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A Review of the Literature on Seed Fate in Whitebark Pine and the Life History Traits of Clark's Nutcracker and Pine Squirrels

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Cover photo

Clark's nutcracker foraging on whitebark pine seeds. Mount Baker-Snoqualmie National Forest, Washington. (Photo by Robin Shoal)

Abstract

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Whitebark pine is a critical component of subalpine ecosystems in western North America, where it contributes to biodiversity and ecosystem function and in some communities is considered a keystone species. Whitebark pine is undergoing rangewide population declines attributed to the combined effects of mountain pine beetle, white pine blister rust, and fire suppression. The restoration and maintenance of whitebark pine populations require an understanding of all aspects of seed fate. In this paper, we review the literature on seed dispersal in whitebark pine. Clark's nutcracker, pine squirrels, and scatter-hoarding rodents are all known to influence whitebark pine seed fate and ultimately affect the ability of whitebark pine populations to regenerate. We also provide a general overview of the natural histories of the most influential species involved with whitebark pine seed fate: Clark's nutcracker and the pine squirrel.

Keywords: Whitebark pine, seed dispersal, Clark's nutcracker, pine squirrels, scatter-hoarding.

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Introduction

Whitebark pine (a list of common and scientific names of all species referred to in this document can be found in app. 1) is a five-needle pine that is restricted in distribution to upland and subalpine habitats in western North America (Arno and Hoff 1989) (fig. 1). It plays a critical role throughout its range as a pioneer species and in stabilizing soils and providing forage and cover for wildlife (Tomback et al. 2001). Whitebark pine communities are typically remote and consequently have not been considered as threatened by human-induced changes as lowland forests. Within the last century, however, whitebark pine throughout its range has been undergoing population declines attributed to the combined effects of mountain pine beetle, white pine blister rust, and fire suppression (Keane 2001, Tomback et al. 2001) (fig. 2).



Figure 1—Range of whitebark pine (U.S. Geological Survey 1999).

These three factors have affected whitebark pine in different ways. Mountain pine beetles kill trees rapidly, and most commonly infect diseased and stressed trees (Cole and Amman 1969, Larsson et al. 1983). During periodic epidemics, healthy trees are also affected, and this causes rapid standwide mortality (Safranyik and Carroll 2006). Climate models predict that conditions are favorable for more



Figure 2—Whitebark pine stand showing damage and mortality from blister rust and mountain pine beetle. Okanogan and Wenatchee National Forests, Washington.

extensive and prolonged outbreaks in the future (Logan and Powell 2001). White pine blister rust is an exotic disease that kills trees slowly; infected trees often persist for years after initially being infected. The cone-bearing branches may be killed many years before the tree itself is killed (McDonald and Hoff 2001), so regeneration in infected stands may be limited. Fire suppression has led to slow population declines over the last century by altering the dynamics of stands in fire-prone regions (Kendall and Keane 2001). In the absence of fire, whitebark pine in these stands is replaced by more shade-tolerant, fire-intolerant species such as subalpine fir and Engelmann spruce.

One or more of these agents have caused mortality in stands throughout the range of whitebark pine. Mortality rates are as high as 90 percent in some stands in the Cascade Range, while disease infects 100 percent of trees in some stands in the Rocky Mountains (Kendall and Keane 2001, Ward et al. 2006). This decline has ramifications for many taxa, most notably Clark's nutcracker, which has evolved a mutualistic relationship with whitebark pine and would be directly affected by its decline (Lanner 1982; Tomback 1978, 1982). Nutcrackers forage on large seeds produced by whitebark pine in autumn and scatter-hoard up to tens of thousands of seeds in subterranean caches to be retrieved later in the year (Tomback 1982).

Seeds that are not retrieved by nutcrackers are able to germinate (Lanner 1982, 1996; Tomback 1983; Tomback and Linhart 1990). Whitebark pine cones are indehiscent (see glossary for definitions) (Price et al. 1998) and therefore nutcracker seed dispersal is required by whitebark pine for population-wide regeneration (Hutchins and Lanner 1982); whitebark pine is an obligate mutualist of Clark's nutcracker. Ultimately, it is possible that declines in whitebark pine may affect this mutualism by offsetting a critical balance between pine and nutcracker populations, resulting in reduced seed dispersal and regeneration (Tomback and Kendall 2001).

Because of their large size and high nutritive value (Lanner 1996, Lanner and Gilbert 1994), whitebark pine seeds are consumed by more than 20 species of vertebrates, in addition to the nutcracker. The interactions between all of these vertebrates and whitebark pine contribute to complexities in seed dispersal because these animals have the potential to influence pine regeneration at the stand level. Although some of these species play an important role in seed dispersal, their role in whitebark pine population dynamics has received little study.

This paper provides a review of the current literature relating to seed fate in whitebark pine. We review the seed harvest, caching, and retrieval behaviors of the vertebrates that are known to directly influence the fate of whitebark pine seeds. We then summarize the life history traits of the species that harvest most whitebark pine seed—Clark's nutcracker, the red squirrel, and the Douglas' squirrel (hereafter collectively referred to as pine squirrels).

Whitebark Pine Seed Fate

Seed fate has a profound effect on population dynamics in plants (Schupp and Fuentes 1995, Vander Wall et al. 2005a, Wang and Smith 2002). Seeds are the primary means by which many species of plants, including whitebark pine, move across landscapes, colonize new areas, and ultimately maintain populations. An understanding of the fates of individual seeds is therefore important for the conservation and restoration of whitebark pine populations.

The seeds of whitebark pine are larger than the seeds produced by most other conifers that occur within its range (table 1). Owing, in part, to their large size, whitebark pine seeds are highly valued as food by many avian and mammalian granivores (table 2). Seeds are rapidly harvested from trees every autumn (Hutchins and Lanner 1982, Tomback 1978). To preclude widespread predation of seeds by such granivores many species of pine, including whitebark pine, have evolved a strategy called masting in which populations synchronize their reproductive activity. Masting results in variations in proportion of seeds effectively dispersed (Kelly 1994). In years of high seed production, granivores are satiated enabling

Nutcrackers provide the sole mechanism of primary seed dispersal for whitebark pine, whose cones are unique in that they are essentially indehiscent.

Table 1—Mean seed weights of North American conifers within the range of whitebark pine

Species of conifer	Mean seed weight
Pine:	Milligrams
digger pine	782.6
foxtail pine	26.8
Great Basin bristlecone pine	10.7
Jeffery pine	122.6
knobcone pine	17.9
limber pine	92.6
lodgepole pine	4.0
ponderosa pine	37.4
Rocky Mountain bristlecone pine	25.1
single-leaf pinyon pine	408.6
sugar pine	216.0
western white pine	16.0
whitebark pine	174.5
Fir:	
grand fir	24.7
noble fir	33.6
Pacific silver fir	41.2
red fir	70.9
subalpine fir	13.0
white fir	40.9
Larch:	
subalpine larch	3.2
western larch	3.3
Spruce:	
Engelmann spruce	3.4
Sitka spruce	2.2
white spruce	2.0
Hemlock:	
mountain hemlock	4.0
western hemlock	1.7
Other:	
Douglas-fir	11.5
western redcedar	1.1

Source: Conner and Lanner 1991, Schopmeyer 1974.

a proportion of seeds to escape predation. In years of low seed production, most seeds are predated and populations of granivores are culled. This has important implications for the number of seeds dispersed within populations and therefore the adaptive evolution of whitebark pine (Siepielski and Benkman 2007b). Overall, the number of seeds effectively dispersed differs in each year owing to many factors: the number of seeds produced within a population of whitebark pine, the size and mobility of populations of several species of granivore, and the availability of alternate foods for such granivores.

Table 2—Vertebrates known to forage on whitebark pine seed

Birds:	
Cassin's finch	<i>(Carpodacus cassinii)</i>
Clark's nutcracker	<i>(Nucifraga columbiana)</i>
common raven	<i>(Corvus corax)</i>
mountain chickadee	<i>(Poecile gambeli)</i>
pine grosbeak	<i>(Pinicola enucleator)</i>
red-breasted nuthatch	<i>(Sitta anadensis)</i>
red crossbill	<i>(Loxia curvirostra)</i>
Steller's jay	<i>(Cyanocitta stelleri)</i>
white-breasted nuthatch	<i>(Sitta carolinensis)</i>
Williamson's sapsucker	<i>(Sphyrapicus thyroideus)</i>
woodpeckers (multiple species)	<i>(Picoides spp.)</i>
Mammals:	
black bear	<i>(Ursus americanus)</i>
chipmunk (multiple species)	<i>(Tamias spp.)</i>
deer mouse (multiple species)	<i>(Peromyscus spp.)</i>
Douglas' squirrel	<i>(Tamiasciurus douglasii)</i>
golden-mantled ground squirrel	<i>(Spermophilus lateralis)</i>
grizzly bear	<i>Ursus arctos</i>
red squirrel	<i>Tamiasciurus hudsonicus</i>
vole (multiple species)	<i>(Clethrionomys spp.)</i>

Sources: Hutchins 1990, Tomback 1978, Tomback and Kendall 2001.

We review the current literature on the attributes of granivores that affect their effectiveness as either seed dispersers or seed predators for whitebark pine. We describe three aspects of whitebark pine seed dispersal and predation. The first two sections review the influence of Clark's nutcracker and pine squirrels on whitebark pine primary seed dispersal and seed predation. These two species account for the majority of seed dispersal and seed predation, respectively (Hutchins and Lanner 1982, Tomback 1978). Information is also provided on the seed harvesting and caching behaviors of nutcrackers and squirrels in other forest types. Also discussed is secondary seed dispersal by mice and chipmunks in other species of North American pine. Although the effectiveness of these rodents as secondary seed dispersers in whitebark pine has not been studied, it has been suggested that they may contribute to seed dispersal (McCaughey and Tomback 2001).

Primary Seed Dispersal by Clark's Nutcracker

Of all of the species involved with whitebark pine seed fate, Clark's nutcracker is the only species that is known to be required for effective seed dispersal. As a result of this relationship, whitebark pine has evolved several unique features among North American pines that facilitate seed harvest by nutcrackers. Whitebark pine seeds are retained in indehiscent cones. The seeds can only be extracted from



Robin Shoad

Figure 3—Mature whitebark pine tree showing rounded, upswept crown. Okanogan and Wenatchee National Forests, Washington. Cones (inset photo) are borne at the ends of the branches.

the cones by nutcrackers. The seeds of whitebark pine are also wingless, which enables nutcrackers to more rapidly harvest and transport seeds. Additionally, the cones of whitebark pine are borne conspicuously at the ends of upswept branches, making it relatively easy for birds to locate cones when flying overhead (Lanner 1982) (fig. 3). The focus of this section is the behaviors of nutcrackers that drive the mutualism between Clark's nutcracker and whitebark pine.

Seed harvest—

Nutcrackers (fig. 4) forage on fresh whitebark pine seeds from July through October. They forage on unripe seeds prior to the onset of cone maturation, as early as mid-July in some years (table 3). Unripe seeds are soft and cannot be removed entirely (Hutchins and Lanner 1982, Tomback 1978), so nutcracker seed harvest rates are low at this time; they harvest whitebark pine seeds at a rate of 4.5 seeds per minute in mid-August, compared to 12.3 seeds per minute in mid-September when cones are ripe (Hutchins and Lanner 1982). Yet in years of poor or moderate



John and Karen Hollingsworth, U.S. Fish and Wildlife Service

Figure 4—Clark's nutcracker.

seed production, the majority of the seeds harvested by nutcrackers may be unripe. In a study of limber pine seed harvest, Lanner and Vander Wall (1980) observed that in one year of moderate seed production, 91 percent of the cones harvested by nutcrackers were not fully ripe.

