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FORAGING OF CLARK'S NUTCRACKERS ON RAPIDLY CHANGING PINE SEED RESOURCES[1]

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Abstract. Singleleaf piñon pine (*Pinus monophylla*) and limber pine (*P. flexilis*) seeds collected and stored by Clark's Nutcrackers (*Nucifraga columbiana*) changed dramatically during fall seed harvests. During August and early September seeds increased in dry mass and caloric value per unit mass. Cones ripened and began to open during mid- to late September. Later, during October and early November, the number of seeds in cones gradually decreased until there were virtually none remaining by mid-November. Nutcrackers modified their foraging behavior to take advantage of these changes. Changes included increased foraging intensity, increased foraging rate, and switching from closed to opening cones during a 3- to 4-week period when both cone types were available.

During the approximately 50- to 75-day harvest period, nutcrackers stored much of the food they would consume over the coming winter, spring, and summer. Nutcrackers stored 1.8 and 2.6 times more energy in the form of pine seeds than they require to survive the winter at subalpine elevations. Changes in nutcracker foraging behavior results in greater numbers of seeds stored, and thus nutcracker efficiency in fall may have far-reaching consequences at other seasons.

Key words: *Clark's Nutcracker; foraging; piñon pine; limber pine; caching; granivory.*

INTRODUCTION

Nearly all of the winter food and much of the food consumed during the breeding season by Clark's Nutcrackers (*Nucifraga columbiana*) is derived from pine seeds collected and stored during a brief period in the fall (Mewaldt 1956, Vander Wall and Balda 1977, Tomback 1978, Vander Wall and Hutchins 1983, Benkman et al. 1984). Length of the fall seed harvest depends on the size of the cone crop and the number of nutcrackers and other animals removing the seeds. Nutcrackers begin feeding on seeds in late July, over 1 month before they are ripe. During late August or early September, nutcrackers begin collecting and storing seeds. Under favorable conditions the storage period lasts 50 to 75 days. By late October or mid-November, when pine seeds have been almost completely depleted, nutcrackers continue to forage on cones but no longer collect significant numbers of seeds for storage. During this period (late July to early November), pine seeds change dramatically both in composition and availability. Previous studies on nutcracker foraging behavior (Vander Wall and Balda 1977; Tomback 1978, 1982; Tomback and Kramer 1980; Hutchins and Lanner 1982; Benkman et al. 1984) have not fully appreciated the dynamic nature of pine seed resources. Given the potentially great impact that this short period in the fall has on nutcracker biology during the ensuing winter, spring, and summer (Vander Wall and Balda 1981, Vander Wall and Hutchins 1983) it is important to understand the dynamics of nutcracker foraging.

The objective of this study is to document how foraging behavior of Clark's Nutcracker changes in response to changes in pine seed resources. To achieve this goal, I show how limber (*Pinus flexilis*) and singleleaf piñon (*Pinus monophylla*) pine seeds and cones change during the fall, how nutcrackers allocate foraging time to these two pines, and how nutcrackers modify foraging behavior in response to changes in seed and cone characteristics. I then describe how changes in foraging rate influences the time it takes nutcrackers to fill the sublingual pouch with seeds. Using these data and information on seed transport and caching behavior, I estimate the total quantity of seeds stored and the impacts of nutcracker fall seed caching on their energetic budget at other seasons.

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STUDY AREA

I conducted this study in the Raft River Mountains of northwestern Utah (41°57′N, 113°20′W). My limber pine study site is situated on a windswept, north-facing slope (2,500 to 2,550 m elevation) overlooking Clear Creek Valley. Conifer trees (i.e., limber pine, subalpine fir [*Abies lasiocarpa*], and Douglas-fir [*Pseudotsuga menziesii*] form a scattered discontinuous cover that is supplemented by a sparse cover of herbs and shrubs. The stand of limber pine is comprised of about 45 cone-bearing trees, but about half of these (at the periphery of the stand) are stunted and produce few cones. The remaining 20 or so trees average about 6 m tall and occupy an area of less than 1 ha. All trees can be seen from the center of the stand. Lanner and Vander Wall (1980) provide a more detailed description of this study site.

About 2 km north of the limber pine study site and separated from it by a deep canyon, an extensive piñon-juniper woodland (*P. monophylla* and *Juniperus osteosperma*) occupies a steep, south-facing slope. I made foraging observations in an approximately 10-ha study site just north of Clear Creek Campground (2,000 to 2,200 m elevation). The piñon pine stand has a mixed age distribution and spacing, including patches of small (1 to 4 m), vigorously growing trees in open areas where sagebrush (*Artemisia tridentata*) and rabbitbrush (*Chrysothamnus nauseosus*) form a shrub understory and patches of large, mature trees in closed-canopied stands with little understory.

METHODS

I observed nutcrackers harvest limber pine seeds at approximately weekly intervals from 2 August to 28 October 1978. During the same period, I watched nutcrackers forage in the piñon pine stand but little data were collected because nutcrackers virtually ignored piñon pine during much of September. In 1980, when piñon pine produced a good crop of cones and limber pine produced no cones, I collected nutcracker foraging data at the piñon pine site at approximately weekly intervals from 10 August to 2 November.

