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The Central Role of Clark's Nutcracker in the Dispersal and Establishment of Whitebark Pine*

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Summary. Whitebark pine (*Pinus albicaulis*) is known to have its seeds harvested and cached in the soil by Clark's Nutcracker (*Nucifraga columbiana*), and unretrieved seeds are known to be capable of germinating and establishing new pines. Many other vertebrates also harvest and feed on these seeds, however, and the roles of these animals as dispersers and establishers of whitebark pine has been uncertain. This work demonstrates that birds other than the nutcracker, rodents, and other mammals do not have the requisite behaviors to systematically disperse or establish whitebark pine, and that the pine is therefore dependent on the nutcracker for its regeneration. These findings support previous suggestions that Clark's Nutcracker is a specialized frugivore that has profoundly influenced the ecology and the evolution of whitebark pine.

Introduction

Several North American soft pines (*Pinus*, subgenus Strobus [Critchfield and Little 1966]) have large wingless seeds that are not dispersible by wind. These seeds are frequently removed from their cones by jays and nutcrackers (Aves: Corvidae), transported some distance, and cached in the soil as a future food resource. When more seeds are cached than are subsequently retrieved and destroyed by predation, the surplus becomes available for germination. Such interactions in western North America involve piñon (*Pinus edulis*), singleleaf piñon (*P. monophylla*), limber pine (*P. flexilis*), southwestern white pine (*P. strobiformis*), and whitebark pine (*P. albicaulis*) (Balda and Bateman 1971, Lanner 1980, Lanner and Vander Wall 1980, Ligon 1978, Tomback 1978, Vander Wall and Balda 1977). Similar dispersal and establishment systems have received study in Europe and Asia where the seeds of four species of stone pine (subsection Cembrae), close relatives of whitebark pine, are harvested, transported, and stored by the Eurasian Nutcracker, *Nucifraga caryocatactes* (Turček and Kelso 1968).

Notably lacking in past studies has been a serious attempt to determine the degree of dependency of a particular pine species on a corvid species for its dispersal and establishment. Dependency would not only have significant ecological consequences for the interacting partners, but would also determine the corvid's potential to act selectively on the pine (Lanner 1980, 1982) and perhaps *vice versa* (Vander Wall and Balda 1981). If, for example, a pine could be effectively dispersed and established only by a given corvid, then the distribution, site preference, spacing, and successional status of the pine would derive in large part from the behavior of the corvid; and many morphological characteristics and physioloical tolerances of the pine would result from the corvid's selective actions in choosing its food and cache site. If, however, a number of seed-caching animals shared the task of dispersing and establishing the pine, then the pine's characteristics would not be attributable to a single species, but would reflect the selective behaviors of all.

The objective of this study is to determine the relative importance to whitebark pine of the various potential dispersers and establishers present in its ecosystem. It has already been shown that whitebark pine seeds, cones, and crowns have numerous adaptations that prevent wind dispersal or passive seed dispersal, and that these adaptations facilitate nutcracker foraging (Lanner 1982). Previous research (Tomback 1978) has identified Clark's Nutcracker (*N. columbiana*) as a disperser of whitebark pine, but without demonstrating unequivocally the role of other animals. Therefore we felt that only by examining the behavior of all animals that forage on whitebark pine seeds would it be possible to determine their relative impacts. Practical considerations dictated restricting observations to diurnal vertebrates.

The study was conducted in Squaw Basin, 40 km east of Moran, Wyoming, in the Bridger-Teton National Forests. This area of high-elevation meadows (2805–2895 m) contains forested moraines and is bounded by the Breccia Cliffs and Absaroka mountains. The vegetation on slopes and ridgetops consists of forests of whitebark pine, Engelmann spruce (*Picea englemannii*), and subalpine fir (*Abies lasiocarpa*), with a few scattered lodgepole pines (*P. contorta*). The basin is dissected by stream channels lined with willows (*Salix* spp.), and contains numerous poorly drained swales supporting herbaceous meadow vegetation. Well-drained open areas support a sagebrush-grass mixture. Scattered small groves of pioneering whitebark

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pine commonly dot the moraines while older stands of whitebark pine, Engelmann spruce, and subalpine fir form a continuous forest overstory (Snethen 1980). Supplementary data were gathered at Mt. Washburn (2,680–3,140 m, Yellowstone National Park, Wyoming) and Surprise Lake (2,960 m, Grand Teton National Park, Wyoming). These two sites have vegetation like that of Squaw Basin, but they lack open-grown cone-bearing whitebark pines. Pure stands of whitebark pine are more common at Mt. Washburn and Surprise Lake than in Squaw Basin.

Methods

Cone-bearing whitebark pines were chosen for observation in a continuous forest, where Red Squirrels were present; and in the open, several hundred meters from the forest edge, where there was no sign of squirrel activity. In each of these two areas ("forest" and "meadow" respectively) 1005 whitebark pine cones, distributed among 14 forest and 21 meadow trees, were observed during the period 3 July to 2 November 1980. Cones were counted at intervals of 1–2 weeks using binoculars and a telescope. Counts were facilitated by "mapping" the cones of each tree on a clear acetate overlay on a plexiglass clipboard, and viewing them from a marked viewpoint 5–25 m from the tree. Partially consumed cones were recorded by estimating from the ground the percentage of seed remaining. Accuracy of these estimates was determined by estimating the number of seeds left in other partially harvested cones removed from the tree and counting the seeds. The prediction line that was obtained did not differ significantly from a slope of 1.0 ($r=0.88$, $n=68$). Cone-count data were converted into seeds using an empirically derived value for the mean number of seeds per cone (50.4 ± 24.2 seeds/cone, $n=91$). Percent of seed crop harvested was plotted against dates for both forest and meadow sites. The resulting curves were then compared to the standard logistic, Gompertz, and Von Bertalanffy curves (Ricklefs 1967) using the GENFIT computer program (written by Kim Marshall, Utah State University).

