squirrels reduces the number of seeds produced and constrains the evolution of cone traits that facilitate seed dispersal, and hence the availability of seeds for dispersal by nutcrackers (Siepielski and Benkman 2007a). This should result in less recruitment, which may be manifested as lower stand densities of mature trees.

Here we use an observational and comparative approach to test the hypothesis that pine squirrels influence stand density of limber and whitebark pines, which is likely an important factor contributing to the structure of the subalpine ecosystems that these conifers dominate (Tomback et al. 2001b). We test the prediction that stand densities should be lower in ranges with pine squirrels than in ranges without pine squirrels. We also evaluate alternative explanations for patterns of variation in the stand densities of these pines.

## METHODS

### *Study areas*

We estimated stand densities of limber pine from six mountain ranges without pine squirrels in the Great Basin and six ranges with pine squirrels from the Rocky Mountains (east of the Great Basin) and the Sierra Nevada (west of the Great Basin; Appendix). The same data for whitebark pine were gathered from five ranges without pine squirrels in the Great Basin and six mountain ranges with pine squirrels from the Rocky Mountains and the Sierra Nevada (Appendix). Whether pine squirrels were present in the Great Basin in the past 20 000 years is doubtful but unknown (Wells 1983, Grayson 1987, Heaton 1990). However, the large expanses of mostly treeless basins between the mountain ranges in the Great Basin would have prevented pine squirrels from colonizing in the recent past (Arbogast et al. 2001). Given the "successful" introductions of pine squirrels to other isolated areas (e.g., Cypress Hills; Benkman et al. 2001), we suspect that the absence of pine squirrels from the more forested mountain ranges (e.g., Snake Range, Nevada) is the result of biogeographic barriers rather than from unsuitability of habitat.

Limber and whitebark pines dominated the study areas, which were located in a relatively narrow range of elevation (2438–3300 m) and latitude (36°46'12"–43°53'24" N; Appendix) to minimize the effects such