Sampling sessions usually lasted 1 day at each site, but in a few instances sampling was done over 2 days. During each session four types of data were collected. First, I took seed samples to document changes in seed mass and caloric content during late summer and fall. One to three cones were randomly selected from each of approximately 10 trees at the end of each sampling session. Edible seeds were removed from each cone, counted, shelled, dried in an oven at 60°C, and individually weighed to the nearest 0.1 mg. Approximately 10 seeds were randomly selected from each seed sample, ground, and the ash-free caloric value of the composite sample determined in a Phillipson microbomb. The mean of three determinations with a range of less than 2% of the mean (usually achieved with three determinations but occasionally as many as five were needed) was deemed an adequate estimate of caloric value. This procedure yielded a point estimate for the caloric content of the composite sample.

Second, I counted cones on selected trees (six limber pine in 1978 and 15 piñon pine in both 1978 and 1980) to document the rate of cone removal by animals (primarily nutcrackers on these sites) and timing of cone opening. Cones were counted from the same vantage point each sampling session. Counts included total cones visible, number of cones with peck marks indicating they had been foraged on by nutcrackers, and cones opening naturally.

Third, I recorded the number of nutcrackers foraging on each pine species as a relative measure of cone-foraging activity during the fall seed harvest. When comparing foraging activity on piñon and limber pines, I express foraging intensity for a sample session as a percent of the most active sample session for that year (measured as number of birds seen working on cones per observer hour) at each study site. It was necessary to use such a relative measure of foraging intensity because topography and stand structure at the two sites were very different, nutcrackers being seen over a much larger area in the piñon-juniper habitat.

Fourth, I gathered time-activity data on foraging nutcrackers to determine foraging time budgets. I measured three aspects of foraging: time to select and handle cones, time to extract seeds, and time to handle seeds. Cone selection included the time to remove and carry a cone to a sturdy perch. I defined seed extraction time as the time from first peck on a cone until a seed was removed. Handling time was the time to manipulate a seed and either eat it or place it in the sublingual pouch. I timed foraging nutcrackers with a stopwatch. I counted number of seeds removed from a cone and estimated handling

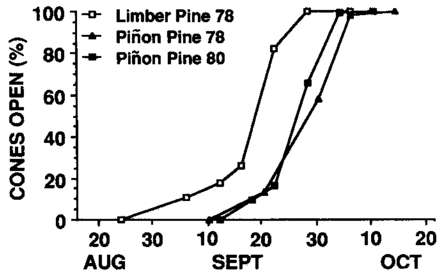

FIGURE 1. Cone opening schedule of limber pine in 1978 and piñon pine in 1978 and 1980.

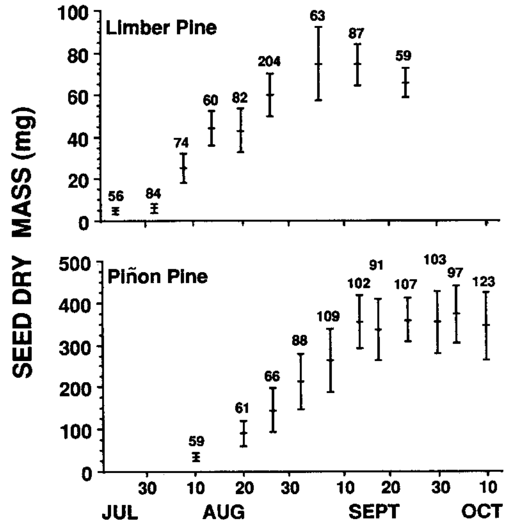

FIGURE 2. Changes in dry mass (mg; $\bar{x} \pm$ SD) of limber pine (1978) and piñon pine (1980) seeds during fall. Numbers above SD bars are sample sizes.

times for each seed by counting seconds. At the termination of foraging, the handling times were totalled, subtracted from total foraging time, and the remaining time (total seed extraction time) was divided by the number of seeds removed to determine mean seed extraction time.

RESULTS

CONE RIPENESS AND CONE COMPOSITION

I considered cones ripe when cone bracts began to separate. In 1978, limber pine cones began opening in early September and by late September virtually all cones were completely or partially open (Fig. 1). Piñon pine followed a very similar pattern of ripening in both 1978 and 1980, ripening 7 to 10 days later than limber pine. In 1978, piñon pine cones contained 8.3 edible seeds (range = 0–34) whereas limber pine cones, which are much larger, contained an average of 44.7 edible seeds (range = 8–95; Table 1). Edible seeds comprised 43.8% of the seeds in piñon pine cones and 77.4% of seeds in limber pine cones.

SEED MASS

The mass of limber pine seeds increased rapidly as they ripened during late July and August 1978 (Fig. 2). Seed mass on 7 September, just prior to cone opening, was significantly higher (LSD, $P < 0.05$) than previous samples and remained constant through 17 September ($\bar{x}$ = 74.2 mg, range = 37–106 mg). Seed mass on 23 September was significantly lower ($\bar{x}$ = 65.8 mg; LSD, $P < 0.05$). The decrease in mean seed mass in late September may have been due to nutcrackers selectively foraging on limber pine trees with larger seeds (Vander Wall, unpubl. data).