Sample cones were collected and examined at each cone observation date to determine cone maturity and contents. The number of filled, discolored, insect-attacked, and second-year aborted seeds per cone were recorded. Mean dry weight of shelled seeds was determined by weighing individually 100 seeds dried at 60° C for 48 h at each sample date. Seed coat thickness was measured on 10 seeds per date with a micrometer. Ten seeds per date were combusted in a Phillipson bomb calorimeter to obtain caloric values. Percent ash was determined from the combusted remains. Germination tests were made on agar-agar substrate in petri dishes, and in pots using a 40–60 (peat moss-sand) soil in the greenhouse after a 90-day "naked stratification" in polyethylene bags at 3° C (USDA Forest Service 1974). The test was run from 13 January to 30 August 1981, and consisted of three replications of 20 seeds/petri dish for each of 10 collection dates.

Seedfall caused by animal foraging was estimated by placing five 1-m^2 wire mesh seed traps randomly beneath sample trees. Data on cones per tree, seeds per cone, area of the tree crown, and number of seeds falling per square meter were used to estimate the proportion of seeds falling to the ground. Traps were designed to exclude animals.

Predation of cached whitebark pine seeds was studied experimentally in the autumns of 1979 and 1980. In 1979 artificial caches were made at depths of 3 cm (simulating nutcracker caches), and 7 cm (simulating squirrel caches), and on the surface, in both forest and meadow areas. Simulated cache depths were based on observations. Three caches containing 10 seeds each were made at each depth. The experiment was repeated in 1980 with 20 replications (12 forest, 8 meadow) of surface and 3 cm-deep caches. Surface caches contained 20 seeds each while 3 cm-deep caches had 10 seeds each in 1980. Seeds were placed in wire mesh trays to facilitate recovery. Final examinations of caches were made in the spring.

Time-budget data were collected on all diurnal vertebrates seen foraging on whitebark pine. Detailed observations (seconds per activity) were made in August, September, and October; and qualitative observations were made throughout the study period. Recognized behaviors were seed harvesting, seed caching, cone harvesting, cone caching, feeding, seed dropping, flight, preening, "play," aggression, and resting. These data were used to calculate the number of seeds harvested and cached per year by animals of each forager species. Data on relative population density of each species were then used to determine relative numbers of seeds harvested by each species.

Estimates of the maximum number of whitebark pine seeds transported by Clark's Nucracker and Steller's Jay per trip to the cache area were made from known volumes of the birds' pouch and esophagus (Vander Wall and Balda 1981). The number of seeds a bird can carry was derived by tightly packing seeds into a water-filled graduated cylinder until the appropriate volume of water was displaced. This measurement was replicated with 3 different groups of seeds at each date and then averaged.

Twenty-five Red Squirrel middens were surveyed to determine the kind and number of trees established on them. The results were compared with 25 non-midden areas sampled by random plots. A split-plot analysis of variance and Least Significant Difference multiple means test ($\alpha=0.05$ and 0.01) were run on these data to test for significant differences. Data on midden area, breast-height diameter (dbh) of all stems, species of trees and cones, and number of annual rings at ground level were collected for each midden. Tree cross-sections or increment cores were aged in the laboratory with a stereomicroscope.

Results

Maturation of whitebark pine seed

Mean dry weight of seeds increased significantly through 31 August. After that date, there was no significant difference between successive means (Student-Newman-Keuls multiple means test, $\alpha=0.05$). Dry weight of a seed averaged 72.09 ± 13.2 mg from 31 August to 1 November. At each date there was considerable variability, as shown by the large standard deviations from the means (Table 1).

Mean calories per ash-free gram showed no significant difference between sampling dates after 13 August. Seedcoat thickness was significantly greater from seed collected after 31 August than before this date ($\alpha=0.05$, Student-Newman-Keuls, Table 1).

Table 1. Changes in weight, coat thickness, germination, and caloric content of whitebark pine seeds from Squaw Basin, Wyoming between July and November 1980

Date	Weight of oven-dry seeds $\bar{X} \pm SD$ mg	Seed coat thickness $\bar{X} \pm SD$ mm	Germination percent	Caloric content of shelled seeds $\bar{X} \pm SD$ cal/ash-free gm	Ash content of seeds percent
22 July	4.06± 0.62	0.17±0.05	0.0	4,808± 8	12.2
5 Aug.	19.52± 6.47	0.23±0.08	1.7	6,202±110	5.1
13 Aug.	48.60±11.71	0.35±0.07* [a]	6.7	7,112±111*	3.8
24 Aug.	50.69±11.24	0.31±0.06	6.7	7,012±110*	2.2
31 Aug.	72.50±10.31*	0.39±0.06*	56.7	7,299±238*	2.6
6 Sept.	73.41±18.57*	0.41±0.09*	8.3	7,241±153*	1.2
17 Sept.	74.10±11.40*	0.41±0.06*	16.7	7,121±199*	1.3
27 Sept.	71.58±14.87*	0.41±0.07*	20.0	7,155± 94*	1.6
11 Oct.	65.82±13.61*	0.42±0.06*	6.7	6,947±174*	2.7
2 Nov.	75.12±12.92*	0.39±0.09*	–	7,012±135*	2.8

[a] * indicates value significantly different ($\alpha = 0.05$) from earlier values according to Student-Newman-Keuls multiple mean test

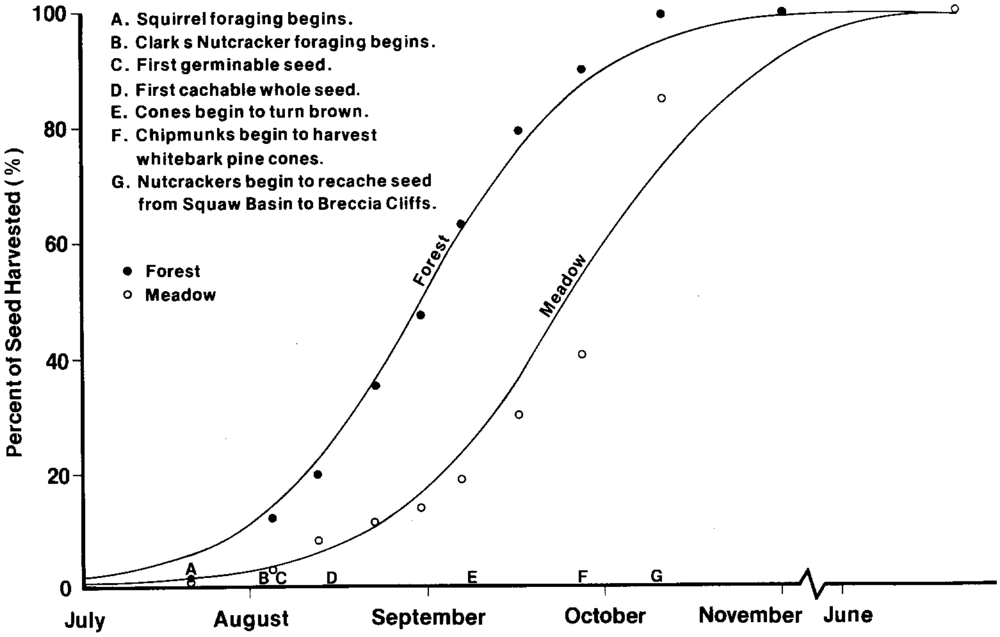

Fig. 1. Seasonal course of whitebark pine seed harvest by vertebrates in Squaw Basin, Wyoming, in 1980

