

## FORAGING STRATEGIES OF CLARK'S NUTCRACKER

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Predators and prey exert a variety of selection pressures on one another, resulting in coevolved systems. Coevolutionary effects also occur between seed predators and plants; these interactions often shape the flora of a community (Janzen, 1971). An especially intense interaction occurs between Clark's Nutcracker (*Nucifraga columbiana*) and several species of pine (*Pinus* spp.), which are its preferred food source. According to my studies in the eastern Sierra Nevada, the use of pine seed has strongly influenced the timing and nature of altitudinal movements and seasonal activities of Clark's Nutcracker in its montane habitat. The effect of this influence is the subject of this paper.

The annual cycle of behavior of Clark's Nutcracker (Figure 1) and its congener, the Eurasian Nutcracker (*N. caryocatactes*), includes the harvest and storage of quantities of conifer seeds when they are plentiful and the subsequent recovery of seed stores when all food is scarce. This food-storage strategy is important to many corvids, especially several other Old and New World jays of the subfamily Corvinae—the genera *Garrulus*, *Aphelocoma*, and *Gymnorhinus* (Turcek and Kelso, 1968). Both species of nutcrackers have behavioral and morphological features adapted to the year-round use of conifer seed as a major food source; this indicates a more specialized condition than that of other jays. One major morphological feature unique to the genus *Nucifraga* is the sublingual pouch—a diverticulum of the floor of the mouth—in which birds transport seeds to storage sites or nestlings (Bock *et al.*, 1973; Mewaldt, 1956). Both species have sturdy, long, and slightly decurved bills with which they tear apart cones of a variety of conifers. An additional bill specialization in the Eurasian Nutcracker—a pressure plate or rhamphothecal bulge in the lower mandible—facilitates cracking the hull of a pine seed squeezed between the mandibles (Formosof, 1933; Stegmann, 1934; Turcek and Kelso, 1968). Whereas the Clark's Nutcracker is monotypic and ranges through the montane regions of western North America from Baja California to Alaska, the European nutcracker consists of 10 subspecies found in Europe and parts of Asia. The distributions of both nutcrackers parallel the range of coniferous forests, especially areas featuring one or more large-seeded species of pine.

My observations indicated that in the south-central eastern Sierra Nevada the Clark's Nutcracker undergoes a seasonal altitudinal migration (Figure 2). Throughout the summer, most nutcrackers are at subalpine elevations. By late summer, when whitebark pine cones (*Pinus albicaulis*) are ripe, nutcrackers harvest and store quantities of whitebark pine seed and then migrate to lower elevations to harvest and store Jeffrey (*Pinus jeffreyi*) and sometimes singleleaf piñon (*Pinus*



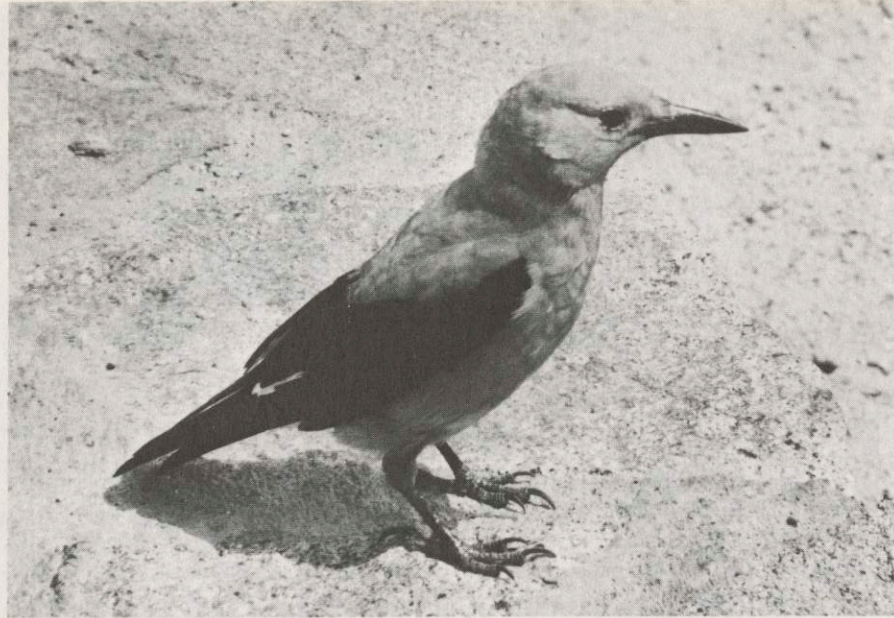


Figure 1. Clark's Nutcracker, *Nucifraga columbiana*.

*monophylla*) pine seed. During winter, most of the nutcracker population remains at lower elevations, feeding on the seeds remaining in cones and seed stores. Nesting begins as early as February; throughout this period both adults and nestlings are sustained by seed stores from lower elevations. Young nutcrackers fledge by late spring and migrate with adults to subalpine elevations, where they are fed whitebark pine seeds from stores made the previous fall, and arthropods. By mid-summer, fresh seed from ripening whitebark pine cones is added to the nutcracker diet. Juvenile nutcrackers become independent in August, freeing adults to harvest and store the new crops of pine seed.

In some years, a portion of the whitebark pine seeds stored by the Clark's Nutcracker are not used and subsequently germinate. Data presented in another paper (Tomback, unpubl. MS) suggest that the nutcracker is a major agent in afforestation of whitebark pine. The relationship between the nutcracker and whitebark pine may, consequently, be mutualistic.

The most important points to come to light from the studies of the Clark's Nutcracker presented here are (1) the timing of activities and altitudinal migrations in relation to the availability of fresh and stored pine seed, and (2) the complexity of the foraging patterns of the nutcracker. These factors together enable the species to feed on pine seed year-round, and suggest that the behavioral ecology of the nutcracker includes a number of "foraging strategies." Abused as the term "strategy" is, I believe its use here is justified. "Strategy" implies that alternative approaches to a problem are available, and one is selected. As will become apparent in the discussion to follow, the nutcracker has several options as to the sequence and nature of some of its activities but appears to have selected the most "adaptive strategy," i.e. the approach yielding the highest return.

The complexity of the yearly cycle of the Clark's Nutcracker and the adaptive significance of the nature and timing of each event indicate a fine tuning of the species to its environment. In support of this idea, the nutcracker



also demonstrates a degree of flexibility in its behavior, which is adaptive in times of food scarcity or harsh conditions. There should be no question that the Clark's Nutcracker is a specialist for both the montane habitat and a year-round diet of pine seed.

### Study Areas and Methods

#### Study Areas

All study areas are in Mono and Madera Counties, California, on the eastern slope of the Sierra Nevada (Table 1, Figure 3). The study was conducted from 1973 to 1976, during four summers and intermittently through three winters and springs. All winter observations and the greater part of the summer observations were made in the vicinity of Mammoth Mountain and Casa Diablo, Mono County, California. The subalpine study areas, Mammoth Mountain and Tioga Pass, feature stands of whitebark pine. The lower elevation study areas, especially Casa Diablo, are characterized by extensive forests of Jeffery pine and stands of piñon pine.

Table 2 illustrates which cone crops were available as food sources in the Mammoth Mountain and Casa Diablo areas during the study. The ranges of monthly temperature and snow depth, recorded on Mammoth Mountain from late fall through spring of each year of the study, are graphed in Figure 4.

#### Methods

I determined the specific elevation for various localities using a Thommen altimeter and U.S. Geological Survey topographic maps. Slope exposures and angles were measured by compass and protractor.

During three periods in summer 1975, and two periods in summer 1976, I used a stopwatch to measure the rates at which nutcrackers extracted whitebark and Jeffrey pine seed from cones. The data obtained from 28 July to 3 August 1976, were divided into rates timed for adults and rates timed for juvenile nutcrackers. Individuals could usually be recognized on a temporary basis by their relative size, light or dark head color, presence or intensity of white facial markings, and their tendency to return to the same stand of trees while harvesting and storing seed. Samples of whitebark pine cones were tested for ripeness during each of the periods on which extraction rates were timed. The degree of ripeness was determined by how easily cone scales were broken off, whether entire seeds or only pieces could be pried loose with a knife, and whether seed hulls were mature, i.e. brown and hard rather than white and soft.

To compute the weight of the whitebark pine seeds, I extracted 200 seeds from cones, weighed them in groups of 10 on a triple-beam balance, and obtained an average weight for one seed. To determine the volume capacity of the seeds, I used a 5 milliliter graduated cylinder filled with a known volume of fine-grained sucrose to measure the volume displacement of a whitebark pine seed. Each seed of a sample of 25 was buried in turn in the sucrose, and the results were averaged.

I determined the average number of whitebark seeds per cone to find how many cones must be harvested to fill a sublingual pouch. I extracted by hand seeds from 50 intact, unharvested cones collected from different sites in the Red's Lake study area on 15 September 1975.

During winter months, fallen Jeffrey pine cones were an important source of seed for nutcrackers, but by midspring few nutcrackers used this source. To investigate this change in foraging behavior, on 23 and 24 April 1975, I gathered 65 fallen cones from the previous fall's crop — 38 cones

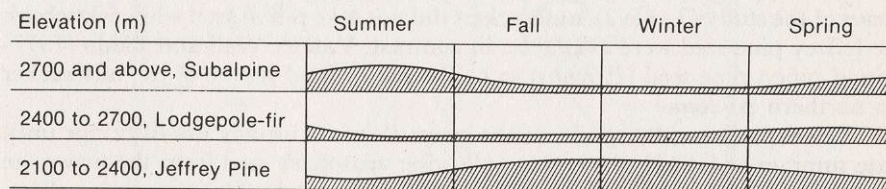


Figure 2. Relative year-round altitudinal distribution of Clark's Nutcrackers in the Mammoth Mountain-Casa Diablo study areas. The total of the shaded portions over the three altitudinal zones represents 100 percent of the population. The shaded area for any given time period within the season adds up to 100 percent.



TABLE 1  
Study Areas

Region	Latitude-longitude	Elevation (meters)	Area (hectares)	Conifer species*
Mammoth Mountain (west slope), Minaret Summit, Red's Lake	37°38' LAT 119° 3' LONG	2,670 to 3,000	650	<i>Pinus albicaulis</i> <i>P. contorta</i> <i>P. jeffreyi</i> (rare) <i>P. monticola</i> <i>Abies magnifica</i> <i>Tsuga mertensiana</i>
Casa Diablo-Little Antelope Valley	37°40' LAT 118°54' LONG	2,100 to 2,300	550	<i>Pinus jeffreyi</i> <i>P. monophylla</i> <i>Juniperus occidentalis</i>
Lee Vining	37°56' LAT 119° 8' LONG	2,160	---	<i>Pinus jeffreyi</i> <i>P. monophylla</i> <i>Juniperus occidentalis</i>
Tioga Pass	37°54' LAT 119°15' LONG	2,980 to 3,150	300	<i>Pinus albicaulis</i> <i>P. contorta</i> <i>Abies magnifica</i>

\* *Pinus albicaulis*, whitebark pine  
*P. contorta*, lodgepole pine  
*P. jeffreyi*, Jeffrey pine  
*P. monophylla*, piñon pine

*P. monticola*, western white pine  
*Abies magnifica*, red fir  
*Juniperus occidentalis*, western juniper  
*Tsuga mertensiana*, mountain hemlock

from the Jeffrey pine belt, 2,205 to 2,355 meters elevation, and 27 cones from the lodgepole-fir belt, 2,370 to 2,520 meters elevation. Cones of the most recent crop could be distinguished by their light, russet-brown color (Sudworth, 1908) and firm texture. Of these 65 cones, I counted the number of fertile (seed-bearing) scales on 42 cones and multiplied each value by two seeds per scale to get the total number of seeds per cone before seeds were shed. For each cone I tallied the actual number of seeds remaining and summed them for each set — 425 seeds from the Jeffrey pine belt and 94 seeds from the lodgepole-fir belt. I analyzed 176 seeds selected from those collected in the Jeffrey pine belt and the 94 seeds from the lodgepole-fir belt for seed quality, separating them into categories of good, aborted, and mealy (insect infested).

### Nature of the Food Source

During the course of my investigation, whitebark and Jeffrey pine seed were the most important and most productive food sources for the Clark's Nutcracker in the eastern Sierra Nevada. Both seeds were eaten fresh or from stores at different times of the year. To a large extent, the periods of use of both seeds were non-overlapping. Although piñon pine produced a cone crop twice in the four years of the study (Table 2), nutcrackers did not take piñon seed while whitebark or Jeffrey pine seed were available. In contrast, Vander Wall and Balda (1977) found piñon pine seed (*P. edulis*) to be the major food source of the nutcracker in northern Arizona.