Piñon pine seeds increased in mass during August and early September, attaining maximum mass by 13 September (1980 $\bar{x}$ = 342.1 mg, range = 179–448 mg), 1 to 2 weeks later than limber pine seeds (Fig. 2). There was a slight decrease in mean seed size on 10 October, but the difference was not significant (LSD, $P > 0.05$). Mean mass of the edible portion of immature piñon and limber pine seeds in early August were similar but still significantly different (i.e., limber pine $\bar{x}$ = 25.2 mg on 8 August 1978; piñon pine $\bar{x}$ = 35.2 mg on 10 August 1980: two-tailed t = 7.23, df = 131, $P < 0.001$). At maturity, ripe singleleaf piñon pine seeds were 4.6 times larger (mean dry mass) than ripe limber pine seeds.

SEED CALORIC VALUE

Limber pine seeds increased steadily in caloric value during August (Fig. 3) but remained fairly

TABLE 1. Composition of limber pine and piñon pine cones in fall 1978.

Species	Number of cones sampled	Seeds per cone: Total ($\bar{x} \pm$ SD)	Seeds per cone: Edible ($\bar{x} \pm$ SD)	Edible range	Percent edible
Limber pine	64	58.8 ± 21.3	44.7 ± 20.0	8–95	77.4
Piñon pine	72	18.9 ± 8.4	8.3 ± 8.3	0–34	43.8

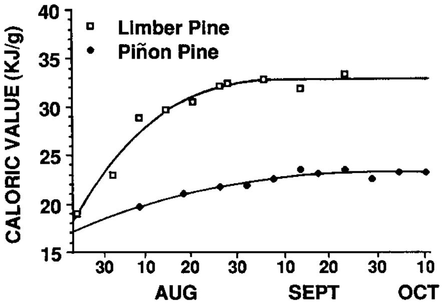

FIGURE 3. Changes in the caloric value (kJ/g) of limber pine (1978) and piñon pine (1980) seeds during fall. Lines fit by eye.

constant after 26 August ($\bar{x}$ = 32.6 kJ/g). Caloric value of piñon pine seed increased only slightly during August (Fig. 3) and reached stable caloric values by 13 September ($\bar{x}$ = 23.1 kJ/g). Mature singleleaf piñon pine seeds contained only 70.9% as much energy per gram dry mass as did limber pine seeds.

The concomitant rapid increase of seed dry mass and caloric value per unit dry mass in August and early September resulted in dramatic increases in the energy content of seeds of these pines (Fig. 4). Estimated energy content of mature limber pine seeds was 2.4 kJ and that of piñon pine seeds about 8.0 kJ. Thus, mature piñon pine seeds contained about 3.3 times more energy per seed.

FORAGING INTENSITY

During August of 1978, nutcrackers were fairly common and conspicuous at both study sites, but they only occasionally foraged for unripe pine seeds (Fig. 5). Collection, transportation, and storage of pine seeds began in late August. Shortly after seed storage began in 1978, most nutcrackers foraged for limber pine seeds and continued harvesting the seeds of that pine intensively until 23 September. During this same period, nutcracker use of piñon pine seeds gradually decreased to near zero by 24 September. Between 24 September and 1 October, the population of nutcrackers shifted foraging from limber pine to piñon pine seeds (Fig. 5). At the time the shift occurred, the limber pine seed crop was nearly depleted and much of the piñon pine seed crop had been consumed by Pinyon Jays (*Gymnorhinus cyanocephalus*), Scrub Jays (*Aphelocoma coerulescens*), and various rodents (e.g., golden-mantled ground squirrels, *Spermophilus lateralis*; cliff chipmunks, *Eutamias dorsalis*). Nutcracker foraging intensity gradually decreased on both pines during October, the seed harvest being virtually over by the end of the month.

The foraging intensity of nutcrackers on piñon pine during 1980, when piñon pine produced a large cone crop and limber pine produced no

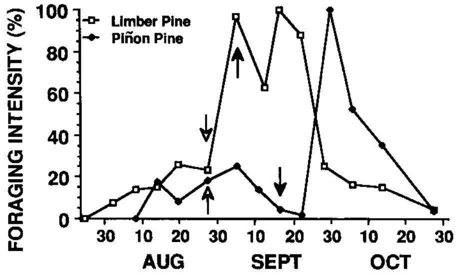

FIGURE 5. Foraging intensity (number of birds seen foraging on cones per hour) of nutcrackers on limber and piñon pine cones in 1978. Because of differences in visibility of nutcrackers at the two study sites, data are standardized as percent of the most active sample day at each site. Open arrows indicate when nutcrackers begin storing seeds; black arrows indicate when the first cones begin opening.

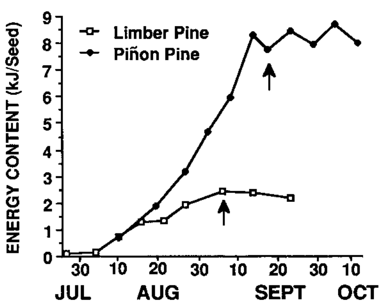

FIGURE 4. Changes in mean energy content (kJ) of limber pine and singleleaf piñon pine seeds. The arrows indicate when the first cones began opening.

