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DISPERSAL OF WHITEBARK PINE SEEDS BY CLARK'S NUTCRACKER: A MUTUALISM HYPOTHESIS

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SUMMARY

(1) Clark's nutcrackers (*Nucifraga columbiana*) store a mean of only 3·7 whitebark pine (*Pinus albicaulis*) seeds per cache, which reduces competition for moisture and space. The mean depth at which seeds are stored, 2·0 cm, is compatible with germination requirements, and many sites selected appear suitable for seed germination.

(2) One nutcracker stores about 32 000 whitebark pine seeds at subalpine elevations each year, which represent 3–5 times its energetic requirements. Although parent nutcrackers feed stored seeds to juveniles, in some years there is probably an excess of seeds stored by the population as a whole.

(3) Experimental results suggest that seeds retrieved from nutcracker caches are as viable as seeds extracted by hand from cones and that seedlings originating in nutcracker caches have a good survival rate: 56% over the first year and 25% by the fourth year.

(4) In comparison with Clark's nutcracker, alternative disperal agents, i.e. rodents and cone disintegration, disperse fewer seeds, disperse seeds shorter distances from parent trees, place seeds in sites less suitable for germination, and/or make large seed caches which lower reproductive potential. Nutcrackers disseminate seeds throughout the subalpine habitat and are, in part, responsible for the 'pioneering' status of whitebark pine.

(5) The evolution of wingless seeds and indehiscent cones in the Cembra pine group was probably a consequence of seed dispersal by an ancestral nutcracker form. It appears that the Clark's nutcracker—whitebark pine interaction is both coevolved and mutualistic.

INTRODUCTION

Clark's nutcracker (*Nucifraga columbiana*) Wilson, a bird of the family Corvidae, harvests and stores pine seeds in the late summer and autumn of each year (Turcek & Kelso 1968; Vander Wall & Balda 1977; Tomback 1977a, b). The stored seeds are used from winter until the new cone crop is available the following summer. Unique to the genus *Nucifraga* is the sublingual pouch, a sac-like extension of the floor of the mouth (Bock, Balda & Vander Wall 1973) which is used to transport seeds. The bill of the nutcracker is sturdy, long, and slightly decurved, and is used to tear into cones and to pry out and open seeds.

According to my observations in the eastern Sierra Nevada (Tomback 1977a, b), each year from late August to the beginning of October, nutcrackers harvest and store clusters of ripe whitebark pine (*Pinus albicaulis* Engelmann) seeds. Each stored cluster will be termed a 'cache'. Caches are buried throughout the forest terrain and also in steep, south-facing slopes which accumulate a minimal snowpack and are used by a local population of nutcrackers. Beginning mid-September, nutcrackers migrate to the Jeffrey pine (*Pinus jeffreyi* Greville and Balfour) belt where they harvest and store seeds of other

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pines. The majority of nutcrackers overwinter there and live on seed caches. Nesting usually occurs during March and April. In late spring, family groups of nutcrackers migrate to subalpine elevations where caches of whitebark pine seeds are the predominant food source until the new crop of cones ripens in mid- or late-summer.

Two recent papers detail the ecological relationship of Clark's nutcracker (Vander Wall & Balda 1977) and another corvid, Piñon jay (*Gymnorhinus cyanocephalus* Wied) (Ligon 1978), with the Colorado piñon pine (*Pinus edulis* Engelmann), a conifer with large, wingless seeds and seed retention in cones. The birds gain an efficiently harvested, energy-rich food source of storable form, and in turn the seed storing habits of the birds disseminate seeds. Similar ecological relationships between hardwood trees and other vertebrate seed dispersers were studied by Stapanian & Smith (1978) and Bossema (1979).

The former authors suggest that the bird-pine relationships are mutualistic and coevolved. Mutualism, defined as a 'mutually beneficial association between different kinds of organisms' (Gove 1968), requires that both species increase their fitness by means of the association. The benefits to the corvids have been documented by Vander Wall & Balda (1977) and by Ligon (1978), and there is little doubt that the fitness of both Clark's nutcracker and Piñon jay is increased by the interaction. However, neither study substantiates the hypothesis that the reproductive success of *P. edulis* is increased.

For the corvid-pine association to be considered mutualistic, other methods of seed dispersal cannot be more successful than that by corvids. If so, the corvids are primarily seed predators. Their seed storing habits lower the fitness of the pine. The alternative hypothesis may be tested in part by determining if the seed dispersal patterns of the birds and the dispersal sites selected provide good conditions for seed germination and seedling survival and by examining the effectiveness of potential alternative dispersal mechanisms.

In this paper I present new data and relevant data from my previous studies to investigate the question of mutualism in relation to another corvid-pine association—that between Clark's nutcracker and whitebark pine. Like the piñon pine, the whitebark pine has large, wingless seeds and seed retention in cones. Unlike the cones of the piñon pine which open in fall, the cones of the whitebark pine are essentially indehiscent (Krugman & Jenkinson 1974; Tomback 1981). The field data presented here were gathered primarily in the summer and fall of 1975 and 1976 in the central region of the eastern Sierra Nevada.

METHODS

Study areas were on the eastern slope of the Sierra Nevada in Mono and Madera Counties, California. The primary study area was a 50-ha section of subalpine forest by Red's Lake on the west side of Mammoth Mountain, about 2830 to 2950 m elevation (Fig. 1). In the northern-most portion of this study area, the southern and south-eastern slopes of a hill, 2955 m high were major seed storage areas for nutcrackers. Conifers in the Red's Lake vicinity include whitebark pine, lodgepole pine (*Pinus contorta* Douglas), some western white pine (*P. monticola* Douglas), red fir (*Abies magnifica* A. Murray), mountain hemlock (*Tsuga mertensiana* Bongard) and an occasional Jeffrey pine. Observations were also made at Tioga Pass, in subalpine forest at approximately 3030 m elevation. The habitat consists of rocky hillocks bearing whitebark and lodgepole pine and red fir, interspersed among wet meadows and small lakes.