Whitebark pine seeds mature throughout the month of August. In late August and September, nutcrackers congregate in loose flocks in whitebark pine stands where they forage predominately on the ripening seeds (Tomback 1978). Caching activity begins with the onset of cone maturation, and nutcrackers typically cache only mature whitebark pine seeds (Tomback 1978). When harvesting and caching seeds, there may be heavy intra- and interspecific competition for seeds. Under such circumstances, nutcrackers may store seeds temporarily within a stand. In locations where pine squirrels were observed actively harvesting whitebark pine cones, Hutchins and Lanner (1982) observed nutcrackers placing seeds in temporary caches within 100 m of the harvest trees. After most seeds had been harvested from cones, nutcrackers were observed retrieving these caches and moving them to cliff faces several kilometers distant. Christensen et al. (1991) observed nutcrackers discriminately harvesting pinyon pine seeds from trees in stands containing the most cones, which would increase foraging efficiency and enable them to more effectively compete with other species for seeds.

The central role of nutcrackers in the regeneration of whitebark pine populations cannot be overestimated: the harvest and scatterhoarding behaviors of Clark's nutcracker provide the only mechanism of primary seed dispersal in whitebark pine.

Table 3—Timing of nutcracker harvest and caching in different locations and for different species of pine

Nutcracker harvest started ^a	Nutcracker caching started ^a	Nutcracker caching completed ^a	Seed essentially mature ^a	Location of study	Elevation of study site	Year of study	Species of pine studied	Size of cone crop ^b	Data source
Late Aug	-	Mid-Dec	Late Aug	Arizona	2000–2350	1969	Colorado pinyon	L	Vander Wall and Balda 1977
Late Aug	-	Late Oct	Late Aug	Arizona	2000–2350	1973	Colorado pinyon	M	Vander Wall and Balda 1977
-	20 Sept	-	-	California	2670–3000	1974	Jeffrey	M-L	Tomback 1977
12 Sept	16 Oct	7 Dec	-	California	2670–3000	1975	Jeffrey	M-L	Tomback 1977
3 Aug	18 Sept	-	Mid-Sept	California	2670–3000	1976	Jeffrey	M-L	Tomback 1977
-	26 Aug	Late Nov	-	Wyoming	2525	1978	Limber	-	Vander Wall and Hutchins 1983
Late July	Late Aug	Late Oct	Mid-Sept	Utah	2500–2550	1978	Limber	M-L	Vander Wall 1988
none	none	none	Mid-Sept	Utah	2500–2550	1980	Limber	S	Vander Wall 1988
20 Aug	28 Aug	Late Oct	Mid-Sept	Colorado	1800–3350	1991	Limber	-	Baud 1993
-	-	Mid-Oct	Mid-Sept	Colorado	2780–2810	1991	Limber	L	Torick 1995
Early Nov	Early Nov	-	-	Colorado	1800–2400	1991	Ponderosa	L	Baud 1993
Early Oct	-	Mid-Nov	Mid-Oct	Colorado	2450–2680	1991	Ponderosa	L	Torick 1995
Mid-Oct	-	-	-	Colorado	-	1991	Rocky Mt bristlecone	-	Baud 1993
Late July	27 Aug	Late Nov	-	Wyoming	1825–2450	1978	Singleleaf pinyon	-	Vander Wall and Hutchins 1983

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Late July	2 Sept	Late Nov	-	Wyoming	1825–2450	1980	Singleleaf pinyon	-	Vander Wall and Hutchins 1983
Late July	28 Aug	Late Oct	Late Sept	Utah	2000–2200	1978	Singleleaf pinyon	M-L	Vander Wall 1988
Early Aug	31 Aug	-	Late Sept	Utah	2000–2200	1980	Singleleaf pinyon	L	Vander Wall 1988
19 July	29 Aug	-	-	California	2670–3000	1973	Whitebark	M-L	Tomback 1977
2 Aug	25 Aug	11 Oct	-	California	2670–3000	1974	Whitebark	M-L	Tomback 1977
1 Aug	8 Sept	16 Oct	Early Sept	California	2670–3000	1975	Whitebark	M-L	Tomback 1977
28 July	-	10 Oct	-	California	2670–3000	1976	Whitebark	M-L	Tomback 1977
13 July	Mid-Aug	Late Oct	Late Aug	Wyoming	2805–3140	1979	Whitebark	-	Hutchins and Lanner 1982
23 July	Mid-Aug	Late Oct	Late Aug	Wyoming	2805–3140	1980	Whitebark	L	Hutchins and Lanner 1982
4 Aug	Mid-Aug	Late Oct	Late Aug	Wyoming	2805–3140	1980	Whitebark	L	Hutchins and Lanner 1982
Early Sept	31 Aug	Late Oct	Early Sept	California	3131-3978	1990	Whitebark	L	Dimmick 1993
Early Aug	12 Sept	Late Oct	Early Sept	California	3131-3978	1991	Whitebark	M-L	Dimmick 1993

Dashes indicate that source does not provide this information.

^a Dates are approximate.

^b L = large, M = moderate, S = small.

Table 4—Number of seeds stored by Clark’s nutcracker per cache and cache depth for different species of pine

Species of pine	Range of cache size	Mean cache size	Cache depth	Source
			<i>Centimeters</i>	
Jeffrey pine	1–9 (n=42)	4.21 ^a	-	Tomback 1977, 1978
limber pine	5–9 (n=2)	7.0	-	Vander Wall and Balda 1977
limber pine	2–5 (n=11)	3.5	-	Baud 1993
ponderosa pine	31 (n=1)	-	-	Torick 1995
whitebark pine	1–15 (n=172)	4.21 ^a	-	Tomback 1977, 1978
whitebark pine	1–14 (n=157)	3.2	-	Hutchins and Lanner 1982
whitebark pine	1–15 (n=54)	3.7	2.0 (n=30)	Tomback 1982
whitebark pine	1–14 (n=155)	3.4	2.5 (n=14)	Vander Wall and Hutchins 1983
whitebark pine	1–24 (n=890)	2–4.2 ^b	3.1 (n=16)	Dimmick 1993

^a Cache size of Jeffrey and whitebark pine were lumped in these studies.

^b Mean differed between years and between nutcracker age classes.

Seed storage—

Nutcrackers store seeds in scattered caches. Caches are placed in a variety of above- and belowground locations. Seeds are commonly placed in subterranean caches, 1 to 5 cm deep (table 4). Caches are made either by side-swiping the bill to create a slight depression or by directly probing into the ground with the bill (Tomback 1998). Caches are always concealed, either by the bird brushing dirt over the seeds or by placing pebbles, twigs, or other objects on top of the cached seeds (Dimmick 1993, Tomback 1978). When a cache is complete, there is no sign of a disturbance (Tomback 1978, Vander Wall and Balda 1977). Nutcrackers have been observed caching the seeds of many different species of conifer, ranging from the large seeds produced by pinyon pines to seeds as small as those produced by Douglas-fir (table 3). Cache size differs and may be correlated with the size of the seed cached (Vander Wall and Balda 1981). Caches of whitebark pine seeds on average contain 1 to 5 seeds compared to ponderosa pine seed caches, which may contain as many as 31 seeds (table 4).

Table 5—Aspect and elevation of communal caching grounds of Clark's nutcracker

Aspect	Elevation	Source
		<i>Meters</i>
South	2525–2750	Vander Wall and Balda 1977
South	2450	Vander Wall and Balda 1977
Southeast	2805–2880	Tomback 1978
Southwest	2265–2325	Tomback 1978
West-southwest	2550–2670	Tomback 1978
South	2805–2985	Hutchins and Lanner 1982
West-northwest	3100–3500	Dimmick 1993

Table 6—Distances and elevations between seed harvest and cache locations of Clark's nutcracker

Species	Distance ^a	Elevation change	Source
			<i>Meters</i>
Colorado pinyon pine	7.5–22 km	530–600	Vander Wall and Balda 1977
Limber pine	4–5 km	-	Vander Wall and Balda 1977
Limber pine	100 m–1 km	-	Vander Wall 1988
Singleleaf pinyon pine	1 m–5 km	-	Vander Wall 1988
Whitebark pine	2.5–12.5 km	500 ^b	Tomback 1978
Whitebark pine	100 m–3.5 km	-	Hutchins and Lanner 1982
Whitebark pine	1 m–3 km	-	Dimmick 1993

^a Numbers are not representative of the mean distance between harvest and cache locations because most sources give the maximum distance and elevation traveled rather than the range of distances.

^b Represents a negative change (decrease) in elevation.

Flocks of up to 150 nutcrackers may use the same area for caching (Hutchins and Lanner 1982). Many of such communal caching areas (Vander Wall and Balda 1977) have been found on steep, south-facing slopes (table 5), which may demonstrate a preference for sites where caches would be available earlier in the season because of rapid snowmelt. In such communal areas, nutcrackers cache seeds independently and without aggression (Hutchins and Lanner 1982, Vander Wall and Balda 1977).

Nutcrackers commonly cache seeds within a few hundred meters of the trees from which they were harvested (Dimmick 1993). However, they may transport seeds to distant and higher or lower elevation cache sites (table 6). Nutcrackers have been known to transport pinyon pine seeds up to 22 km in distance and 600 m in elevation between seed sources and caching grounds (Vander Wall and Balda 1977, 1981).



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Figure 5—A clump of whitebark pine seedlings resulting from a multiseed cache. Okanogan and Wenatchee National Forests, Washington.

Many of the caching behaviors of nutcrackers are advantageous for population-wide regeneration in whitebark pine.

Nutcrackers bury seeds in a variety of locations, including but not limited to meadows, closed-canopy forests, puddles, and dry slopes (Hutchins and Lanner 1982, Tomback 1978, Torick 1995). Nutcrackers also place caches aboveground in crevices in trees and rocks (Dimmick 1993, Tomback 1978). Observational studies have noted that nutcrackers in the Sierra Nevada Mountains in California appear to place most of their whitebark pine seed caches at the bases of large trees and rocks and in open pumice (Dimmick 1993, Tomback 1978). Nutcrackers also use a variety of substrates for burying caches. In the most comprehensive study of nutcracker caching to date, needle litter and gravel were the most commonly used substrates for whitebark pine seed storage (Dimmick 1993). There has been no research published to support the widely cited perception that Clark's nutcrackers preferentially cache in recent burns or clearings.

Many of the caching behaviors of nutcrackers are advantageous for population-wide regeneration in whitebark pine. Because of their wide-ranging caching behavior, nutcrackers give whitebark pine a pioneering advantage over trees with

wind-dispersed seeds. The number of seeds placed by nutcrackers in one cache often results in a multigenet growth form because whitebark pine seedlings tolerate crowding (Furnier et al. 1987, Linhart and Tomback 1985) (fig. 5). Additionally, the depths of nutcracker caches overlap the range of depths from which seedlings can successfully germinate (Tomback 1982).

Conversely, the sites selected by nutcrackers for caches are not always optimal for seedling survival. Nutcrackers most commonly place caches in needle litter or in microsites that are unshaded (Dimmick 1993). Whitebark pine seedlings are susceptible to death by heat stress and desiccation in their first summer, and seedling survivorship in whitebark pine is significantly lower for seeds growing in needle litter and full sun (McCaughey 1990). Nutcrackers also commonly place caches in cliffs and rocky slopes where vegetation is minimal (Dimmick 1993, Hutchins and Lanner 1982, Tomback 1978). Because rodent cache theft is likely to be lower in such places, nutcrackers may be selecting these habitats for their caches to minimize cache theft by rodents (Hutchins and Lanner 1982). However, whitebark pine seed caches placed by nutcrackers on cliffs or rocky areas likely face relatively high mortality rates as seedlings and may be unlikely to mature into cone-bearing adults.