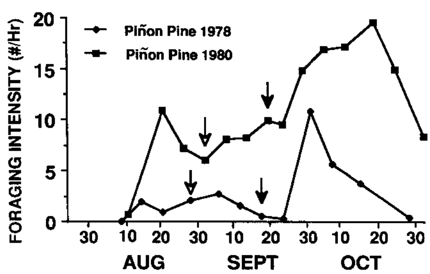

FIGURE 6. Foraging intensity (number of birds seen foraging on cones per hour) of nutcrackers on piñon pine cones in 1978 and 1980. Open arrows indicate when nutcrackers begin storing seeds; black arrows indicate when the first cones began opening.

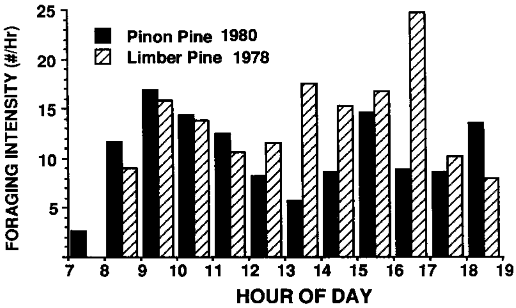

FIGURE 7. Mean foraging intensity (number of birds seen foraging on cones per hour) of nutcrackers on limber pine (1978) and singleleaf piñon pine (1980) during the course of a day when seeds were being stored. Sizes of most samples ranged from 3 to 12 hr.

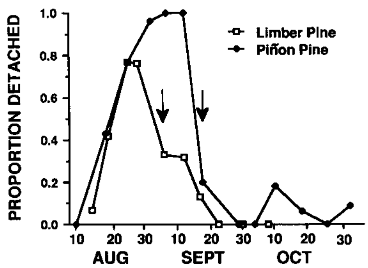

FIGURE 8. Proportions of limber pine (1978) and singleleaf piñon pine (1980) cones that nutcrackers detached and carried to foraging perches. Arrows indicate when cones first began opening.

cones, was markedly different than that of 1978 (Fig. 6). By late August 1980, the number of foraging nutcrackers was already similar to that recorded at the peak of the 1978 harvest. The number of foraging nutcrackers in late September and October well exceeded the number observed in 1978, due, apparently, to the larger piñon pine seed crop and lack of a limber pine seed crop. The seed harvest continued into early November, when observations were terminated.

The diel pattern of foraging is illustrated in Figure 7. Nutcrackers arrived at the foraging site before sunrise, before a human observer could see clearly. They began foraging immediately. Foraging continued throughout the day, punctuated by individuals departing with loads of seeds in their sublingual pouches and others returning to collect more seeds. On hot, sunny days, foraging activity often decreased in mid-afternoon and then increased again in late afternoon (Fig. 7). This was especially true of the piñon pine study site, which occupies a south-facing slope at low elevation that can become very hot at midday.

FORAGING BEHAVIOR

Foraging of nutcrackers on cones can be divided into three components: cone selection, seed extraction from cones, and seed handling. Cone-selection behavior by nutcrackers in fall changes as a function of cone ripeness. Early in the seed harvest, nutcrackers removed seeds from closed, green cones by hammering between cone scales with their bills. Nutcrackers detached many of these cones (Fig. 8) and carried them to firm, interior branches where they wedged them in crotches to extract seeds. Time required to select a cone was difficult to estimate owing to the subjective nature of determining when a nutcracker was looking for a cone. Prior to cone opening (mid-September for limber pine, late September for piñon pine), cone selection time was estimated by determining the interval between foraging bouts during which nutcrackers actively searched for a new cone. For piñon pine, this consumed a mean of 80.5 sec (SD = 88.4, n = 22) and for limber pine, 55.0 sec (SD = 46.3, n = 30). Differences between cone-selection times were not significant (two-tailed $t = 1.35$, df = 50, $P > 0.05$). After cones opened, nutcrackers stopped detaching cones from trees (Fig. 8). Rather than work intensively on single cones, they hopped through the crowns of cone-bearing trees peering into cones. Numerous cones were selected (perched on, looked into, or probed at) and from zero to about 20 seeds extracted from each.

Mean seed-extraction times of nutcrackers foraging on both pines decreased steadily from early August to mid-September, reaching a minimum during the last week of September (Fig. 9). The decrease in seed-extraction times was due to abscission of cone bracts as cones ripened, permitting nutcrackers to penetrate the woody tissue surrounding seeds more easily. Seed-extraction times were lowest just after 50% of the cones had opened; 23 September for limber pine, 29 September for piñon pine. Seed-extraction times increased steadily in October as seeds in cones became depleted (Fig. 9). On sample dates for which there were sufficient data to compare nutcracker seed-extraction rates on detached vs. attached cones, nutcrackers tended to handle cones in such a manner as to minimize seed-extraction time. For example, on 19 August 1980, at a time when nutcrackers were beginning to detach and carry