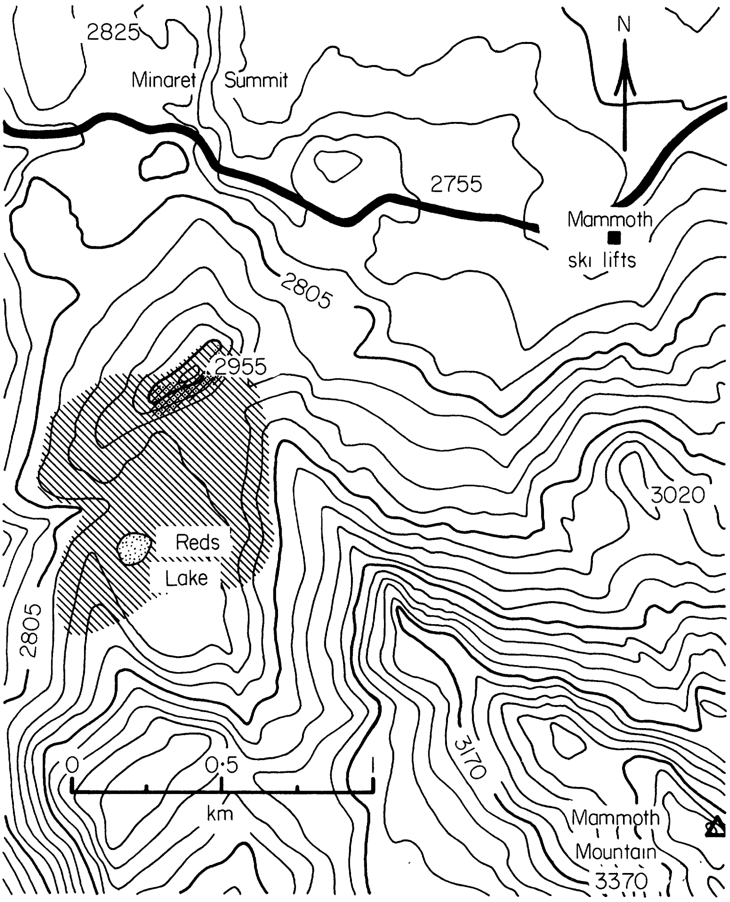

FIG. 1. The Red's Lake study area in relation to Mammoth Mountain and vicinity. (Based on part of U.S. Geological Survey Topographical map, N3730-W11900/15.) Hatched area = 50 ha study area. Cross-hatched area = storage slope.

Number of seeds per cache

I observed fifteen nutcrackers at close range—by means of Bushnell 7 × 35 wideangle binoculars—place 119 seeds in twenty-four caches (range 1–6 caches per bird) in terrain throughout the Red's Lake vicinity in September, 1975. On 6 and 7 June 1976, at Tioga Pass I observed two nutcrackers recover thirty caches (twenty-three and seven respectively) representing a total of seventy-eight seeds stored the previous autumn.

Depth of caches and cache site characteristics

When nutcrackers dig up seed caches, their excavations remain, except in pumice or gravel. Usually, the birds open seeds on the site, leaving behind seed coats (Tomback 1980). Measurements of such excavations yield data on seed cache depth. In July 1975, I measured twenty-six cache excavations at Tioga Pass, where the predominant substrate was mineral soil and duff.

During the summer and autumn of 1975 in the Red's Lake study area, I found ninety-four recently-germinated clusters of pine seedlings, which probably originated from nutcracker caches buried in 1974. Although this origin cannot be confirmed, these seedling clusters appeared in the same terrain where nutcrackers had stored seeds the previous year. The seed coats on or near the seedlings together with the number of cotyledons (see Mirov 1967), confirmed that the seedlings were whitebark pine. Also recorded were the following site characteristics for each cluster: substrate type, distance to nearest tree, slope aspect, slope angle, and date.

Seed storage effort

In many cases, individual nutcrackers could be distinguished on a short-term basis by differences in body size, colour, and facial markings. Consequently, nutcrackers observed harvesting seeds could often be recognized when they returned after flying off to store seeds. Sometimes only one nutcracker harvested seeds from a particular group of trees and then returned to the same locale, even the same tree, after storing seeds. When two or three nutcrackers harvested seeds in adjacent trees, I could follow each nutcracker for a time and be certain my data included only one observation for each bird. Also, to avoid gathering data from the same birds more than once, I worked in different parts of the Red's Lake area within the same day. However, it is possible one or more individuals provided more than one set of data.

Seed capacity of the sublingual pouch was determined for thirteen nutcrackers by counting the number of seeds each bird placed in its pouch from the time it began to harvest (deflated pouch) to the time it departed for storage areas with an inflated pouch. [Variations in pouch load may correlate with age, sex, size, and/or distances travelled (Bossema 1979).] Using these same thirteen birds and three others, I determined the time required to harvest a pouch load of seeds. Also recorded was the time taken by ten nutcrackers to store a pouch load of seeds and return to harvest more seeds.