Cones produced by species of the genus *Pinus* are usually not fully ripe until late summer or fall. However, partially ripe whitebark seed from the new cone crop became an important component of the nutcracker diet at subalpine elevations by midsummer of each year of the study. The time of summer that nutcrackers began harvesting seed varied as much as two weeks for whitebark pine and possibly more for Jeffrey pine from year to year. In 1973, nutcrackers began harvesting whitebark seed as early as 19 July but not until 1 and 2 August in



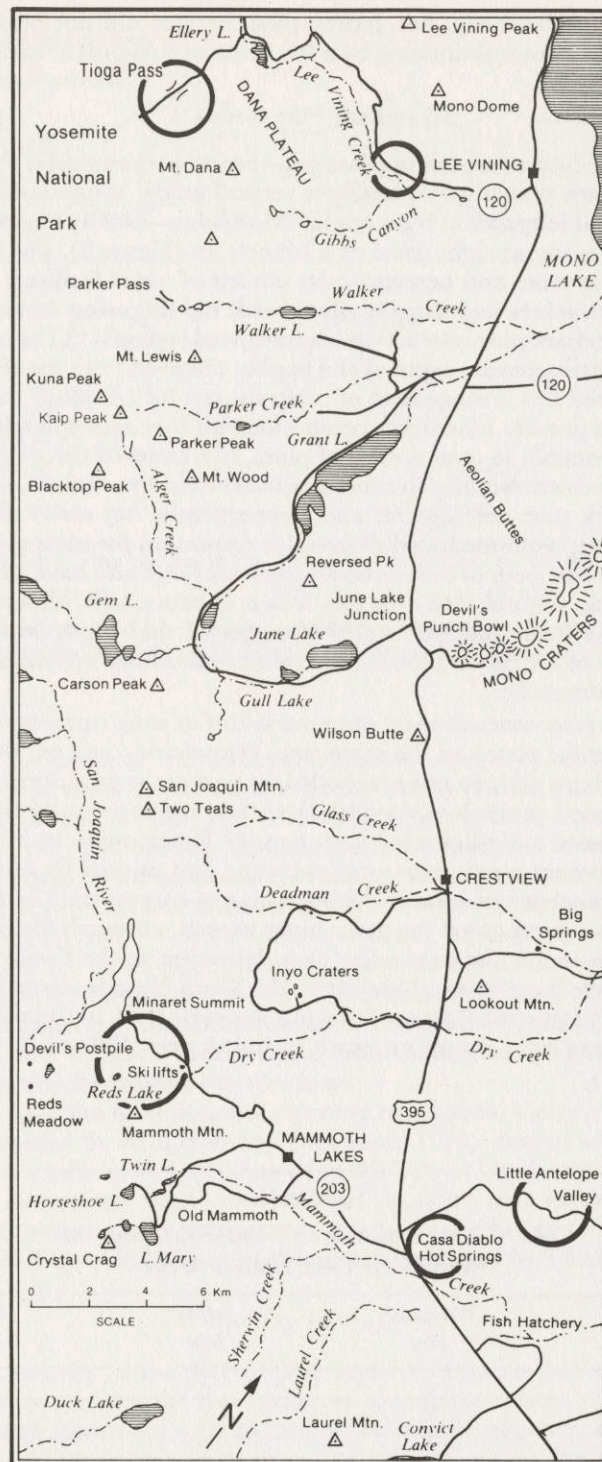


Figure 3. Map of the south-central region of the eastern slope of the Sierra Nevada, showing study areas.



1974 and 1975, respectively. For Jeffrey pine, harvest did not begin until 12 September in 1975 but was initiated by a few birds on 3 August or earlier in 1976.

#### Whitebark Pine Cones

Whereas the branches of most pines grow nearly perpendicular to the trunk, those of whitebark pine grow at nearly a vertical angle. Whitebark pine cones develop with their long axis at right angles to branches—usually in pairs, clusters, or circlets of as many as eight cones at a branch tip (Figure 5). The vertical arrangement of branches and perpendicular circlets of cones facilitate harvesting of seeds by nutcrackers and suggest, along with the following factors, that the nutcracker-whitebark pine interaction is a coevolved system: (1) The cone circlets at the tip of the branches are exposed and readily observed from the air. Selection may have favored this arrangement of cones in part for "display" purposes. (2) The branch tips provide nutcracker perch sites with easy access to adjacent cone circlets. (3) In contrast to most species of pines, ripe cones of the whitebark pine do not open. Seeds are retained in cones until harvested by animals. (4) The seeds of the whitebark pine are wingless and, consequently, not easily dispersed by wind. In contrast, wind-mediated dispersal is important for most species of the genus *Pinus*. (5) The seeds of the whitebark pine are large and have a high caloric value (Tomback, unpubl. MS)—factors which enhance seed attractiveness for animals. Vander Wall and Balda (1977) suggested that many features of the cones and seeds of the piñon pine are the result of a similar mutualistic interaction with the nutcracker.

Whitebark pine cones showed some variation in cone ripeness from tree to tree and among the cones on the same tree. Whitebark cones on low branches and on the northern side of a tree are shaded for part of the day; during my study, these cones ripened as much as a month later than the cones at the top of a tree, which were exposed to sunlight for longer periods. For example, by 19 September 1976, lower cones on many trees were as unripe and unused by nutcrackers as cones on top branches had been at the beginning of August in 1976. Differential cone ripeness has been noted for other pines as well, although for most species the time difference may be only a few days. However, at the Pacific Southwest Forest and Range Experimental Station in the Sierra Nevada, cones from stands of sugar pine (*P. lambertiana*) on south-facing slopes ripened 10 days to two weeks earlier than cones from stands on north-facing slopes (William B. Critchfield, pers. commun.).

TABLE 2  
Cone Crops Available as Food Sources in the  
Mammoth-Casa Diablo Areas

	<i>Whitebark pine</i>	<i>Jeffrey pine</i>	<i>Piñon pine</i>
1973	X	0	0
1974	X	X	X
1975	X	X	0
1976	X	X	X

X = moderate to heavy cone crop.

0 = light or no cone crop.



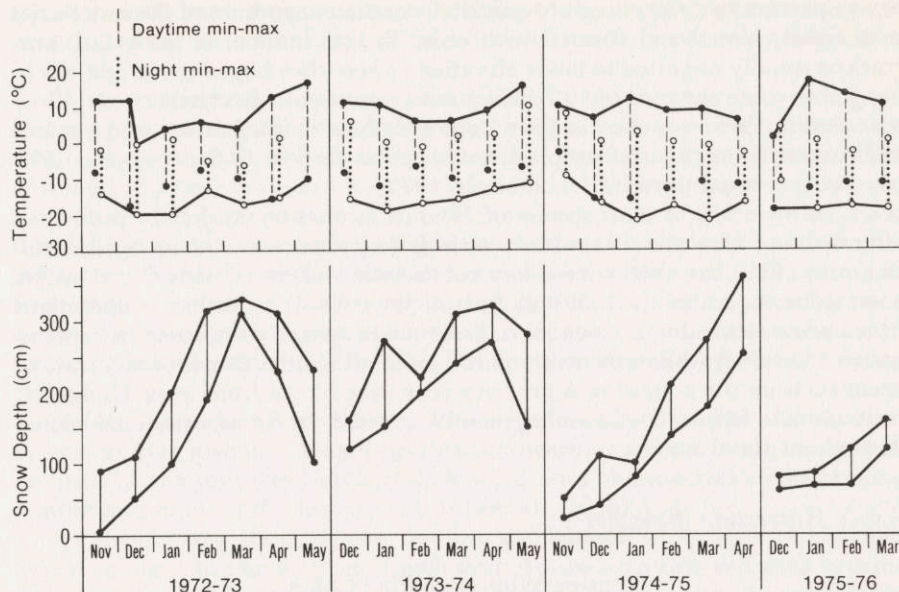


Figure 4. Monthly daytime and nighttime minimum and maximum temperatures and monthly minimum and maximum snow depths recorded on Mammoth Mountain, 2,910 meters from 1972 to 1976.

When the cones of the whitebark pine are unripe or partially ripe, oleoresin — a thick, sticky substance secreted by woody material of the cone as well as by other parts of the pine tree — accumulates over cone scales in large droplets. Tough, wet, and fibrous, the cone scales are detached at midsummer only with much effort by the nutcracker. While harvesting seed, nutcrackers become covered on their breast and throat with red color from anthocyanins — pigments in cones (Mirov, 1967) — from contact with the broken ends of scales.

As whitebark cones ripen, the cone material dehydrates, causing scales to separate slightly from the central core (Krugman *et al.*, 1974). During this time, the seed endosperm firms and seedcoats become woody, turning from light to medium brown in color. Much of the resin coating and deposits on the cone harden, thereby decreasing the stickiness.

In the field the final phase of ripening of whitebark pine cones proceeded rapidly (as noted by Krugman and Jenkinson, 1974), during which an increasing number of nutcrackers participated in the harvest. By the time the cones were fully ripe, nutcrackers began to store seed, an event that varied in occurrence by as much as two weeks from year to year. Storage behavior became evident by 25 and 29 August in 1973 and 1974, respectively, and by 8 September in 1975.

#### Jeffrey Pine Cones

Characteristics of the Jeffrey pine and its cones do not appear to be as strongly influenced by the nutcracker as are characteristics of the whitebark pine, although features of such an interaction may be obscured by other factors. Jeffrey pine cones open and rapidly shed winged seeds. The arrangement of branches and cones is similar to that of most pines.

Nutcrackers rarely harvested seed from unripe Jeffrey pine cones in midsummer. Most of the cones at that time were green in color; those with purple-



brown patches had ripened more quickly from direct exposure to the sun. Scales were tightly closed and covered with resin. In late summer or early fall, nutcrackers usually migrated to lower elevations where they began to harvest ripening Jeffrey pine seed. About 12 September, nutcrackers first harvested Jeffrey pine seed in 1975; however, in 1976 I observed a few birds harvest seed as early as 3 August. Storage of Jeffrey pine seed began as early as 18 September in 1976 but did not begin until mid-October in 1975.

Like the cones of most species of *Pinus*, the cones of the Jeffrey pine open after ripening. However, in my study areas Jeffrey pine cones did not open simultaneously. One tree might have any combination of cones with closed scales, open scales, or scales open on only part of the cone. In addition, a tree might have open cones from previous years. Some cones opened completely in September and October, while others remained closed all winter. Cones of any state of openness from the present or a previous year were blown from trees. Unopened cones which fell and were subsequently covered by snow remained closed throughout the winter.

### *Adult Harvesting Behavior*

#### Unripe Whitebark Pine Cones

The process of harvesting unripe whitebark pine seed appeared to involve complex motor patterns for nutcrackers. When a nutcracker landed in a tree to harvest seed, the bird assumed a firm stance with legs spread slightly apart to stabilize the center of gravity. Whitebark cones range in length from about  $3.5 \pm 9$  centimeters (Sudworth, 1908). Depending on the size of the cone involved and its position and proximity to other cones, a nutcracker perched either upright or sideways in any of a variety of ways when harvesting seed. For example, it (1)



Figure 5. Whitebark pine branches rise vertically from trunks. Cones grow in circlets at branch tips, the long axes of the cones perpendicular to the branch. Consequently, the cones are clearly displayed and very accessible to birds.



stood on the cone it was harvesting, (2) gripped cones in the cluster other than the cone it was harvesting or cones in an adjacent cluster, (3) gripped the vertical branch bearing the cone cluster or an adjacent branch, or (4) any combination of the above.

After securing a base, a nutcracker stabbed its bill repeatedly into a cone, loosening and tearing off scales. When beginning to work on a new cone or a new area on the same cone, a bird used "power stabs" several times in succession. That is, it pulled its neck and head up and back with bill directed down and assumed a nearly vertical body posture by straightening its legs. As each blow was struck, the body dropped into a horizontal position, adding force to the blow. For tearing action, the bird reared its head and neck back and directed blows from different angles. Sometimes, while gripping tightly with its claws, a nutcracker hung over a cone in an upside-down posture as it tore into scales. Occasionally, a nutcracker seized a loosened scale with its bill and then ripped it off with a twisting pull.

Adult nutcrackers harvesting whitebark pine seed were often accompanied by one to four juveniles, which perched on nearby cones or in adjacent trees. Frequently, the juveniles fluttered their wings in a characteristic food-begging posture and emitted the hunger call (Mewaldt, 1956).

In unripe cones, the seeds were not firm and had soft white hulls; nutcrackers were able to remove only pieces of such seed. As cones ripened and seeds became more firm, birds removed whole seeds with more frequency. As each piece of seed or whole seed was removed, a nutcracker swallowed it directly or placed it in the sublingual pouch to feed dependent juveniles. The two actions could be distinguished. To place seed material in the sublingual pouch, a bird gave a slight backward toss of the head, lifting the bill. This action propelled the seed into the pouch from an opening anterior and lateral to the base of the tongue (Bock *et al.*, 1973).

A bird sometimes rested freshly extracted seed material on a cone or adjacent branch. Holding the material or seed in place with a claw, the nutcracker used its bill to clean the seed of adhering cone material or shifted the seed into position to be swallowed or placed in the sublingual pouch. Occasionally, a nutcracker detached an entire whitebark cone and carried it to an anvil — a large rock, stump, or bare branch. While resting the cone on the anvil and holding it between the feet, the nutcracker made typical bill stabbing movements to dislodge cone scales.

During the entire time a nutcracker spent harvesting seed from a cone, the bird was extremely vigilant and paused briefly every few seconds to glance up in a different direction. Birds of prey that caused alarm reactions and that occurred regularly in all study areas included the Red-tailed Hawk (*Buteo jamaicensis*) and Cooper's Hawk (*Accipiter cooperii*). Species that caused alarm reactions but occurred infrequently were the Prairie Falcon (*Falco mexicanus*) and Goshawk (*Accipiter gentilis*).

Bill-wiping was a frequent behavior pattern of harvesting nutcrackers because of the thick resin and woody debris from unripe cones. After extracting seed for a period of time and especially before feeding juveniles, a nutcracker flew to a dead tree or bare branch in a lodgepole pine or red fir and bill-wiped vigorously. Each side of the bill was alternately rubbed from base to tip against a side of the branch.

In midsummer, individuals were selective about the cones chosen for harvesting seed. They often landed on several cones in succession, testing each with several bill stabs, apparently locating the ripest cone before settling down to harvest. Also at this time, groups of birds tended to use the same stands of trees each



day and ignored trees on adjacent slopes and in other parts of the subalpine study areas. The cones in the stands of trees frequented by nutcrackers generally were riper than the cones from the other locations.

#### Unripe Jeffrey Pine Cones

The behavior and motor patterns of two birds observed harvesting unripe Jeffrey seed on 3 August 1976 were similar to those used to harvest unripe whitebark pine seed. Because Jeffrey cones are larger—14 to 30 cm in length—nutcrackers often stood on the same cone from which they were harvesting seed. They directed bill stabs into the cones, loosening scales, and apparently were not bothered by the prickles on cone-scale tips.

#### Extraction Rates for Unripe Pine Cones

In 1975 the average time required by a nutcracker to extract seed material from unripe whitebark cones was one item every 31 seconds (Table 3). In 1976 the average rate was one item every 28 seconds. During the same period in 1976, the few extraction attempts observed for unripe Jeffrey pine cones averaged one item every 61 seconds (Table 3). The extraction of Jeffrey seeds was significantly slower (Table 3). Based on these data, the use of Jeffrey cones as a food source in midsummer appeared to be less efficient than the use of whitebark pine cones.