Seeds collected prior to August 5 failed to germinate; while lots collected on that date and thereafter showed variable results (Table 1).

Whitebark pine cones were still moist and pulpy in August, and seed coats were thin and fragile. Consequently, nutcrackers and other animals were unable to extract whole seeds from the cones until 15 August. Before this date, nutcrackers left shell fragments lining the cone, and acquired only fragments of seed.

Cones dried and turned dull brown by 7–10 September. The scales then loosened and the cones fell apart when briskly handled. Though cones of whitebark pine are described as indehiscent by Shaw (1914), 24.8% of those collected after 7 September parted their scales 4–8 mm from tip to tip ($n = 141$). This allowed the seeds to be seen but not to fall out of the cone.

Cone Contents

Ninety-one cones collected on and after 31 August were disassembled, and the contents analyzed. First-year ovule abortions caused by lack of pollination were not tallied, as they do not produce a normal-size seed.

The cones ranged in length from 23–89 mm ($x = 53.2 \pm 13.2$ mm), and contained 6–110 viable seeds ($\bar{x} = 41.2 \pm 23.4$), which comprised 82% of the total seeds.

Seed Crop Depletion

As animals intensified their harvesting efforts, the rate of seed depletion increased rapidly in both forest and meadow plots (Fig. 1). Both the forest and meadow curves correlate closely with the logistic growth curve: $r^2 = 0.99$ in the forest and $r^2 = 0.96$ in the meadow. The harvest was considerably earlier in the forest than in the meadow areas. Thus, in the forest, 50% of the seed crop had been harvested by 31 August, while in the meadow, this point was not attained until 25 September. By 1 November, no seeds remained on forest trees and only 0.1% of the original seeds remained on trees in the meadow. We observed no whitebark pine cones falling, independent of animal foraging, during several hundred hours of observations in whitebark pine forests from 1977–1981. Seed trap analysis showed that 4.2% of the filled whitebark pine seed dropped to the soil surface, probably due to foraging animals, in 1980.

Seed Predation

Seed predation was strongly influenced by proximity of the seeds to the soil surface. No surface-broadcast seeds, whether in the forest or the meadow, survived from September to the following July in a test during 1979–1980. Many shell fragments were left in the seed trays, indicating onsite consumption, though some of the seeds may have been stored for later use. In tests conducted during 1980–1981, only 7% of the surface-bradcast seeds survived 2 weeks of exposure under crowns of cone-bearing whitebark pines, and only 1 seed of 400 survived to 26 June. That seed had an aborted embryo and was probably left behind for that reason. Of 260 seeds collected under 4 trees and from the 5 seed traps in fall 1980, 30.0% were filled and judged sound (compared to 82% of seeds in cones), 25.8% had aborted, and 44.2% were discolored and judged ungerminable. By June 1981, no seeds remained under these trees.

Arttificial seed caches at 3 cm (depth of nutcracker cache) yielded different results for forest and meadow plots. In the 1979–1980 study, only 43.3% of the seeds cached in the forest survived until the next June, whereas all of the seeds cached in the meadow survived. Similar experiments in 1980–1981 showed only 10.0% survival in the forest ($n = 12$ caches) but 62.9% survival in the meadow ($n = 8$ caches).

All of the seeds cached at 7 cm depth survived predation in both forest and meadow in 1979–1980. This experiment was not repeated in 1980–1981. Cutting tests on 100-seed subsamples of the seeds used in these experiments showed 89% filled seed in 1979–1980 and 82% filled seed in 1980–1981.

Animal Interaction With Whitebark Pine Seeds

Many of the diurnal birds and mammals that were observed in whitebark pine stands did not harvest the whitebark pine seeds. These include the Gray Jay (*Perisoreus canadensis*), Common Flicker (*Colaptes auratus*), Cassin's Finch (*Carpodacus cassinii*), rosy finch (*Leucosticte* sp.), Pine Siskin (*Spinus pinus*), Dark-eyed Junco (*Junco hyemalis*), pine marten (*Martes americana*), coyote (*Canis latrans*), and weasel (*Mustela* sp.). Gray Jays were never seen foraging on whitebark pine seed during 3,463 seconds of foraging observations (Table 2). Their caching was limited to placing fresh carrion or boli on pine or spruce branches. Two Magpies (*Pica pica*) were seen in Squaw Basin, but they did not forage on conifer seeds. No evidence of whitebark pine cones or seeds was found in 13 coyote scats examined at Squaw Basin in 1980. The following 11 vertebrates did forage on seeds of whitebark pine and require consideration as possible seed dispersers.

Table 2. Time (seconds) spent by birds and mammals foraging on whitebark pine seeds as a percent of total foraging time in whitebark pine stands between 15 August and 11 October 1980

	Total foraging time seconds	% Time spent successfully foraging on whitebark pine seeds		% Time spent unsuccessfully foraging on whitebark pine seeds
		in trees	on ground	
Clark's Nutcracker	42,401	97.5	0.2	1.3
Steller's Jay	2,541	24.5	14.0	6.9
Raven	572	78.7	0	21.3
Pine Grosbeak	1,797	91.7	0	2.3
Mountain Chickadee	1,235	7.6	0	13.0
Red-breasted Nuthatch	262	0	0	100.0
Red Squirrel	852	60.0	15.8	0
Chipmunk	1,625	35.4	20.8	8.1

Clark's Nutcracker (*Nucrifraga columbiana*)

The nutcracker was by far the most frequently observed resident vertebrate to forage in whitebark pine trees (Table 3). At all times of year birds were observed alone or in small, loosely organized flocks. Foraging was almost entirely restricted to whitebark pine seed still in the cone (97.5%), though some ground foraging on fallen seeds also occurred (0.2%, Table 2). Seed extraction rates from whitebark cones were relatively low in mid-August but increased markedly in September (Table 4). One bird harvested 74 seeds at the rate of 32 seeds/minute on 19 September. During the mast season, less than 1% of nutcracker foraging time was devoted to insects. On 17 August, a juvenile nutcracker briefly pecked at a subalpine fir cone, but harvested no seeds. Engelmann spruce and lodgepole pine seeds were not harvested by Clark's Nutcracker. Seeds of all of these species were present in cones of the current year's crop or, in the case of lodgepole pine, from the serotinous cones of previous years.