Seed mass and caloric value

The average mass of the edible portion of a whitebark pine seed was determined by weighing a sample of 100 whole whitebark pine seeds. I cracked the seeds, separated the edible portions (embryo and endosperm) from the seed coat and nucellus, and weighed them.

The edible portions of ten whitebark pine seeds were crushed into fine particles, mixed thoroughly and oven-dried to constant mass. Two samples, each approximately 1 g, were weighed and combusted in an oxygen bomb calorimeter (Parr Instrument Co., Inc., Model 1211) to determine their caloric values.

Seed viability and seedling survival

Twenty whitebark pine seeds extracted by hand from cones and twenty seeds recovered from nutcracker caches a few weeks after storage were sliced in half through the centre of the seed embryo, placed in separate Petri dishes, immersed in a 0·1% solution of tetrazolium chloride (2,3,5-triphenyltetrazolium chloride) and incubated in the dark at room temperature for 60 min (see Machlis & Torrey 1956). Seed embryos stained red after treatment were considered viable.

The first-year survival rates of seedlings which probably germinated from nutcracker caches were determined in the field as follows: On 18 September 1975, I selected two small plots with seedling clusters in the Red's Lake vicinity. One plot was 1–3 m from whitebark and lodgepole pines with a 2°–12° westerly exposure and contained fifty-four seedlings in twelve clusters. The other plot was on open, almost level ground, about 10 m from the nearest cone-bearing pine tree; it had thirty-one seedlings in fourteen clusters. The seedlings in both sites were in the succulent stage, between 1–3 weeks old (Mirov 1967). On 4 June 1976 and 18 September 1976, the condition and number of seedlings remaining in both areas were recorded.

RESULTS AND DISCUSSION

Whether or not the whitebark pine benefits from interacting with Clark's nutcracker depends on the effectiveness of the bird as a seed disperser. Data bearing on critical aspects of this problem should provide support for or against the mutualism hypothesis.

Number of seeds per cache

The number of whitebark pine seeds per cache stored by nutcrackers in the Red's Lake area ranged from 1 to 10 (mean and S.D. = $5\cdot0 \pm 2\cdot4$, median = 5). Cache sites selected there were mostly on the forest floor and in pumice substrate. At Tioga Pass, the number of seeds per cache retrieved by nutcrackers ranged from 1 to 15 (mean and S.D. = $2\cdot6 \pm 2\cdot7$, median = 2). Caches were recovered from soil on small, rocky hillocks adjacent to meadows. Although the number of seeds per cache in the two types of terrain differed significantly ($t = 4\cdot90$, d.f. = 23, $P < 0\cdot001$), the combined samples may be more representative of the overall variation in number of seeds per cache stored by nutcrackers. Combined cache sizes ranged from 1 to 15 seeds with a mean and S.D. of $3\cdot7 \pm 2\cdot9$ and median of three seeds per cache. Regional differences in cache size may relate to substrate quality or probability of cache losses to rodents (i.e. smaller caches where rodent densities are high). The larger the cache, the greater the competition for moisture, space, and light among seedlings, and hence greater reproductive loss to whitebark pine.

Cache site quality: micro-habitat characteristics and seed depth

It is important to assess how closely the 'sowing' behaviour of the nutcracker fills the germination requirements of whitebark pine seeds. Koller (1972) considered water supply, energy (radiation for photosynthesis and environmental temperature), supply of carbon dioxide, soil type, mineral supply, and competition from other plants as the most important factors affecting germination, and Baker (1950) added mechanical resistance of the substrate to the seed shoot.

The depth at which nutcrackers bury caches may be as important in seed germination as micro-habitats. According to Hoffman (1924), the optimum depth is proportionate to seed size—largest seed (*Pinus ponderosa* Douglas), optimum about 2·5 cm, lower limit 7·5 cm, and smallest seed (*Thuja plicata* Donn) lower limit at about 1·3 cm. Whitebark pine seeds are larger than ponderosa pine seeds and should germinate at similar or lower depths varying with soil type and moisture content (Arndt 1965 in Koller 1972). Under nursery conditions, *P. albicaulis* and other large seeds are covered with about 1·25 cm of soil (Krugman & Jenkinson 1974).

Excavations made by nutcrackers recovering seeds at Tioga Pass indicated that seeds were buried 1·0–3·0 cm in depth ($\bar{x} = 2\cdot0 \pm 0\cdot77$ cm), a possible overestimate if nutcrackers dig deeper than the deepest seed. However, it appears that nutcrackers are placing whitebark pine seeds at depths suitable for germination.

Micro-habitats in which nutcrackers store whitebark pine seeds are listed in Table 1, with relative frequencies of use in Tomback (1977b) and Fig. 2 based on observations of

TABLE 1. Micro-habitats selected by nutcrackers for storing seeds (from Tomback 1977b)

Ground cover (under)	Objects (next to)	Trees (on or in)	Plants (next to stems)
volcanic gravel	rocks	roots	*Eriogonum*
pumice	fallen branches	holes	*Arctostaphylos*
forest litter	fallen trees	cracks	*Phyllodoce*
Soil	base of tree	under bark	*Cassiope*
			Castanopsis
			Artemesia