Cache retrieval—

Many granivores, especially granivorous rodents, use their sense of smell to locate buried seeds. Nutcrackers have a poor sense of smell, however, and retrieve their buried caches by memorizing the exact locations in which they were placed (Balda and Kamil 1992, Kamil and Balda 1985, Vander Wall 1982). In captivity, nutcrackers retain memory of their caches with high accuracy for 180 days and with diminishing accuracy for nearly 300 days (Balda and Kamil 1992).

While the abilities of nutcrackers to remember the locations of their caches have been well studied in laboratory settings, cache recovery in the wild has not been studied in as much depth. Cache recovery of pine seed has been observed mostly in early spring through summer (Tomback 1977, 1978; Vander Wall and Hutchins 1983). Nutcrackers in the Sierra Nevada have been observed recovering seeds from ground caches in February and March at mid-elevation sites (2100 m) and in late May and early June at high-elevation sites (2650 to 3150 m) (Tomback 1978). In Wyoming, nutcrackers have been recorded recovering seeds in June and July (Vander Wall and Hutchins 1983).

Nutcrackers recover their own caches by flying directly to cache sites and immediately removing seeds (Vander Wall 1982). Nutcrackers also pilfer the caches of other individuals by engaging in extensive or prolonged searches of the

ground surface (Vander Wall 1982, Vander Wall and Hutchins 1983). Nutcrackers increase their chances of locating such seed stores by searching for germinating seedlings (Vander Wall and Hutchins 1983; Lorenz, unpublished data) or by concentrating search effort near landmarks where nutcrackers in general are more likely to concentrate caches (Vander Wall 1982). There are no data on the proportion of seeds acquired by individual nutcrackers from personal caches as opposed to pilfered caches.

It is widely known that nutcrackers are pine seed specialists who consume pine seed throughout the year (Bent 1946, Bradbury 1917, Giuntoli and Mewaldt 1978, Mewaldt 1956, Tomback 1977, Vander Wall and Hutchins 1983). However there is no information on the degree to which nutcrackers rely specifically on cached seed because nutcrackers have been observed foraging on seeds retained in cones throughout the year. The cones of large-seeded pines, such as whitebark and pinyon pine, provide seeds from July through mid-autumn (Lanner and Vander Wall 1980, Tomback 1978, Vander Wall and Balda 1977). After this time, nutcrackers may forage on seeds of wind-dispersed conifers at lower elevations through June of the following year (Tomback 1977, 1978; Lorenz, unpublished data). Despite current gaps in the literature, there is likely considerable variation in an individual's reliance on seed caches among years depending on factors such as the availability of alternate foods, winter severity, and breeding status.

Seed Predation by Pine Squirrels

Research on seed dispersal in large-seeded pines has focused on the harvesting and caching behaviors of birds. Benkman (1995) argued that such a focus is unwarranted and regardless of the mutualistic associations between birds and pines, predatory interactions strongly influence all aspects of plant demographics (Crawley 2000, Fleming and Estrada 1993). A shift in focus to encompass all aspects of whitebark pine seed fate is thus necessary for a comprehensive understanding of regeneration in whitebark pine.

Major invertebrate predispersal seed predators include cone worms and cone beetles (Bartos and Gibson 1990). Predispersal predators of whitebark pine seed also include the avian and mammalian granivores that forage on cones and collect fallen seed from the ground. Postdispersal predators include granivores such as Clark's nutcracker and the pine squirrel, and less specialized omnivores such as bears that consume seeds opportunistically.

Pine squirrels (red and Douglas' squirrels) are the most effective predispersal seed predators of whitebark pine because of their methods of seed harvest

(Hutchins and Lanner 1982), and nearly all of the seeds harvested by pine squirrels are consumed or unable to germinate (Hutchins and Lanner 1982, McCaughey and Tomback 2001). Thus predation of whitebark pine cones by pine squirrels affects the dispersal probabilities of whitebark pine seed. In regions facing strong selective pressure from pine squirrels, nutcrackers disperse fewer seeds compared to regions where pine squirrels are absent (Siepielski and Benkman 2007a). This is because pine squirrel predation in stands results in trees with fewer seeds per cone and an increase in cone defenses such as an increase in cone scale thickness and a decrease in the number of seeds per cone (Siepielski and Benkman 2007a). Consequently, pine squirrels are able to exert selection pressures on whitebark pine that are arguably as strong as the selective pressures exerted by whitebark pine's mutualistic partner, Clark's nutcracker. The influence of pine squirrels on seed fate in whitebark pine is considerable and should not be underestimated. However, because there is limited information on the influence of pine squirrels on whitebark pine seed fate, most of the information presented in this section is from studies of their harvest, storage, and retrieval behaviors in other forest types.

Seed harvest—

Red squirrels and Douglas' squirrels forage extensively on conifer seed, and their life history traits revolve around seed availability. Although whitebark pine seeds are valued by pine squirrels because of their large size (Hutchins and Lanner 1982, Smith 1968b, Tomback and Linhart 1990,), the range of whitebark pine overlaps only a small portion of the range of the pine squirrel. Consequently, squirrels in most parts of their range forage on the smaller seeds of wind-dispersed conifers (Shaw 1936; Smith 1968b, 1970; Tevis 1953).

Pine squirrels harvest whitebark pine cones up to 6 weeks before seeds are ripe and several weeks before nutcrackers begin harvesting seeds (Hutchins and Lanner 1982). Hutchins (1982, 1994) observed that squirrels harvest whitebark pine cones more intensively before seeds have ripened. Seeds in cut unripe cones are not fully developed, and consequently their predation is a reproductive loss for the tree (McCaughey and Tomback 2001).

Pine squirrels generally inhabit stands in which there are multiple species of conifer. This is because different species of conifer generally produce mast crops of cones in different years, making it more likely that squirrels will have a consistent supply of food year to year. Mixed stands of whitebark pine, spruce, and fir are good habitat for pine squirrels because they provide a more reliable food source and protective shelter (Reinhart and Mattson 1990). Pine squirrels are often uncommon in or absent from pure whitebark pine stands because cone production is not

Pine squirrels harvest whitebark pine cones up to 6 weeks before seeds are ripe and several weeks before nutcrackers begin harvesting seeds.

reliable between years (Mattson and Reinhart 1997, Reinhart and Mattson 1990). Overall, whitebark pine trees in mixed stands are likely to have more cones harvested by squirrels than whitebark pine trees in pure stands or isolated in meadows (Hutchins 1982).

The amount of seeds harvested by squirrels differs and is dependent on stand characteristics. Benkman et al. (1984) found that in mixed limber pine stands, as much as 89 percent of the cone crop was harvested by squirrels, with as little as 1 percent remaining for dispersal by Clark's nutcrackers. In nearby pure stands, most cones remained on the tree and available for nutcrackers. Similarly, Hutchins (1982) found that squirrels harvested nearly 64 percent of the available whitebark pine seed in forests of whitebark pine, subalpine fir, and Engelmann spruce, but harvested no cones from isolated whitebark pines in meadows.

Seed storage—

Because the availability of conifer seed differs yearly, squirrels store food to survive periods of food shortage. When harvesting for storage purposes, squirrels rapidly cut and drop large numbers of cones; they have been observed cutting the small cones of giant sequoia trees at a rate of 500 cones in 30 minutes (Shellhammer 1966). Squirrels gather such cut cones within days of harvest and store them for later use.

Squirrels usually cache whole conifer cones. However, in some cases they extract the seeds from the cones of whitebark and limber pines before storage (Benkman et al. 1984, Hutchins and Lanner 1982). Unlike the scatter-hoarding behaviors of nutcrackers, pine squirrels typically larder-hoard, storing all of their seeds in a few locations within their territory (Finley 1969, Hurly and Lourie 1997). It is common for cones and seeds to be buried within middens, which are piles of loose cone scales that have accumulated beneath favored feeding perches (Finley 1969, Vahle and Patton 1983) (fig. 6). To be effective for cone storage, middens must have a cool and moist interior that prevents cones from opening (Finley 1969, Shaw 1936, Smith and Mannan 1994). Where moisture is limited, squirrels select middens for cone storage that are on north-facing slopes or heavily shaded by the canopy. Middens on south-facing slopes or in the open are not typically used for cone storage (Finley 1969, Smith and Mannan 1994).

The number of conifer cones stored by squirrels in middens differs depending on the presence of potential competitors and food availability (Finley 1969, Gurnell 1984). Middens may contain enough food to last 1 year (Ferron et al. 1986, Gurnell 1984, Smith 1968b). Middens as large as 85 m² in diameter and 0.4 m deep have been found. Such middens often reflect the work of many generations of squirrels (Finley 1969, Rusch and Reeder 1978). Estimates of 16,000 spruce cones, 3,000



Anne L. Casey, U.S. Forest Service

Figure 6—A red squirrel pausing near its midden. Coronado National Forest, Arizona.

whitebark pine cones, and 8,800 lodgepole pine cones in some middens exemplify the industriousness of pine squirrels (Hurly and Lourie 1997, Schmidt and McCaughey 1990, Smith 1968b).

Squirrels without access to suitable middens may store cones under piles of brush or logs or within tree cavities (Finley 1969, Gurnell 1984, Hatt 1943, Shellhammer 1966). Pine squirrels also scatter-hoard cones in subterranean caches (1 to 30 cones) (Carey 1991, 1995; Hurly and Lourie 1997). Hurly and Lourie (1997) found that pine squirrels in Alberta cached lodgepole pine cones both in large, central middens (1,000 to 8,000 cones) and in numerous scatter-hoards (1 to 5 cones). Approximately 40 percent of the cones stored by squirrels in this population were scatter-hoarded. The scatter-hoarding behavior of pine squirrels may be underreported because scatter-hoarded cones are less visible than cones stored in larders.

For multiple reasons, seeds stored by pine squirrels are unlikely to establish as seedlings. Seeds are usually not extracted from cones before being stored, which precludes germination. When caching individual seeds, squirrels larder-hoard whitebark pine seeds in caches between 6.5 and 40 cm deep and ranging from 14 to 55 seeds (Hutchins and Lanner 1982). This inhibits regeneration by preventing germinants from being able to grow upwards enough to penetrate the surface of the midden and by causing overcrowding. The squirrels' tendency to place caches

Estimates of 16,000 spruce cones, 3,000 whitebark pine cones, and 8,800 lodgepole pine cones in individual middens exemplify the industriousness of pine squirrels.

at the bases of large, live trees and under the canopy of forests inhibits seedling growth. Moreover, as squirrels cache and retrieve cones from their larders, materials are continually turned over, making establishment impossible for most seeds (Gurnell 1984, Hatt 1943). Hutchins and Lanner (1982) found significantly fewer surviving whitebark pine seedlings on middens compared to randomly selected portions of the forest floor.

Cache retrieval—

Pine squirrels recover stored seed mainly in winter when fresh seed is unavailable (Smith 1968b). Squirrels will retrieve seeds up to several years after they have been cached (Smith 1968b). The amount of seed recovered from caches in a given year depends on a number of factors, especially the size of the previous year's cone crop and the amounts and availability of alternate food sources. Consecutive years of cone crop failure may result in the consumption of all cached seeds (Smith 1968b).

The conventional view of seed dispersal as a short-term, discrete event is being replaced by an understanding of the complex interactions between animals and plants that occur for an extended period after a seed arrives on a substrate.

Secondary Seed Dispersal by Scatter-Hoarding Rodents

For many systems with vertebrate-mediated seed dispersal, research has historically focused on the relationship between the plant and the animal most directly involved with the transport of the seed away from the parent plant. However, in many systems, the travels of seeds do not always end with this first phase of dispersal (Chambers and MacMahon 1994, Vander Wall et al. 2005b). Moreover, the secondary phases of dispersal are often as influential to plant population dynamics as the first phase (Chambers and MacMahon 1994). It is now apparent that many plant-disperser interactions involve multiple stages of varying degrees of effectiveness, occurring in two or more phases. The conventional view of seed dispersal as a short-term, discrete event is being replaced by an understanding of the complex interactions between animals and plants that occur for an extended period after a seed arrives on a substrate.