Nutcrackers foraged on cones as early as 13 July 1979 (Surprise Lake), 23 July 1980 (Brooks Lake, 35 km northeast of Squaw Basin), and 4 August 1980 (Squaw Basin). At this time they were unable to pull whole seeds from the closed cone due to the thin seed coaats (Table 1). Some seeds were dropped to the ground by nutcrackers, but only rarely recovered by them. From 15 to 23 August, the birds cached the new seed crop, while continuing to recover, and recache, the previous year's seeds. Many of these cached seeds had already germinated. Nutcrackers cached seeds by bringing them up from the pouch, one by one, and pushing them into the soil with their bills. Only whitebark pine seeds were cached in 35,986 s of observations. We only observed seeds being cached either within 100 m of the harvest site, or 3.5 km away on the Breccia Cliffs. Caches were made at the bases of trees, rocks, or annual plants, in dense moss growth, or in the open. Some cache locations were heavily shaded by the forest canopy, while others were on

Table 3. Number of visits to whitebark pine trees by potential dispersers of whitebark pine seed in the study sites[a]

	Number of visits							
	Squaw Basin		Mt. Washburn		Surprise lake		Grand total	
	Total	per hour	Total	per hour	Total	per hour	Total	per hour
Clark's Nutcracker	448	3.4	544	14.3	79	4.8	1,071	5.7
Gray Jay	89	0.7	8	0.2	0	0	97	0.5
Steller's Jay	11	0.1	11	0.3	1	0.1	23	0.1
Raven	15	0.1	18	0.5	3	0.2	29	0.2
Mountain Chickadee	26	0.2	37	1.0	0	0	63	0.3
Red-breasted Nuthatch	4	<0.1	1	<0.1	0	0	5	<0.1
Pine Grosbeak	13	0.1	6	0.2	2	0.1	21	0.1
Red Squirrel	116	0.9	5	0.1	4	0.2	125	0.7
Chipmunk	10	0.1	4	0.1	3	0.2	17	0.1
Golden-mantled ground squirrel	0	0	1	<0.1	0	0	1	<0.1

[a] Periods of observation were as follows: Squaw Basin, 133.4 h; Mt. Washburn, 38.0 h; Surprise Lake, 16.6 h; total = 188.0 h

Table 4. Foraging rates of vertebrates harvesting whitebark pine seeds from cones between August and November 1980

	Number of seeds harvested per minute of foraging time											
	Clark's Nutcracker		Steller's Jay		Raven		non-corvid birds		Red Squirrel		Chipmunk	
	$\bar{X}\pm$SD	n	$\bar{X}\pm$SD	n	$\bar{X}\pm$SD	n	$\bar{X}\pm$SD	n	$\bar{X}\pm$SD	n	$\bar{X}\pm$SD	n
15–18 August	4.5±3.4	8	–		–		–		51.3±20.7	17	–	
7–10 Sept.	10.7±2.9	3	0.7±0.5	4	0.6±0.4	3	0.7±0.4	6	36.7±17.0	7	–	
17–19 Sept.	12.3±8.1	10	–		–		–		14.8±20.5	3	–	
27–29 Sept.	–		–		–		–		–		1.8±0.9	5
10–12 Oct.	2.8±1.7	5	–		–		–		–		–	
1–2 Nov.	0	2	–		–		–		–		–	

open meadow. Seeds were cached on all exposures, near a spring, on a streambank, and even in a puddle of water. As the seed crop dwindled in mid-October, mutcrackers spent a great deal of time recovering seeds from the Squaw Basin meadows, transporting them to the steep, southwest-facing Breccia Cliffs, and re-caching them. By 2 November, nutcrackers were almost totally dependent on cached seeds for their food supply, and on occasion pecked through 10 cm of snow to recover them.

Nutcrackers cached singly or in flocks of up to 150 birds. On Mt. Washburn, groups of 10–15 birds were seen caching within a 100-m^2 area on several occasions with no signs of aggression.

Cache size ranged from 1–14 seeds ($\bar{x} = 3.2 \pm 2.8$ seeds/cache, $n = 157$). One-seeded caches predominated (35%) followed by 2- and 3-seeded caches (18.5% and 18%), with larger caches present in successively lower frequencies. Our calculations indicate a nutcracker's pouch can hold an average of 92.7 ± 8.9 seeds, assuming a pouch capacity of 20 ml (Vander Wall and Balda 1977).

Number of Whitebark Pine Seeds Cached

An estimate of the number of seeds cached per individual nutcracker in 1980 was made after splitting the caching season into two time periods: *early* (15 August–10 September) and *late* (11 September–2 November). This was necessary because seed extraction rate increases significantly in mid-September; and birds become more active in harvesting and caching seed, and spend less time on maintenance.

The following formula was used: $T_{\mathrm{fp}} + T_{\mathrm{fc}} + T_{\mathrm{c}} + T_{\mathrm{m}} =$ Time to make a single caching trip where T_{fp} is the average time it takes a nutcracker to fill its pouch (93 seeds at 9.68 s/seed *early*, and 93 seeds at 6.6 s/seed *late*); T_{fc} is the mean flight time to and from the Breccia Cliffs cache site (7.0 km round trip at 47.1 km/h, Vander Wall and Balda 1981); T_{c} is the mean time to cache a pouchload of seeds (assumed to be about 10 min from our observations and Vander Wall and Balda 1977); and T_{m} the mean time spent on maintenance and social behavior (preening, displacing other birds from cones, etc.), assumed to be 15 min per trip *early*, and 7.5 min *late*. Adding these values gives the total time per round trip as 2,934 s (*early*), and 2,197 s (*late*). During both early and late periods, caching activity is most pronounced during about 9 h of the day, despite changes in daylength.