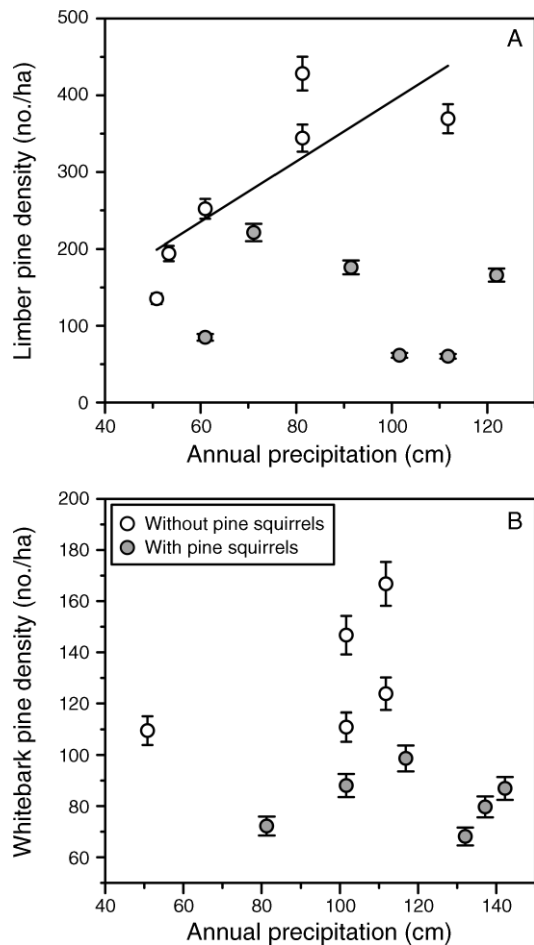


FIG. 1. The relationship between stand density and annual precipitation for (A) limber and (B) whitebark pines among areas with and without pine squirrels. Values shown are means  $\pm$  2 SE. The only statistically significant relationship is for limber pine in the absence of pine squirrels ( $r = 0.81$ ,  $df = 5$ ,  $P = 0.05$ ). Below, the sites are listed from left to right; if values for the abscissa are identical the site with the lower stand density is listed first. Limber pine sites with pine squirrels: Avintaquin, Utah; Pike's Peak, Colorado; Ward, Colorado; Onion Valley, California; Horseshoe Meadows, California; and Rocky Mountain National Park, Colorado. Limber pine sites without pine squirrels: White Mountains, California; Spring Mountains, Nevada; Toiyabe Range, Nevada; Snake Range, Nevada; Schell Creek Range, Nevada; and Ruby Mountains, Nevada. Whitebark pine sites with pine squirrels: Union Pass, Wyoming; Salt River Range, Wyoming; Sonora Pass, California; Galena Peak, Idaho; Saddlebag Lake, California; and Mt. Rose, California. Whitebark pine sites without pine squirrels: Pine Forest Range, Nevada; East Humboldt Range, Nevada; Jarbidge Mountains, Nevada; Independence Mountains, Nevada; and Ruby Mountains, Nevada.

variation might have on stand density. Siepielski and Benkman (2007a) provide some additional details on study locations. Although we did not survey for white pine blister rust (*Cronartium ribicola*) or bark beetles (*Dendroctonus ponderosae*), both causing extensive

mortality of limber and whitebark pines (Tomback et al. 2001b), we did not notice advanced signs of damage from blister rust or bark beetles in most study areas. Thus, mortality from either of these causes should not confound comparisons between areas with and without pine squirrels.

#### Stand densities in regions with and without pine squirrels

We used the point-center-quarter method (Mueller-Dombois and Ellenberg 1974) to estimate limber and whitebark pine stand densities. During late August and early September 2004, we located mature pine stands (i.e., trees producing female cones) within each mountain range and marked one transect through the approximate center of each stand; the starting point was haphazardly chosen. We recorded the distance to and diameter at breast height (hereafter dbh) of the nearest cone-bearing pine tree in each of four quadrants at 10 locations spaced approximately 500 m apart along each transect. Because of the patchy distribution of these pines within a range, our estimate of density should be viewed as an estimate of the density of trees within limber or whitebark pine stands rather than a range-wide density. We recorded dbh to test and control for differences in age or stage of succession, which could potentially confound our comparisons. We used one-tailed two-sample  $t$  tests to test the prediction that stand densities of each conifer were greater in regions without pine squirrels than in regions with pine squirrels. Kruskal-Wallis tests were used to compare size class (dbh) distributions. All model assumptions were met.

#### Stand density and abiotic factors

Variation in the stand density of limber and whitebark pines is also likely affected by abiotic conditions (e.g., Lepper 1974, McCaughey and Weaver 1990, Schoettle and Rochelle 2000, Tomback et al. 2001a). To address this possibility, we examined the correlation between stand density and several abiotic factors that may affect these pines: elevation, latitude, and annual precipitation. Elevation and latitude were recorded using a GPS unit, and estimates of annual precipitation were determined from a climate database (available online).<sup>2</sup>

## RESULTS

#### Stand densities in regions with and without pine squirrels

Stand densities in the absence of pine squirrels were about double those in regions with pine squirrels (Fig. 1). Limber pine stand densities were over twice as great in mountain ranges without pine squirrels (overall mean  $\pm$  SE =  $287 \pm 46$  trees/ha) than in ranges with pine squirrels ( $128 \pm 28$  trees/ha; one-tailed test,  $t_{10} = 2.96$ ,  $P = 0.005$ ). We note that our estimate of the stand densities

<sup>2</sup> (<http://www.ncgc.nrcs.usda.gov/products/datasets/climate/data>)

TABLE 1. Pearson correlation coefficients between several abiotic factors and stand densities of limber and whitebark pines in areas with and without pine squirrels.