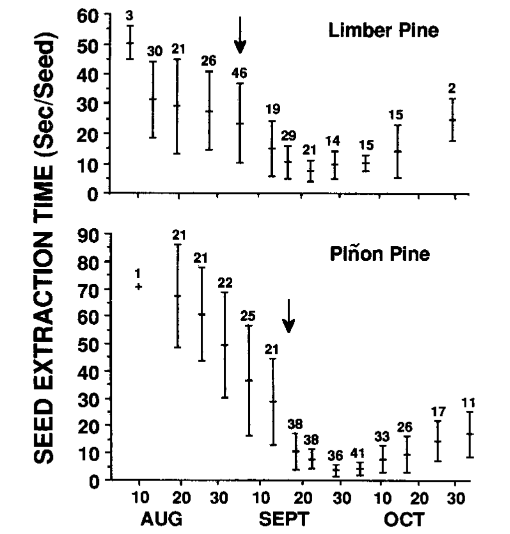

FIGURE 9. Seed extraction time (sec/seed; $\bar{x} \pm$ SD) for nutcrackers harvesting limber pine (1978) and singleleaf piñon pine (1980) seeds during fall. Numbers above SD bars are sample sizes. Arrows indicate when cones first began opening.

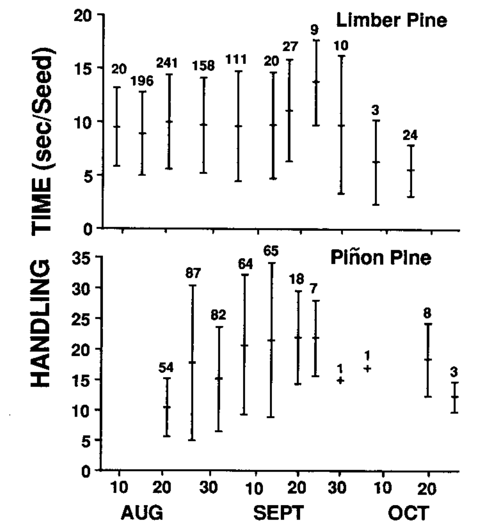

FIGURE 10. Handling times (sec/seed; $\bar{x} \pm$ SD) of nutcrackers eating limber pine (1978) and piñon pine (1980) seeds. Numbers above SD bars are sample sizes.

most piñon pine cones to feeding perches (Fig. 8), they removed seeds significantly faster from detached ($\bar{x}$ = 58.2 ± 22.5 sec/seed) than attached ($\bar{x}$ = 94.4 ± 52.7 sec/seed) cones (two-tailed $t = 2.65$, df = 38, $P = 0.01$). Time to detach cones, which was unknown in most cases, would contribute to mean seed-extraction time on detached cones, but the difference between attached and detached cones would probably still be significant. On 18 and 19 September, however, when nutcrackers had begun to forage almost exclusively on attached cones, they removed seeds significantly faster from attached ($\bar{x}$ = 8.9 ± 4.6 sec/seed) than detached ($\bar{x}$ = 16.6 ± 7.8 sec/seed) cones (two-tailed $t = 3.88$, df = 43, $P < 0.01$). Similar but less marked results were found for limber pine.

Nutcrackers handled mature (September) limber pine seeds ($\bar{x}$ = 9.7, SD = 4.6) significantly faster than mature piñon pine seeds ($\bar{x}$ = 21.1, SD = 11.3) (two-tailed $t = 6.56$, df = 127, $P < 0.001$; Fig. 10). Nutcrackers handled limber pine seeds at a nearly constant rate throughout August and September, but their seed-handling rates decreased significantly in October (two-tailed $t = 4.93$, df = 91, $P < 0.001$). Nearly all of the piñon pine seeds extracted by nutcrackers during August were removed from the cone in pieces because the seed coats had not yet fully hardened. Seeds that nutcrackers extracted at this time were handled for significantly shorter periods than those extracted in September (two-tailed $t = 3.85$, df = 217, $P < 0.001$). For seeds placed in the sublingual pouch, modal handling time was approximately 1 sec (800 of 839 cases for piñon pine, range = 1–14 sec; 1,466 of 1,477 cases for limber pine, range = 1–5 sec). During this brief period, nutcrackers frequently bill-clicked seeds rapidly in their bill as they moved the seed to the back of their mouth and into the pouch. This behavior, in addition to checking quality and assessing handling method (Ligon and Martin 1974, Vander Wall and Balda 1977, Johnson et al. 1987), seemed to play a role in maneuvering the seed into the pouch, especially when the pouch was nearly full.