Assuming a harvest season of 80 days, 1,053 trips are made each year by each nutcracker. Assuming 93 seeds/trip, about 98,000 seeds are cached per individual per year.

Steller's Jay (Cyanocitta stelleri)

Steller's Jays are elusive birds that, because of their dark plumage and long periods of silence, are rather inconspicu-

Table 5. Comparative harvest of whitebark pine seeds by vertebrates in Squaw Basin, Wyoming, 1980, calculated from time-budget data

	Extraction rate (seed/min)[a]	Time spent foraging (min/day)[b]	Harvest duration (day/season)[b]	Seeds harvested (seeds/individual)	Relative abundance (%)	Relative number of seeds harvested (seeds/1,000,000)[c]
Clark's Nutcracker	7.9	180	91	129,000	70	364,000
Steller's Jay	0.7	120	55	4,620	2	370
Raven	0.6	30	53	954	2	76
Chickadees & Nuthatches	0.7	120	56	4,700	7	1,320
Red Squirrel	43.4	240	84	875,000	18	633,000
Chipmunk	1.7	120	35	7,140	2	575

[a] Seasonal average from observations of 15 August–11 October
[b] Estimate from daily activity patterns
[c] Calculated by multiplying the preceding two columns and adjusting to 1,000,000 seed base

ous within the whitebark pine forest. They were usually seen alone or in pairs, and were far less common visitors to whitebark pine trees than were nutcrackers (Table 3). These jays first appeared in the whitebark pine forests in early September, when cones were mature. They began harvesting seeds on 7 September 1980. About 25% of their foraging time was spent harvesting whitebark pine seed from cones in trees (Table 2), though their foraging was less efficient than that of the nutcracker (Table 4). Ground foraging for fallen whitebark pine seeds occupied 14% of their foraging time in whitebark pine stands (Table 2). Steller's Jays were sometimes unable to break off cone scales with their bills to extract seed. Therefore, they often foraged on seeds previously exposed by nutcrackers. Steller's Jays tore seeds apart with their bills to consume small pieces of female gametophyte and embryo tissue, and thus did not pass seed through their digestive tract undamaged. Jays placed no more than 5 whitebark pine seeds in their elastic esophagi, although calculations based on data from Vander Wall and Balda (1981) indicate they can hold up to 34 seeds.

Steller's Jays were seen caching whitebark pine seeds in a witches'-broom, under lichen growth on a branch, and in a branch crotch; but not in the soil.

They often foraged on the ground in company with nutcrackers. They were never seen uncovering a nutcracker cache, and no aggression occurred between the two species during foraging or caching.

Raven (*Corvus corax*)

Ravens are relatively uncommon visitors to whitebark pine trees (Table 3) and were seldom observed foraging on seed. Their large bodies and bills make it difficult for them to forage efficiently on whitebark pine cones (Table 4). They sat above the cones and reached down, pulling off cone scales to expose the seeds. After acquiring 1–2 seeds, they flew down to a rocky south-facing slope. We did not see them caching seeds.

Pine Grosbeak (*Pinicola enucleator*)

On 9 September, small, wandering flocks of Pine Grosbeaks were first observed searching through cones. They obtained whitebark pine seeds by pulling off the cone scales with their stout beaks, or took seeds exposed by nutcracker foraging. Their foraging rate was far lower than that of the nutcracker (Table 4). They dropped seed 2.3% of the observed foraging time (Table 2). They tore seeds apart with their bills, and thus did not pass undamaged seeds through the digestive tract. We did not see them caching seeds.

Mountain Chickadee (*Parus gambeli*)

Mountain Chickadees are resident throughout the year in whitebark pine stands and move through the forest in small flocks. They were never seen foraging on the ground, and most of their foraging in trees was for insects. After 6 September however, 7.6% of their tree foraging time in whitebark pine stands was spent harvesting whitebark pine seeds in trees (Table 2). The seeds are too large for them to handle efficiently and most were dropped. One bird dropped 6 of 7 consecutively harvested seeds. Chickadees tore seeds apart with their bills to consume small pieces of seed, and thus did not pass undamaged seeds through the digestive tract. No caching of whitebark pine seeds was observed.

Red-breasted Nuthatch (*Sitta canadensis*)

Red-breasted Nuthatches occasionally foraged among whitebark pine cones but we never saw them succeed in harvesting seeds (Table 2).

Red Squirrel (*Tamiasciuris hudsonicus*)

Red Squirrels are common and conspicuous inhabitants of subalpine conifer forests, including stands of whitebark pine that are large enough to provide territories with the necessary requirements of food and cover. After Clark's Nutcracker, they were the most commonly observed vertebrates visiting whitebark pine trees (Table 3). Red Squirrels spent 60% of their total foraging time in trees foraging on whitebark pine cones (Table 2) and 11.3% in Engelmann spruce cones. 15.8% of their foraging time was spent collecting whitebark pine seeds dropped on the ground by other animals, and 12.9% harvesting seeds of herbaceous plants. Red Squirrels' foraging rate was much higher than that of any other animal because they almost always harvested the whole cone, especially in August and early September (Table 4). They started their harvest earlier than the other animals – by 13 July 1979 (Surprise Lake), and 22 July 1980 (Squaw Basin). Observations of cones in middens during 1980 indicated that whitebark pine was the first species harvested, followed by Engelmann spruce (18 August), subalpine fir (11 September), and lodgepole pine (27 September).

Cone caching began 4 August 1980 at Squaw Basin, but at Surprise Lake occasional cones were cached as early as 13 July 1979. All the cones cached in 114 observations were cached on or in "middens" – extensive areas piled with the cone debris of many years (Finley 1969). Of the time spent caching food, 61.4% was devoted to whitebark pine cones, 16.9% to whitebark pine seeds, 11.8% to Engelmann spruce cones, 6.3% to lodgepole pine cones, and 0.5% to subalpine fir cones (based on 7,304 s of observations). A few mushrooms and herbaceous plant seeds were also cached.