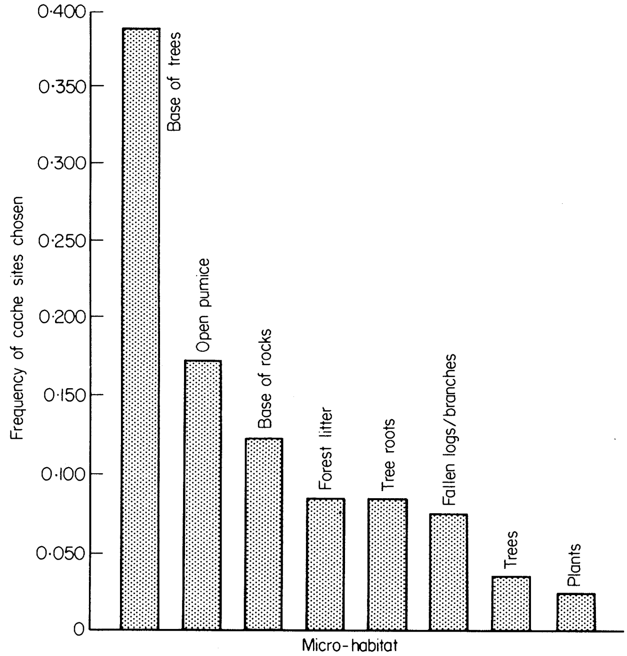

FIG. 2. The relative frequency of use of different micro-habitats by nutcrackers storing seeds.

fifty-two nutcrackers making eighty whitebark pine seed caches in the vicinity of Mammoth Mountain.

Nutcrackers did not use moist areas where caches could spoil before germination. I have observed fungal growth on and in seeds retrieved from damp sites on the forest floor or from Jeffrey pine cones buried under snow. *Rhizoctonia* and *Pythium* attack newly-germinated conifer seedlings (Baker 1950), and although some fungi form symbiotic associations with conifer roots, others produce toxins (Janzen 1977). Infected seeds waste a nutcracker's time and energy and deplete food stores. Avoiding damp sites minimizes reproductive loss to the whitebark pine from seed spoilage. The whitebark pine is an arid-site conifer (*sensu* Fritts 1974), and excess moisture may be particularly harmful to seedlings.

Whitebark pine seedling survival potential of the seed storage sites can be evaluated as follows (see Fig. 2). Seeds stored among tree roots and in trees (about 9% and 3%, respectively) are lost if there is inadequate growing space, moisture, or light, and seeds will not germinate under bark or in cracks or holes of trees.

Most caches (39%) were within 1·5 m of the base of a mature conifer (Fig. 2). Whitebark pine is intolerant of shade (Baker 1950). Such shaded sites are unlikely to produce mature individuals. Also, competition for light, moisture, and space may occur later between neighbouring trees.

Some moisture is required for seed germination and seedling growth. The Red's Lake subalpine climate is warm and dry and many nutcracker caches are on steep slopes with southern exposures; hence seeds and seedlings are subject to conditions of aridity, wind and excess insolation. The most common substrate, pumice, drains water rapidly, and forest litter traps moisture; neither are optimal substrates (Baker 1950). Caches next to or under the broad base of sulphur flower (*Eriogonum umbellatum* Torrey), account for many of the observations 'Plants' in Fig. 2.

Micro-habitat characteristics of ninety-four seedling clusters (presumably from nutcracker caches, although this is not critical to the evaluation) in the Red's Lake area (Table 2) compared with the micro-habitat frequencies in Fig. 2 suggest which sites used have the best reproductive potential. Seeds germinate in open pumice despite the aridity of surface layers, perhaps after a series of storms since seedlings appear during the wettest times of the summer. Seedling clusters near to or in sulphur flower plants occur beyond expectation from Fig. 2, and tree base sites below expectation. The sulphur flower probably provides cool, moist conditions at its base, during the early heat-sensitive stage of seedling growth, whereas tree sites are usually covered with forest litter. Nutcrackers tend to store seeds in south-facing slopes (Table 2), but whether such sites favour seedling survival is not known. Although cache sites next to trees, in trees, or in forest litter are poor (but still support seedlings), other sites (about 40% of total, Fig. 2) are potentially favourable.

The volcanic origin of Mammoth Mountain accounts for the pumice substrate over most of the Red's Lake area, but in other montane regions soil predominates and may favour seedling establishment. At Tioga Pass, nutcrackers frequently bury caches in soil.

Additional reproductive loss occurs when nutcrackers bury whitebark pine seeds below 2400 m elevation in the Jeffrey pine belt. I have never observed a whitebark pine tree at these elevations, and Sudworth (1908) does not mention any below subalpine elevations, suggesting conditions are unsuitable for the species.

Number of seeds stored v. seeds required

Central to the mutualism question is whether nutcrackers use all of the seeds they store each year, i.e. whether unused seeds are available for whitebark pine population recruitment. The total number of whitebark pine seeds stored by a single nutcracker in one season was estimated with the data presented in Table 3.

Values B and C (Table 3) are based on the following observations. The late-summer and autumn climate at subalpine elevations in the eastern Sierra Nevada is dry with maximum temperatures frequently above 26 °C (Tomback 1978). Nutcrackers usually harvest and store whitebark pine seeds in the cooler hours of the day, 2–3 h after sunrise and 2–3 h in the afternoon and early evening. Harvesting activity is interrupted as nutcrackers search for ripe cones, give alarm calls, and/or mob predators (Tomback 1977b). A conservative estimate of the daily time spent in harvesting and storing seeds per individual is 4·5 h.