FILLING THE SUBLINGUAL POUCH

Nutcrackers were first seen filling their sublingual pouches with limber pine seeds on 26 August (1978) and with piñon pine seeds on 2 September (1980), indicating that seed storage had begun. After these dates, the number of seeds placed in the pouch per observer hour rapidly increased while the number of seeds eaten per observer hour decreased (Fig. 11). The decrease in number of seeds eaten during late August and early September is due to a concomitant increase in amount of energy contained in a seed (Fig. 4). Prior to filling their pouch, nutcrackers usually ate a few

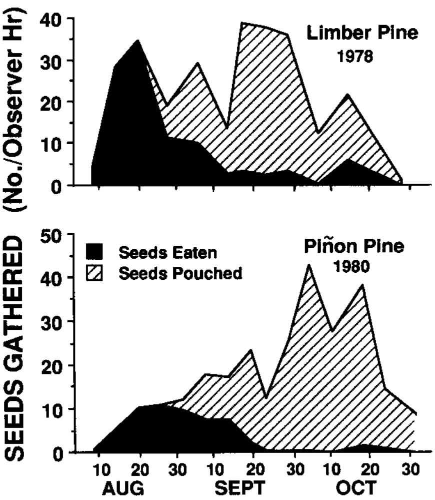

FIGURE 11. Changes in number of pine seeds eaten and placed in the sublingual pouch during the seed harvest. Placing seeds in the pouch signifies the initiation of seed caching.

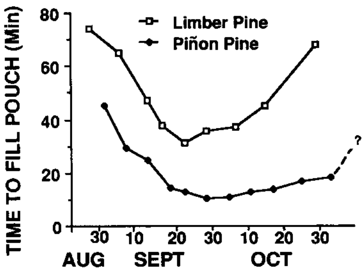

FIGURE 12. Changes in the time required to ingest four to eight seeds and then fill the sublingual pouch with seeds during the fall as cones ripen (August), open (mid- to late September), and eventually become depleted of seeds (October).

seeds. In 28 cases where a bird was observed to switch from eating to pouching limber pine seeds, the mean number of seeds consumed was 7.5 (SD = 6.8; range = 1–13). For piñon pine the mean number of seeds consumed was 4.0 (SD = 3.5; n = 35; range = 1–5). These data are minimum estimates because some birds may have eaten seeds before I observed them. Once a nutcracker began filling its pouch with seeds, eating did not occur again until they emptied the pouch.

Nutcrackers extracted a mean of 4.4 seeds from each piñon pine cone when feeding and 6.6 seeds per cone when collecting seeds for storage. Data for limber pine were 8.5 and 9.1 seeds/cone, respectively. The greater number of seeds taken from limber pine is due largely to the fact that limber pine cones contained more seeds (Table 1).

I collected six nutcrackers believed to be carrying full loads of piñon pine (*P. monophylla*) seeds. The mean quantity of seeds was 19.8 g and 19.7 ml; the maximum load (38 *P. monophylla* seeds) was 30.6 g and 28.5 ml. The number of seeds carried was lower than that reported by Vander Wall and Balda (1977) because *P. monophylla* seeds are much larger than *P. edulis* seeds. If one assumes 20 ml to be the average capacity of the sublingual pouch, then the pouch can hold approximately 120 limber pine seeds and 30 singleleaf piñon pine seeds. Based on these quantities of seeds, I calculated how long it would take a nutcracker to eat four singleleaf piñon pine or eight limber pine seeds and then fill its pouch at different times of the seed harvest (Fig. 12). At all times, nutcrackers can fill their pouch faster with piñon pine than with limber pine seeds, a difference attributable to the larger size of piñon pine seeds. For both species of pine, filling time was a U-shaped function during the fall, the descending arm of the curve due to faster seed extraction times as cones ripened and the ascending arm due to seed depletion in cones (Fig. 12). I calculated that it would take a nutcracker slightly over 45 min to fill its pouch with piñon pine seeds on 2 September but by late September this activity would take only 10 min 36 sec. When nutcrackers first began filling pouches with limber pine seeds on 26 August, I estimated that they required 74 min to fill their pouch; by 23 September the estimated time had decreased to 31 min 12 sec.

SEED TRANSPORT

Nutcrackers transported most limber pine seeds to a wind-swept ridge that served as a cache area just west of the seed-collecting site. Numerous nutcrackers intermixed their caches on this cache area and did not defend cache sites or portions of the caching area. Most observed transport flights ranged from 100 to 1,000 m, with a few birds transporting seeds greater than 1,000 m. Nutcrackers transported seeds of piñon pine harvested at low elevations to subalpine cache areas, which were also used communally. The maximum observed distance along flight paths repeatedly used by nutcrackers—hundreds of sightings of numerous individuals—was 5 km. Most birds carried seeds at least 3 km. A few nutcrackers were seen caching seeds in the piñon-juniper study site, just a few meters from where the seeds were collected, but more often birds transported seeds out of the piñon-juniper habitat. Nutcrackers hauling seeds usually made nonstop flights directly from a foraging area to a caching area.

To determine how much time a transport flight took in these situations, I timed nutcrackers as they flew between landmarks both upslope (to caching areas, pouch full) and downslope (to collecting areas, pouch empty) along a 20% grade. Distances travelled were measured on a topographic map. Mean downslope speed was 19.4 m/sec (SD = 1.5 m/sec, n = 11); mean upslope speed was 13.1 m/sec (SD = 2.3 m/sec, n = 18). Based on these mean flight speeds, mean round-trip flight time for limber pine (2.0 km) was 123 sec and for piñon pine (10.0 km) was 617 sec.