Seed dispersal in whitebark pine has not been studied in detail, but it has traditionally been considered a single-phase event in which nutcrackers disperse seeds from a parent plant to favorable sites. In other species of western pine with both wind- and bird-dispersed seeds, recent work has changed traditional perceptions of seed dispersal. For example, the seeds of ponderosa and Jeffery pines were traditionally considered to be dispersed by the wind. The seeds of Colorado pinyon and single-leaf pinyon pine have been described as dispersed entirely by birds. Studies tracking the movements of such seeds over time have revealed that granivorous rodents are involved, and at times required, for effective seed dispersal in these species.

Many species of rodents store seeds in small (one to three seeds), shallow (5 to 20 mm deep) subterranean caches. The term “scatter-hoarding rodents” is used widely as a term for this guild. Some examples of scatter-hoarding rodents that participate in the harvest of pine seeds include chipmunks, ground squirrels, kangaroo rats, pocket mice, and deer mice. Their scatter-hoarding behavior enables population regeneration in some species of North American pines (Vander Wall 1992b).

Whitebark pine is different from other North American pines because it is the only species with indehiscent cones. Effective seed dispersal requires Clark's nutcracker and this has been well documented (Hutchins and Lanner 1982, Tomback 1978, Tomback and Linhart 1980). However, scatter-hoarding rodents demonstrably affect seed fate in whitebark pine (Hutchins and Lanner 1982, McCaughey and Weaver 1990, Tomback 1980). The outcome of their interactions with whitebark pine seed and their overall role in whitebark pine seed fate has not been studied (McCaughey and Tomback 2001).

This section provides a review of the current literature on whitebark pine seed harvest by scatter-hoarding rodents and their seed storage and cache retrieval behaviors with other pines. Seed storage and cache retrieval by such rodents has been studied in Jeffery pine, sugar pine, and pinyon pines in western North America. Although storage and retrieval behaviors of these rodents have not been formally studied in whitebark pine, information on their behaviors in other systems may contribute to an understanding of the complexities of whitebark pine seed fate.

Seed harvest—

Chipmunks and deer mice have weak jaw muscles compared to pine squirrels, and they therefore are not as efficient in harvesting seeds compared to nutcrackers and pine squirrels (Hutchins and Lanner 1982, Tomback 1978). A relatively small proportion of the whitebark pine cones are cut down by these scatter-hoarding rodents (Hutchins and Lanner 1982) (fig. 7).

Scatter-hoarding rodents more commonly forage on and collect seed that has fallen on open ground. In experimental settings, whitebark pine seed that was surface sown in stands was removed by rodents within 24 hours (Hutchins and Lanner 1982, McCaughey and Weaver 1990). It is important to note, however, that relatively little whitebark pine seed naturally drops to the ground (Hutchins and Lanner 1982). Scatter-hoarding rodents likely exert more influence on whitebark pine seed dispersal by pilfering seeds from nutcracker and pine squirrel caches. Over the course of 9 months, theft of simulated nutcracker caches ranged from 57 percent in subalpine, Engelmann spruce forests, to 90 percent in whitebark pine stands (Baud



Robin Shoat

Figure 7—A chipmunk harvesting seeds from a whitebark pine cone. Okanogan and Wenatchee National Forests, Washington.

1993, Hutchins and Lanner 1982). Rodent theft of seeds from pine squirrel larders has not been studied.

Seed storage—

In North America, scatter-hoarding rodents contribute to population-wide regeneration in several species of pine. Their seed storage behaviors have been studied most thoroughly in Jeffery, sugar, and pinyon pine. Jeffery and sugar pines have seeds with wings. Although primary dispersal is enabled by the wind, recent studies have shown that secondary dispersal by rodents may be required for germination and seedling establishment (Vander Wall 1992b, Vander Wall et al. 2005b). Pinyon pine seeds are wingless and are dispersed by birds. The first phase of seed dispersal in pinyon pines is enabled by Clark's nutcracker and the pinyon jay. Rodents are involved in secondary seed dispersal in pinyon pines both by collecting seeds dropped during seed harvest by birds, and by stealing cached seeds (of birds and other rodents) that they are able to smell buried under the soil surface.

A comparative study of the effectiveness of six species of rodent as dispersers for pinyon pines found that seeds harvested by deer mice and least chipmunks were

10 times more likely to germinate compared to seeds dispersed by kangaroo rats and pocket mice (Hollander and Vander Wall 2004). This is because most of the pine seeds obtained by deer mice and chipmunks are immediately cached in shallow, subterranean caches (Hollander and Vander Wall 2004; Vander Wall 1993, 2003; Vander Wall and Joyner 1998). Seeds are buried mostly in caches of one to four seeds and are transported between 1 and 69 m from the seed source (Vander Wall 1992b, 1993). Cache depth of scatter-hoarded seeds ranges from just below the soil surface to 8.0 cm, and most caches are buried approximately 5 to 15 mm deep (Thayer and Vander Wall 2005; Vander Wall 1992b, 1993, 1997).

Microsites chosen by scatter-hoarding rodents for caching are different than the microsites chosen by avian dispersers. In studies of seed dispersal in sugar and pinyon pines, rodents placed the majority of their caches near or under shrubs (Thayer and Vander Wall 2005, Vander Wall and Joyner 1998). Rodents are subject to predation by aerial foraging raptors, so rodents may be more likely to cache under the protection of shrubs to reduce predation risk (Thayer and Vander Wall 2005). In a comparative study of caching behaviors in Steller's jays and yellow pine chipmunks on sugar pine seeds, 100 percent of rodent caches were associated with potential nurse shrubs, compared to 42 percent of jay caches (Thayer and Vander Wall 2005). Rodents also most commonly place caches in mineral soil, whereas Steller's jays and Clark's nutcrackers most commonly place caches in needle litter (Dimmick 1993, Thayer and Vander Wall 2005, Vander Wall 1993, Vander Wall and Joyner 1998). Seedlings of many species of pine, including whitebark pine, show increased survivorship when grown in mineral soil and protected from full sun (McCaughey and Weaver 1990; Vander Wall 1992a, 1997).

Cache retrieval—

Chipmunks and deer mice use both spatial memory and scent to locate buried seeds. They may use their spatial memory to locate their own caches, but they rely on scent to raid the caches of other animals (Vander Wall 1991, 2000). The ability of chipmunks and deer mice to successfully locate a cache by scent is affected by soil type and moisture (Briggs and Vander Wall 2004; Vander Wall 1998, 2000).

Few of the seeds that chipmunks and deer mice encounter and steal are immediately consumed. Vander Wall and Joyner (1998) found that 75 percent of Jeffrey pine seed caches that are pilfered by chipmunks are recached immediately in new sites. Individuals aid their own fitness by stealing and recaching seeds previously cached by neighbors (Vander Wall 1995a). Individuals also monitor their own seed stores for evidence of pilferage and recache their own stores multiple times. Caches of larger seeds contain fewer seeds, and are placed farther apart than the caches of

smaller seeds. Both of these strategies reduce the likelihood of cache theft, suggesting that rodents give preferential treatment to large seeds (Vander Wall 1995b, 2003).

As seeds are monitored, pilfered, and repilfered by different individuals, they may be moved more than four times before germinating (Vander Wall and Joyner 1998). In a study of seed dispersal in Jeffrey pine, Vander Wall and Joyner (1998) found that only 1 percent of seeds germinating from chipmunk caches had remained in their original cache site through the winter.

The proportion of seeds that successfully germinate and establish from the caches of scatter-hoarding rodents and birds differs between years depending on factors such as population size, the availability of alternate foods, and the number of seeds produced. Actual germination rates from caches made by birds are not currently known because birds may cache over many square kilometers and these seeds are not easily tracked. Conversely, multiple studies have examined germination rates from seeds scatter-hoarded by rodents; rodent caches are easier to track because rodents cache within 100 m of the seed source. Of Jeffrey pine and bitterbrush seeds experimentally presented to and cached by chipmunks in two studies, approximately 14 percent of seeds scatter-hoarded and 69 percent of caches made by scatter-hoarding rodents survived to germination (Vander Wall 1995a, Vander Wall and Joyner 1998).

Life History Traits

Clark's nutcracker and the pine squirrel have the most direct influence on the fate of whitebark pine seed. This section reviews key aspects of the evolutionary biology, annual cycle, and natural histories of Clark's nutcracker and pine squirrel.

Clark's Nutcracker

Clark's nutcracker is a conifer-seed specialist (Lanner 1996, Tomback 1983, Tomback and Linhart 1990). On a landscape scale, conifers do not produce the same amounts of seed every year. Years of heavy seed production, or "mast-years," are often followed by 1 to 3 years of low or moderate production. Nutcrackers therefore must be highly opportunistic and adaptable in order to survive years of low seed production. Many aspects of the nutcracker's life history, such as their varied diet and their yearly movements, reflect this opportunistic nature. Other aspects, including morphology and the timing of the breeding season, reflect their dependence on conifer seed. To understand the life history of Clark's nutcrackers, it is important to consider both their adaptability and their dependence on conifer seed.

To understand the life history of Clark's nutcrackers, it is important to consider both their conifer seed dependence and their adaptability.



Dave Herr, U.S. Forest Service

Figure 8—A Clark's nutcracker in its first year, showing the pink mouth lining, which contrasts with a black mouth lining in adults. Deschutes National Forest, Oregon.

Morphology—

Clark's nutcracker is a gray bird with contrasting black-and-white markings on its wings and tail (fig. 4). It is sexually monomorphic in plumage, but males are heavier (mean mass 137 g) than females (mean mass 123 g) (Mewaldt 1948), and males have longer tails and wings and a longer, wider bill (Mewaldt 1958). Adult nutcrackers have varying amounts of white plumage on their faces—some individuals have white extending in a broad patch from the bill to the eye while others have only a small patch of white near the bill. Juveniles in their first summer have a gray face and can reliably be distinguished from adults by the color of the mouth; juveniles have a pink mouth, and adults have a black mouth (Mewaldt 1958) (fig. 8). Juveniles molt their plumage during the postjuvenile molt, which extends from July to January in their first year. After this time, hatch-year birds are distinguishable from adults only by faded, brown-tinged wing and tail feathers (which are glossy black in adults). This usually requires scrutiny of the bird in hand. By midsummer of the following year, adults and second-year birds are indistinguishable even in the hand (Mewaldt 1958).

Clark's nutcracker is unusual among passerines in having an extended molt. Most songbirds initiate molt after their breeding season, and the molt is completed within weeks. Nutcrackers begin the annual molt of all feathers in late winter. Molt lasts for up to 9 months, extending from the start of the breeding season throughout

Table 7—Estimates of the number of seeds of different species of pine carried in the sublingual pouch of Clark’s nutcracker

Species of conifer seeds carried	Mean number of seeds in sublingual pouch	Source
Colorado pinyon pine	55 (n=5)	Vander Wall and Balda 1977
Ponderosa pine	34 (n=1)	Grinnell et al. 1930
Singleleaf pinyon pine	72 (n=1)	Grinnell and Storer 1924
Whitebark pine	65 (n=1)	Grinnell and Storer 1924
Whitebark pine	77 (n=13)	Tomback 1978

the postfledging period and well into autumn (Mewaldt 1958). The extended molt enables nutcrackers to be active during all times of the year, but especially in the fall, while harvesting conifer seeds, at a time when many passerines are molting and have reduced flight capabilities.