Comparison	Abiotic factor		
	Elevation	Latitude	Annual precipitation
Limber pine			
Limber pine with pine squirrels	-0.37	0.64	-0.18
Limber pine without pine squirrels	-0.10	0.67	0.81*
Overall	-0.28	0.56†	-0.02
Whitebark pine			
Whitebark pine with pine squirrels	0.15	-0.69	0.09
Whitebark pine without pine squirrels	0.55	-0.40	0.56
Overall	-0.51	-0.09	-0.19

\* $P = 0.05$ , † $P = 0.06$ ; all other comparisons  $P > 0.10$ .

of reproductive (producing female cones) limber pine in Rocky Mountain sites (overall mean = 188 trees/ha) is comparable to 12 sites sampled throughout Colorado by Schoettle and Rochelle ([2000]; mean = 210 trees/ha based on data in their Table 4). Similarly, whitebark pine stand densities were 1.6 times greater in ranges without pine squirrels ( $132 \pm 11$  trees/ha) than in ranges with pine squirrels ( $82 \pm 5$  trees/ha; one-tailed test,  $t_9 = 4.40$ ,  $P = 0.0009$ ).

Size-class distributions (dbh) did not differ between ranges with ( $23.7 \pm 7.2$  cm [mean  $\pm$  SD];  $35.9 \pm 10.9$  cm) and without ( $24.8 \pm 8.6$  cm;  $37.1 \pm 10.7$  cm) pine squirrels for either limber ( $\chi^2 = 1.0$ ,  $df = 1$ ,  $P = 0.32$ ) or whitebark pines ( $\chi^2 = 1.57$ ,  $df = 1$ ,  $P = 0.21$ ), respectively.

#### Stand density and abiotic factors

With the exception of annual precipitation, no abiotic factor was significantly correlated with stand densities of either pine (Table 1). The stand densities of limber pine increased with increases in annual precipitation, but only in the absence of pine squirrels (Fig. 1A, Table 1). Although not statistically significant ( $P = 0.33$ ), a similar pattern is apparent for whitebark pine in the absence of pine squirrels as well (Fig. 1B, Table 1). In contrast, no relationship between stand density and precipitation was evident for either pine in the presence of pine squirrels (Fig. 1, Table 1). Although stand densities of limber pine tended to increase with increases in latitude across all sites (Table 1), the differences in stand densities cannot be explained by differences in latitude because there was no difference in mean latitude between areas with and without pine squirrels (Table 1,  $t_{10} = 0.61$ ,  $P = 0.56$ ).

#### DISCUSSION

The lower stand densities of limber and whitebark pines in the presence than absence of pine squirrels are consistent with the hypothesis that the ecological and evolutionary effects of pine squirrels limit recruitment and, thus, the density of these pines. Pine squirrels may therefore act to limit recruitment before other factors

become limiting to stand density. Once seed limitation by pine squirrels is removed and tree densities increase, then other factors, namely precipitation, appear to limit stand densities (Fig. 1A). Thus, the extent to which at least limber pine stand densities increase in the absence of pine squirrels appears limited by precipitation. Whether stand densities would converge at the lowest levels of precipitation regardless of the presence and absence of pine squirrels is unknown. Pine squirrels and precipitation may, however, jointly limit pine recruitment at the lowest levels of precipitation. If so, then the absence of pine squirrels may be critical in allowing limber pine and perhaps whitebark pine to extend into relatively arid regions of the Great Basin. Before we further discuss these findings, we address several alternative hypotheses that could potentially explain the lower stand densities in the presence of pine squirrels.

#### Alternative hypotheses

One hypothesis is that differences in stand densities result from variation in stand age. We do not know why stand age would differ in a consistent manner between the different regions. Moreover, we did not detect differences in tree size distributions (tree size is positively correlated with tree age in both limber [Knowles and Grant 1983] and whitebark pines [Snethen 1980]), between ranges with and without squirrels for both pines. This indicates that differences in stand ages are unlikely to account for the observed differences in stand densities of limber and whitebark pines between ranges with and without pine squirrels.