#### Ripe Whitebark Pine Cones

During the last week of ripening of whitebark cones, the effort required by nutcrackers to remove cone scales decreased, and the birds frequently extracted whole, intact seeds. When cones were fully ripe, nutcrackers easily broke off cone scales with bill stabs, and seed extraction thus progressed at a rapid rate.

A cone harvested by a nutcracker, as opposed to other vertebrate seed predators, had a characteristic appearance. Sometimes nutcrackers removed only the scales facing upwards or sideways, leaving behind a partly hollow cone, and rarely only a core (Figure 6). Other species of birds removed only a few scales and seeds at most. Rodents usually chewed off the scales around the cone, leaving a central core.

Earlier in the summer most nutcrackers were found together in the same stands of whitebark pine, presumably because of differential cone ripeness from one area to another. By mid-September nutcrackers were dispersed throughout the subalpine belt. They continued to show selectivity about cones by landing on and testing several in succession before harvesting seed.

Before filling its sublingual pouch with ripe seed, a nutcracker usually spent two to three minutes harvesting seed for its own consumption. Whenever a seed was removed for eating, the nutcracker briefly tested the seed before cracking the hull to determine whether or not it was good. While moving the seed up and down in its bill, the bird opened and closed its mandibles rapidly around the seed, making audible clicks. Nutcrackers probably determined the suitability of seeds by their weight and the sound they made when rattled against the mandibles; unsuitable seeds were immediately dropped. This seed testing behavior was also reported for nutcrackers by Vander Wall and Balda (1977) and for Piñon Jays (*Gymnorhinus cyanocephalus*) by Ligon and Martin (1974). Nutcrackers cracked seed hulls by holding a seed between their mandibles and applying pressure. As a result, most seeds tended to split along the sides, which bear remnants of seed wings (Figure 7). For hard-to-crack seeds or seeds from caches made the previous



TABLE 3  
Pine Seed Extraction Rates

Cone maturity	Dates	Number of rates	Number of individuals	Whole seed or piece of seed per number of seconds		Mean length of timed run and S.D. in seconds
				Mean rate and S.D.*	Median rate	
<i>Pinus albicaulis</i>						
	1975					
Unripe, a**	4 Aug-3 Sep	83	47	1/31 $\pm$ 1/16	1/28	189 $\pm$ 125
Partially ripe, b***	4 Sep-6 Sep	23	13	1/21 $\pm$ 1/10	1/20	82 $\pm$ 34
Ripe, c	10 Sep-13 Sep	63	33	1/7 $\pm$ 1/3	1/6	48 $\pm$ 30
	1976					
Unripe, d†	28 Jul-3 Aug	81	34	1/28 $\pm$ 1/16	1/23	90 $\pm$ 40
<i>Pinus jeffreyi</i>						
Unripe, e††	3 Aug	5	2	1/61 $\pm$ 1/35	1/54	63 $\pm$ 42
Ripe, f	21 Sep-23 Sep	46	20	1/10 $\pm$ 1/3	1/10	30 $\pm$ 16

\* Standard Deviation.

\*\* a vs b median test, two-tailed  $.02 < p < .05$ .

\*\*\* b vs c median test, two-tailed  $p < .001$ .

† d vs e Mann-Whitney U test, one-tailed  $p = .006$ .

†† e vs f Mann-Whitney U test, one-tailed  $.0001 < p < .0002$ .

fall, nutcrackers often used their perch like an anvil, and, while holding a seed in place with a toe, they hammered with their bill. Both hulling patterns occur in the Eurasian Nutcracker (Formosof, 1933; Stegman, 1934; Turcek and Kelso, 1968).

According to my observations of six nutcrackers consuming a total of 49 seeds, each individual extracted, tested, removed the hull from, and swallowed one seed every 8 to 72 seconds. On the average, one seed was processed every  $17 \pm 15$  seconds.

By mid-October the nutcrackers at subalpine elevations were still selective about the whitebark cones from which they gathered seed and often tested several cones in succession before harvesting. Most cones were partly empty, and the few cones still filled with seed—usually on the lower branches—had still not completely ripened. As a result, only a few seeds were gathered from any one cone. Thus, the process of harvesting required more time late in the season. Nutcrackers were highly nomadic in the subalpine belt, traveling in small flocks from area to area where they searched through stands of whitebark pine.

#### Ripe Jeffrey Pine Cones

In late August, the incidence of nutcrackers found in the Jeffrey pine belt increased (Figure 1). Groups of nutcrackers made short-term excursions, often of only a few hours' duration, from the subalpine belt to the Jeffrey pine belt. At the lower elevations, individuals perched in Jeffrey pines and prodded at several different cones on each tree, occasionally harvesting seed. The purpose of these flights, as suggested by these activities, may have been to "test" the degree of cone ripeness and evaluate the numbers of cones available. Usually by





Figure 6. Characteristic appearance of whitebark pine cones after nutcrackers have harvested seed.

late September (Figure 1), nutcrackers remained in the Jeffrey pine belt—especially in the lower areas where piñon pine is abundant—and began to harvest ripe Jeffrey pine seed.

Even in years with an abundant crop of piñon cones, nutcrackers preferred to harvest and store Jeffrey pine seed. In 1974, piñon and Jeffrey cones ripened simultaneously, but Jeffrey cones were harvested most frequently. In 1976, piñon cones ripened two to three weeks after the Jeffrey cones, but nutcrackers only rarely attempted to take piñon seed while Jeffrey seed was available. Until piñon cones are fully ripe and completely open, the cones are especially resinous and the scales tough and fibrous.

Nutcrackers harvested Jeffrey pine seed solitarily, in pairs, or in small flocks of about three to ten birds. Birds were quiet while harvesting seed, but group vocal interactions occurred intermittently, especially alarm calls in response to birds of prey circling over the area. Birds settled on Jeffrey pine cones for only a short time; they quickly sorted through the open scales for seed before moving on to another cone. Open cones lose their seeds rapidly, especially during strong winds, and may retain only a few. For ripe whitebark pine cones, a nutcracker spent an average of 48 ( $\pm 30$  seconds) harvesting seed from a single cone ( $n = 63$  cones) and remained on one cone as long as 188 seconds. A nutcracker spent an average of only 30 ( $\pm 16$ ) seconds on a single Jeffrey pine cone ( $n = 46$  cones), remaining only as long as 64 seconds.

Nutcrackers spent more time harvesting cones with scales not fully open than those with open scales. To extract seed from closed cones, the birds used bill stabs and forced open the scales. After this treatment, the scales looked frayed or shredded. When a nutcracker located a seed, it used its bill like a forceps and extracted the seed from between scales. With about equal frequency, the seed was removed with the seed-wing attached to the seed or with it detached and lodged in the cone. A nutcracker always removed the wing from a Jeffrey pine seed before placing the seed in its sublingual pouch. Holding the seed in the bill with wing protruding, a nutcracker usually shook its head vigorously to loosen the wing, or closed the mandibles tightly against the wing with a scissor-like action. If this failed, the nutcracker rubbed the wing against cone scales to break



it off. To clean debris from a seed, the nutcracker used a cone as support, holding the seed in place with its toes.

Before hulling and eating seeds, and often before placing seeds in the sublingual pouch, nutcrackers tested the quality of the seed in the same way they tested a whitebark seed. Good seeds and those with withered (aborted) embryos or mealy contents probably differed both in weight and in the sound they made when rattled between the mandibles.

#### Extraction Rates for Ripe Pine Cones

In 1975, whitebark pine cones ripened rapidly in the first weeks of September. The mean extraction rate for partly ripe cones during the transition period of 4 to 6 September was one seed every 21 seconds (Table 3), a faster rate than that for unripe cones ( $0.2 < p < .05$ , median test). Some nutcrackers began to harvest seed in quantity and make seed stores on 8 September. The numbers of nutcrackers engaged in these activities increased rapidly in the following days. Extraction rates for ripe cones from 10 to 13 September averaged one seed every seven seconds, a highly significant difference ( $p < .001$ ) in comparison to the transition period rate. The onset of seed storing behavior thus appeared to be correlated with a greatly increased efficiency of seed extraction, and also probably with seed coat maturity. Vander Wall and Balda (1977) reported that the extraction rate for piñon pine averaged one seed every 27 seconds.

From 21 to 23 September 1976, I timed extraction rates of ripe Jeffrey pine seed for 20 individual nutcrackers (Table 3). The mean of one seed every 10 seconds was a highly significant increase ( $.0001 < p < .0002$ ) over the mean extraction rate recorded on 3 August 1976 for unripe Jeffrey pine seed.

#### Juvenile Harvesting Behavior

Although the majority of juveniles still depended on adults for pine seed at midsummer, a number of young birds began to harvest whitebark pine seed by the beginning of August. These juvenile nutcrackers were probably the offspring of the earliest nesting pairs.



Figure 7. Before consuming whitebark pine seeds nutcrackers usually remove the hulls, either by cracking the seeds between the mandibles or using an "anvil."



The major differences in harvesting behavior between adults and juveniles were not in the motor patterns involving the detachment of scales and extraction of seed, but rather in the time wasted between harvesting bouts and in motor coordination. On the whole, juveniles harvesting whitebark pine seed were less efficient at extracting pine seed for the following reasons: (1) After selecting a cone cluster, juveniles—unlike older nutcrackers—did not begin harvesting immediately. They were easily distracted and sometimes prodded desultorily among the other cones in the cluster or among the nearby foliage. (2) Juveniles were awkward on their perch. They had difficulty finding a balanced position for harvesting and shifted their perch often. At least three times in the course of the study, I observed juveniles lose their balance while jabbing into cone scales, topple off their perch, and fall a meter or more before recovering and landing in a lower branch. Adults never fell off their perch. (3) Initial stabs into a cone by juveniles were unsure and did not have the same force as those of older nutcrackers. (4) Juveniles were not as coordinated when manipulating extracted seed material and dropped several items per cone. Adults only occasionally dropped seed material.

Later in the season, when juveniles began harvesting Jeffrey pine seed, these differences in harvesting efficiency were not as obvious.

#### Extraction Rates

The mean extraction rate of unripe whitebark pine seed for 12 juveniles from 28 July to 3 August 1976 was one seed every  $25 \pm 31$  seconds (median = one/23

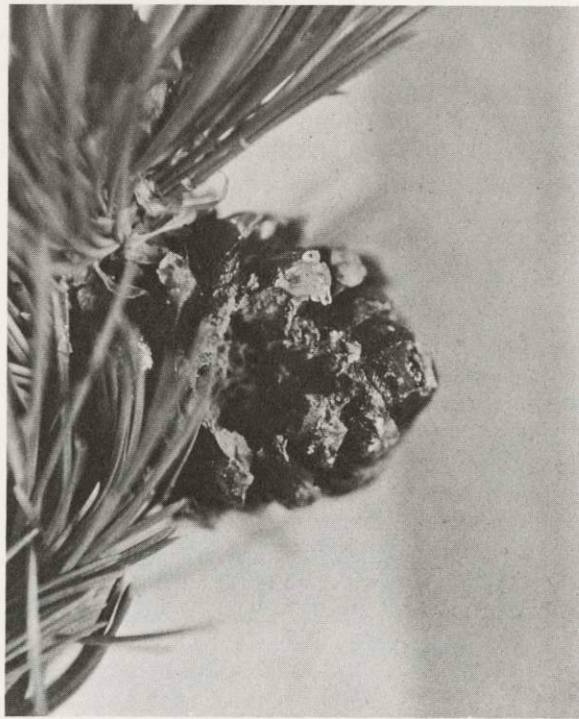


Figure 8. Whitebark pine cone from which seed was harvested by a nutcracker. By October, intact cones are rare.



sec, number of rates = 22, mean length of timed run =  $83 \pm 34$  sec). A median test comparing juvenile extraction rates with rates for adults during the same period (Table 3) did not indicate a statistical difference. However, the awkwardness of juvenile nutcrackers extracting seed seemed to make them somewhat less efficient than adults if only because the time between bouts of harvesting activity was greater. Additional data must be obtained before this can be stated conclusively.

### Seed Competitors

When whitebark and Jeffrey cones became ripe, a number of bird and mammal species began to feed on the seed. The few agonistic encounters that I observed between the nutcracker and other seed predators clearly indicated that the nutcracker was dominant among all the other species including the sciurids mentioned below. However, one or more of these animals often foraged in close proximity to a harvesting nutcracker, even on adjacent cones, without eliciting an aggressive response.

During late summer and fall, the following bird species were common at all elevations and occasionally fed both on whitebark and Jeffrey pine seed from cones: Williamson's Sapsucker (*Sphyrapicus thyroideus*), Hairy Woodpecker (*Picoides villosus*), White-headed Woodpecker (*P. albolarvatus*), Mountain Chickadee (*Parus gambeli*), White-breasted Nuthatch (*Sitta carolinensis*), and Cassin's Finch (*Carpodacus cassinii*). The Red Crossbill (*Loxia curvirostra*) and Pine Grosbeak (*Pinicola enucleator*) were transient through the subalpine belt in late summer and fall, feeding primarily on pine seed.

Several species of squirrels fed on ripe whitebark and Jeffrey pine seed. The Golden-mantled Ground Squirrel (*Spermophilus lateralis*) gnawed on cones, both in trees and on the ground, to extract the seed; several species of chipmunks (*Eutamias* spp.) harvested seed from trees by gnawing on cones; and the Chickaree (*Tamiasciurus douglasi*) cut down cones from trees and buried them in the ground. The Chickaree seemed to be the nutcracker's most efficient vertebrate seed competitor, because it removed a number of cones from each tree before nutcrackers could use them. The Chickaree's habit of cutting down and storing whole cones rather than harvested seed may maximize the quantity of seed stored in relation to time and energy expended. But this method may also have the advantage of removing as much seed as possible as quickly as possible before nutcrackers begin harvesting.