Clark’s nutcrackers have several distinctive morphological adaptations for their conifer seed diet. Their bill is long, decurved, and sharply pointed, which enables them to chisel into cones and extract seeds from narrow cracks in cone scales (Vander Wall and Balda 1981). Nutcrackers have evolved strong flight capabilities relative to sympatric species, which aids them when searching for cone-bearing trees and when transporting seeds (Vander Wall and Balda 1981). They are capable of transporting more than one seed at a time because of a unique, expandable pouch below the tongue (Bock et al. 1973). This sublingual pouch has an approximate volume of 28 ml (Vander Wall and Balda 1981), and an individual nutcracker can carry up to 20 percent of its body weight in seeds. A nutcracker is therefore capable of transporting approximately 150 whitebark pine seeds at a time, although it is more common for individuals to carry 50 to 70 seeds (Tomback 1977) (table 7).

The nutcracker’s brain is also morphologically specialized for its reliance on conifer seed. Within the lower section of bird and mammal brains is a complex that controls certain memory-related tasks. This portion of the brain, called the hippocampal complex, controls spatial memory in birds. The hippocampus of Clark’s nutcracker is larger than those of noncaching birds of similar size (Basil et al. 1996). This enlarged hippocampus enables nutcrackers to remember the locations of tens of thousands of individually buried seeds for nearly a year (Balda and Kamil 1992). Nutcrackers remember the locations of caches by memorizing the positions of objects surrounding their caches; the positioning of landmarks, rather than the distances to them, is the tool used to locate hidden caches (Kamil and Cheng 2001, Vander Wall 1982). There is also evidence that nutcrackers are able to

A nutcracker is capable of transporting approximately 150 whitebark pine seeds at a time.



Figure 9—Range of Clark's nutcracker (Ridgeley et al. 2005) in gray. Range of whitebark pine (U.S. Geological Survey 1999) overlaid in black crosshatch.

remember not only the locations but also the sizes of the seeds that they place in each cache (Möller et al. 2001).

Distribution—

The range of Clark's nutcracker is restricted to west-central North America (fig. 9). Its breeding range extends northward to central British Columbia, east to the front range of the Rocky Mountains, westward to the Coast Ranges, and south nearly to the border of the United States and Mexico (Tomback 1998). Many populations of nutcrackers are relatively isolated. Populations inhabit and likely regularly breed in isolated high-elevation forests in the Great Basin of Nevada; on Cerro Potosi in Nuevo Leon, Mexico; in the Black Hills of South Dakota; and in the Olympic Mountains of Washington (Peterson 1988, Smith et al. 1997, Tomback 1998). In years of low conifer seed production, nutcrackers have been observed far outside their typical range. They are reported irregularly in Alaska and eastern parts of North America, and these extralimital movements have been attributed to widespread cone crop failures (Davis and Williams 1957, Fisher and Myres 1979, Vander Wall et al. 1981).

Nutcrackers remember the locations of caches by memorizing the positions of objects surrounding their caches.



Michel Rogg

Figure 10—The only other member of the genus *Nucifraga* is the spotted nutcracker, which disperses seeds for several species of pine throughout Eurasia.

In years of low conifer seed production, nutcrackers have been observed far outside their typical range.

Systematics and related species—

Within the class Aves, Clark’s nutcracker is a songbird, in the order Passeriformes, family Corvidae, genus *Nucifraga*. Species in the family Corvidae are linked taxonomically by some common morphological traits. Overall, corvids are regarded as social and highly intelligent birds (McGowan 2001). The only other member of the genus *Nucifraga* is a Eurasian species, the spotted nutcracker, of which there are at least seven recognized subspecies (Goodwin 1986, Madge and Burn 1994) (fig. 10). Many of the life history traits of the spotted nutcracker are similar or identical to those of Clark’s nutcracker. Most notably, both species have coevolved with pines in the subsection Cembrae (section *Strobus*, subgenus *Strobus*, genus *Pinus*), and their annual cycles revolve around seed availability.

Within the family Corvidae, nutcrackers appear to be most closely related to the crows (Goodwin 1986). However, several species of New World jays have convergently evolved traits similar to those of the nutcracker. The blue jay of eastern North America and the western scrub jay of the Southwestern United States have evolved traits for effective seed dispersal in oaks and beeches. The Steller’s jay of western North America opportunistically harvests and disperses seeds of both deciduous and coniferous trees (Lanner 1996). Of the jays, the pinyon jay (fig. 11) is most specialized in conifer seed dispersal and has several morphological adaptations similar to those of the nutcracker: exceptional spatial memory, morphological



Dave Herr, U.S. Forest Service

Figure 11—A sympatric species, the pinyon jay, which disperses the seeds of North American pinyon pines. Clark's nutcracker and the pinyon jay share many similarities in life history traits and morphological adaptations that reflect their reliance on pine seeds. Deschutes National Forest, Oregon.

adaptations for carrying multiple seeds, a long sharp pointed bill, and strong flight capabilities for transporting seeds long distances (Vander Wall and Balda 1981). In general, however, nutcrackers are considered the most specialized food-hoarding and seed-eating corvid (Vander Wall and Balda 1981).

Diet—

Despite its evolutionary history with whitebark pine, Clark's nutcracker does not require whitebark pine for survival. The range of Clark's nutcracker extends beyond the range of whitebark pine in the Southwestern United States. Seeds from other large-seeded pines including limber, southwestern white, and pinyon pine replace those of whitebark pine as important food in the southern parts of the nutcracker's range (Samano and Tomback 2003, Vander Wall 1988, Vander Wall and Balda 1977). In western Montana, Giuntoli and Mewaldt (1978) found that even where the ranges of nutcrackers and whitebark pine overlap, whitebark pine seed on average accounted for less than 20 percent of the annual diet of nutcrackers (app. 2). Ponderosa pine seed accounted for more than half of the annual diet over 3 years, compared to 19 percent whitebark pine seed, 13 percent insects and spiders, and 11 percent Douglas-fir seed. In other parts of their range, nutcrackers are known to forage and sometimes to rely on seeds of Great Basin bristlecone pine, Rocky mountain bristlecone pine, Monterey pine, ponderosa pine, Jeffery pine, and Douglas-fir (table 8). The cones of these conifers ripen asynchronously throughout

Despite its evolutionary history with whitebark pine, Clark's nutcracker does not require whitebark pine for survival; local populations of nutcrackers are able to persist in the absence of whitebark pine.

Table 8—Species other than whitebark pine on which Clark’s nutcrackers forage for seed

Species used as forage ^a	Source
Bush chinquapin	Roth and Vander Wall 2005
Colorado pinyon pine	Christensen et al. 1991, Tomback 1977, Vander Wall and Balda 1977, Vander Wall et al. 1981
Douglas-fir	Giuntoli and Mewaldt 1978, Vander Wall et al. 1981
Great Basin bristlecone pine	Lanner 1988
Jeffrey pine	Tomback 1978
Limber pine	Benkman et al. 1984, Lanner and Vander Wall 1980, Tomback and Kramer 1980, Torick 1995, Vander Wall 1988, Vander Wall and Balda 1977,
Monterey pine	Davis and Williams 1957
Ponderosa pine	Baud 1993, Giuntoli and Mewaldt 1978, Torick 1995
Rocky Mountain bristlecone pine	Baud 1993
Singleleaf pinyon pine	Vander Wall 1988, Vander Wall et al. 1981
Southwestern white pine	Benkman et al. 1984, Samano and Tomback 2003, Vander Wall and Balda 1977

^a Nutcrackers have been cited as making caches of all of these species except Monterey pine.

the fall (Krugman and Jenkinson 1974). Within any given region, nutcrackers therefore must be highly mobile and move throughout the landscape during the year to exploit the available seeds of the different species of conifer.

The amount of conifer seed in the diet of nutcrackers differs by month (app. 2). Throughout the year, nutcrackers opportunistically consume foods other than conifer seed. Insects may account for the majority of the nutcracker’s diet in summer (Giuntoli and Mewaldt 1978). Nutcrackers have readily adapted to human food and are attracted to bird feeders, picnic grounds, and human habitations at moderate and high elevations. They also eat songbird eggs and young, consume carrion, forage on pollen cones, and prey upon small mammals, amphibians, and birds (Cottam 1945; Dixon 1956; French 1955; Giuntoli and Mewaldt 1978; Lorenz, unpublished data; MacCracken 1949; Mulder et al. 1978).

Territoriality and pair bonds—

Avian territories are most commonly defined as established, defended patches for breeding purposes. Territoriality is commonly exhibited in passerines during a short, 2- or 3-month breeding season during which there is competition among individuals for food. Territories typically incorporate a nest site and sufficient resources for reproduction. Territory size is correlated with body size (Schoener 1968) because resources need to be economically defensible (Brown 1964). Trespassing by conspecifics is not tolerated, and food resources and mates are

actively defended. In most species, territories are established and defended by singing males. Plumage coloration and songs in males aid in territorial defense and mate acquisition.

Rolando and Carisio (2003) found that the spotted nutcracker of Eurasia restricts territorial behavior to its nest site, and the same appears to be true for Clark's nutcracker. Mewaldt (1956) reported three nests of Clark's nutcracker in Montana located within 500 m of each other. During the breeding season, conspecifics were observed traveling within 100 m of a nesting pair without being challenged (Mewaldt 1956).

Both male and female breeding nutcrackers often become quiet and secretive during the breeding season (Mewaldt 1948). During the initial stages of the breeding season, males may act as sentinels while females are tending the nest or young. Territorial defense is generally reserved for predators. Potential predators are often met with aggressive mobbing by resident nutcrackers. Mobbing behavior by one individual acts to attract other nutcrackers within range of hearing, and predators may be driven away from nests by nutcrackers from multiple breeding territories (Mewaldt 1948, Tomback 1998).

In the closely related spotted nutcracker and pinyon jay, males and females form pair bonds that typically last multiple breeding seasons, and it is likely that Clark's nutcracker does the same (Marzluff and Balda 1992, Swanberg 1956). Adult nutcrackers observed foraging outside of the breeding season and caching in autumn appear to be paired (Mewaldt 1956).

Breeding biology—

Adult nutcrackers forage on freshly harvested and previously cached seeds and insects during the spring breeding season (Giuntoli and Mewaldt 1978). Observations of nesting nutcrackers across years suggest that adults attempt to breed only in years that they have sufficiently large seed stores (Tomback 1998).

In years when breeding occurs, nutcrackers initiate the breeding season in midwinter, up to 3 months earlier than most passerines (Bendire 1889, Bradbury 1917, Mewaldt 1956). Not only is the breeding season early, it is also lengthy, extending into late summer. This extended period enables young nutcrackers to develop mentally and physically before being faced with the challenges of seed harvesting, seed caching, and independence (Dimmick 1993, Vander Wall and Hutchins 1983).

Nutcrackers initiate the breeding season by building nests. Nest-building typically takes less than a week and occurs in February and March (Campbell et al. 1997, Mewaldt 1956). Nests are bulky to provide adequate insulation for the eggs



Nicholas T. Ernst

Figure 12—A Clark's nutcracker brooding its nestlings. Okanogan and Wenatchee National Forests, Washington.

and nestlings during the early breeding season. Nests may be placed anywhere from 2 to 24 m above ground, usually in conifers (Bradbury 1917, Mewaldt 1956). Nutcracker nests have been found in ponderosa pine, Douglas-fir, pinyon pine, western juniper, and mountain mahogany in mid-elevation coniferous forests, and in subalpine fir and whitebark pine at high elevations (Bent 1946; Bradbury 1917; Campbell et al. 1997; Mewaldt 1956; Quigley and Dixon 1956; Lorenz, unpublished data). Compared to most other songbirds, however, few nutcracker nests have been reported, and more study is needed on habitat selection by breeding nutcrackers and productivity within populations.