During the harvest period, the number of nutcrackers in the Red's Lake area ranged from seventy-five at the peak of the season to about ten at the close of the season. In 1974

TABLE 2. Frequency distribution (*f*) of micro-habitat characteristics of ninety-four seedling clusters surveyed in 1975

Micro-habitat (see Fig. 2)	(*f*)	Substrate	(*f*)	Distance to nearest tree (m)	(*f*)	Slope aspect	(*f*)	Slope angle	(*f*)	Month observed	(*f*)
Base of trees*	0·21	Pumice	0·89	0–1·9	0·20	S	0·30	level	0·37	July	0·47
Open pumice	0·42	Forest litter	0·11	2–5	0·21	SW	0·25	2–5°	0·16	Aug	0·21
Forest litter	0·01			6–10	0·48	SE	0·04	5–10°	0·38	Sept	0·32
Plants†	0·36			>10	0·11	W	0·02	>10°	0·09		
						N	0·02				
						level	0·37				

* 0–1·5 m from base.

† Cache buried next to or under base of plant *Eriogonum umbellatum*.

TABLE 3. Data pertaining to nutcracker harvesting behaviour

	Seeds per pouchload	Time to fill pouch (min)	Time to store and return (min)
Range	35–150	4–16	7–50
mean ± S.D.	77 ± 37	10 ± 3·9	14 ± 13
n	13	16	10
	A. Total time: harvest, store, and return, min	B. Number trips per day	C. Number seeds stored per bird-day
Range	11–66	4–24	140–3600
mean	24	11	850

and 1975, nutcrackers harvested and stored whitebark pine seeds for 38 and 47 days, respectively. With a good cone crop, one nutcracker could store about 850 seeds per day (Table 3) for about 42 days, thus storing about 35 000 whitebark pine seeds per year in about 9500 caches (at 3·7 seeds per cache). Many nutcrackers made at least one trip per day with full pouches to lower elevation cache sites. If we assume a single trip, a bird would store about 9% of the total (or about 3000 seeds) at lower elevations. The remaining 32 000 seeds would be stored in about 8500 caches in the Red's Lake area.

If twenty-five birds (the most common number observed) each stored 32 000 seeds in the Red's Lake area, this totals about 800 000 seeds or about 200 000 caches within 50 ha. With a mean and S.D. of 45 ± 16 seeds per whitebark pine cone (Tomback 1977b), nutcrackers must harvest about 18 000 cones to obtain this quantity.

An estimate of how many whitebark pine seeds are used each year requires calculation of the energetic requirements of a single nutcracker during the time caches are recovered in the Red's Lake area—from about April to July (Tomback 1977b). Although insects and spiders occur in the nutcracker diet (Giuntoli & Mewaldt 1978), it is assumed that all energetic requirements are filled by whitebark pine seeds.

Calculations of energy and seed requirements are based on laboratory determinations of metabolism in three winter- and three summer-acclimatized nutcrackers. Metabolic rates were determined by measuring oxygen consumption (Beckman 755 paramagnetic oxygen analyser) in post-absorptive birds at chamber temperatures ranging from −10 to 44 °C. Values were converted to rates of heat production (W/kg). Details of the experimental methods and seed requirement calculations are reported in Laudenslager and Tomback (unpublished) and are summarized below. Conversions from energy to seed requirements use the following data: The dry mass of the edible part of each whitebark pine seed is approximately 0·080 g, which is about 50·1% the dry mass of the whole seed. The results of two calorimetric determinations for the dry mass of the edible portion of whitebark pine seeds were 7802 and 7631 cal g^{-1}. For conversion, Laudenslager and Tomback (unpublished) used the mean of the two caloric values, 7716 cal g^{-1} or 32·284 kJ g^{-1}.

Calculations of minimum seed requirements are based on basal metabolic rate in the nutcracker thermoneutral zone, 20–30 °C. Winter-tested birds produced a mean of 11·98 W/kg (J/s/kg), while summer-tested birds produced a mean of 11·38 W/kg. Calculations of maximum seed requirements are based on metabolic rates at mean monthly temperatures (April, −2·1, May, 5·1; June, 7·8; July, 10·5 °C, D. F. Tomback, unpublished data) with a 20% increment for 'free activity'. (At 0 °C, winter-tested birds produced a mean of 17·62 W/kg, and summer-tested birds produced a mean of 15·98

W/kg.) A mean nutcracker body weight of 130 g was used in all calculations, and winter heat production rates were used for April and May and summer rates for June and July.

From April to July, the minimum energy requirement for a single nutcracker is about 16 000 kJ, 6000 seeds, or about 1600 caches. The maximum energy requirement during this period is about 25 500 kJ, 10 000 seeds, or about 3000 caches. These values compare favourably to the calculated requirements of 11 000 seeds for the same months, based on the equation for passerine existence energy (Weiner & Glowacinski 1975) and free existence energy increment (Weins & Innis 1974), which appears in Tomback (1977a).

The estimated number of whitebark pine seeds one nutcracker stores at subalpine elevations represents between three and five times as much seeds as it requires. According to Vander Wall & Balda (1977) a nutcracker stores between 2·2 and 3·3 times the amount of piñon seeds it needs each year. However, the period of *P. edulis* seed use differs from that of whitebark pine. Juveniles are fed by adults with whitebark pine seeds from subalpine elevations from the time they fledge until late summer (Tomback 1977b) Therefore, each parent nutcracker must gather enough seeds from stores to feed itself and its young. Assuming this responsibility is divided equally between the male and female, each parent would feed half its young from its own seed stores.