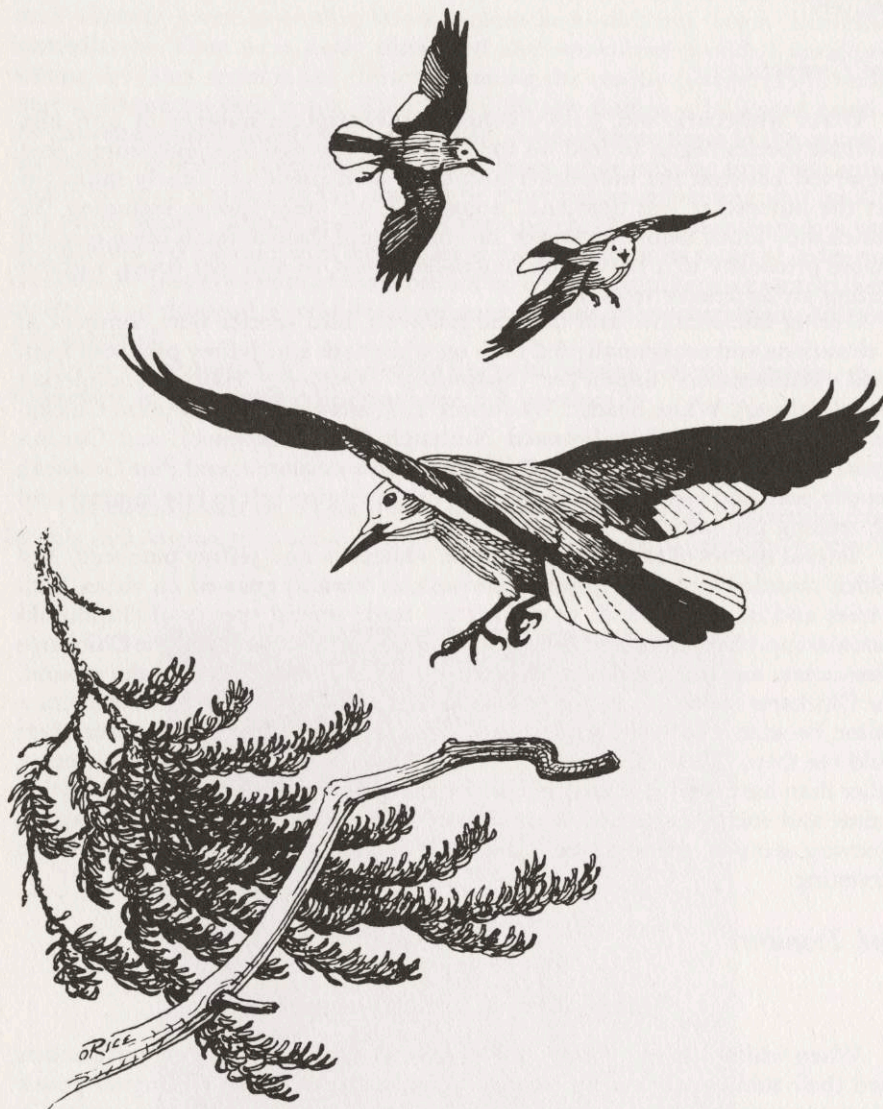
### Seed Transport

#### Sublingual Pouch and Seed Capacity

When whitebark and Jeffrey pine seed storage activities began, nutcrackers filled their sublingual pouches as they harvested seed. A full sublingual pouch bulges noticeably in the throat region of the bird, resembling a large goiter in position and size. By means of the sublingual pouch, nutcrackers transported harvested seed to storage sites.

To determine the seed capacity of the sublingual pouch, I followed 13 individuals from cone to cone and tree to tree as they harvested seed and filled their sublingual pouches before departing to store seeds. A single pouch-load ranged from 35 to 150 whitebark pine seeds. ( $\bar{X} = 77 \pm 37$  seeds, median = 58 seeds). Because I was not certain the sublingual pouch was completely empty when the birds arrived and began harvesting, the number of seeds re-





Clark's Nutcracker, *Nucifraga columbiana*. Drawing by Orville O. Rice.



corded for each pouch-load may be about 10 too few. According to my volumetric measurements for whitebark pine seed ( $n = 25$ ), seeds ranged from .15 cubic centimeters to .40 cc each and  $\bar{X} = 0.26 \pm 0.054$  cc. Using this value, the volume of a full sublingual pouch was as great as 39 cc, and had a mean and median of 20 cc and 15 cc respectively.

The weight of a single whitebark pine seed ranged from .14 to .19 grams ( $n = 200$  seeds and  $\bar{X} = 0.16 \pm 0.011$  grams); consequently, the average pouch-load of 77 seeds weighed 12.3 grams. Using the data on nutcracker body weight averages reported by Giuntoli (1963), I calculated that a pouch-load of seeds represented from about 4 to 17 percent of the weight of a nutcracker ( $\bar{X} = 9\%$ ).

For a sample of 50 cones, the numbers of mature seeds per cone ranged from 21 to 86 ( $\bar{X} = 45 \pm 16$  seeds per cone, median = 42). If nutcrackers used all seeds in a single cone—which is not the case early in the season—they would require from 0.4 to 7 cones ( $\bar{X} = 1.7$  cones) to make one pouch-load of seed.

A review of the findings of other workers indicated considerable variation in the number of seeds transported in the sublingual pouch, Giuntoli (1963) found from 1 to 46 whitebark seeds with an average of eight in the sublingual pouches of 13 nutcrackers collected at different times of the year. Grinnell and Storer (1924) collected an individual with 65 whitebark pine seeds in its pouch and another individual with 72 piñon seeds. Vander Wall and Balda (1977) found the average number of piñon seeds carried by five individuals to be 55 or 13 percent of the body weight of the nutcrackers, with a maximum load of 95 seeds. For ponderosa pine (*Pinus ponderosa*), Grinnell *et al.* (1930) collected an individual with 34 seeds in its pouch, and Giuntoli (1963) found a range of 1 to 92 seeds per pouch-load for 20 individuals, with an average of 25 seeds.

Similar variation in the numbers of seeds transported per pouch-load were found for the Eurasian Nutcracker. Values reported for the Siberian stone pine (*Pinus sibirica*) ranged from 50 to 167 seeds per pouch-load (Gorodkov, 1916; Pallas, 1911; Randla, 1964; Reimers, 1956; Schonbeck, 1956; Suchkin, 1938). For Japanese stone pine (*Pinus pumila*) seed, a pouch-load was found to consist of 218 seeds (Mezhenny, 1961).

Based on the weights reported for pouch-loads of 120 and 90 seeds, 35.9 and 22.2 grams respectively (Reimers, 1956), I calculated that an average of 3.7 seeds of the Siberian stone pine weighed 1.0 gram. I used the average weights given for the Eurasian Nutcracker by Dement'ev (1970) to calculate the percentage of body weight represented by the various pouch-loads, and found a range from 4.6 to 27 percent with an average somewhere near 14 percent. According to Löhrl (1970), Eurasian Nutcrackers transport cones of the Swiss stone pine (*Pinus cembra*) over short distances. The cones weigh as much as 96 grams or more, and thus represent a load of about 33 to 50 percent of the body weight of the bird.

Because of the dense foliage and height of the Jeffrey pine—about 38 to 43 meters (Sudworth, 1908)—I could not follow individual nutcrackers to determine how many Jeffrey pine seeds constituted a full pouch-load. Whitebark pine trees are only 5 to 15 meters tall (Sudworth, 1908).

### Seed Storage

#### Initiation of Seed Storage

During my investigation, the timing of the onset of whitebark pine seed storage behavior by nutcrackers varied at most by two weeks from year to year.



The earliest date recorded for the beginning of seed storage was 25 August in 1974. The latest date of storage initiation was 8 September in 1975. A delay in cone ripening in 1975 was the consequence of late and heavy snows the previous spring (Figure 4). By mid-October—as early as 10 October in 1976 and as late as 16 October in 1975—whitebark pine seed storage behavior had ceased.

Jeffrey pine seed storage began sometime after the first nutcrackers had settled in the Jeffrey pine belt, as early as 18 September in 1976 and as late as mid-October in 1975. The 1975 timetable was also the consequence of late snows the previous spring (Figure 4). The only date obtained for the cessation of Jeffrey pine seed storage was 7 December in 1975. Seed storage probably ends somewhat earlier in most years.

### Caching Behavior

Both adult and juvenile nutcrackers participated in storing whitebark and Jeffrey pine seed. After harvesting a pouch-load of seeds, a nutcracker traveled to an area where it concealed many small clusters of seeds in a variety of sites, until the sublingual pouch was empty. I will refer to each cluster of seeds as a single "cache." "Stores" are defined as the collective caches of all nutcrackers of the population.

Nutcrackers tended to be very secretive while making seed caches and worked individually or, rarely, in pairs. When a nutcracker selected an area for seed storage, it landed and hopped along the ground, turning its head from side to side while scrutinizing the terrain. The nutcracker paused at a chosen site and quickly dug a shallow trench a few centimeters in length with sideswiping, digging motions of the bill tip. Next, to remove seeds from the sublingual pouch, the nutcracker tossed its head backward slightly several times in succession. Each seed was placed in the trench, forming a small cluster or cache. In gravelly soil or pumice, no trench was dug and the seeds were merely pushed one at a time into place with the bill. A single cache consisted of 1 to 15 seeds ( $\bar{X} = 4.2 \pm 2.9$  seeds per cache,  $n = 214$  caches, Tomback, unpubl. MS). After completing a cache, the nutcracker covered the trench with soil, again using sideswipes of the bill, and surveyed the cache-site. The bird then moved on, making a series of caches in the same area or making another series of caches a distance away—until the sublingual pouch was empty. The nearest-neighbor distances between caches in a series ranged from 10 to 300 cm ( $\bar{X} = 67 \pm 69$  cm,  $n = 113$  inter-cache distances, Tomback, unpubl. MS). During this procedure, the nutcracker frequently paused and glanced around the area. If a nutcracker or Steller's Jay (*Cyanocitta stelleri*) landed nearby, the storing nutcracker flew into a tree or flew off some distance before returning to continue its caching. Sometimes Steller's Jays were apparently unnoticed by nutcrackers storing seed. After the nutcrackers left the area, the jays flew to the cache sites and retrieved the seeds.

Nutcrackers occasionally stored whitebark seed on a short-term basis to be retrieved later and stored in another location. I observed this behavior three times during the course of my study. On two occasions, the nutcracker went directly to several sites in succession, digging up a seed cache at each and placing the seeds in its bulging sublingual pouch. It then flew off and presumably stored the pouch contents elsewhere. For the third observation, I have more detail. A nutcracker with a full sublingual pouch had been harvesting seed from a whitebark pine cone. It stopped harvesting and flew to the top of a 2.5-meter-tall lodgepole pine (*Pinus contorta*). The bird then landed on the ground near the tree, dug up two seeds from a spot in open pumice, and



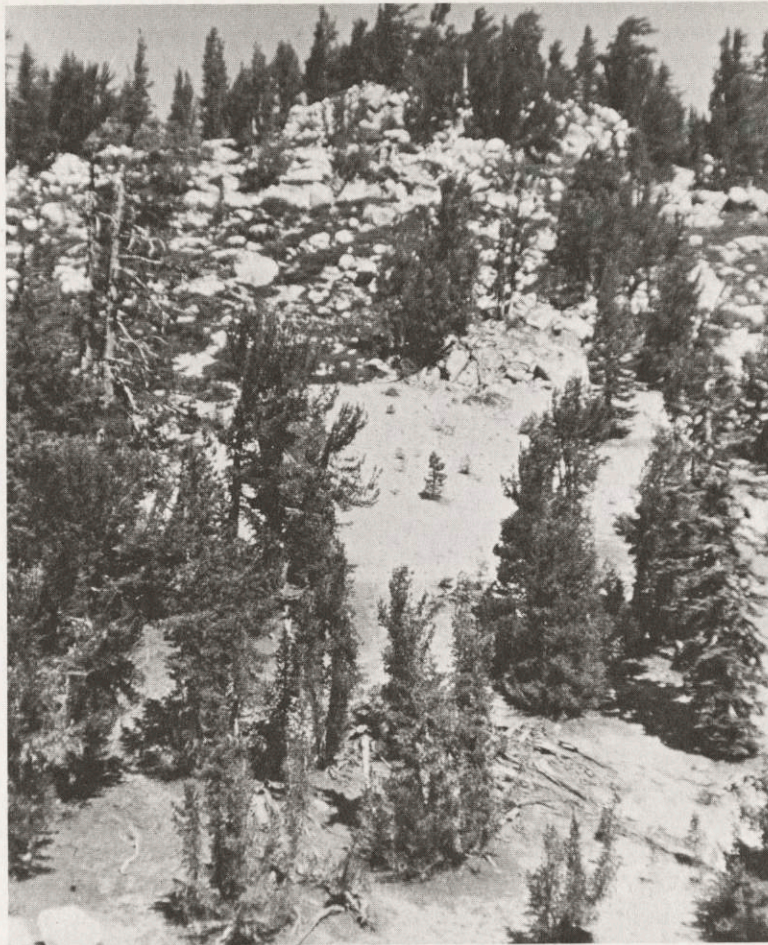


Figure 9. South-facing convergent storage slope in the Red's Lake study area (see text for explanation). Note stand of whitebark pine in foreground.

moved off one half meter and removed three seeds from the base of a sulphur flower plant (*Eriogonum umbellatum*). The bird then flew to the top of another small tree, paused briefly and then landed on the ground nearby. There it recovered two more caches in open pumice—consisting of two seeds each—and a final cache of two seeds from the base of another sulphur flower plant. As each cache was recovered, the bird placed the seeds in its sublingual pouch. I do not know whether the same individual that recovered the seed caches had buried them originally.

#### Divergent and Convergent Storage Areas

*Divergent Seed Storage.* During each seed-storage trip, an individual selected either what I term a “divergent” or “convergent” area in which to store seed. A bird storing seed “divergently” made seed caches anywhere on the forest floor where there were stands of either whitebark, Jeffrey, or piñon pine. An individual landed on the ground not far from the trees from which it had harvested seed and made a series of caches. Often the bird then flew a distance of about 10 to 50



meters farther to make more caches, and so on until the pouch-load had been stored. At Tioga Pass, nutcrackers used only the divergent mode of seed storage; all birds stored seed in the rocky hillocks which bear stands of whitebark pine and rise above the adjacent meadowland. Divergent seed caching by nutcrackers in any altitudinal belt resulted in a scattering of seed stores over a large area and variety of terrain.