SEED CACHING

Seed caching is a stereotyped sequence of behaviors comprised of searching for a cache site, loosening the soil with jabs of the bill, inserting one or more seeds into the soil, raking soil and litter over the cache site, and, in many cases, placing a large piece of litter on the site (Vander Wall and Balda 1977). Time to prepare piñon pine seed caches, including time to select a site, ranged from 10 to 17 sec (n = 9 caches, 17 seeds). This is equivalent to 7.7 sec/seed. Similar times were observed in another field study (Vander Wall and Balda 1977) and in an experimental study (Vander Wall 1982). Thus, a pouch full of piñon pine seeds (30 seeds) takes about 230 sec to cache; a pouch of limber pine seeds (120 seeds) requires about 920 sec.

QUANTITY OF SEEDS STORED

To estimate the amount of seeds stored by nutcrackers, it is necessary to know the number of days on which seeds were stored, the number of transport flights made per day, and the capacity of the sublingual pouch. The storage season for limber and piñon pines in 1978 lasted from late August to late October, about 65 days. In 1980, nutcrackers stored piñon pine seeds from the first few days of September through November. When I discontinued observations on 2 November, many nutcrackers were still actively harvesting seeds (Fig. 6). The harvest probably continued until about mid-November, for a total harvest period of about 75 days. Since flight time and caching time are approximately constant during the fall, the maximum number of transport flights made each day during the fall varied inversely with time required to fill the sublingual pouch (Fig. 12). I make the conservative assumption that nutcrackers spend 50% of their active day (about 330 min) collecting seeds. I further assume that individual nutcrackers foraged at a rate equal to the population mean (Figs. 9 and 10) and, in 1978, apportioned their foraging effort between piñon and limber pines at the same ratio as did the population on the two study areas (Fig. 5). Given these assumptions, nutcrackers in 1978 began the seed harvest on about 26 August by making three transport trips, two of limber pine and one of piñon pine seeds. The estimated number of trips gradually increased to 13 by 29 September and then decreased, as nutcrackers and other animals depleted the seed crop, to zero by 30 October. The total estimated number of transport trips made by each nutcracker during this period was 136 loads of limber pine seeds and 246 loads of piñon pine seeds. In 1980, when nutcrackers foraged only for piñon pine seeds, they made five trips per day at the beginning of the harvest season (2 September), 13 trips per day at the height of the harvest (29 September to 4 October), decreasing gradually to one trip per day by mid-November. Each individual made an estimated 598 trips during the fall. Over the course of the 1978 seed harvest, nutcrackers stored an estimated 16,300 limber pine seeds and 7,400 piñon pine seeds. In 1980, nutcrackers stored an estimated 17,900 piñon pine seeds. This is equivalent to 3.73 kg (edible dry mass) stored by each nutcracker in 1978 and 6.12 kg stored in 1980.

Vander Wall and Balda (1977) estimated that nutcrackers required 49,484 kJ to survive at subalpine elevations from mid-October to mid-April. How far could the stored food reserves of these nutcrackers go toward meeting their metabolic needs during this period? Based on caloric contents of 32.6 kJ/g for limber pine and 23.1 kJ/g for piñon pine (Fig. 3), the quantity of limber and piñon pine seeds stored in 1978 represented 97,700 kJ and the piñon pine stored in 1980 contained 141,400 kJ of energy. Assuming an assimilation efficiency of 90%, the limber and piñon pine seeds stored in 1978 represented 1.8 times the required energy to pass the winter and spring at subalpine elevations, whereas the cache of piñon pine seeds in 1980 would have contained 2.6 times the required energy.

DISCUSSION

Limber pine and piñon pine seeds change rapidly during late summer and fall. Major components of this change include increases in caloric content and, although not measured in this study, increases in digestible carbohydrates, proteins, and lipids as seeds mature during August and early September. During the same period, cone bracts loosen and begin to open making the seeds easier for nutcrackers to extract. These seed and cone characteristics eventually stabilize by mid-September. But shortly thereafter depletion of the seed crops by nutcrackers and other animals makes seeds more difficult for nutcrackers to find, causing rates of energy acquisition to decline to near zero by mid-November.

Changes in cones and seeds were accompanied by changes in nutcracker foraging behavior. Early in the seed harvest (July) nutcrackers expend a portion of their time and energy extracting unripe seeds from tightly closed green cones. The energetic rewards at this time probably did not equal the energetic expenditure because the seeds were very small and of little caloric value (cf. Fig. 4). The main advantage to nutcrackers of foraging on pine seeds at this time may have been to gain information on the quantity and quality of the future seed crop. Advance knowledge of the seed crop may allow nutcrackers to respond to future seed shortages before they actually occur (Vander Wall et al. 1981). Nutcrackers increased their foraging intensity (measured as number of birds foraging/hour, Figs. 5 and 6) as well as their foraging rates (decrease in seconds to extract seeds from cones, Fig. 9) in response to ripening of seed and cones. Changes in their foraging tactics increase their ability to forage rapidly. For example, as cones began to open, nutcrackers shifted from feeding on detached cones, which they carried to interior branches to extract seeds, to foraging on open cones in the canopies of trees. This shift greatly increased seed extraction rates. Nutcrackers further increase foraging efficiency by selecting the most productive trees in a stand on which to forage, selecting cones that contain a greater number of edible seeds, and accurately sorting edible from inedible seeds as they extract them from cones (Vander Wall and Balda 1977; Vander Wall, unpubl. data).