A second hypothesis is that limber and whitebark pines occur in higher stand densities in regions without pine squirrels because of reduced competition with other subalpine conifers such as Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*), which are less common in the Great Basin than in the Rocky Mountains (e.g., Wells 1983). Two observations suggest this is probably not an adequate explanation. First,

other conifers were a minor component in all the study areas as both limber and whitebark pines were always the dominant species. Second, the densities of limber and whitebark pines were high in ranges where other subalpine conifers occurred commonly and pine squirrels were absent. For instance, the Snake Range has extensive areas of Engelmann spruce and a similar diversity of conifers as in the Rocky Mountains (Wells 1983), yet the density of limber pine was high (Fig. 1A).

A third hypothesis is that differences in soil productivity and nutrient availability affect stand density (e.g., McCaughey and Weaver 1990). Although both pines appear to grow best on poorly developed, well-drained soils (McCaughey and Weaver 1990, Schoettle and Rochelle 2000), Lepper (1974) found that stand densities were unrelated to measured soil characteristics for 54 stands of limber pine from throughout its range. Thus, differences in soil alone probably do not account for the higher stand densities in the absence of pine squirrels.

Undoubtedly, we have not discussed every alternative explanation for the observed differences in limber and whitebark pine stand densities between regions with and without pine squirrels. Moreover, we lack statistical comparisons for most factors. The possibility also exists that some of the factors discussed above may interact synergistically. The transition between seed and mature tree is complex and involves a suite of factors (McCaughey and Tomback 2001, Tomback et al. 2001a, b, Wang and Smith 2002). In fact, we suspect that differences in tree density at the site level can largely be attributed to factors (some of which we discussed above; e.g., precipitation, Fig. 1A) other than the presence or absence of pine squirrels (see also Schoettle and Rochelle 2000). However, despite the fact that other factors contribute to variation in the stand densities of these pines, we still detected consistent differences replicated in two species between areas with and without pine squirrels. Although experimental studies are ultimately necessary to clarify the role for squirrel predation and other factors in limiting the densities of these pines, these comparative data suggest that seed predation and evolution in response to selection exerted by pine squirrels has cascading effects.

#### *Pine squirrels as keystone species and selective agents*

Pine squirrels have important ecological effects, because they are strong preemptive competitors and reduce the number of seeds available for dispersal by nutcrackers (Benkman et al. 1984, Siepielski and Benkman 2007a). Such high levels of seed predation alone could limit recruitment. For example, Castro et al. (1999) suggested that regeneration of relict Scots pine (*P. sylvestris nevadensis*) forests is limited by high levels of seed predation from granivorous birds (see also Peters et al. 2003). Pine squirrels also act as keystone selective agents in at least two ways. First, selection exerted by

pine squirrels reduces the proportion of the cone that is allocated to seeds resulting in fewer seeds per cone (Benkman 1995, Siepielski and Benkman 2007a). Second, the increased seed defenses against pine squirrels lower the seed removal rates of nutcrackers (Siepielski and Benkman 2007a). We hypothesize that the combined competitive and evolutionary effects of pine squirrels limit seed dispersal and thus recruitment, which is manifested as lower stand densities in areas with pine squirrels. In the absence of pine squirrels, their selection is relaxed and selection exerted by nutcrackers causes an increase in both the numbers of seeds per cone and a cone structure where seeds are more accessible for dispersal by nutcrackers. In effect, we have a "seed addition experiment" in the absence of pine squirrels.

Tree density is an important property of most forested ecosystems, because it influences the structure of plant and animal communities, nutrient cycling, landscape hydrology, and recruitment (e.g., Harper 1977, Tinker et al. 1994, Turner et al. 2003). Limber and whitebark pine subalpine ecosystems are no exception. First, these conifers are the dominant trees in many subalpine communities in western North America (Lanner 1996, Tomback et al. 2001b) and thereby provide habitat for a diverse array of organisms (Tomback and Kendall 2001). Second, because tree size distributions were comparable between regions with and without pine squirrels, the greater stand densities of each pine contribute to greater biomass production in the absence of pine squirrels. Elevated levels of biomass result in greater influxes of energy and nutrients (Barbour et al. 1987) and can serve as carbon sinks (Reich et al. 2006). Third, these pines act to regulate runoff from the snowpack and reduce soil erosion in upper-elevation watersheds as well as regulate stream flow (Tomback et al. 2001b). Finally, these pines facilitate forest succession, as they are a pioneer species in recently disturbed habitat and facilitate the survival and growth of other plants (Tomback and Kendall 2001, Baumeister and Callaway 2006).