After 16 September 1980, squirrels began making large seed caches from their cached cones. These were made by extracting a single seed from a cone, running several meters to place the seed in a deep hole in the midden, and then running back to the cone to get another seed. Cones were not brought to the hole. This took a mean of 63.8 ± 36.5 s/seed cached ($n = 34$). Caches were placed 6.5–40 cm deep ($\bar{x} = 15.2 \pm 12.3$ cm, $n = 6$; 4 of these caches were 11–11.5 cm deep). The number of seeds per cache ranged from 14–55 ($\bar{x} = 28.8 \pm 19.2$ seeds/cache; $n = 4$), although Kendall (1980a) found up to 176 seeds in a single cache. In a 14- and a 31-seed cache, all the seeds were found to be filled.

Establishment of Conifers on Squirrel Middens

The squirrel middens surveyed in this study ranged in area from 15 m^2 to 158.5 m^2 ($\bar{x} = 64.2\ m^2 \pm 37.8\ m^2$, $n = 25$) and totaled 1,605.3 m^2. They varied in depth from a superficial layer of scattered cone parts to deposits at least 30 cm thick, comprised of unincorporated cone litter material on the surface and successively more decomposed material beneath the surface. Squirrels dig deep holes for cone storage in the midden, especially around the roots of large trees that have been engulfed by the midden. Probably because of this disturbance, large numbers of dead trees were found on midden surfaces and along their edges. A split-plot analysis of variance showed significantly fewer living tree stems in the lower size classes, growing on midden surfaces than on randomly sampled forest floor. Thus, for example, whitebark pine seedlings (≤ 1 cm diam.) and small saplings (< 10 cm diam.) were far less likely to be found on midden surfaces than on forest floor ($P < 0.05$, Student-Newman-Keuls multiple mean test). The youngest whitebark pine growing on a midden had 30 annual rings at the root collar, indicating that not a single seedling of this species had succeeded in establishing and maintaining itself in the past 29 years on over 1,600 m^2 of midden surface. Three germinating seedlings were found on two middens in early June, but all were dead by September. The youngest whitebark pines on middens ranged in age from 30 to 246 years ($\bar{x} = 82.5 \pm 67.9$ years, $n = 15$). Engelmann spruce establishment showed the same pattern, with significantly fewer seedlings and small saplings on middens than on random forest floor. The youngest spruce on a midden was 20 years old. But subalpine fir showed the opposite pattern. There was a significantly greater number of fir stems less than 1 cm dbh on midden edges, and a 6-year-old seedling was collected from a midden. Despite the relative rarity of subalpine fir in Squaw Basin (Snethen 1980), dense stands of his species occur on middens where squirrels have stored fir cones. In fact, middens can often be located from a distance by the ring of subalpine fir surrounding them.

Chipmunk (Eutamias sp.)

Chipmunks were relatively uncommon visitors to whitebark pine trees (Table 3). Most of their time was spent on the ground in close proximity to sagebrush (*Artemisia tridentata* Nutt.). Considerable time observing these animals in 1980 and 1981 revealed a preference for herbaceous plant materials (*Lupinus, Epilobium,* etc.), at least until these plants die back in mid-September. Tree-foraging activities directed at whitebark pine cones occupied 35.4% of the total time devoted to foraging in whitebark pine stands. About 8% of the foraging time in these stands led to unsuccessful attempts (i.e. dropped seed, etc.). Their foraging rate was well below that of the Red Squirrel or Clark's Nutcracker (Table 4). Foraging for whitebark pine seeds dropped on the ground, by themselves and other animals, occupied almost 21% of the foraging time spent in whitebark pine stands by chipmunks (Table 2). At Squaw Basin chipmunks did not ascend whitebark pine trees until 27 September in 1980, when cones were mature and the scales loose. We observed no caching of seeds. Three chipmunk burrows were inspected to about 20 cm from the entrances, without finding stored whitebark pine seeds. On 24 June 1980 at Surprise Lake, a chipmunk was observed uprooting and consuming a whitebark pine seedling.

Golden-mantled Ground Squirrel (Spermophilus lateralis)

This species occurs on the upper slopes of Mt. Washburn but was not observed on the Squaw Basin study site. Ground squirrels were once observed foraging on a whitebark pine cone in a tree. The seeds were pouched but eaten as soon as the squirrels reached the ground. We observed no caching of seeds.

Grizzly and Black Bears (Ursus arctos horribilis, U. americanus)

Grizzly bears were never observed foraging in whitebark pine but recent activity was evident. A squirrel midden at Squaw Basin was torn apart by a grizzly bear between 5 and 13 August 1980. The large amount of fecal material left behind contained only one intact seed of several thousands ingested. Four other samples of grizzly feces found on Mt. Washburn on 1 June 1980 and 18 June 1981 contained only 2 filled, undamaged seeds. A collection of black bear feces from Squaw Basin contained 1 undamaged whitebark pine seed. All fecal collections were within 25 m of a ravaged squirrel midden.

Discussion

Our results clearly show that the only reliable establishment mechanism for whitebark pine in Squaw Basin is the germination of seeds cached by Clark's Nutcracker, and that the caching behavior of the nutcracker is conducive to successful establishment.

When the rate of nutcracker foraging began to increase in mid-August (Fig. 1, meadow curve), seeds were already mature and germinable (Table 1). Their large size and high caloric content combined to make them a far more attractive and advantageous food for nutcrackers than the seeds of other conifers in the area (Lanner 1980, 1982). Their thickened seed coats allowed them to be pulled out of the cones, manipulated in the bill, pouched, unpouched, and cached in often stony soil – all without damage. Germinability tests indicate that seeds cached at almost any time in the harvesting season had the potential of becoming seedlings. When, in early September, cones dried out and became more frangible, the nutcrackers' harvesting activities were further facilitated. Nutcrackers are, however, capable of removing the seeds from unripe cones as well.

Energy contents of these whitebark pine seeds compare closely with those reported by Lanner (1982), though his were expressed in cal$\cdot$gm^{-1} of seed contents, rather than as cal$\cdot$ash-free gm^{-1}, as is done here. Thus his values range 6,432–7,308 cal gm^{-1} for seeds from different cones, while ours range 6,202–7,299 cal$\cdot$ash-free gm^{-1}. The low germination rates in our laboratory tests are difficult to interpret. Little is known of whitebark pine seed biology. However, dormancy, perhaps due to seed-coat impermeability or immature embryos (Pitel and Wang 1980), may postpone germination of many seeds until the second or third year (USDA Forest Service 1974).