Two to five eggs are laid within days of completion of the nest (Mewaldt 1956). Unlike most passerines, male nutcrackers share incubation and brooding duties with the female (Mewaldt 1952), which enables both sexes to retrieve seeds from personal caches (fig. 12). Incubation lasts approximately 3 weeks. After hatching, the nestlings remain in the nest for 20 days before fledging. As the young approach fledging, they demand constant feeding by both adults. Nestlings are fed regurgitated conifer seeds and insects (Bendire 1889, Bradbury 1917, Dixon 1934, Mattes 1994, Mewaldt 1956). Stored seeds may be important for the survival of nestling nutcrackers, whereas insect material is likely critical for growth and development (Dixon 1934, Mewaldt 1956). Nutcracker young typically fledge in April and May.

Shortly after the young fledge, snow begins melting in subalpine areas, especially on the south-facing slopes where adults placed caches the previous fall. The adults with their newly fledged young move to these caching grounds to retrieve stored seeds and forage on germinating seedlings (Vander Wall and Hutchins 1983). Young are proficient fliers by early summer, although they often remain dependent on their parents for food. The young are highly vocal, and one or several may follow their parents throughout each day, begging loudly (Vander Wall and Hutchins 1983).

Juvenile nutcrackers are dependent on their parents for 2 or 3 months after fledging. Independence occurs gradually over several weeks. In mid-July, young nutcrackers start learning to find caches on their own by locating germinating seedlings (Vander Wall and Hutchins 1983). Young birds likely learn this technique by following their parents as they search for cached food. Juvenile nutcrackers also practice cache and retrieval behaviors by “playing,” in which they cache and retrieve nonedible objects (Vander Wall and Hutchins 1983).

Adult nutcrackers may harvest unripe seeds from whitebark pine cones as early as July (Tomback 1978, Vander Wall and Hutchins 1983). First-year birds also attempt to harvest unripe seeds from cones, although typically their rate of seed retrieval is far slower than those of adults (Dimmick 1993), because the young birds have difficulties perching and balancing on cones, prying scales apart, retrieving intact seeds, and balancing on branches (Tomback 1978). Aggression by juveniles toward adults may be high as seed stores are depleted and juveniles must subsist on unripe seeds; juveniles often successfully supplant adults foraging on cones (Vander Wall and Hutchins 1983). As the seed harvest season progresses, juveniles become more efficient at harvesting seeds (Vander Wall and Hutchins 1983). This is facilitated by ripening of the cones, which increases seed harvesting rates for all birds.

Ripening of the cones coincides with the beginning of the seed-caching period for adults. Juveniles do not begin caching seeds until late in the season, typically after adults have been caching for weeks (Vander Wall and Hutchins 1983). This is a critical time in the lives of newly independent young birds. Their ability to learn harvesting and caching techniques may determine their likelihood of surviving to adulthood and securing a mate in following years.

Winter survival—

Clark's nutcrackers forage primarily on conifer seeds in winter (Giuntoli and Mewaldt 1978) (fig. 13), and the availability of seeds likely affects their movements in winter (Davis and Williams 1957, 1964; Fisher and Myres 1979; Vander



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Figure 13—A Clark's nutcracker perched during a midwinter snow storm. Okanogan and Wenatchee National Forests, Washington.

Based on observations of returning migrants, nutcrackers may spend up to 10 months, or the majority of the year, on wintering grounds.

Wall et al. 1981). In years of moderate or high cone production, most nutcrackers appear to be high-elevation residents or short-distance altitudinal migrants (Campbell et al. 1997, Grinnell and Storer 1924, Tomback 1978).

Widespread and simultaneous failures in cone crops can cause population irruptions (migration to areas outside the usual range of Clark's nutcracker) in some years. Extralimital sightings include multiple reports of nutcrackers in the Eastern United States (Bryant 1895, Coale 1911, Fisher 1943, Mitchell 1894) as well as in southern and coastal California (Davis and Williams 1957, 1964), the Desert Southwest (Presnall 1936, Westcott 1964), and eastern Canada (Fisher and Myres 1979). Most of these sightings occur from August to December, at the time that cone crops in low production years would be depleted. Population irruptions are common in other North American birds that rely on conifer seeds, such as the pine siskin, red crossbill, and white-winged crossbill (Gill 1995). The spotted nutcracker of Eurasia undergoes similar although less frequent population irruptions in times of low seed availability (Formosof 1933, Mattes 1994, Swanberg 1956). Irruptions of Clark's nutcracker have been observed at 5- to 15-year intervals (Davis and Williams 1957, 1964), although more recent work indicates that minor extralimital movements may be occurring as frequently as every 3 or 4 years (Fisher and Myres 1979).

Although extralimital sightings have been well documented, seasonal migrations of nutcrackers within their normal range are poorly understood. There is

evidence that migrations occur regularly and perhaps even annually in some populations. Vander Wall et al. (1981) documented both northward and southward migrations of thousands of nutcrackers through the Great Basin in the autumns of 1977, 1978, and 1979. Based on observations of returning migrants, nutcrackers may spend up to 10 months, or the majority of the year, on such wintering grounds. Although there is no evidence that nutcrackers transport seeds while on migration (Vander Wall et al. 1981), they have been seen caching seeds while on wintering grounds (Davis and Williams 1957). Migrants will participate in the harvest of seeds with resident populations and may attempt to breed on their wintering grounds (Vander Wall et al. 1981). Several species of bird follow such semiannual, irregular migration patterns and are described as facultative partial migrants (Podulka et al. 2004). Movement patterns in such species are unpredictable as they respond to changes in the abundance of specialized foods.

Population trends—

Information on population trends in Clark's nutcracker is available from two sources, the North American Breeding Bird Survey (BBS; coordinated by the U.S. Geological Survey), and the Christmas Bird Count (CBC; coordinated by the National Audubon Society). Both counts are standardized across North America and have been ongoing since 1966 and 1900, respectively. The BBS is conducted in June, and the CBC is conducted in December of each year. Both counts are intended to provide a long-term data set for investigating general trends in populations.

Results from the BBS show a slight overall increase in numbers of Clark's nutcracker across its range since 1966. In the past 20 years, counts in the Rocky Mountains and Great Basin have recorded fairly stable or slight increases in numbers. Conversely, counts have recorded consistent declines in the Cascade Range and Sierra Nevada (Sauer et al. 2005). Results from the CBC suggest that populations of nutcrackers rangewide have remained stable in the past 40 years (National Audubon Society 2002).

Although these data are available and currently provide the only measure of population trends in Clark's nutcracker, there are many limitations to BBS and CBC data because of inconsistencies between surveys and years. The value of such counts lies in the sheer volume of data gathered over long time periods. The BBS data are particularly limited in value for monitoring species like Clark's nutcracker that are not actively nesting when the counts are actually being conducted, and that are nonterritorial and wide-ranging. For example, Mewaldt (1948) found that the densities of nutcrackers on transects in Montana varied by a factor of eight between months because of variation in conifer seed availability. Overall, a more reliable

Pine squirrels are efficient cone harvesters and harvest the majority of available white-bark pine seeds in some years and locations.

method of surveying nutcracker populations is needed before conclusions can be made on population trends.

Pine Squirrels

Pine squirrels—red and Douglas’ squirrels—are important components of white-bark pine ecosystems (Mattson et al. 2001, McCaughey and Tomback 2001). As discussed earlier, pine squirrels are efficient cone harvesters and harvest the majority of available whitebark pine seeds in some years and locations (Hutchins and Lanner 1982). Because of their efficiency, the selective pressures exerted by pine squirrels on conifers are considerable. In limber and whitebark pine, the presence of pine squirrels has led to cone traits that hinder avian seed dispersal: the production of sterile scales at the base of the cone, the production of thicker seed coats, and a reduction in number of seeds per cone (Benkman 1995, Benkman et al. 1984, Siepielski and Benkman 2007a). Furthermore, pine squirrel harvest activities in a stand may competitively exclude Clark’s nutcrackers (Benkman et al. 1984, Siepielski and Benkman 2007a).

Despite their predatory effects, pine squirrels are important components of whitebark pine communities. Pine squirrels are important prey items for many predators. They form a major component of the diet of the northern goshawk throughout its range in North America (Squires and Reynolds 1997 and references therein). Likewise, American martens, the threatened Canada lynx, great horned owls, and red-tailed hawks prey on pine squirrels in parts of their ranges (Clark et al. 1987, Rusch and Reeder 1978, Tumilson 1987). Squirrel middens also are important components of whitebark pine communities because the pine squirrel’s cone-storing habits make large quantities of whitebark pine seeds available for grizzly and black bears (Mattson and Reinhart 1994). This squirrel-related food source has direct consequences for interactions between grizzly bears and humans in some regions (Mattson and Reinhart 1997). In years of small whitebark pine cone crops when squirrel middens are not available, bears migrate to areas where they are in more contact with humans (Mattson et al. 1992). For diverse reasons, therefore, a review of the life history traits of the pine squirrel is important when considering mechanisms of seed dispersal in whitebark pine.

Morphology—

Pine squirrels are small (200 to 250 g) diurnal tree squirrels (Steele 1999). Both species are specialized for foraging on conifer seeds. Their small bodies enable them to forage on the relatively small branches of conifer trees. With the exception of the nocturnal flying squirrels, pine squirrels are the smallest arboreal squirrels in



Donna Dewhurst, U.S. Fish and Wildlife Service

Figure 14—A red squirrel foraging on spruce cones. Anchorage, Alaska.

North America. They have well-developed jaw musculature for their small size, which facilitates harvesting of large conifer cones. Sexes are not considered dimorphic, although males are commonly heavier than females (Steele 1998, 1999). Size varies intraspecifically in pine squirrels. Smaller individuals inhabit forests of small, soft cones, and larger squirrels predominate in forests of large, heavily armored cones (Lindsay 1986).

Red and Douglas' squirrels are superficially similar in appearance and morphology. However, red squirrels can be distinguished from Douglas' squirrels in the field by slight differences in the color of their coats. The red squirrel is generally more reddish dorsally and white or pale yellow ventrally (fig. 14). The Douglas' squirrel is gray or olive-brown above and yellowish to deep orange below (Steele 1999). In addition to pelage color, there are differences in size and reproductive rates of red and Douglas' squirrels, that aid in survivorship of the two species in their respective habitats (Smith 1981). The red squirrel has larger jaw muscles, a larger body, and a reproductive rate that is apparently less influenced by changes in cone production than that of the Douglas' squirrel. These factors increase the fitness of the red squirrel in the more open lodgepole and ponderosa pine stands of the eastern Cascade Range and Rocky Mountains, where the intensity of light in the forest is higher and the food supply is more consistent between years than in coastal forests. The opposite factors aid in survival in Douglas' squirrel in the

The pine squirrel's cone-storing habits make large quantities of whitebark pine seeds available for bears.

coastal forests of the Pacific coast, where stands are dense and dark and cone crops fluctuate more drastically (Smith 1981).

Distribution—

The range of the red squirrel extends from the Appalachian Mountains of northern Georgia, into the boreal forests to the Arctic Circle, south to the border of Mexico, and westward to the Rocky Mountains and eastern slopes of the Cascade Range and into the Rocky Mountains and south to the border of Mexico (fig. 15). It is absent from the Great Plains, the southeastern lowlands, and the Pacific coast of North America (Steele 1998). The red squirrel is most commonly found in coniferous forests but may take up residence in mixed stands, especially in the eastern portions of its range (Layne 1954, Steele 1998).