*Convergent Seed Storage.* In addition to storing seed divergently, many nutcrackers in each study area also used the same hillside or slope(s) for some of their seed storage (Figure 9). As a result, these communal or convergent storage slopes contained a high density of seed stores.

In the Red's Lake vicinity, the south- and southeast-facing slopes of a small, steep hill to the west of Mammoth Mountain were used for convergent seed storage by the nutcrackers harvesting seed from adjacent stands of whitebark pine (Table 4). Also, I observed birds carry seed two kilometers to the slopes, and suspected that some nutcrackers brought seed over even longer distances. The nutcrackers in the Mammoth area also transported seed to a steep west-by-southwest-facing slope above the Pumice Flat area of Red's Meadow (Table 4).

In the Casa Diablo-Little Antelope Valley study area, a steep, southwest-facing hillside served as a convergent storage slope for Jeffrey and piñon pine seed (Table 4).

The Slender-billed Nutcracker in the Ural Mountains stores seed both throughout forested areas and on communally used tundra slopes above timberline (Bibikov, 1948); this subspecies, too, stores seed divergently and convergently.

#### Characteristics of Convergent Storage Slopes

The selection of a slope for communal use by nutcrackers seemed to depend on several characteristics. All three slopes are (1) adjacent to large stands of pines used by nutcrackers as food sources, (2) covered by a deep layer of pumice or gravelly soil that is volcanic in origin, and (3) face a direction that maximizes exposure to direct sunlight—from southeast to west by southwest (Table 4). All three slopes are steep, with inclinations varying from 22° to 30°.

Vander Wall and Balda (1977) found similar characteristics in the convergent storage slopes chosen by Clark's Nutcrackers in northern Arizona.

In the mountains of Khamar-Daban, the Slender-billed Nutcracker stores convergently in alpine slopes and burned areas (Reimers, 1953). The Slender-billed Nutcracker in the Urals stores convergently in slopes above timberline (Bibikov, 1948; Kuznetsov, 1959).

TABLE 4  
Macro-habitat Features of  
Convergent Storage Areas

<i>Convergent storage slope location</i>	<i>Slope exposure</i>	<i>Angle</i>	<i>Elevation (meters)</i>	<i>Soil type</i>
Hill west of Mammoth Mountain	SE and S	22° to 29°	2,805 to 2,880	pumice
Casa Diablo	SW	29°	2,265 to 2,325	gravel
Above Pumice Flat	WSW	25° to 30°	2,550 to 2,670	pumice



In the Mammoth Mountain study areas, nutcrackers flew to convergent slopes alone, in pairs, or in small flocks. Once at a slope, the flocks dispersed and each bird worked by itself. After storing a pouch-load of seed, the individuals often returned to the same stand of trees to continue their harvest.

In the Casa Diablo area, I observed throughout the day a steady stream of nutcrackers flying between the southwest-facing convergent storage area and the adjacent forest. I counted as many as 15 nutcrackers in the air at one time; but the birds usually travelled alone, in pairs, or small groups of 3 to 5 birds. Within about two hours of sunset, the number of nutcrackers going to the storage slope decreased, as the birds began to forage and engage in social interactions in preparation for roosting (Tomback, 1978).

#### Cache Sites

Nutcrackers selected certain micro-habitat features as sites for both convergent and divergent storage. The various types of microhabitat features used by nutcrackers are listed in Table 5 and Figure 10.

In the volcanic pumice covering Mammoth Mountain and vicinity, sulphur flower plants occur in high density. Nutcrackers frequently hid seeds at the base of these plants (Table 5). At Tioga Pass, where there was no convergent slope, nutcrackers frequently stored seed at the bases of trees on rocky rises (Figure 11).

I never observed nutcrackers use the shores of lakes, stream banks, meadowland or any other damp areas, clumps of grass or sedge, clumps of short-lived flowering plants, fine-grained soil without a covering of forest litter, or hard-packed substrate as sites to store seed.

During the fall of 1973, 1974, and 1975, I observed 52 nutcrackers at close range make 80 separate caches in the vicinity of Mammoth Mountain. The relative frequencies of micro-habitat sites selected by these birds may reflect to some extent the relative frequency of occurrence of the different micro-habitat sites in a study area rather than the order of preference by nutcrackers (Figure 4). In several cases, however, the data do reflect nutcracker partiality; for example, the bases of trees are preferred over tree roots and the latter are preferred over storage in the tree itself, and open pumice is preferred over pine needle litter.

TABLE 5  
Micro-habitat Features

<i>Ground cover</i>	<i>Objects</i>	<i>Trees</i>	<i>Plants</i>	<i>Other</i>
Volcanic gravel	rocks	roots	Sulphur flowers, <i>Eriogonum</i>	rocky rises above meadows
Pumice	fallen branches	holes cracks	Manzanita, <i>Arctostaphylos</i>	exposed rock
Pine needle litter	logs trees	under bark	Heather, <i>Phyllodoce</i> and <i>Cassiope</i> Chinquapin, <i>Castanopsis</i> Sagebrush, <i>Artemisia</i>	rock rubble



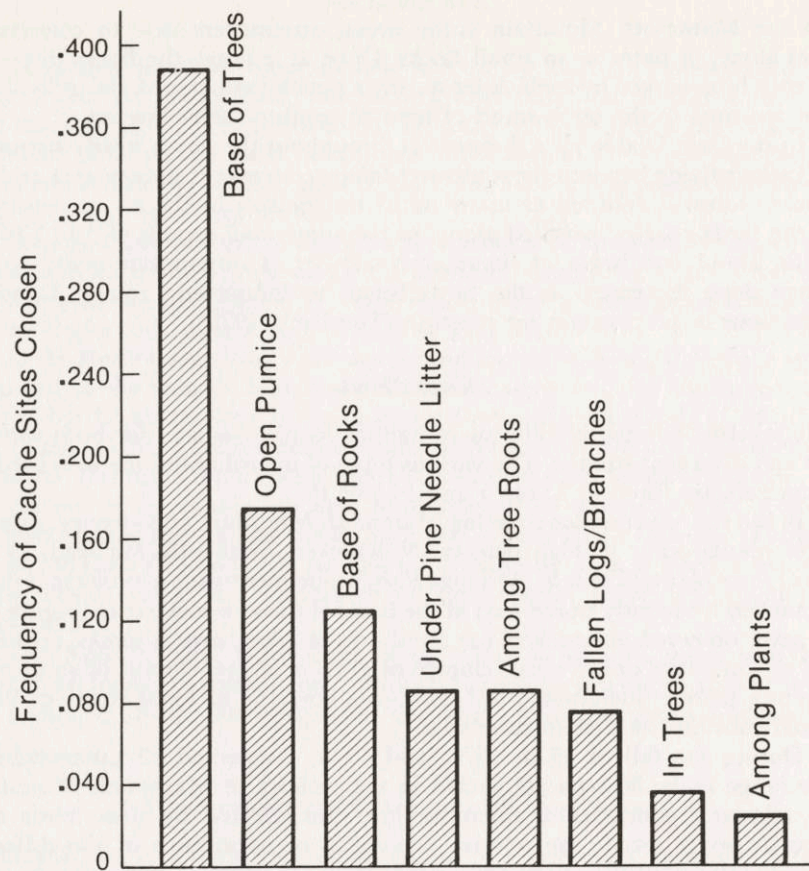


Figure 10. The relative frequency of the use of different micro-habitat features by nutcrackers for storing seed.

The various subspecies of the Eurasian Nutcracker use similar micro-habitat sites. Seeds are stored under peeling bark and on exposed rocky sites (Kishchinskii, 1968), among spruce stands (Mezhenny, 1961), under stones, in loose conifer litter on the forest floor (Bibikov, 1948; Reimers, 1959) and by shrubby trees and under plants (Kuznetsov, 1959). In addition, the Eurasian species places seeds under a covering of moss or lichen (Bibikov, 1948; Kishchinskii, 1968; Reimers, 1959; Swanberg, 1951).

#### Distances Between Feeding Areas and Cache Sites

During the period of harvest and storage of whitebark pine seed, nutcrackers not only stored whitebark seed at subalpine elevations, but also transported seeds to convergent storage slopes at lower elevations. Subalpine seed storage generally occurred in early morning and late afternoon hours, and transportation of seeds to lower areas from about 09:00 to 16:00 hours. During the longer flights, nutcrackers travelled alone, in pairs, or in small groups which frequently perched in the tops of tall trees, resting and exchanging vocalizations.

In the vicinity of Mammoth Mountain, nutcrackers with full sublingual pouches headed northeast and flew downslope out of sight in the general direction of the Casa Diablo area. At Casa Diablo, nutcrackers with full throat



pouches often flew toward the southwest-facing convergent storage slope from the general direction of Mammoth Mountain and the adjacent Sherwin area. The straight-line flight from the Mammoth Mountain vicinity to Casa Diablo is 12.5 km, with a 500-meter decrease in elevation. From Casa Diablo, the nearest subalpine habitat is in the Sherwin and Laurel Mountain drainages, a minimum of 4.5 km flying distance.

In addition to flights in the direction of Casa Diablo from the Red's Lake area, a stream of nutcrackers flew to and from the storage slope above Pumice Flat. Whereas some nutcrackers stored seed in the upper portion of the Pumice Flat slope and returned to the harvest, others continued their flight downslope, storing seed as low as 2,550 meters and travelling as far as 2.5 km from parts of the Red's Lake area.

In the Tioga Pass area, nutcrackers in groups of one to ten transported the seeds northeast along the pass and downslope in the direction of Lee Vining Canyon, a distance of about eight to ten km. I observed individuals store seeds among the sagebrush and piñon pine on the steep, south-facing slope of the canyon.

Transportation of seeds by nutcrackers over long distances to storage slopes has been reported by other workers. Vander Wall and Balda (1977) observed that nutcrackers fly 7.5 to 22 km from pine stands to storage slopes, with an altitudinal gain of between 530 and 600 meters. As recounted by Guintoli (1963), Mewaldt saw nutcrackers in northern Idaho on 30 September 1950 harvest ponderosa pine seed and transport it two to three miles (about three to five km). The Thick-billed Nutcracker was observed transporting hazelnuts six km from hazel-coppices to coniferous forest where they were stored (Swanberg, 1956). Sutter and Amann (1953) and Reimers (1958) reported that Slender-billed

On 16 and 17 October 1975, at the end of the whitebark pine seed harvest, I sampled micro-habitat sites of the type used by nutcrackers for seed caches along a 60-meter vertical transect of the lower elevation convergent storage slope at Casa Diablo. I recovered a total of 22 seed caches by this method, representing 58 seeds. Twelve caches (54%) consisted entirely of whitebark pine seed, and the remainder entirely of Jeffrey pine seed. The whitebark seed represented 41 percent by number of the total recovered seed. On 22 September 1976, I briefly searched an area on the convergent storage slope at Casa Diablo and located 10 seed caches, representing 16 seeds. Of these caches, four were of whitebark pine seed and contained five seeds in total.

Giuntoli's (1963) analysis of the stomach contents of nutcrackers collected at different elevations and times of the year in Montana by Mewaldt (1948) also indicated that nutcrackers had transported and stored whitebark pine seed at low elevations.

### *Timing of Seed Recovery*

#### Late December to Late March

During winter months, the majority of nutcrackers concentrated in the Jeffrey pine belt, especially in areas of Jeffrey pine-piñon-juniper-sagebrush ecotone. A small number of nutcrackers overwintered at subalpine elevations and were transient through the lodgepole-fir belt (Figure 2), especially when severe storms forced them down from subalpine elevations.

During my investigation, the subalpine belt accumulated a snowpack that varied in depth from about 40 to 160 cm from year to year (Figure 4). After severe weather, snow also accumulated in the lodgepole-fir and Jeffrey pine belts



as low as the conifer-sagebrush ecotone. However, after several days of mild weather at these lower elevations, large patches of snow melted off terrain with a southern exposure, inducing the recovery of seeds from this slope by nutcrackers.

On open, level ground and inclines exposed to direct sunlight for part of the day, snow melt also proceeded quickly. Within the areas prone to snow melt, the snow around the base of objects such as trees, rocks, and logs—especially on the south side—showed the first decrease in snow depth. Snow cover on dense plant growth, such as sagebrush (*Artemisia*) and manzanita (*Arctostaphylos*), melted more quickly than snow on adjacent ground.

In winter months, the nutcrackers at subalpine elevations occasionally recovered caches of whitebark pine seed from sites with a minimal cover of snow—such as rocky ledges or exposed cliffs. However, deep snow pack probably frustrated any large-scale use of seed stores at this time.

By the end of February or early in March, nutcrackers in the Casa Diablo study area began to include in their diet whitebark, Jeffrey, and/or piñon pine seeds stored in the convergent slope the previous fall. During this same period, some nutcrackers initiated courtship displays, vocalizations, and nest-building behavior.

#### Late March to Late June

In the Jeffrey pine belt, mild temperatures in spring caused rapid snow melt in all except the most sheltered areas, exposing most divergent seed storage areas.

Throughout the spring months, some nutcrackers migrated to higher elevations, where they fed primarily on seeds recovered from convergent slopes. In the Mammoth Mountain and Tioga Pass areas, snow usually melted off in wide rings around objects on level areas by the end of May. Melt-off also occurred throughout areas with any southern exposure. The use of divergent seed stores by nutcrackers at subalpine elevations usually began by the first of June. A small number of nutcrackers, about 15 to 30, remained in the lower elevation study areas throughout the spring and early summer (Figure 2). In both the Casa Diablo and Lee Vining study areas, nutcracker family groups consisting of adults and newly-fledged young made their appearance by the beginning of May. By the beginning of June, family groups of nutcrackers appeared at subalpine elevations; some of these were probably from nests at elevations above the Jeffrey pine belt, whereas others migrated up from the Jeffrey pine belt. Throughout June, the subalpine population of nutcrackers continued to increase as more family groups and individuals moved up from other altitudinal belts (Figure 2). Dixon (1934) also observed family groups of nutcrackers in late May and early June between 2,550 and 3,150 meters elevation in the June Lake-Reversed Peak drainage, which is on the eastern slope of the Sierra Nevada between Tioga Pass and the Mammoth Mountain vicinity (Figure 3).