Efficient exploitation of pine seeds extends beyond responding to seasonal changes in value and availability of seed of a particular species. Preferences among the species of seeds produced is also important. Early in the fall of 1978, nutcrackers foraged more frequently for the medium-sized seeds of limber pine and largely ignored the larger seeds of singleleaf piñon pine. Although I did not have sufficient data to quantitatively compare the energetic benefits of foraging on limber vs. piñon pine seeds, several lines of evidence suggest that nutcrackers first exploited the most valuable resources (as measured by energy gain). First, limber pine cones ripen and begin opening about 7 to 10 days earlier than do piñon pine cones. The opening of cones greatly increases seed extraction rates. Second, limber pine seeds, although smaller, contain more energy per unit dry mass than piñon pine seeds. This is apparently due to a higher concentration of lipids in limber pine seeds (Botkin and Shires 1948). Third, limber pines grow much closer to subalpine caching areas. Consequently, loads of seeds can be transported to storage areas quickly. The switch of nutcrackers from limber pine to piñon pine in the last week of September 1978 (Fig. 5) was coincident with seed depletion from limber pine cones. A sample of 22 open limber pine cones collected on 8 October, for example, contained a mean of only 1.5 seeds per cone. Seed depletion resulted in greater time to find a cone on which to forage and greater seed extraction times once a cone was found.

Nutcrackers are well adapted, both morphologically and behaviorally, to collect and transport pine seeds (Bock et al. 1973; Vander Wall and Balda 1977, 1981; Tomback 1978). The set of traits nutcrackers exhibit makes it possible for them to store more pine seeds than any other member of the pine-seeds eating guild except the red squirrel (*Tamiasciurus hudsonicus*), which stores whole cones (Hutchins and Lanner 1982). I view the ability of nutcrackers to quickly respond to rapidly changing pine seeds as a component of their adaptive strategy to efficiently exploit temporarily abundant seed sources. During a year of good seed production, nutcrackers can store considerable quantities of pine seeds. In the Raft River Mountains in 1978 and 1980, nutcrackers stored 1.8 and 2.6 times the energy in the form of pine seeds they were likely to need the following winters. These estimates agree with those made by others (Vander Wall and Balda 1977, Tomback 1982). The effective reserve may be even greater since nutcrackers derive a portion of their metabolic needs from other food sources in winter (Giuntoli and Mewaldt 1978). I believe the estimated quantity of seeds stored reported here to be conservative due to the assumption that nutcrackers invest only 50% of their time harvesting, consuming, transporting, and storing seeds during the fall. The remainder of their time is spent in social interactions, foraging for other foods, vocalizing, avoiding predators, etc. Because the birds left the seed harvesting area frequently to transport seeds to cache areas, it was impossible to determine precisely what proportion of time individuals dedicated to harvesting seeds. During early September, nutcrackers spend considerable time in nonforaging activities, but at the height of the seed harvest (late September to early October), nutcrackers appear to dedicate nearly all of their time in the piñon pine and limber pine habitats to collecting seeds. During this period of intense activity, the proportion of time spent harvesting is probably much more than 50%. Thus, the estimated number of seeds stored is likely to be a minimum estimate.

One aspect of the nutcracker's seed harvesting behavior seems, at first glance, to be counterproductive if maximizing seeds stored is the primary objective. Why should nutcrackers transport seeds 1 to 5 km to cache areas—at other study sites they often transport seeds much further (e.g., Vander Wall and Balda 1977)—when they could store them closer to harvest trees, resulting in a considerable saving of time and a greater quantity of seeds stored? Nutcrackers did, in fact, store some seeds near harvest trees, but the amount probably did not exceed 10 to 20% of total seeds stored. The reason that nutcrackers do not cache more seeds in the harvest areas is not clear but may be due to higher levels of cache robbing by rodents (e.g., golden-mantled ground squirrels, chipmunks, deer mice, *Peromyscus maniculatus*) in the piñon-juniper woodland and limber pine forests than is likely to occur on subalpine wind-swept ridges and cliff faces, more frequently utilized cache sites. Nutcrackers that cache under harvest trees may increase the number of seeds they store but suffer a decrease in the number of seeds actually available in late winter or spring.

Some of the advantages to nutcrackers of storing more food than they require were discussed by Vander Wall and Balda (1977). Foremost among these is that nutcrackers continue to use stored seeds long after winter is over. Nutcrackers use stored pine seeds to finance the energetic costs of early breeding (Vander Wall and Balda 1981), to feed their nestlings (Mewaldt 1956), and to feed fledglings throughout the summer (Vander Wall and Hutchins 1983). Seeds may even be recovered from caches in August, as new seeds are ripening in trees (pers. observ.). The ability of nutcrackers to track changes in resource value permit them to increase the number of seeds they store. This ability has a significant impact on nutcracker biology at other times of year, and in years of low to moderate seed production, it may determine whether nutcrackers successfully survive the winter and breed in the spring.

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