Nutcrackers commonly have clutches of two and three eggs (Bent 1946), and most nutcracker family groups in my study areas had three young, with two young next highest in frequency. With no data available on the relative occurrence of non-breeding and breeding birds in the population and the number of successfully fledged offspring per breeding pair, a general model is presented for determining whether the overall nutcracker population in an area stores more seeds than it consumes. In the model, the ratios are based on 32 000 seeds stored per individual, 10 000 seeds required per individual, and 5000 seeds required for each offspring [Weins & Innis (1974) considered juveniles to be metabolically similar to adults] fledged, from April to July per parent. The combined frequency of first-year (non-breeding) nutcrackers and those that have not bred successfully is designated as f_0, and the frequency of individuals that have fledged 1, 2, 3, and 4 young are designated as f_1, f_2, f_3, and f_4, respectively. The value resulting from the model is the ratio R_s of the total number of seeds stored by the population of nutcrackers to the total number of seeds required.

$$R_s = f_0(3{\cdot}2) + f_1(2{\cdot}1) + f_2(1{\cdot}6) + f_3(1{\cdot}3) + f_4(1{\cdot}1).$$

To illustrate how this equation functions, values are used which are compatible with field observation but not the result of a population census. They may overestimate fledging success:

$$f_0 = 0{\cdot}20, f_1 = 0{\cdot}10, f_2 = 0{\cdot}25, f_3 = 0{\cdot}35, \text{ and } f_4 = 0{\cdot}10.$$

Here R_s would equal 1·8 and thus 45% of the seeds stored would not be retrieved by nutcrackers. In the Red's Lake area, where twenty-five nutcrackers might store 800 000 whitebark pine seeds in one season, an R_s of 1·8 indicates about 350 000 superfluous seeds or 95 000 unused caches.

Of the unretrieved caches there would be losses to rodents, spoilage, and storage in sites not favourable to seed germination. However, in some years a large fraction of nutcracker seed stores may be available for afforestation, particularly since germination may occur before many caches are retrieved.

Seed viability and seedling survival

The viability of seeds which were harvested, carried in the sublingual pouch, and buried by nutcrackers was compared to that of seeds taken directly from cones. The tetrazolium dye test indicated that seventeen of the seeds extracted by hand were viable, whereas nineteen of the seeds buried by nutcrackers were viable, suggesting at least equal viability (Fisher Exact Probability test, $P = 0{\cdot}25$). However, the seeds in nutcracker caches should be of better overall quality than the complement of seeds in a cone. Nutcrackers discriminate between good and inedible (i.e. aborted, insect-infected, or diseased) piñon and whitebark pine seeds by rattling each harvested seed in their mandibles (Vander Wall & Balda 1977; Tomback 1977b).

For a short-term test of seedling survivorship, two sites with seedling clusters, presumably germinated from nutcracker caches, were selected in the Red's Lake area. Survival rates of seedlings within each group were calculated twice in 1976 (Table 4). There were no significant differences in seedling survival between the two groups (χ^2 test, $P = 0{\cdot}30$), and the combined first-year survival rate was 56%.

In 1975 I found more than 600 seedlings presumed to be from nutcracker caches in the Red's Lake area, of which about 300 (50%) were expected to survive through summer, 1976. About 30% or more of these 600 seedlings were present in September 1976.

On 5 August 1979, I examined Site 1 again. After five growing seasons, seedlings survived in six or 50% of the original twelve clusters for a total of fourteen seedlings or 26% of the original number. Clusters now contained a mean and S.D. of 2·3 ± 2·0 seedlings per cluster (range: 1–6 seedlings per cluster).

TABLE 4. Mean survival rates for seedlings within a cluster and among the total seedlings in one group

	First winter % survival within a cache (mean ± S.D.)	First winter overall % survival of seedlings	First winter plus second summer % survival within a cache (mean ± S.D.)	First winter plus second summer overall % survival of seedlings
Site 1 12 clusters 54 seedlings	68 ± 39%	76%	59 ± 42%	65%
Site 2 14 clusters 31 seedlings	63 ± 35%	47%	59 ± 38%	41%

Evaluation of the mutualism hypothesis

As in the case of the nutcracker—*P. edulis* interaction, the benefits gained by the nutcracker as a *P. albicaulis* seed predator are clear. (a) The seeds are energy-rich. The nutritive contents rank high among conifers in both caloric and fat content per gram (see Grodzinski & Sawicka-Kapusta 1970). (b) The seeds are large and wingless (narrow remnants may occur). Since nutcrackers harvesting winged pine seeds remove the wings before placing seeds in the sublingual pouch (Tomback 1977b), both features increase the foraging efficiency of the nutcracker, maximize the number of seeds stored per harvest period by nutcrackers, and enable the birds to remove *P. albicaulis* seeds rapidly from competing seed predators (Tomback 1977b; Smith & Balda 1979). (c) The cones are indehiscent (but see Tomback 1981). The ripe seeds are retained in the cone during late summer and autumn, guaranteeing the nutcracker a full 'packet' when it forages through an intact cone. In contrast, some winged seeds of dehiscent cones are dislodged or blown out immediately after cone opening. Consequently, indehiscent cones increase foraging efficiency by decreasing search time and by maximizing return for the effort required to break into the cone. (Indehiscent cones should not be confused with the fire-adapted serotinous cones, such as occurs in *P. contorta* (Lotan 1976)).

The corvid-pine mutualism hypothesis is supported if evidence suggests that both species are increasing their fitness by means of the association. Only when the seed source is adapted to corvid-mediated seed dispersal and increases population recruitment by this means can the interaction be considered mutualistic. Two conditions must be satisfied to support this latter possibility: (1) the corvid is an effective seed disperser for the species, and (2) other potential seed dispersal mechanisms are less effective.

Some evidence for the effectiveness of Clark's nutcracker as a disperser (Condition 1) comes from the results presented in the last section. Estimates of the number of seeds stored and the energetic requirements per nutcracker suggest that a population may store more seeds than it will use when the whitebark pine cone crop is good (good to excellent cone crops occurred in Red's Lake from 1973 to 1976, Tomback 1977b). By storing extra seeds, nutcrackers may compensate for losses to rodents and spoilage or a poor cone crop in overwintering areas.