The range of the Douglas' squirrel is limited to coniferous forests of the Pacific coast, from coastal British Columbia, through the Cascade Range of Washington and Oregon, and south to central California (Steele 1999) (fig. 16). The ranges of red and Douglas' squirrels are allopatric except for two areas in the Pacific Northwest (Johnson and Cassidy 1997, Steele 1999). A small zone of



Figure 15—Range of red squirrel (Patterson et al. 2005) in brown. Range of whitebark pine (U.S. Geological Survey 1999) overlaid in black crosshatch.



Figure 16—Range of Douglas' squirrel (Patterson et al. 2005) in brown. Range of whitebark pine (U.S. Geological Survey 1999) overlaid in black crosshatch.

sympatry occurs in eastern Oregon and in the Cascade Mountains of southern British Columbia and northern Washington. Both species may coexist in forests of Engelmann spruce, Pacific silver fir, subalpine fir, and mountain hemlock (Smith 1981) in the transitional forest types in the Cascade Range. Past reports of hybridization in these areas were based on observed differences in pelage color. It is now believed that the two species do not hybridize, and observed pelage differences are the result of converging morphological traits (Lindsay 1986).

Systematics—

The family Sciuridae is the second largest family in the order Rodentia, with 276 recognized species worldwide. Family Sciuridae is diverse and includes members of about 50 genera, including pine squirrels, chipmunks, marmots, ground squirrels, flying squirrels, and other tree squirrels (Duff and Lawson 2004). Pine squirrels have a deep reddish pelage and morphological adaptations to a conifer seed diet, which distinguishes them from other tree squirrels. They are endemic to North America, where there are 25 recognized subspecies of red squirrel and three subspecies of Douglas' squirrel.

Diet—

Pine squirrels are conifer-seed-eating specialists (Ferron et al. 1986). Densities of pine squirrels in stands differ over time in response to seed availability (Carey 1991, Flyger and Gates 1982, Klenner and Krebs 1991, Smith 1970, Yeager 1937). In the Pacific Northwest, pine squirrels rely on the seeds of western hemlock, Douglas-fir, grand fir, Sitka spruce, and western redcedar west of the Cascade crest. East of the crest and in the intermountain West, they forage most extensively on lodgepole pine, ponderosa pine, Engelmann spruce, subalpine fir, and Douglas-fir (Smith 1968a, 1970). They prefer cones containing seeds with the highest caloric value (Smith 1970).

In late spring and summer, conifer seed is not ripe enough for consumption, and a variety of fresh foods may be consumed. Fungi are important food items—more than 45 species of fungi are consumed by squirrels in the Pacific Northwest (Smith 1968a). Secondary food sources are numerous and include tree buds and flowers, pine cambium and phloem, fleshy fruits, insects, and songbird eggs and nestlings (Ferron et al. 1986, Flyger and Gates 1982, Smith 1968a). Pine squirrels also forage extensively on conifer pollen cones in summer if other foods are unavailable, although large quantities of pollen cones may be needed because they have relatively low caloric value. Squirrels commonly remove the branch containing pollen cones when foraging, thereby precluding cone production on such branches in the future. Pine squirrels thus can cause extensive tree and stand damage while foraging.

Squirrels subsist on stored conifer seed in winter and supplement their diet opportunistically as food stores are depleted. In winter and spring, this comes at a great loss to living trees. Squirrels strip bark and forage on cambium, phloem, buds, and shoots (Smith 1968b). They preferentially consume bark of pines infected by rusts (*Peridermium* and *Cronartium*) because infected bark has a high sugar content (Hoff 1992, Smith 1968a). Extensive stand damage in years of food shortage may occur because of tree girdling and the destruction of new tree growth (Sullivan and Sullivan 1982, Sullivan and Vyse 1987, Sullivan et al. 1993).

Territoriality—

Pine squirrels aggressively defend their caches against all potential competitors, including conspecifics, chipmunks, and Clark's nutcrackers (Carey 1991, Hutchins and Lanner 1982, Smith 1968a, Torick 1995). Such aggressive resource defense is imperative for individual survivorship because squirrel larders sustain individuals throughout the winter and early spring (Smith 1968b). The cone larders are often centrally located in a circular-shaped territory, making food defense as economical

as possible (Hatt 1943, Smith 1968a). Pine squirrels establish territorial boundaries around their food stores by aggressive chases and territorial calls. Territories are defended year-round.

Both males and females defend territories and are equally intolerant of intruders (Smith 1968a). Where the ranges of Douglas' and red squirrels overlap, the two species defend territories interspecifically (Smith 1981). Territorial defense is particularly heated in autumn when cones are being harvested and there is increased competition from juveniles. Territory overlap or breakdown may occur in some populations when defensible food is depleted, such as in late winter and spring (Smith 1968a, 1968b). Pine squirrels may leave their territories and migrate more than 5 km under such circumstances (Rusch and Reeder 1978).

As long as a squirrel has sufficient food stores and is capable of defending its cone-bearing trees and caches, its territory is its permanent, year-round residence (Buchanan et al. 1990, Kemp and Keith 1970, Smith 1968a, Sullivan 1990, Sullivan and Klenner 1992). Many species of conifer in western North America produce large crops of cones at intervals of 3 to 5 years, and this periodicity is synchronized within populations (Krugman and Jenkinson 1974). Successive years with no cone crop result in high mortality in pine squirrels and emigration of the remaining population (Smith 1968b). Because seeds are the primary food source of squirrels, squirrels inhabiting homogenous stands are at a disadvantage because there are few alternative seed sources in consecutive years of low cone production. Stands of pure whitebark pine stands may therefore be devoid of squirrels in most years (Hatt 1943, Mattson and Reinhart 1997).

Breeding biology—

As in most rodents, pine squirrels do not pair and are promiscuous. Territoriality in both sexes prevents interaction except for a single day in which a female is in estrous and permits males into her territory. Several males will fight for dominance throughout the day of a female's estrous, and dominance might change among several males over the course of this day (Koford 1982, Smith 1968a). Females control the timing of copulation and therefore can select the male with which she will mate. Gestation is approximately 30 days.

Pine squirrels may breed in spring (February–May) or late summer (July–September). They typically bear one litter each year, although there are instances of females producing two litters in one year, apparently in response to surpluses of food (Ferron et al. 1986, Koford 1982). Conversely, females in poor-quality habitat or following years of poor cone production may forego reproduction for a year (Kemp and Keith 1970, Smith 1968a). A single litter may be born in late

summer in years following cone crop failure but in which the current year's cone crop is moderate or heavy. Such late summer breeding provides females with a large supply of fresh conifer seed during lactation.

Most litters are born in spring, and young are weaned and independent 2 months after birth. The timing of spring breeding enables the young of the year to establish territories in late summer prior to cone harvesting. Although still dependent on their mother, young squirrels explore the area within 2.6 km of their natal territory in search of suitable habitat in which to establish their own territory (Kemp and Keith 1970, Larsen and Boutin 1994). Females may assist their young by expanding their territory prior to juvenile dispersal and subsequently giving up parts of their territory to their young or dispersing themselves (Larsen and Boutin 1994, Price 1992, Price and Boutin 1993). Juveniles that inherit their mother's territory show low predator-induced mortality in autumn, compared to dispersing juveniles, but they have lower winter survival rates (Larsen and Boutin 1994). These juveniles may face heavier intraspecific competition, which directly affects survivorship as juvenile survivorship is closely correlated with cone productivity and the amount of food an individual is able to store (Halvorson and Engeman 1983, Larsen and Boutin 1994).

Cone harvesting and storage behaviors in pine squirrels appear to be inherent. Juveniles will participate in the cone harvest in the year of their birth, although typically they are unable to secure larders large enough to enable breeding the following year. Most pine squirrels first breed at 2 years of age (Hatt 1943, Kemp and Keith 1970, Rusch and Reeder 1978).

Winter survival—

Pine squirrels do not hibernate and do not undergo torpor of any kind. They remain active throughout the winter although they may seek shelter for days at a time during major weather events. A high body temperature and fat deposits enable pine squirrels to survive extreme cold (Steele 1998). Their ability to survive the winter also depends on the insulating qualities of their nests and the amount of food they have stored.

Nest site selection is critical for winter survival and effective thermoregulation (Smith 1968a). Although natural cavities appear to be preferred where available, pine squirrels most commonly build vegetative nests (composed of grasses, mosses, bark, and leaves) in the canopies of trees. Squirrels often place nests in large-diameter trees with many interlacing branches, which provide canopy escape routes (Rothwell 1979, Vahle and Patton 1983). Because squirrels subsist on stored cones

during the winter months, most nests are built within 30 m of middens (Rothwell 1979; Smith 1968a, 1968b; Vahle and Patton 1983).

Conclusion

Clark's nutcracker, pine squirrels, and scatter-hoarding rodents are the primary vertebrate species that influence whitebark pine seed fate and ultimately affect the ability of whitebark pine populations to regenerate. Clark's nutcracker is well-known for its mutualistic role as a seed disperser for whitebark pine, and it also acts as a seed predator in many circumstances. Pine squirrels are highly effective seed predators. Scatter-hoarding rodents are confirmed seed predators. They are confirmed seed dispersers for many species of pine, and although their role has not been studied in whitebark pine, they likely disperse seeds in some populations.

However, seed dispersers can be transformed into seed predators, and mutualistic partnerships can become exploitative interactions as a result of fluctuations in cone productivity on a landscape scale, predator abundance, and inter- and intra-specific competition. The roles of these granivores vary both spatially and temporally—roles vary spatially in relation to the distribution of whitebark pine trees and alternative food sources on the landscape, and they vary temporally in response to demographic changes within their populations.

These variations affect whitebark pine seed fate in complex ways. Spatially, not all whitebark pine trees are equally likely to have their seeds dispersed in a manner that will enable germination. Trees in pure stands and isolated trees in open areas will have the greatest proportion of their seeds harvested by Clark's nutcrackers (Christensen and Whitham 1991, Hutchins and Lanner 1982, Reinhart and Mattson 1990) and fewer of their seeds will be lost to pine squirrel predation. Conversely, whitebark pine in mixed stands would have a greater proportion of their cones harvested by pine squirrels, and the likelihood of regeneration for such individuals is lower. Whitebark pine regeneration is also influenced by temporal changes in nutcracker and rodent populations. All of these animals show plasticity in foraging behavior and have evolved to survive periods of low whitebark pine seed production. Short-term and small-scale changes in food availability will affect species differently than long-term, widespread, and simultaneous changes in seed production.

As whitebark pine populations continue to decline owing to white pine blister rust, mountain pine beetle attacks, fire suppression and, in the future, global warming, it will become increasingly important for successful whitebark pine restoration to consider the complex and variable roles that vertebrates play in whitebark pine

Clark's nutcracker, pine squirrels, and scatter-hoarding rodents are the primary vertebrate species that influence whitebark pine seed fate and ultimately affect the ability of whitebark pine populations to regenerate.

Successful restoration and management of whitebark pine depends on recognizing the complexities of interactions between multiple vertebrate species and whitebark pine.

seed fate. There are many gaps in our knowledge of the interactions among Clark's nutcracker, pine squirrels, scatter-hoarding rodents, and whitebark pine. This paper provides a review of the current literature to inform managers who are interested in restoring and managing whitebark pine ecosystems.