The more rapid depletion of seeds borne on forest trees than on meadow trees was due mainly to predation by Red Squirrels. Squirrels initiated their harvesting earlier than did nutcrackers, they were more efficient in their harvest, and they exerted dominance over nutcrackers in agonistic encounters. We believe these are sufficient reasons to explain the more rapid depletion of seeds in the forest than in the meadow where squirrels were absent. Our failure to observe the passive falling of whitebark pine cones supports the contention of Lanner (1982) that these cones do not normally fall from the tree, but are forcibly removed or disassembled on the tree by animals, mainly nutcrackers and squirrels. The likelihood of fallen seeds germinating and becoming established is thereby diminished. The same conclusion must be drawn from the almost total failure of surface-broadcast seeds to survive until the next growing season. The higher survivability of seeds buried at "nutcracker depth" and the absence of predation on those at "squirrel depth" demonstrate that seed burial is indeed as effective anti-predator strategy. We doubt, however, that seeds at "squirrel depth" (7 cm) often germinate and establish successfully, because their hypocotyls, even when elongated, are too short (3–4 cm) to permit frequent emergence of the cotyledons above the soil surface. Bossema (1979) also observed that acorns exposed on the soil surface disappeared due to predation much more rapidly than buried acorns.

The pattern of nutcrackers caching many of their harvested seeds within 100 m of the harvest site explains the frequent regeneration under the canopy of whitebark pine, i.e., its tendency to behave as climax species (Lanner 1980). Such all-aged stands are common in soft pine species whose seeds are dispersed by corvids (Lanner 1980) but not among typical white pines whose seeds are wind-dispersed (R. Lanner, unpublished). The long-distance dispersal to the Breccia Cliffs is similar to the pattern described by Tomback (1978) in the Sierra Nevada, though far short of the very long dispersal flights – to 22 km – reported by Vander Wall and Balda (1977). Caching seeds close to the harvest site and subsequently re-caching them on the Breccia Cliffs would appear to increase the number of seeds nutcrackers can harvest. By caching them near the source, the nutcracker eliminates the need for time-consuming flights to the cliffs and can therefore concentrate more intensively on the harvest. Later, when the harvest is complete, seeds can be moved to the cliffs without foregoing harvesting opportunities.

It is advantageous for nutcrackers to cache seeds in the open because of the much lower rate of seed predation. Caching in the open also produces benefits for future nutcracker populations, for three reasons. First, seeds germinating in the open are subject to less shading and root competition, and are more likely to become successfully established. This would make possible the survival of more established trees to seed-bearing age than would be the case within the dense whitebark pine-spruce forest, and would help to guarantee a food source for future nutcracker populations. Second, whitebark pines establishing in the open develop larger crowns capable of producing bigger seed crops than those formed on the small, narrow crowns of forest-grown trees. And finally, these seed crops are inaccessible to the Red Squirrel, the nutcracker's only strong competitor for whitebark pine seeds. Having many of its seeds cached in the open benefits whitebark pine as well, by assuring its establishment.

Our observations of caching sites disagree with those of Tomback (1978), who "...never observed nutcrackers use the shores of lakes, stream banks, meadowland, or any other damp areas..." Moist cache sites are not necessarily disadvantageous, despite the possibility that seeds may spoil (Tomback 1981). We have successfully germinated whitebark pine seeds taken from a partially-rotted cone found in wet debris 25 cm deep in a squirrel midden. According to Finley (1969), squirrels frequently cache cones under water, and the storage conditions retain seed freshness for long periods.

Nutcrackers outnumber other seed predators. They harvest more whitebark pine seeds and do so more efficiently than any other predator except the squirrel. They specialize on whitebark pine seeds, when available, almost to the exclusion of other foods, and they carry large numbers of seeds to sites near and distant. For all these reasons, nutcrackers are substantially more effective dispersers than other vertebrates. In addition, they cache seeds in quantities well beyond their metabolic needs (Vander Wall and Balda 1977) sufficiently deep in the soil to reduce predation and desiccation, yet shallow enough to permit seedling establishment; and they do so on sites favorable to whitebark pine growth (Lanner 1980). This syndrome of behavioral traits makes them the only potential dispersers capable of systematically regenerating whitebark pine. Some other vertebrates may occasionally be effective as *dispersers*, some rarely as *establishers*, but only the nutcracker performs both roles.

Steller's Jay is an insignificant disperser because of its small numbers and the small number of seeds it caches. Though this corvid is reported to cache piñon seeds in the soil (Vander Wall and Balda 1981), its cache sites in Wyoming were in trees, and could not support seedling establishment. Ravens were even less effective as establishers for the same reasons, despite the report by Reimers (1959, in Turček and Kelso 1968) that they store seeds of Siberian and Japanese stone pines, presumably in soil caches. Grosbeaks, chickadees, and nuthatches eat small numbers of seeds at or near the point of harvest. Chickadees and nuthatches cache conifer seeds in branch and bark crevices, but are not known to cache seeds in the soil (Smith and Balda

1979). The small numbers of seeds these birds may drop on the ground are highly vulnerable to predation by ground-foraging animals. They may therefore be dismissed as effective agents of dispersal and establishment.

The Red Squirrel is the most voracious harvester of whitebark pine seeds, and would seem an ideal candidate for the roles of disperser and establisher, but this is not so. The squirrel's small territories, 0.5 to 3 acres according to Smith (1970), limit its transport distance; and the squirrel's absence from open areas outside the forest suggest it is ineffective in dispersing seeds to points not already forested. The midden surface, where the squirrel does all of its cone and seed caching, is not a suitable substrate for pine or spruce regeneration, though it is obviously suitable for subalpine fir regeneration; and on several occasions squirrels have been observed eating newly germinating seedlings. When the squirrel buries seeds, they are usually placed too deep in the soil or midden debris for successful germination and establishment. Pines that might get established in the midden are likely to die of root damage due to the constant digging-up and churning of midden material by the squirrel. With respect to whitebark pine and Engelmann spruce, our findings support the position of Hatt (1943) and Finley (1969), that Red Squirrels are not important agents of afforestation; rather than that of Klugh (1927), Bailey (1931), and MacClintock (1970) who did consider these mammals effective tree establishers. Of course, occasional establishment of these conifers can be expected, but as a random event, not regularly. The strong tendency of subalpine fir to regenerate on and at the edge of middens is, however, another matter. The seeds of firs are, probably because of their resin-filled blisters, a food of last resort for rodents and squirrels (Abbott 1962; Howard and Cole 1967, Smith 1970). We suggest that when other seeds are available, fir cones tend to be pushed aside and ignored, and that when the cones disintegrate to release the seeds, as is normal for *Abies* cones, some of the seeds germinate. Species of North American *Abies* frequently become established on organic seedbeds (USDA Forest Service 1965). Therefore it seems reasonable to speculate that the Red Squirrel is an agent of subalpine fir regeneration, but more observations are needed.