In regard to the extremes of the montane climate, the first few years of a seedling's life appear most crucial (Baker 1950). The early survival rates of seedlings originating in nutcracker caches, i.e. about 50% over the first year and 25% by the fourth year, are comparable to those recorded in forestry experiments for other conifers (Baker 1950, and references therein).

The reproductive loss consequent to seedling growth under crowded conditions (i.e. 1–15 seedlings originating from a single cache) may be less for the whitebark pine than for the Colorado piñon and other species of corvid-dispersed pines. An important dispersal pattern of *P. albicaulis* is tight clumps of individual trees, i.e. a 'multi-trunk' tree. Sudworth (1908) described this form as follows: 'often in clusters of from 3 to 7 trees, as if growing from the same root'. Each trunk may arise from one seedling of a cache (Lueck 1980). Thus, a major effect of nutcracker seed dispersal is an extremely 'clumped' pattern for whitebark pine. Seedling cluster size distribution is compared with nutcracker cache sizes in the Red's Lake area in Table 5. Limber pine (*P. flexilis*), another subalpine pine with large, wingless seeds, has its seeds dispersed by nutcrackers and also occurs in an extremely 'clumped' pattern (Woodmansee 1977; Vander Wall & Balda 1977; Tomback & Kramer 1980; Lanner & Vander Wall 1980). Both Clausen (1965) and Weaver & Dale (1974) found a high frequency of whitebark pine clumps. Of the 6000 whitebark pine trees

TABLE 5. Percent occurrence of seedling cluster sizes and the number of seeds per nutcracker cache in the Red's Lake area

No. of seeds per cache or seedlings per cluster	Percent occurrence of seedling clusters or singles	Percent occurrence of nutcracker cache sizes
1	12·5	8·3
2 + 3	17·0	33·3
4 + 5	30·0	8·3
6 + 7	17·0	37·5
8 + 9	14·0	8·3
10–15	9·5	4·2
	$\bar{x} = 5{\cdot}3$ $n = 94$ clusters/singles	$\bar{x} = 5{\cdot}0$ $n = 24$ observations

surveyed by Clausen (1965) at elevations between 3000 and 3350 m in the eastern Sierra Nevada, about 70% were of the 'multi-trunk' form with 5 to 6 trunks per 'tree' most common.

The assessment of the nutcracker as a seed disperser reveals no serious problems which support the alternative hypothesis. In fact, based on the preliminary data presented, the quantity and quality of nutcracker seed dispersal is impressive.

Next, the effectiveness of alternative means of whitebark pine seed dispersal (Condition 2) must be evaluated. Wind is not an important dispersal agent for whitebark pine for the simple reason of morphology. Whitebark pine seeds are wingless and thus not likely to be blown any distance.

Potential dispersal agents for the whitebark pine, alternative to nutcrackers, are other vertebrates. While no other avian species at subalpine elevations disperses seeds as effectively as the nutcracker, there are several species of rodents which store conifer seeds.

According to my observations in both the Red's Lake and Tioga Pass study areas, Douglas squirrel (*Tamiasciurus douglasii* J. A. Allen) cuts down quantities of whitebark pine cones in late summer and autumn of each year (Tomback 1977b). The cones are stored intact in piles or middens, usually at the base of a tree; and, although the seeds may remain viable for a year or longer, they remain in cones. Seeds from cone middens of *Tamiasciurus* squirrels rarely are in a substrate or situation suitable for germination. Particularly, most whitebark pine seedlings arising from middens may not receive enough sunlight (Finley 1969). Also, seed dispersal distances from parent trees are restricted by squirrel home range size.

Deer mice (*Peromyscus maniculatus* Le Conte) occur at subalpine elevations and make numerous, large seed caches (20–30 seeds, Abbott & Quink 1970) throughout the forest floor. Deer mice cannot gnaw into and remove seeds from intact whitebark pine cones and, instead, probably gather seeds which are small and from open cones. Also, the olfactory sense of deer mice enables them to find and use up most of their seed stores (Howard, Marsh & Cole 1968, Abbott & Quink 1970).

Chipmunks (*Eutamias spp.*) also bury caches in late summer and autumn (Tevis 1953), but many of these caches are underground and are used during hiberation (Ingles 1965). West (1968) suggests that some surface caches of chipmunks may germinate and produce mature trees. I have watched chipmunks harvest whitebark pine seeds in trees by gnawing off cone scales. Although chipmunks may be disseminating whitebark pine seeds, they are less efficient than nutcrackers: (1) Their seed caches are large (West 1968), which means greater reproductive loss. (2) Fewer seeds are stored since chipmunks spend considerable time harvesting seeds from a single whitebark pine cone, and the capacity of their cheek pouches is small in relation to the nutcracker sublingual pouch. (3) Chipmunks are restricted to a home range, so terrain types in which caches are buried and seed dispersal distances are limited. (4) Both the *Tamiasciurus* squirrels and Clark's nutcracker remove cones or seeds so quickly that chipmunks may be able to gather whitebark pine seeds only briefly in late summer. (5) Like other sciurids, chipmunks rely on olfaction to find their caches (Cahalane 1942) and may recover most of their seed stores. Although some whitebark pine population recruitment maybe a consequence of rodent seed dispersal, rodents are less effective dispersers than are nutcrackers. In fact, at high population densities, rodents may compete for seeds and empty nutcracker caches (Tomback 1980).