The extent of the snow melt and consequent availability of seed stores each spring appeared to be an important factor in the timing of the migration of nutcrackers up to subalpine elevations. As early as 31 May 1974, I observed a flock of seven nutcrackers at 2,700 meters in the Rock Creek drainage—about 30 km south-southeast of Mammoth Mountain. Snow melt-off at subalpine elevations was extensive at that time. By 4 June 1976, several family groups were already present at Tioga Pass, and at least two groups were in the Red's Lake area of Mammoth Mountain. Because of the mild winter and spring in 1976 (Figure 4), snow melt-off had been extensive by the beginning of June. However, following the late and severe storms of spring 1975, snow persisted in large patches in all subalpine areas through July, and family groups did not appear at higher elevations until the beginning of that month.



## Late June to Late July

Small numbers of nutcrackers (Figure 2) remained in the conifer-sagebrush ecotone during this period. In these lower areas, nutcrackers depended on opportunistic foraging and, to a lesser extent, the remaining seed stores.

The migration of individuals and family groups to subalpine elevations continued throughout early July (Figure 2). Pine seed recovered from divergent seed stores made the previous fall also was the primary food of the nutcrackers at subalpine elevations during this period. Unripe seed from the new crop of whitebark cones became an important food source as early as 19 July in 1973 and by the beginning of August in the other years of the study.

*Seed-recovery Behavior*

Solitary nutcrackers recovered seed caches most often in winter and spring. Sometimes pairs of nutcrackers traveled together to seed storage sites; however, when the subordinate nutcracker—presumably the female, which is the smaller of the sexes (Mewaldt, 1948)—located the seeds, it was often displaced at the cache site by the other bird. In summer months, adult nutcrackers recovering seed stores were frequently accompanied by one to four begging juveniles.

The following summarizes the typical behavior sequence used by nutcrackers retrieving seed stores: A nutcracker perched in a tree adjacent to a convergent or divergent cache site. From this observation point it looked around the immediate forest area, possibly for predators and other nutcrackers, and also surveyed the terrain adjacent to the tree. After a pause of a few seconds to several minutes, the nutcracker landed nearby on the slope or forest floor. In winter and spring, the nutcracker usually selected a snow-free patch or a site with a minimum of snow under the canopy of a small tree or on the steep, wind-swept portion of a slope. In late spring and early summer, nutcrackers most



Figure 11. Nutcrackers frequently store seed next to rocks and trees: In warm weather, snow depth decreases faster around these objects than on adjacent terrain.



often selected newly exposed, wet ground adjacent to a snow patch.

To recover seed, the nutcracker probed the ground at the selected site, thrusting the bill down through the snow and/or forest litter and soil. Occasionally, the bird either miscalculated its position or another nutcracker or seed predator had already removed the seed cache; in either case the nutcracker changed its position and probed again for the seed cache. If seeds were located, the nutcracker dug with side-swipes of the bill, enlarging the hole and thus exposing the entire cache. As the nutcracker removed the seeds from the site, it tested the seeds for spoilage and then either ate them immediately or placed the seeds in its sublingual pouch. Sometimes, the nutcracker flew into a nearby tree and consumed the seeds. Frequently, after recovering one cache, a nutcracker proceeded to uncover several more caches in the immediate area.

Before eating the seeds, nutcrackers usually removed the hulls, either cracking the seeds between the mandibles or flying to an "anvil." The anvil was used either to support a partly-cracked seed while the nutcracker picked out its contents, or as a base on which to open seeds with hammer-like blows of the bill. Certain objects used repeatedly as nutcracker anvils included stumps of trees, logs, and flat-surfaced rocks, and were littered with pieces of seed hulls.

The means by which nutcrackers locate seed stores is not entirely known. My observations suggest that individual nutcrackers recall the areas and perhaps the specific sites in which they stored seed the previous fall. Orientation at the site may be in relation to the micro-habitat feature originally selected for storage of the cache. This problem is treated in more detail elsewhere (Tomback, unpubl. MS).

During the time that snow was present in the study areas, the sites chosen by nutcrackers during seed-cache recovery had several characteristics in common. The caches were often recovered from deep needle litter or soil in a circle of bare ground around the base of trees and rocks; the bare soil or needle litter was often wet, indicating very recent snow melt-off.

### *Feeding on Cones in Winter*

Unharvested seed from the cones remaining on trees was a major food source for the nutcracker at subalpine elevations for one or two months following a good whitebark pine crop and at lower elevations for winter and part of spring following a good Jeffrey pine cone crop. By deriving a significant portion of their diet from this source, nutcrackers in effect reserved seed stores for periods of harsh winter and for use later in spring, especially during the nesting period when the alternative seed source was exhausted.

In the Casa Diablo-Little Antelope Valley area, groups of nutcrackers travelled through the forest, going from one Jeffrey pine to the next, generally sampling only a few cones on each tree. If part of a cone was closed, the nutcracker forced the scales open and extracted the seed, which was then tested for quality within the mandibles by "bill clicking." If the seed was good, the nutcracker consumed it on the spot. Similarly, Mewaldt (*in* Giuntoli, 1963) reported nutcrackers feeding on seeds from ponderosa pine cones remaining on trees in late March.

During winter and spring, nutcrackers foraged not only among the remaining Jeffrey pine cones on trees but also among cones that had fallen to the ground. Flocks of nutcrackers searched among the fallen cones silently and intensely, individuals often only a meter apart. At times small groups of harvesting nutcrackers—both in trees and on the ground—were dispersed throughout the



Casa Diablo area, whereas at other times a loose, large association of nutcrackers formed in one part of the Jeffrey pine forest.

While foraging through fallen cones, nutcrackers first took seeds that had dropped out of the cones onto the ground nearby, and then searched through open cone scales for the remaining seeds. Sometimes, a nutcracker rolled a cone over to expose any closed portion. If the bottom of the cone was not rotted, the nutcracker forced open the closed scales and removed seeds. Cones on the ground also served as hiding places for insects and spiders, which nutcrackers fed on as they were encountered.

Any noise or disturbance in the area or an alarm call from a nutcracker sent the entire group flying into the low branches of nearby trees. After a few minutes, the flock of nutcrackers returned to the ground.

Juniper berries, when available, were also a frequent food source in the conifer-sagebrush ecotone. I observed nutcrackers harvest juniper berries during harsh snow storms. Only rarely did they forage through cones at such times.

### *Transition from Feeding on Cones to Feeding on Seed Stores*

Until about mid-spring, nutcrackers continued to forage on the cones left on trees and on the ground. Both modes of foraging decreased in frequency during April, while the emphasis on the recovery of stored seed increased. On 22 April 1975, during the entire day only once did I observe a group of nutcrackers searching for seed in cones; on 2 and 3 May 1975, I did not observe any such foraging attempt. In contrast, on 4 March 1975 I observed eight separate groups of nutcrackers either taking seeds from cones on trees or cones on the ground.

The most obvious explanation for the transition in foraging emphasis from cones to seed stores was the reduced availability of seeds in cones. To test this idea, I examined fallen Jeffrey cones from two groups—one group collected between 2,205 and 2,355 meters in the Jeffrey belt and the other from between 2,370 and 2,520 meters in the lodgepole-fir belt. Using these cones, I obtained several types of data (see *Methods*).

Counting the fertile cone scales on a sample of 42 cones from both altitudinal belts, I determined that the number of fertile seeds produced by a Jeffrey pine cone before seed dispersal ranges from 160 to 338 seeds per cone (mean and standard deviation and median were  $222 \pm 39$  and 216 seeds, respectively). By the end of April, the number of seeds, regardless of quality, remaining in fallen cones collected in the Jeffrey pine belt ( $n = 38$ ) ranged from 0 to 55 seeds per cone (mean and standard deviation and median were  $11 \pm 11$  and 8 seeds, respectively). The seeds remaining in the cones collected in the lodgepole-fir belt ( $n = 27$ ) ranged from 0 to 22 seeds per cone (mean and standard deviation and median were  $3.5 \pm 5.6$  and 2 seeds, respectively). Analysis by median test indicated that the difference in the number of seeds remaining in cones between the two altitudinal groups was highly significant ( $p < .001$ ).

One explanation for this may be different degrees of seed predator pressure in the Jeffrey pine belt and the lodgepole-fir belt. In spring, Jeffrey pine seed probably is readily taken by sciurids newly emerged from hibernation and several species of birds in addition to the nutcracker. As expected, the use of Jeffrey seed would be most intense above the Jeffrey pine belt where the large size of the seed relative to the size of the seeds of white fir (*Abies concolor*), red fir (*A. magnifica*), and lodgepole pine would make it especially attractive. To determine whether the seeds remaining in cones were actually edible, I analyzed 270 seeds from fallen cones, 176 from the Jeffrey pine belt and



94 from the lodgepole-fir belt. Overall, 14.8 percent of the seeds were good, 15.9 percent were aborted, and 69.2 percent were meally from insect infestation. The actual numbers of good, aborted, and meally seeds from the Jeffrey pine belt were 27, 15, and 130 seeds, respectively, and from the lodgepole-fir belt, 9, 28, and 5 seeds, respectively. The differences between the two altitudinal belts were statistically significant ( $p < .001$ ).

### *The Jeffrey Pine Seed Moth*

The meally Jeffrey pine seeds were the result of larval infestation by the Jeffrey pine seed moth (*Hedulia injectiva*) and also possibly by its relative *Laspheyresia piperana*, which usually infests ponderosa pine seed (Thomas W. Koerber, pers. commun.). Moth eggs are laid on Jeffrey pine cones the spring before the cones ripen. Newly hatched larvae burrow into undeveloped seeds. In the course of its growth to the pupal stage, a single larva consumes the contents of an average of 3.5 Jeffrey pine seeds before its final emergence the following spring. Of 54 cones collected and analyzed by Koerber, Okamura, and Ruckes, Jr. (unpubl. MS), only eight (14.8%) were free of larvae; each infested cone carried 1 to 41 larvae with averages from 5 to 15 larvae for different samples of cones. The reduction of viable seed per cone as a result of seed moth infestation ranges from 1 to 60 percent (Koerber, Okamura, and Ruckes Jr., unpubl. MS), indicating that the seed moth is a formidable competitor of the nutcracker.

On the basis of the data obtained from my analysis of seed quality, I computed how many seeds on the average would be available to nutcrackers foraging through fallen cones by late April. If an average of 11 seeds remained in a cone from the Jeffrey pine belt and 3.5 seeds in a cone from the lodgepole-fir belt, and only 14.8 percent of these remaining seeds were good, then a nutcracker would find on the average only 1.6 good seeds per cone in the Jeffrey pine belt and 0.5 good seeds per cone at higher elevations. Although a nutcracker might derive some nutritional benefit from those meally seeds still containing larvae, such seeds would probably be indistinguishable from other meally seeds and thus be rejected. Thus, in spring, this method of foraging, to sort through cone scales for seed and then select the good seed, probably yielded very little for the time and energy expended; and increased reliance on seed stores was probably more efficient.

### *Supplementary Food Sources*

#### Insects

As daytime temperatures increased during March (Figure 4), nutcrackers at all elevations took insects and spiders in large quantities, supplementing their use of seed stores. Beginning in late May or early June at subalpine elevations, adult and juvenile nutcrackers foraged through grasses and sedges for insects. Many mosquitoes and other dipterans were available at the edges of lakes and in wet meadows. Nutcrackers gleaned insects from the vegetation and engaged in flycatching at the lake shores, where they were often accompanied by flocks of Violet-green Swallows (*Tachycineta thalassina*).

In the Jeffrey pine belt, especially at its lower limits, nutcrackers occasionally flew from low perches to the ground nearby to catch insects and engaged in flycatching from perches at any height. Nutcrackers continued to take insects and spiders encountered while foraging through fallen cones. If a nutcracker located an ant nest, it spent several minutes consuming ants in numbers. All nutcrackers



occasionally picked bark off trees and prodded woodpecker-like into tree stumps and rotting logs to locate insects. Dixon (1934) reported that nutcrackers in the June Lake area (Figure 2), obtained wood-borers by digging into rotting logs and a variety of other insects by flycatching. Mewaldt (*in* Guintoli, 1963) described how on 21 March a nutcracker flaked bark from dead pine branches and fed on something it had uncovered. After analyzing the stomach contents of 428 nutcrackers, Guintoli (1963) found that the most frequently occurring insect orders were Coleoptera, Hymenoptera, and Orthoptera.

#### Scavenging and Predatory Behavior

Like most corvids, the Clark's Nutcracker is highly opportunistic in its feeding habits. In addition to taking conifer seed, spiders, insects, and berries, the nutcracker takes bird eggs and nestlings (French, 1955; Munro, 1919) and carrion (Bradbury, 1917; Munro, 1919). At all times of the year, nutcrackers visit bird feeders, trash bins, and camping sites for food scraps.

Although many behavior patterns and morphological features of the species are adapted to a diet of conifer seed, the tendency toward specialization does not imply that the use of particular foraging methods or a food source always yields the highest return if alternatives are available. The following observations, which I and others made in the eastern Sierra Nevada, indicate that the nutcracker may scavenge and prey on other animals even if fresh seed or seed stores are available.

In May 1973, in Inyo National Forest, Mono County, California, at about 2,370 meters, John Derby of the U.S. Forest Service (*pers. commun.*) watched as two nutcrackers fed on a Belding Ground Squirrel (*Spermophilus beldingi*) road kill.

On 28 August 1973, on route 203 in the same area, at 2,450 meters elevation, I observed a nutcracker tearing off and eating shreds of meat from a run-over chipmunk (*Eutamias* sp.) until it flew off with the carcass. At this time, the nutcracker population in the area was harvesting seed from an abundant cone crop of whitebark pine.