Glossary

allopatric—Occurring in separate, nonoverlapping geographic areas. This term is often used to describe populations of related organisms unable to crossbreed because of geographic separation.

cache—In relation to seed dispersal by animals, refers to a discrete site selected by an animal for temporary cone or seed storage. Caches may contain one or many cones or seeds depending on the species of animal storing and the species plant being stored.

corvid—A bird in the family Corvidae, a family of passerine birds that contains the crows, ravens, rooks, jackdaws, jays, magpies, and nutcrackers. Collectively its members are called corvids, and there are more than 120 species.

granivore—An animal that selectively eats seeds.

indehiscent—A fruit or cone that does not split open to scatter its seeds when mature.

keystone—A species that has a disproportionate effect on ecosystem function relative to its abundance or biomass.

larder-hoard—Method of food storage by animals in which items are concentrated in one or few caches. Larders are visited multiple times.

masting—An event that results when plants within a population synchronize their reproductive activity. Generally, masting describes not only abundance but also paucity of seed production. However, a “mast year” usually means a year in which plants produce a significant amount of seed. It is thought that masting occurs as an evolutionarily stable strategy through which plants are able to influence the size of animal populations that predate on the seed.

midden—An accumulation of cone debris that collects beneath the preferred feeding perches of squirrels. Squirrels may use middens for food storage.

molt—The gradual shedding and replacement of the feather coat in birds.

mutualism—An interaction between two or more species where both species derive benefit. Mutualisms can be lifelong interactions involving close physical and biochemical contact (known as symbiosis) such as those between plants and mycorrhizal fungi; they can also be briefer, nonsymbiotic interactions, such as those between flowering plants and pollinators or seed dispersers. Mutualisms may be facultative (optional) or obligatory.

passerine—A bird of the order Passeriformes also known as perching birds or song birds. Passerines are characterized by feet with three toes directed forward without any webbing or joining, and one toe directed backward. More than half of all species of bird are passerines.

population irruption—A density-dependent form of migration that is independent of predictable seasons, tides, or similar geographic events. In species of seed-eating birds, irruptions are population-wide responses to the absence of seed crops and result in individuals occurring outside of their defined range.

primary seed dispersal—Transport of seeds away from the parent plant to the site of first deposition.

scatter-hoarding—A method of food storage by animals in which items are cached in many locations throughout an individual's home range. Unlike larders, scatter-hoards are usually visited only once for caching and once for retrieval.

secondary seed dispersal—Movement of seeds from the site of initial deposition to all subsequent sites prior to seed germination.

songbird—A bird of the order Passeriformes in which the vocal organ is structurally more complex and more muscular than in other birds. Songbirds consequently have the most varied and intricate vocalizations among birds.

sympatric—Occupying the same or overlapping geographic areas without interbreeding. This term is used to describe populations of closely related species.

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English Equivalent

When you know:	Multiply by:	To find:
Centimeters (cm)	0.39	Inches
Meters (m)	3.28	Feet
Kilometers (km)	.62	Miles
Square kilometers (km ²)	.386	Square miles
Square kilometers (km ²)	247.1	Acres
Hectares (ha)	2.47	Acres
Milligrams (mg)	.015432	Gram

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Appendix 1:

Common and Scientific Names

Common name	Scientific name ^a
Plants (trees and shrubs):	
Beeches	<i>Fagus</i> spp.
Bitterbrush	<i>Purshia tridentata</i> (Pursh) DC.
Bush chinquapin	<i>Chrysolepis sempervirens</i> (Kellogg) Hjelmqvist
Digger pine	<i>Pinus sabiniana</i> Dougl. ex Dougl.
Douglas-fir	<i>Pseudotsuga menziesii</i> (Mirb.) Franco
Engelmann spruce	<i>Picea engelmannii</i> Parry ex Engelm.
Foxtail pine	<i>Pinus balfouriana</i> Grev. & Balf.
Giant sequoia	<i>Sequoiadendron giganteum</i> (Lindl.) Buchh.
Grand fir	<i>Abies grandis</i> (Dougl. ex D. Don) Lindl.
Great Basin bristlecone pine	<i>Pinus longaeva</i> D.K. Bailey
Jeffery pine	<i>Pinus jeffreyi</i> Grev. & Balf.
Knobcone pine	<i>Pinus attenuata</i> Lemmon
Korean stone pine	<i>Pinus koraiensis</i> Siebold <i>et</i> Zucc.
Limber pine	<i>Pinus flexilis</i> James
Lodgepole pine	<i>Pinus contorta</i> Dougl. ex Loud.
Monterey pine	<i>Pinus radiata</i> D. Don
Mountain hemlock	<i>Tsuga mertensiana</i> (Bong.) Carr.
Alderleaf mountain mahogany	<i>Cercocarpus montanus</i> Raf.
Noble fir	<i>Abies procera</i> Rehd.
Oaks	<i>Quercus</i> spp.
Pacific silver fir	<i>Abies amabilis</i> Dougl. ex Loud.
Colorado pinyon pine	<i>Pinus edulis</i> Engelm.
Ponderosa pine	<i>Pinus ponderosa</i> P.& C. Lawson
Red fir	<i>Abies magnifica</i> A. Murr.
Rocky Mountain bristlecone pine	<i>Pinus aristata</i> Engelm.
Siberian stone pine	<i>Pinus sibirica</i> Du Tour
Single-leaf pinyon pine	<i>Pinus monophylla</i> Torr. & Frém.
Sitka spruce	<i>Picea sitchensis</i> (Bong.) Carr.
Southwestern white pine	<i>Pinus strobiformis</i> Engelm.
Subalpine fir	<i>Abies lasiocarpa</i> (Hook.) Nutt.
Subalpine larch	<i>Larix lyallii</i> Parl.
Sugar pine	<i>Pinus lambertiana</i> Dougl.
Swiss stone pine	<i>Pinus cembra</i> L.
Western hemlock	<i>Tsuga heterophylla</i> (Raf.) Sarg.
Western juniper	<i>Juniperus occidentalis</i> Hook.
Western larch	<i>Larix occidentalis</i> Nutt.
Western redcedar	<i>Thuja plicata</i> Donn ex D. Don
Western white pine	<i>Pinus monticola</i> Dougl. ex D. Don
White fir	<i>Abies concolor</i> (Gord. & Glend.) Lindl. ex Hildebr.
White spruce	<i>Picea glauca</i> (Moench) Voss
Whitebark pine	<i>Pinus albicaulis</i> Engelm.

Common name	Scientific name
Birds:	
Blue jay	<i>Cyanocitta cristata</i>
Cassin's finch	<i>Carpodacus cassinii</i>
Clark's nutcracker	<i>Nucifraga columbiana</i>
Common raven	<i>Corvus corax</i>
Crows	<i>Corvus spp.</i>
Great horned owl	<i>Bubo virginianus</i>
Mountain chickadee	<i>Poecile gambeli</i>
Northern goshawk	<i>Accipter gentiles</i>
Pine grosbeak	<i>Pinicola enucleator</i>
Pine siskin	<i>Carduelis pinus</i>
Pinyon jay	<i>Gymnorhinus cyanocephalus</i>
Red crossbill	<i>Loxia curvirostra</i>
Red-breasted nuthatch	<i>Sitta canadensis</i>
Red-tailed hawk	<i>Buteo jamaicensis</i>
Scrub jay	<i>Aphelocoma coerulescens</i>
Spotted nutcracker	<i>Nucifraga caryocatactes</i>
Steller's jay	<i>Cyanocitta stelleri</i>
Western scrub jay	<i>Aphelocoma californica</i>
White-breasted nuthatch	<i>Sitta carolinensis</i>
White-winged crossbill	<i>Loxia leucoptera</i>
Williamson's sapsucker	<i>Sphyrapicus thyroideus</i>
Woodpeckers	<i>Picoides spp.</i>
Mammals:	
American marten	<i>Martes americana</i>
Black bear	<i>Ursus americanus</i>
Canada lynx	<i>Felix lynx</i>
Chipmunks	<i>Tamias spp.</i>
Deer mice	<i>Peromyscus spp.</i>
Douglas' squirrel	<i>Tamiasciurus douglasii</i>
Flying squirrels	<i>Glaucomys spp.</i>
Golden-mantled ground squirrels	<i>Spermophilus spp.</i>
Grizzly bear	<i>Ursus arctos</i>
Ground squirrels	<i>Ammnospermophilus spp., Spermophilus spp.</i>
Kangaroo rats	<i>Dipodomys spp.</i>
Least chipmunk	<i>Tamias minimus</i>
Marmots	<i>Marmota spp.</i>
Tree squirrels	<i>Sciurus spp.</i>
Pocket mice	<i>Perognathus spp.</i>
Red squirrel	<i>Tamiasciurus hudsonicus</i>
Voles	<i>Microtus spp., Myodes spp.</i>
Yellow pine chipmunk	<i>Tamias amoenus</i>

Insects and diseases:

Cone beetles	<i>Conophthorus</i> spp.
Cone worms	<i>Dioryctria</i> spp., <i>Eucosma</i> spp.
Limb rust	<i>Peridermium</i> spp.
Mountain pine beetle	<i>Dendroctonus ponderosae</i> Hopkins
White pine blister rust	<i>Cronartium ribicola</i> Fisch.

^a Scientific names and authorities of plants are from U.S. Department of Agriculture, Natural Resources Conservation Service (2007).

Appendix 2

Table 9—Stomach contents of 426 Clark’s nutcrackers from western Montana expressed as volume (percent) and frequency (percent) by months

Year	Month	Num-ber	Volume (and frequency) as percentages					Mam-mals
			Ponderosa pine	Whitebark pine	Douglas-fir	Misc. plants	Arthropods	
1946	Oct	6	48 (100)	5 (17)	45 (67)		2 (50)	
	Nov	5	2 (80)		98 (100)		T (20)	
	Dec	8	1 (38)		99 (100)		T (12)	
1947	Jan	7	55 (72)	3 (14)	42 (43)		T (29)	
	Feb	10	37 (100)	28 (60)	34 (50)	1 (10)	T (70)	
	Mar	25	24 (68)	5 (32)	69 (80)	T (16)	1 (44)	1 (44)
	Apr	16	46 (88)	9 (25)	36 (69)	1 (6)	8 (62)	
	May	22	31 (64)	29 (77)	14 (36)	T (5)	25 (96)	1 (5)
	Jun	8	16 (25)	46 (88)			38 (100)	
	Jul	9	2 (10)	62 (100)			T (33)	36 (100)
	Aug	13		84	(100)	1 (8)	14 (100)	1 (8)
	Sep	6		87	(100)		13 (33)	
	Oct	13	55 (93)	13 (46)			32 (85)	
	Nov	16	56 (94)	38 (88)			4 (44)	2 (19)
	Dec	18	47 (95)	33 (89)			4 (33)	16 (28)
1948	Jan	11	48 (100)	52 (91)		T (9)	T (27)	
	Feb	12	40 (100)	56 (100)			4 (42)	
	Mar	12	51 (100)	37 (100)		1 (8)	9 (83)	2 (8)
	Apr	17	39 (94)	23 (59)		8 (47)	22 (71)	8 (24)
	May	12	30 (83)	38 (92)		T (8)	26 (100)	6 (17)
	Jun	4	6 (50)	51 (75)			30 (100)	13 (25)
	Jul	20	1 (5)	19 (70)			T (5)	76 (100)
	Aug	0						
	Sep	3	95 (100)				5 (67)	T (33)
	Oct	0						
	Nov	41	96 (100)			T (5)	2 (32)	2 (5)
	Dec	0						
1949	Jan	21	91 (100)			T (5)	T (5)	9 (38)
	Feb	24	94 (100)				3 (37)	3 (17)
	Mar	24	86 (100)				4 (46)	10 (33)
	Apr	23	85 (100)				15 (91)	
	May	20	82 (100)			T (5)	18 (90)	
Weighted summation ^a			52.4 (80)	19.3 (42)	11.2 (15)	0.7 (6)	13.3 (59)	3.1 (12)

^a Volume percent = $S_w^v = \sum (N_1 V) / N_2$ when S_w^v = weighted summation of volumes, N_1 = number that month, V = percent of volume that month, and $N_2 = 426$ samples. Frequency percent, = $S_w^f = \sum (N_1 F) / N_2$, when S_w^v = weighted summation of frequencies, and F = percent frequency that month

Source: Reproduced from Giuntoli and Mewalt (1978).

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