Chipmunks are unlikely agents of whitebark pine seed dispersal or establishment. They devoted only minor attention to pine seeds, as also noted by Heller (1971) in the Sierra Nevada. They handled the large seeds clumsily and often dropped them. Their major foraging effort was devoted to herbaceous plants, as noted in other studies (Tevis 1952, 1953a, b; Broadbrooks 1958; Heller 1971), Any pine seed they might cache would probably be buried far too deep to germinate, as chipmunk caches have been found to average 28 cm in depth (Broadbrooks 1958). Most chipmunk activity at Squaw Basin was in open meadow areas, but by the time these animals began foraging on whitebark pine seeds, over half of the seed crop had already been depleted. These conslucions are in marked contrast to those of several authors who, without presenting supporting data, have asserted that chipmunks are important agents of afforestation (Gordon 1943; Tevis 1953b; Shtil'mark 1963; MacClintock 1970). We saw no evidence that chipmunks influence tree regeneration.

The limited observations of the golden-mantled ground squirrel suggest it is insignificant as an agent of dispersal or establishment of whitebark pine. This is further supported by its absence from Squaw Basin, the infrequency of its tree-climbing (Tevis 1953b), and the great depth of its caches (MacClintock 1970).

Black bears and grizzlies raid squirrel middens to feed on lipid-rich whitebark pine seeds, especially in the fall, preceding hibernation (Mealey 1975; Picton 1978; Kendall 1980a, b). We agree with Kendall (1980a) that bears do not obtain whitebark pine cones by breaking branches from tree crowns, but rely on squirrel hoards. None of the thousands of trees we examined showed signs of the extensive crown damage that would inevitably result from such large animals trying to harvest cones from the tips of limber, ascending limbs. While it is possible that bears are occasional dispersers and establishers of whitebark pine by means of viable seeds germinating in their scats, we have no evidence this occurs, and believe it would be a rare event. The bear scats in our study area were all close to the raided squirrel middens, and usually under the forest canopy.

Nocturnal rodents – mainly mice and voles – are unlikely to be significant dispersers. Though they may harvest the small amount of seeds that fall to the ground ($\sim 4\%$), our artificial cache experiments indicate most of these are consumed on the spot. Abbott and Quink (1970) showed that most caches of eastern white pine (*P. strobus*) seed made by mice and voles were less than 15 m from the seed source. They also found that when cached seeds germinated, the rodents ate the seedlings. They therefore concluded that mouse and vole caches were of minor importance to pine seedling establishment. On the other hand, West (1968) reported the early survival of seedlings of ponderosa pine (*P. ponderosa*) that were presumably growing from rodent caches, so it is possible – though not yet established – that rodents effect regeneration close to the seed source. Tomback (1978) mentions seed predation by some of the vertebrates we observed, as well as by some not found in our study area, but she presents no data useful in evaluating a dispersal or establishment role for any of them except the nutcracker.

Estimates of the number of seeds cached by a nutcracker during a harvest season are subject to numerous difficulties. Vander Wall and Balda (1977), basing their calculations on length of the harvest, number of flights per day, and number of seeds carried per flight, estimated that a nutcracker could cache 22,000–33,000 piñon seeds per season. Our estimate of nearly 98,000 seeds is based on the timed behavior of birds whose cache site was relatively close to the harvest site. We have no site-specific estimates of the number of seeds required to provide for a bird's metabolic requirements, and those of its young, until the maturation of the next crop. Vander Wall and Balda (1977) estimated that an adult nutcracker needed less than 10,000 piñon seeds, which are approximately twice as large as whitebark pine seeds, to survive from October to April. We suggest that a very large fraction of the 98,000 seeds cached per nutcracker in Squaw Basin would escape retrieval by nutcrackers and predation by other animals, and would provide a substantial seed bank for establishment of whitebark pine. Our observations of three cone crops, two of them in mast years, suggest to us that the size of the nutcracker's harvest is a function of the size of the seed crop: that harvesting and caching continue as long as cones and seeds are available. If so, then regeneration of whitebark pine is most likely to occur in years following mast years, from seeds surplus to the needs of nutcrackers. A great deal of work needs to be done on the demographics of cached seeds, however, before these questions can be answered with satisfaction.

The dependence of whitebark pine on Clark's Nutcracker adds weight to earlier suggestions that the distribution, site occurrence, clumping of stems, and successional status of whitebark pine (Lanner 1980) reflect the behavior of the nutcracker. It also provides a necessary precondition to the argument that cone and seed morphology and anatomy, and crown shape of this pine have resulted from the natural selective action of nutcrackers on a white pine ancestor, resulting in the speciation of whitebark pine and its congeners of subsection Cembrae (Lanner 1982).

Finally, the behavior of Clark's Nutcracker is quite similar to that of "specialized frugivores" as predicted by McKey (1975), though nutcrackers are technically granivores. Specialized frugivores receive all or most of their carbohydrate, lipid, and protein needs from fruits. They are the principal dispersal agents for the species that make up most of their diet, and they have co-evolved with those species. They are further characterized by a reliability of visitation and the likelihood they will deposit intact seeds in favorable sites. They start to remove the crop immediately upon maturation, and they are more dependent, therefore more attuned to their major food species, than other dispersers. Recent work shows that juvenile Clark's Nutcrackers are almost totally dependent on cached pine seeds recovered by adult birds for many weeks after fledging (Vander Wall and Hutchins, in prep.). Therefore, in all of these aspects Clark's Nutcracker fits closely the description of a specialized frugivore that provides a high quality of dispersal.

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