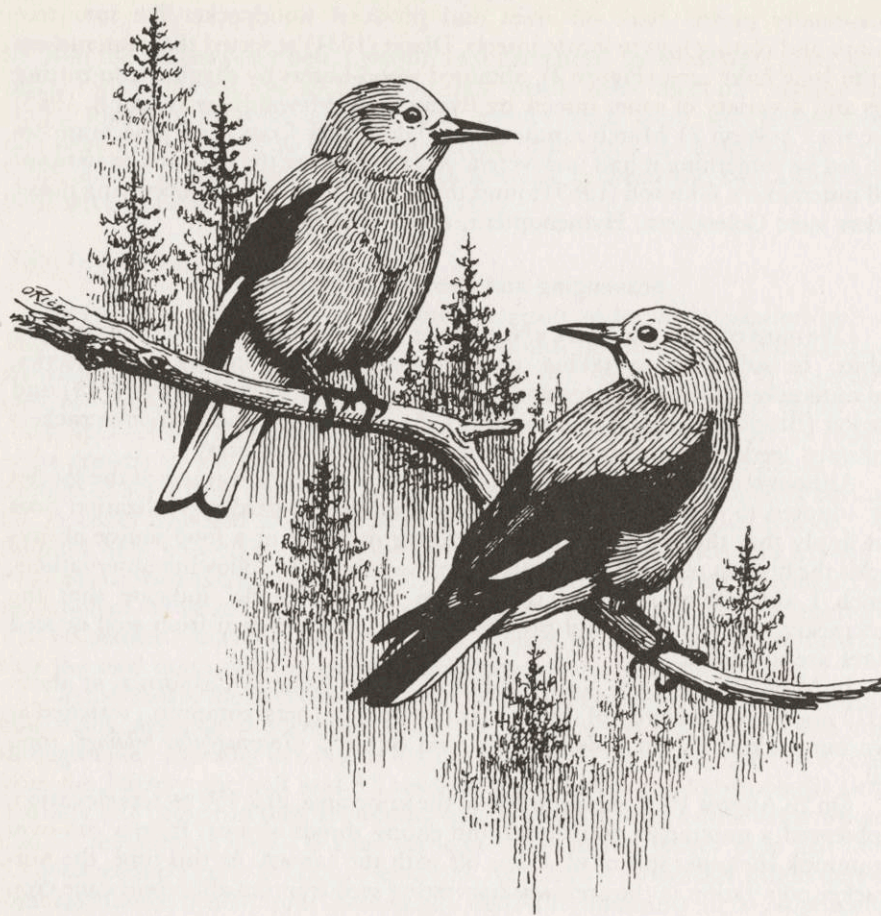
There are only a few known accounts of predatory behavior by nutcrackers. In April 1935, in Mono County, California, Dixon (1956) witnessed an adult nutcracker attack and kill a Belding Ground Squirrel and then strip off the meat, which it took to nestlings. On the same trip, he twice recorded chipmunks being attacked by nutcrackers; one escaped but the other was killed and eaten.

On 19 May 1975, in a meadow at Tioga Pass, Mono County, California, at 3,040 meters, Brian Schultz (*pers. commun.*) observed an adult nutcracker struggle with, and kill, a Mountain Vole (*Microtus montanus*) by stabbing the vole with its bill. The nutcracker fed on the rodent for a few minutes and then flew off with the carcass.

Subsequently, Mulder, Schultz, and Sherman (*unpubl. MS*) have reported the occurrence at Tioga Pass of many more incidents of predation by nutcrackers on rodents during the springs of 1975, 1976, and 1977. The Dana Meadows area, which is frequented by a large population of nutcrackers in spring and summer, provides an unusual abundance of prey species.

During my study of the nutcracker in the Mammoth Mountain region, I never observed an incident of predatory behavior, even though several species of sciurids were common in the area. In general, it seems that the frequency of predation and scavenging by nutcrackers in any area may be related to the





Clark's Nutcracker, *Nucifraga columbiana*. Drawing by Orville O. Rice.

terrain, the type and abundance of prey species, and perhaps the quality and quantity of conifer seed available in the vicinity at the time.

Giuntoli (1963), in his analysis of nutcracker stomach contents, reported finding hair, fragments of bone, teeth, pieces of skin, and whole feet, all belonging to various species of rodents. Mammal remains were present in stomachs of nutcrackers collected at various months of the year, from October 1946 to May 1949, with a frequency of occurrence ranging from 0 to 44 percent per month ( $n = 29$  months, mean and standard deviation  $11 \pm 14\%$  per month).

The summer food of the Slender-billed Nutcracker in the Northern Urals included an occasional vole, shrew, or small bird (Bibikov, 1948). For birds collected in fall from mountains of East Saian and Khamar-Daban, Reimers (1954) reported mammal remains in the stomachs of two of the 56 specimens collected in autumn. Dement'ev *et al.* (1970) listed small passerines, bird eggs, and some amphibians and reptiles as part of the year-round diet of the Slender-billed Nutcracker; and Mezheny (1961) found that the frequency of occurrence of vertebrates in the diet of this subspecies was about 13.9 percent in fall ( $n = 43$  stomachs) and around 15 percent for the other seasons of the year ( $n = 98$  stomachs) for specimens collected in the Adycha River Basin in Siberia.



### *Factors Affecting the Sequence of Activities and Timing of Seasonal Altitudinal Migration*

The timing, sequence, and nature of the activities of the Clark's Nutcracker in the eastern Sierra Nevada appear highly adaptive in terms of making efficient use of fresh and stored pine seed. For this reason, many of these activities may be termed "strategies." Both the ecological significance of the most important foraging-related behavior patterns and the effect of these patterns on several other nutcracker activities are discussed at length below.

#### Harvesting Unripe Pine Cones

In midsummer the majority of nutcrackers harvested seed from unripe whitebark pine cones, although unripe Jeffrey pine cones were also available. This preference may be the result of three factors: (1) Snow melt occurred latest in the year at the highest elevations. This attracted nutcrackers to the subalpine belt to use newly available seed stores and to exploit the abundance of insects resulting from standing water from snow melt. This placed nutcrackers in proximity to the ripening crop of whitebark cones. (2) More importantly, when seed stores were depleted and nutcrackers began to harvest unripe seed, it was far more efficient to use whitebark pine seed, which ripened somewhat earlier than Jeffrey pine seed. The significant difference in extraction rates (Table 3) indicated whitebark pine seed to be the most efficiently obtained seed at the time. Also, the seed of the whitebark pine is larger than the seed of the Jeffrey pine and, assuming comparable caloric value per gram, there would be a higher return in terms of effort expended to harvest whitebark pine seed. Extraction of piñon seed from unripe cones required so much effort that nutcrackers made few attempts until the fall season. (3) An equally important consideration was that the size of the whitebark pine seed and the retention of seed in the cone made it highly attractive to a number of avian and rodent species, especially after the cones had ripened. By exploiting whitebark seed as early as possible, and by removing quantities of seed for storage as soon as it was ripe, nutcrackers were able to compete effectively against the combined efforts of the other species.

#### Onset of Whitebark Pine Seed Storage

The timing of the transition from the sporadic harvest of seed for immediate consumption to the harvest of seed for storage was probably based on seed ripeness. Before seeds could be stored, they had to be extracted whole and be mature enough to have hard, protective hulls. The proximate factor triggering this behavior probably was the increased efficiency with which ripe seeds were harvested in comparison with unripe or partially ripe seed (Table 3).

#### Transition to Harvest and Storage of Jeffrey Pine Seed

By the end of September the whitebark pine seed harvest had peaked, and nutcrackers at supalpine elevations became nomadic, going from area to area extracting whatever seed remained in whitebark pine cones. More time and travel were required to fill the sublingual pouch before storing seed. At this



time, nutcrackers began to migrate down to the Jeffrey pine belt; by mid-October, the majority of nutcrackers had settled at lower elevations (Figure 2) where they harvested and stored Jeffrey and, later, piñon pine seed. The average rate of extraction of seeds from ripe Jeffrey pine cones was significantly faster than that from unripe cones (Table 3).

Pressure from other seed competitors probably favored the rapid and intense harvest and storage of Jeffrey pine seed by nutcrackers. An especially important factor was the removal of seed from cones before it was consumed by the final instar of the larvae of the Jeffrey pine moth.

#### Seed Storage Sites and Areas

Nutcrackers cached seeds in sites characterized by a variety of micro-habitat features. These features, listed in Table 5, either facilitated the accessibility of seeds after snowstorms and/or tended to preserve seeds from spoiling. In part, they may also have served as visual cues to aid in the recovery of seed stores.

Volcanic gravel, pumice, and pine needle litter, especially on steep slopes, drained moisture readily and probably prevented spoilage of seeds. The snow on the ground at the base of objects such as trees, rocks, fallen branches, logs, and tree roots, tended to soften and melt before the snow on adjacent areas; when these sites were used for seed storage, they allowed nutcrackers to reach their caches at the earliest possible time after snow storms and with the least amount of digging. The snow on top of dense, creeping plants such as manzanita, heather (*Phyllodoce* sp. and *Cassiope* sp.), and chinquapin (*Castanopsis* sp.) also tended to soften and melt before the snow in other areas. Seeds stored in trees—in cracks, crevices, under bark, and in holes—were readily accessible at any time of year. Steep, wind-swept, rock-strewn slopes remained clear of snow, even after severe storms. Seeds stored on these slopes among rocks and rubble and on gravelly ledges were always accessible.

In the Dana Meadows area at Tioga Pass, the interspersed rocky rises and hillocks drained more readily during snow melt-off than did the adjacent meadows and lake shores. Since these rises usually bear whitebark pine trees, they were frequently used by nutcrackers for divergent seed storage.

Nutcrackers seemed to select convergent storage areas on the basis of certain gross features, which, in combination with micro-habitat features, allowed the earliest access to seed stores. All convergent storage areas used in the Mammoth Mountain-Casa Diablo area had southern exposures, a 22° to 30° angle of steepness, and large, bare areas of volcanic pumice or gravel. The direct exposure to sun and steepness of the slopes insured that the convergent areas underwent the earliest and most rapid snow melt-off of all the terrain in the vicinity. The volcanic soil, a feature characteristic of the Mammoth and Casa Diablo areas, drained well and provided some protection against seed spoilage.

#### Convergent versus Divergent Seed Storage

Storing seeds in both convergent and divergent areas, in both the subalpine and Jeffrey pine belts, was a strategy that used the sequence of winter and spring weather and snow conditions to increase the likelihood that a supply of stored seed would always be available.

The use of one particular slope in an area for seed storage by many nutcrackers was probably not for any social purpose, but rather because the selected slope had physical characteristics that facilitated access to seed stores in winter and spring.



At all elevations, the convergent slopes accumulated the least amount of snow and underwent the most rapid snow melt. As a result, nutcrackers could always retrieve seed stores from convergent slopes by digging through minimal depths of snow. In winter the divergent stores in the same area were usually inaccessible because of excessive snow cover. By placing some seed caches in convergent areas, nutcrackers had food available during the harshest periods of the year.

However, by the end of winter or after a prolonged period of harsh weather, the quantity of convergent seed caches available per individual certainly diminished. Thus in milder weather, a switch to the use of divergent seed stores was probably adaptive and reserved the remaining convergent stores for use during subsequent severe weather.

In spring months, snow melted rapidly in the intense sunlight of montane elevations. As the divergent storage areas lost some of their snow cover, nutcrackers took seed caches as they became accessible. As storms were spaced farther apart and weather became milder, nutcrackers had access to more and more of their divergent seed stores. Divergent seed storage thus regulated or rationed the availability of seed caches, so some stores were protected by snow cover. The protection of some stores by snow probably minimized the chance discovery of an individual's caches by other nutcrackers, and discouraged exploitation of seed stores by squirrels and other rodents. Mezhenny (1961) noted that squirrels searching for nutcracker seed stores were impeded by snow.

#### Seed Storage and Seasonal Altitudinal Migration

The significance of seed stores in both convergent and divergent areas at subalpine, as well as lower, elevations becomes apparent when related to the species' annual cycle of altitudinal migration. During my investigation, the majority of nutcrackers overwintered in the Jeffrey pine belt, where they had access to seed stores on the convergent slope during periods of severe weather. During periods of mild weather, the birds had some access to divergent seed stores of Jeffrey and piñon pine seed. In winter months, at subalpine elevations, snow accumulation on the convergent slopes probably discouraged the recovery of seed stores in any quantity. This may be one reason why few nutcrackers overwintered at the higher elevations.

In spring months, snow melt-off in divergent storage areas at lower elevations was extensive. Seeds from both convergent and divergent areas provided food for adults nesting at lower elevations and, at a later date, for their young. At the same time, the mild weather between storms in March and April decreased the snow depth on the subalpine convergent slopes, providing access to whitebark pine seed stores for the nutcrackers which had migrated to higher elevations to nest.

As family groups of nutcrackers migrated to subalpine elevations during late spring and early summer, progressive snow melt-off in divergent storage areas made available previously inaccessible caches of whitebark pine seed. The family groups continued to use these divergent stores well past the time they began to harvest the new whitebark pine seed crop. Nutcrackers remaining at lower elevations during late spring and summer months also used whatever divergent seed stores were left.

#### Proportions of Pine Seed in the Nutcracker Diet

Figure 12 illustrates the relative use of whitebark and Jeffrey/piñon pine



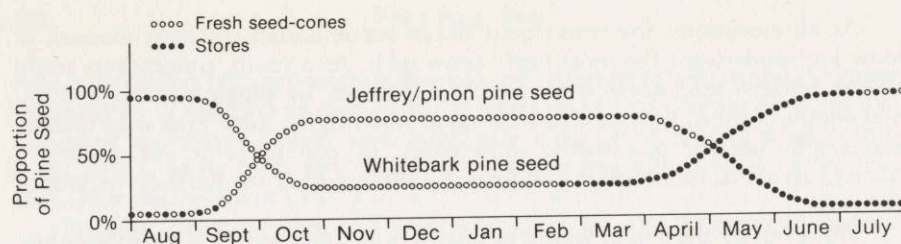


Figure 12 Estimated relative proportions of whitebark and Jeffrey-piñon pine seed in the nutcracker diet throughout the year.

seed by nutcrackers during an "ideal" year when all cone crops are produced. The quantities of seed considered are relative and not absolute values. The proportions were derived from observations of the use of seed stores and seed from cones in relation to the distribution of nutcrackers over various elevations throughout the year. In general, whitebark pine seed is the primary pine seed in the nutcracker diet from late spring to the end of summer. Jeffrey and piñon pine seed are the major seeds taken in fall, winter, and early spring, supplemented by some whitebark pine seed.