It is well established that seed predators can have strong effects on patterns of recruitment and the dynamics of plant populations, with subsequent effects on community structure (e.g., Janzen 1971, Crawley 1992, Orrock et al. 2006). Accordingly, seed predators often exert strong selection pressures on phenotypic traits (e.g., seed defenses such as conifer cones; Benkman et al. 2003, Siepielski and Benkman 2007b) or life history strategies (e.g., masting; Janzen 1976, Benkman et al. 2003) that increase fitness by reducing seed predation. While these patterns have been documented repeatedly in nature, the extent or possibility that selection induced changes by seed predators at one phenotypic level influence higher organizational levels such as ecosystems has rarely been examined. Our results, and those of Benkman and Siepielski (2004), begin to bridge this gap

and suggest that selection by predators on plant reproductive traits can have important effects at the ecosystem level. Combined with a growing body of literature (e.g., Whitham et al. 2006), these results suggest that selection on heritable traits in a single species can affect ecosystem dynamics.

## ACKNOWLEDGMENTS

B. Duval, T. Parchman, J. Pauli, L. Santisteban, D. F. Tomback, and one anonymous reviewer provided helpful comments on earlier drafts of this manuscript. We also especially thank J. Orrock who suggested a key analysis. This research was supported by NSF grants (DEB-0344503, DEB-0455705, and DEB-0515735) awarded to C. W. Benkman. Additional support was provided to A. M. Siepielski by the American Ornithologists' Union, The Explorer's Club, the Department of Biology at New Mexico State University, and the Wyoming Native Plant Society.