One important alternative seed dispersal mechanism remains to be considered: what is the fate of whitebark pine seeds which have not been harvested? The literature is unclear on this point, although some experimental evidence suggests that cones may eventually abscise and disintegrate (Krugman & Jenkinson 1974). However, controlled experiments may not elucidate the true fate of cones and seeds (Tomback 1981). If cones do detach and disintegrate later in the year, the cones are likely to fall near the parent tree. This may be adaptive, since cones may land in sites suitable for germination but not under the canopy of the tree. However, a few seeds to a full cone complement of seeds may be dropped in one site, and many of these seeds are likely to be taken by rodents. Even if a number of the seeds per cone produce seedlings, only a few seedlings may eventually contribute to population recruitment (e.g. a multi-trunk tree) because of competition for space, light, and moisture. Reproductive loss from this dispersal mechanism may be high.

My observations in the field suggest that cones which have been partly emptied by nutcrackers have a lower probability of disintegrating (Tomback 1981). Most of the old cones I observed on trees were intact nutcracker-foraged cones or cone cores left by chipmunks. Of the old *P. albicaulis* cones I examined on the ground in the eastern Sierra Nevada in August and September 1979, 21% were intact shells of nutcracker-harvested cones, 11% were chipmunk cores, 46% were small, closed cones containing only aborted (withered embryos) seeds, and 21% were cones in various states of disintegration (total $n = 28$). No potentially viable whitebark pine seeds remained in any of these cones (Tomback 1981).

However, if seed dispersal by cone disintegration is as effective as seed dispersal by nutcrackers, the argument rests on relative numbers of seeds dispersed by these two mechanisms. During 8–15 September 1979, the number and conditions of *P. albicaulis* cones of the current crop were censused along transects at Cathedral Peak and Budd Lake in Yosemite National Park and Red's Lake on Mammoth Mountain. The numbers of trees surveyed per location were 36, 10, and 45, respectively, and the cone crops ranged from fair to moderate in each location. Of the new cones on each transect, from 75 to 100% of the cones had already been foraged in by nutcrackers and chipmunks, and some animals were still gathering seeds (Tomback 1981). With so few cones escaping vertebrate predators/seed cachers each year and with so many seeds cached in suitable sites, it is unlikely that cone disintegration is the primary seed dispersal mechanism for *P. albicaulis*, but it does improve the reproductive potential of seeds which have been overlooked by vertebrates. Possibly, cone disintegration as well as indehiscence are adaptations for a primarily nutcracker-mediated seed dispersal system.

The information presented thus far, although by no means conclusive, supports the hypothesis that the association between Clark's nutcracker and whitebark pine is mutualistic. In effect, the nutcracker is not the only disperser of whitebark pine seeds, but it is the disperser which is likely to contribute the greatest number of individuals to whitebark pine populations.

One additional factor must be evaluated in relation to the ecology of the whitebark pine—nutcrackers disperse seeds to locations where there are none to few whitebark pine trees, i.e. a 'pioneering' effect. Many of the nutcracker cache sites as well as seedlings were in open areas 10 m or more from the nearest cone-bearing whitebark pines(Table 2). Young whitebark pine trees of various ages grew on the nutcracker seed storage slope, were common in other parts of the Red's Lake area, and appeared to be invading the margins of the old lake bed adjacent to the present day Red's Lake. Nutcrackers, therefore, not only disseminate whitebark pine seeds, but spread the pine throughout the subalpine habitat, defining limits of its occurrence and shaping forest structure.

The 'pioneering' consequences of nutcracker seed dispersal may be illustrated by data I gathered in August and September 1979 on regeneration of a 2-ha intense subalpine burn between *c.* 3210 and 3295 m elevation on the west slope of Cathedral Park, Yosemite National Park (D. F. Tomback unpublished). Belt transects of the burn indicated substantial whitebark pine regeneration since the 1975 fire. The number of whitebark pine seedlings per cluster on five transects averaged from 1 to 4 ($\bar{x} = 1{\cdot}7 \pm 1{\cdot}0$, $n = 31$ sites, D. F. Tomback unpublished). During field work in September, nutcrackers flew into the burned area and stored seeds, which are the likely source of regeneration.

Whitebark pine is closely related to several other species with wingless seeds and indehiscent cones (*P. sibirica* Du Tour, *P. cembra* Linnaeus, *P. pumila* Regel, and *P. koraiensis* Siebold and Zuccarini) which together constitute the 'Cembra' pines (Mirov 1967). With the exception of whitebark pine, seeds of the Cembra pines are disseminated by one or more subspecies of the Eurasian Nutcracker (*N. caryocatactes* Linnaeus). At the European centre of origin of the Cembra group, it is conceivable that seed dispersal by nutcrackers, or an ancestral corvid form, was a major factor in the evolution of wingless seeds and indehiscent cones. The nutcrackers, in turn, probably evolved a preference for seeds of the Cembra pines, which were the most efficient to harvest and store, and appropriate behaviour patterns.

Morphological features of nutcrackers also reflect the intense interaction with Cembra pines. The sturdier bill of the thick-billed subspecies of the Eurasian nutcracker (*N. c. caryocatactes*) correlates with thicker seed coats on seeds of *P. cembra*. The evolution of the sublingual pouch (Bock, Balda & Vander Wall 1973) may also be the result of this association.

Consequently, it appears that the relationship between Clark's nutcracker and the whitebark pine, as well as the relationship between several subspecies of the Eurasian nutcracker and other Cembra pines, is coevolved as well as mutualistic.

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