Giuntoli (1963) analyzed the occurrence of pine seed in the stomachs of nutcrackers collected at various elevations and months over three and one half years in west central Montana. His results suggest that the annual pattern of altitudinal migration and the use of conifer seeds by the nutcracker at various elevations were comparable to my observations in the eastern Sierra Nevada. Also, the general results indicate that nutcrackers in Montana stored whitebark pine seed at low elevations in addition to storing it in the subalpine zone, just as I have observed in the eastern Sierra Nevada.

### *Early Nesting*

The availability of seed stores enables the Clark's Nutcracker to begin nesting in late winter or early spring, at a time when little other food may be found. The conifer seeds fed to young nutcrackers have a higher caloric content per gram weight than the insect diet of most other young passerines. Insects have about 4,000 calories per gram while the pine seeds used by both Clark's Nutcracker and the Eurasian Nutcracker have at least 5,000 calories per gram (Grodzinski and Sawicka-Kapusta, 1970).

In the eastern Sierra Nevada, young nutcrackers fledged by late spring and migrated with adults to subalpine elevations. There, they were fed by adults primarily on whitebark pine seed from caches made the previous fall. When cones ripened in late summer, juveniles harvested seed and made their own seed stores, freeing adults for the same task.

Early nesting by the Clark's Nutcracker may (1) insure that the young will be independent by the time the new cone crop has ripened, (2) provide a long maturation period for the young, and/or (3) increase the survival rate of young by not exposing them to the unusually rigorous conditions of montane winters until they are of a comparatively advanced age.

### *Cone Crop Failure and Nutcracker Irruptions*

The annual cycle of the Clark's Nutcracker, as described in this paper, is related to a year-round diet of pine seed. When major cone crop failures occur,



nutcrackers leave the area in the fall when they would normally be making seed stores. During widespread food shortages, nutcrackers have been found to wander hundreds of kilometers from the Sierra Nevada (Davis and Williams, 1957). In addition to nutcracker irruptions from the Sierra Nevada, irruptions have been documented in Arizona and New Mexico. Nutcrackers have been reported as far east as Oklahoma, Texas, Kansas, and Missouri in irruptive years (Davis and Williams, 1964), although the eastern extent of their range is the Black Hills of South Dakota.

Davis and Williams (1957, 1964) have analyzed all nutcracker irruptions from the Sierra Nevada from 1898 to 1961. To examine the cause of these irruptions, they obtained cone crop ratings beginning in 1933 for the major conifers of the Sierra Nevada—ponderosa and Jeffrey pine, sugar pine, and white fir. Unfortunately, cone crop ratings were not available for whitebark pine. For three of the four nutcracker irruptions since 1933, Davis and Williams found a pattern of two years of good cone crops among all the conifers followed by a general cone crop failure in the third year. They hypothesized that nutcracker irruptions resulted from a build-up of nutcracker numbers over the two years in which food was especially abundant, followed in the third year by a mass exodus of nutcrackers when insufficient food was available for the large population.

My observations in the eastern Sierra Nevada, in conjunction with a re-examination of the cone crop data obtained by Davis and Williams (1957, 1964), indicate that the explanation for nutcracker irruptions—at least in the Sierra Nevada—may be more straightforward than the population build-up theory. Throughout most of the Sierra Nevada there are two major seed sources for the nutcracker, either whitebark pine and Jeffrey pine or whitebark pine and ponderosa pine (Jeffrey pine and ponderosa pine replace each other geographically). I believe that a cone crop failure of one pine species of each pair may be offset to some degree if the other pine has a good cone output. Major irruptions of the Clark's Nutcracker should always occur in the fall of years when whitebark pine and both Jeffrey and ponderosa pine fail to produce cones. The whitebark pine seed usually transported to and stored at lower elevations may actually serve as insurance for nutcrackers in case the Jeffrey or ponderosa pine cone crops are poor.

Contrary to the Davis and Williams hypothesis (1957), the size of the nutcracker population in relation to cone crop failure may not be the prime determinant of irruptions. Simultaneous failure of both the whitebark pine and Jeffrey-ponderosa pine cone crops, regardless of the level of the nutcracker population, may be the only factor required to trigger an irruption.

More than 30 irruptions of the Eurasian Nutcracker were documented between 1753 and 1933 (Formosof, 1933). The irruptions of the Eurasian Nutcracker (*N. c. macrorhynchos*) were stimulated by cone crop failures of the Siberian stone pine, the primary food source of this Asiatic race in most of its range.

In addition to both species of nutcrackers, a number of other New and Old World boreal seed-eating birds also irrupt periodically from their habitat. Bock and Lepthien (1976) found correlations between irruptions of these other avian species and ratings of seed production of both New and Old World species of conifers and birches. Although the bird populations in the western forests of the United States did not conform to the general patterns found by Bock and Lepthien—possibly because of the availability of a greater diversity of seed sources—the conclusions of Bock and Lepthien are in basic agreement with my explanation for the irruptions of the Clark's Nutcracker from the Sierra Nevada: "Seed crop size is the prime moving and synchronizing force."



### Summary

My investigation of the year-round activities of Clark's Nutcracker, *Nucifraga columbiana*, yielded the following results: (1) Nutcrackers have an array of complex behavior patterns related to the harvest and storage of pine seed and subsequent recovery of seed caches. (2) It was more efficient in terms of the rate of seed extraction and return per-effort-expended for nutcrackers to harvest unripe whitebark pine seed rather than unripe Jeffrey pine seed. (3) The onset of storage of whitebark pine seeds coincided with their ripening, allowing nutcrackers to extract the seeds from cones at a maximum rate. (4) The transition to the harvest and storage of Jeffrey pine seed occurred when few seeds remained in whitebark pine cones. (5) Nutcrackers stored seeds at sites that underwent the earliest snow melt-off and preserved seeds from rotting. (6) The slopes chosen as convergent storage areas accumulated a minimal amount of snow, thus allowing nutcrackers access to seed stores throughout winter and spring. (7) Divergent storage areas underwent a gradual snow melt-off, which regulated the availability of an individual's seed stores. A cover of snow probably discouraged theft of seed stores by rodents and other nutcrackers. (8) Stores of Jeffrey, piñon, and whitebark pine seed at lower elevations were recovered during winter and early spring; most whitebark pine seed stores were recovered during late spring and summer. (9) The use of seeds recovered from stores to feed young enabled nutcrackers to begin nesting early in spring when other food was scarce. (10) In any year, a widespread and simultaneous cone-crop failure of whitebark pine and Jeffrey and/or ponderosa pine should result in an irruption of nutcrackers from the Sierra Nevada.

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## LITERATURE CITED

- BIBIKOV, D. I.  
1948 On the ecology of the nutcracker. Trudy Pechorskogo-Ilychskogo Gosudarstvennogo Zapovednika, No. IV, pt. 2:89-112.
- BOCK, C. E., and L. W. LEPTHIEN  
1976 Synchronous eruptions of boreal seed-eating birds. Amer. Nat., 110:559-571.
- BOCK, W. J., R. P. BALDA, and S. B. VANDER WALL  
1973 Morphology of the sublingual pouch and tongue musculature in Clark's Nutcracker. Auk, 90:491-519.
- BRADBURY, W. C.  
1917 Notes on the nesting habits of the Clark Nutcracker in Colorado. Condor, 19:149-155.
- DAVIS, J., and L. WILLIAMS  
1957 Irruptions of the Clark's Nutcracker in California. Condor, 59:297-307.  
1964 The 1961 irruption of the Clark's Nutcracker in California. Wilson Bull., 76:10-18.
- DEMENT'EV, G. P., *et al.*  
1970 Birds of the Soviet Union. Vol. V. Israel Program for Scientific Translations, Jerusalem.
- DIXON, J. B.  
1934 Nesting of the Clark Nutcracker in California. Condor, 36:229-234.  
1956 Clark Nutcrackers preying on ground squirrels and chipmunks. Condor, 58:386.
- FORMOSOF, A. N.  
1933 The crop of cedar nuts, invasions into Europe of the Siberian Nutcracker (*Nucifraga caryocatactes macrorhynchus* Brehm) and fluctuations in numbers of squirrels (*Sciurus vulgaris* L.). Jour. Animal Ecol., 2:70-81.
- FRENCH, N. R.  
1955 Foraging behavior and predation by Clark Nutcracker, Condor, 57:61-62.
- GIUNTOLI, M.  
1963 An analysis of food habits of the Clark Nutcracker (*Nucifraga columbiana*). Unpubl. M.A. thesis, Department of Biological Sciences, San Jose State College.
- GORODKOV, B. N.  
1916 Observations on the life of the cedar pine (*Pinus sibirica* Mayr) in Western Siberia. Trudy Botanicheskogo Muzeya Imperatorskoi Akad. Nauk No. XVI:153-172.
- GRINNELL, J., J. DIXON, and J. M. LINSDALE  
1930 Vertebrate natural history of a section of northern California through the Lassen Peak region. University of California Press, Berkeley.
- GRINNELL, J., and T. I. STORER  
1924 Animal life in the Yosemite. Univ. California Press, Berkeley.
- GRODZINSKI, W., and K. SAWICKA-KAPUSTA  
1970 Energy values of tree-seeds eaten by small mammals. Oikos, 21:52-58.
- JANZEN, D. H.  
1971 Seed predation by animals. Ann. Rev. Ecol. and Syst., 2:465-492.
- KISHCHINSKII, A. A.  
1968 Kedrovka-*Nucifraga caryocatactes kamtschatkensis* Barr.-Hamm. and *N. c. macrorhynchus* Brehm. Pitsy Kolymского Nagorya, pp. 100-109.
- KRUGMAN, S. L., and J. L. JENKINSON  
1974 *Pinus* L. Pine. In: Seeds of woody plants in the United States. Forest Service, U.S. Department of Agriculture, Washington, D.C., pp. 598-638.



- KRUGMAN, S. L., W. I. STEIN, and D. M. SCHMITT  
1974 Seed biology. In: Seeds of woody plants in the United States. Forest Service, U.S. Department of Agriculture, Washington, D.C., pp. 5-40.
- KUZNETSOV, N. I.  
1959 On the ecology of the nutcracker in the Mid-Urals. Byulletin Moskovskovo Obshchestva Ispytatelei Prirody Otdel Biologicheskii, 64:132-33.
- LIGON, J. D. and D. J. MARTIN  
1974 Piñon seed assessment by the Piñon Jay, *Gymnorhinus cyanocephalus*. Animal Behav., 22:421-429.
- LÖHRL, H.  
1970 Der tannenhäher (*Nucifraga caryocatactes*) beim Sammeln und Knacken von Nüsschen der Zirbelkiefer (*Pinus cembra*). Anzeiger der Ornithologischen Gesellschaft in Bayern, 9:185-196.
- MEWALDT, L. R.  
1948 Nesting habits and some general notes on Clark's Nutcracker (*Nucifraga columbiana* Wilson). Unpubl. M.A. thesis, Montana State University, Missoula.  
1956 Nesting behavior of the Clark Nutcracker. Condor, 58:3-23.
- MEZHENNY, A. A.  
1961 Food competitors, enemies and diseases. In: Ecology and economics of the Yakut Squirrel, O. V. Egorov, ed. Akademiya Nauk, Moscow, pp. 124-129.
- MIROV, N. T.  
1967 The Genus *Pinus*. Ronald Press Co., New York.
- MUNRO, J. A.  
1919 Notes on some birds of the Okanagan Valley, British Columbia. Auk, 36:64-74.
- PALLAS, P. S.  
1811 Zoographia Rosso-Asiatica. Vol. I, pp. 397-398.
- RANDLA, T. E.  
1964 A greedy nutcracker. Priroda, 52:95.
- REIMERS, N. F.  
1953 The food of the nutcracker and its role in the dispersal of the cedar-pine in the mountains of Khamar-Daban. Lesnoe Khozyaistvo, No. 1:63-64.  
1954 On the biology of the nutcracker in South Cisbaikal. Zoologicheskii Zhurnal, Vol. 33:1358-1364.  
1956 The role of nutcrackers and murine rodents in the pine woods of southern Cisbaikal. Byulletin Moskovskovo Obshchestva Ispytatelei Prirody-Otdel Biologicheskii, 61:35-39.  
1958 The reforestation of burns and forest tracts devastated by silkworms in the mountain cedar-pine Taiga of Cisbaikal and the role of vertebrate animals in the process. Byulletin Moskovskovo Obshchestva Ispytatelei Priroda Otdel Biologicheskii, 63:49-56.  
1959 Birds of the cedar-pine forests of south central Siberia and their role in the life of the cedar-pine. Trudy Biologicheskogo Instituta, Sibirskogo Otdelenie.
- SCHONBECK, H.  
1956 Der Tannenhäher (*Nucifraga caryocatactes* L.) in der Steiermark. Mitteilungsheft No. 5/56D. Landesmus. Joanneum, pp. 68-82. Graz.
- STEGMANN, B. K.  
1934 On the phylogeny of the nutcracker (Kedrovka). Doklady Akademii Nauk USSR, 2:267-269.
- SUCHKIN, P. P.  
1938 Birds of Soviet Altai. Moscow-Leningrad.
- SUDWORTH, G. B.  
1908 Forest trees of the Pacific slope. Forest Service, U.S. Department of Agriculture.



- SUTTER, E., and F. AMANN  
1953 Wie weit fliegen vorrattssammelnde Tannenhäher. Orn. Beobachter, 50:89-90.
- SWANBERG, P. O.  
1951 Food storage, territory, and song in the Thick-billed Nutcracker. Proc. Xth Internatl. Ornith. Congr.:545-554.  
1956 Territory in the Thick-billed Nutcracker. *Nucifraga caryocatactes*. Ibis, 98:412-419.
- TOMBACK, D. F.  
1978 Pre-roosting flight of the Clark's Nutcracker. Auk (in press).
- TURCEK, F. J., and L. KELSO  
1968 Ecological aspects of food transportation and storage in the Corvidae. Commun. Behav. Biol., Part A, 1:277-297.
- VANDER WALL, S. B., and R. P. BALDA  
1977 Coadaptations of the Clark's Nutcracker and the piñon pine for efficient seed harvest and dispersal. Ecol. Monogr., 47:89-111.

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