## LITERATURE CITED

- Arbogast, B. S., R. A. Browne, and P. D. Weigl. 2001. Evolutionary genetics and Pleistocene biogeography of North American tree squirrels (*Tamiasciurus*). *Journal of Mammalogy* 82:302–319.
- Bailey, J. K., J. A. Schweitzer, B. J. Rehill, R. L. Lindroth, G. D. Martinsen, and T. G. Whitham. 2004. Beavers as molecular geneticists: a genetic basis to the foraging of an ecosystem engineer. *Ecology* 85:603–608.
- Barbour, M. G., J. H. Burk, and W. D. Pitts. 1987. *Terrestrial plant ecology*. Benjamin-Cummings Publishing Company, Menlo Park, California, USA.
- Baumeister, D., and R. M. Callaway. 2006. Facilitative effects of *Pinus flexilis* during succession: a hierarchy of mechanisms benefits other plant species. *Ecology* 87:1816–1830.
- Benkman, C. W. 1995. The impact of tree squirrels (*Tamiasciurus*) on limber pine seed dispersal adaptation. *Evolution* 49:585–592.
- Benkman, C. W. 1999. The selection mosaic and diversifying coevolution between crossbills and lodgepole pine. *American Naturalist* 153:S75–S91.
- Benkman, C. W., R. P. Balda, and C. C. Smith. 1984. Adaptations for seed dispersal and the compromises due to seed predation in limber pine. *Ecology* 65:632–642.
- Benkman, C. W., W. C. Holimon, and J. W. Smith. 2001. The influence of a competitor on the geographic mosaic of coevolution between crossbills and lodgepole pine. *Evolution* 55:282–294.
- Benkman, C. W., T. L. Parchman, A. Favis, and A. M. Siepielski. 2003. Reciprocal selection causes a coevolutionary arms race between crossbills and lodgepole pine. *American Naturalist* 162:182–194.
- Benkman, C. W., and A. M. Siepielski. 2004. A keystone selective agent? Pine squirrels and the frequency of serotiny in lodgepole pine. *Ecology* 85:2082–2087.
- Benkman, C. W., A. M. Siepielski, and T. L. Parchman. 2008. The local introduction of strongly interacting species and the loss of geographic variation in species and species interactions. *Molecular Ecology* 17:395–404.
- Castro, J., J. M. Gómez, D. García, R. Zamora, and J. A. Hódar. 1999. Seed predation and dispersal in relict Scots pine forests in southern Spain. *Plant Ecology* 145:115–123.
- Clark, C. J., J. R. Poulsen, D. J. Levey, and C. W. Osenberg. 2007. Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. *American Naturalist* 170:128–142.
- Crawley, M. J. 1992. Seed predators and population dynamics. Pages 157–191 in M. Fenner, editor. *Seeds: the ecology of regeneration in plant communities*. C.A.B. International, Oxon, UK.
- Grayson, D. K. 1987. The biogeographic history of small mammals in the Great Basin: observations on the last 20,000 years. *Journal of Mammalogy* 68:359–375.
- Harper, J. L. 1977. *Population biology of plants*. Academic Press, New York, New York, USA.
- Heaton, T. H. 1990. Quaternary mammals of the Great Basin: extinct giants, Pleistocene relicts, and recent immigrants. Pages 422–465 in R. M. Ross and W. D. Allmon, editors. *Causes of evolution a paleontological perspective*. University of Chicago Press, Chicago, Illinois, USA.
- Holt, R. D. 1994. Linking species and ecosystems: where's Darwin? Pages 273–279 in C. Jones and J. Lawton, editors. *Linking species and ecosystems*. Chapman and Hall, London, UK.
- 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.
- Janzen, D. H. 1971. Seed predation by animals. *Annual Review of Ecology and Systematics* 2:465–492.
- Janzen, D. H. 1976. Why bamboos wait so long to flower. *Annual Review of Ecology and Systematics* 7:347–391.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos* 69:373–386.
- Knowles, P., and M. C. Grant. 1983. Age and size structure analyses of Engelmann spruce, ponderosa pine, lodgepole pine, and limber pine in Colorado. *Ecology* 64:1–9.
- Lamont, B. B., D. C. Le Maitre, R. M. Cowling, and N. J. Enright. 1991. Canopy seed storage in woody plants. *Botanical Review* 57:277–317.
- Lanner, R. M. 1996. *Made for each other: a symbiosis of birds and pine*. Oxford University Press, New York, New York, USA.
- Lepper, M. G. 1974. *Pinus flexilis* James, and its environmental relationships. Dissertation. University of California, Davis, California, USA.
- McCaughy, W. W., and D. F. Tomback. 2001. The natural regeneration process. Pages 105–120 in D. F. Tomback, S. F. Arno, and R. E. Keane, editors. *Whitebark pine communities: ecology and restoration*. Island Press, Washington, D.C., USA.
- McCaughy, W. W., and T. Weaver. 1990. Biotic and microsite factors affecting whitebark pine establishment. Proceedings. Symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. Intermountain Research Station, United States Department of Agriculture, Ogden, Utah, USA.
- Moles, A. T., and M. Westoby. 2002. Seed addition experiments are more likely to increase recruitment in larger-seeded species. *Oikos* 99:241–248.
- Mueller-Dombois, D., and H. Ellenberg. 1974. *Aims and methods of vegetation ecology*. Wiley, New York, New York, USA.
- Orrock, J. L., D. J. Levey, B. J. Danielson, and E. I. Damschen. 2006. Seed predation, not seed dispersal, explains the landscape-level abundance of an early-successional plant. *Journal of Ecology* 94:838–845.
- Paine, R. T. 1969. A note on trophic complexity and species diversity. *American Naturalist* 100:91–93.
- Parchman, T. L., and C. W. Benkman. 2002. Diversifying coevolution between crossbills and black spruce on Newfoundland. *Evolution* 56:1663–1682.
- Peters, S., S. Boutin, and E. Macdonald. 2003. Pre-dispersal seed predation of white spruce cones in logged boreal mixedwood forest. *Canadian Journal of Forestry Research* 33:33–40.
- Reich, P. B., S. E. Hobbie, T. Lee, D. S. Ellsworth, J. B. West, D. Tilman, J. M. H. Knops, S. Naeem, and J. Trost. 2006.

- Nitrogen limitation constrains sustainability of ecosystem response to CO<sub>2</sub>. *Nature* 440:922–925.
- Schoettle, A. W., and S. G. Rochelle. 2000. Morphological variation of *Pinus flexilis* (Pinaceae), a bird-dispersed pine, across a range of elevations. *American Journal of Botany* 87: 1797–1806.
- Siepielski, A. M., and C. W. Benkman. 2007a. Convergent patterns in the selection mosaic for two North American bird-dispersed pines. *Ecological Monographs* 77:203–220.
- Siepielski, A. M., and C. W. Benkman. 2007b. Selection by a pre-dispersal seed predator constrains the evolution of avian seed dispersal in pines. *Functional Ecology* 21:611–618.
- Smith, C. C. 1970. The coevolution of pine squirrels (*Tamiasciurus*) and conifers. *Ecological Monographs* 40:349–371.
- Snethen, K. L. 1980. Whitebark pine (*Pinus albicaulis* Engelm.) invasion of a sub-alpine meadow. Thesis. Utah State University, Logan, Utah, USA.
- Steele, M., L. A. Wauters, and K. A. Larsen. 2005. Selection, predation and dispersal of seeds by tree squirrels in temperate and boreal forests: are tree squirrels keystone granivores? Pages 205–221 in P. M. Forget, J. E. Lambert, P. E. Hulme, and S. B. Vander Wall, editors. Seed fate: predation, dispersal and seedling establishment. C.A.B. International, Oxon, UK.
- Tinker, D. B., W. H. Romme, W. W. Hargrove, R. G. Gardner, and M. G. Turner. 1994. Landscape-scale heterogeneity in lodgepole pine serotiny. *Canadian Journal of Forest Research* 24:897–903.
- 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. 2001. Clark's Nutcracker: agent of regeneration. Pages 89–104 in D. F. Tomback, S. F. Arno, and R. E. Keane, editors. Whitebark pine communities: ecology and restoration. Island Press, Washington, D.C., USA.
- Tomback, D. F., A. J. Anderies, K. S. Carsey, M. L. Powell, and S. Mellmann-Brown. 2001a. Delayed seed germination in whitebark pine and regeneration patterns following the Yellowstone fires. *Ecology* 82:2587–2600.
- Tomback, D. F., S. F. Arno, and R. E. Keane. 2001b. The compelling case for management intervention. Pages 3–25 in D. F. Tomback, S. F. Arno, and R. E. Keane, editors. Whitebark pine communities: ecology and restoration. Island Press, Washington, D.C., USA.
- Tomback, D. F., and K. C. Kendall. 2001. Biodiversity losses: the downward spiral. Pages 243–262 in D. F. Tomback, S. F. Arno, and R. E. Keane, editors. Whitebark pine communities: ecology and restoration. Island Press, Washington, D.C., USA.
- Turnbull, L. A., M. J. Crawley, and M. Rees. 2000. Are plant populations seed-limited? A review of seed sowing experiments. *Oikos* 88:225–238.
- Turner, M. G., W. H. Romme, and D. B. Tinker. 2003. Surprises and lessons from the 1988 Yellowstone fires. *Frontiers in Ecology and the Environment* 1:351–358.
- Wang, B. C., and T. B. Smith. 2002. Closing the seed dispersal loop. *Trends in Ecology and Evolution* 17:379–385.
- Wells, P. V. 1983. Paleobiogeography of montane islands in the Great Basin since the last glaciopluvial. *Ecological Monographs* 47:89–111.
- Whitham, T. G., et al. 2006. A framework for community and ecosystem genetics: from genes to ecosystems. *Nature Review Genetics* 7:510–523.

#### APPENDIX

Type of conifer, site, and region, whether or not pine squirrels are present, elevation, coordinates, and mean diameter at breast height (dbh) of trees at the study site (*Ecological Archives* E089-167-A1).