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HANDLING OF PINYON PINE SEED BY THE CLARK'S NUTCRACKER[1]

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Abstract. Clark's Nutcrackers (*Nucifraga columbiana*) are dependent on pine seeds as a food source for both nestlings and adults. Here we report on how nine captive individuals open pinyon pine (*Pinus edulis*) seeds. Two hulling methods were used: *crushing,* squeezing and cracking the seed coat and separating it from the endosperm while holding the seed in the bill; and *pounding,* holding a seed between the feet and perch and pounding on it forcefully with the bill until the seed coat cracks. On average, birds crushed 43.7% of their seeds, but three birds pounded over 70% and one crushed over 90%. Seeds that were pounded were significantly wider and had thicker coats than those crushed. Large birds crushed seeds of greater size than did small birds. Pounding took 2.5 times longer than crushing, however, individuals specializing on pounding opened seeds as fast with that technique as other birds did by crushing. Bill-clicking of seeds may function in assessment of hulling method. Seeds that nutcrackers were apparently uncertain of how to open were clicked more than seeds they were apparently certain of how to open. Nutcrackers are efficient seed handlers; they use the less costly crushing technique whenever possible, become very proficient at pounding open seeds, and use a very general behavior (bill-clicking) to assess which hulling technique is the most profitable means of opening a seed. The variability in handling behavior we document leads us to suggest that tests of optimal prey choice be based on profitability of prey to, and choice of prey by, individual predators.

Key words: Behavior, bill-clicking, coevolution, handling time, optimal foraging, Nucifraga columbiana, *pine seed, pinyon pine.*

INTRODUCTION

Clark's Nutcrackers (*Nucifraga columbiana*), high alpine permanent residents, are dependent on pine seeds as a food source for both nestlings and adults (Mewaldt 1956, Giuntoli and Mewaldt 1978, Tomback 1978, Vander Wall and Balda 1977, 1981, Vander Wall and Hutchins 1983). Such dependency is likely to select for high efficiency in using that resource and indeed, previous research indicates nutcrackers are highly proficient in harvesting pine seeds (see Vander Wall and Balda 1977, Tomback 1978, Tomback and Kramer 1980, Vander Wall 1982, Balda and Turek 1984, Kamil and Balda 1985).

Here we examine an unexplored yet potentially important aspect of pine seed handling behavior; the means by which nutcrackers separate the hard seed coat from the energy rich endosperm. Previous reports (Vander Wall and Balda 1977, Tomback 1978, Bunch et al. 1983) indicate nutcrackers use two methods to hull seeds. The first, which we term "crushing," involves squeezing and cracking the seed coat and separating it from the endosperm while holding the seed in the bill. The name "nutcracker" probably comes from this technique (Newton 1894). In the second, or "pounding" method, birds hold a seed firmly between their feet and perch and pound on it forcefully with the bill until the seed coat cracks. The seed coat is then pried away and the endosperm removed and swallowed.

Individual nutcrackers may eat tens of thousands of pine seeds in their lifetime, thus they should become proficient in handling pine seeds. Seed profitability increases as handling time decreases (e.g., Krebs 1976), therefore, nutcrackers should use the hulling method which is fastest. This choice of hulling method may depend on seed size, bill size, or an individual bird's ability and experience. Individual birds should also be capable of accurately and rapidly assessing which method to use on a seed, especially if the difference in time investment is great.

We report here on how captive nutcrackers use the two hulling methods while eating pinyon pine (*Pinus edulis*) seeds. We emphasize how individuals of differing bill size minimize handling costs by adjusting hulling methods to seed size. We also provide data that suggest that the pre-

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TABLE 1. Nutcrackers' bill volumes, percentage of seeds crushed, and mean handling times for seeds pounded and seeds crushed. Sample sizes in parentheses. F and P refer to one-way ANOVAs comparing handling times of seeds crushed versus pounded.

Bird	Bill volume (mm³)	% Seeds crushed	Handling times (sec) Crushed	Handling times (sec) Pounded	F	P
1	66.5	54% (24)	54.9 (13)	80.6 (10)	1.22	0.14
2	74.4	91% (23)	114.1 (19)	305.4 (2)	—	—
3	60.3	27% (22)	16.4 (6)	52.7 (16)	2.39	0.07
4	65.9	42% (24)	24.0 (11)	156.2 (13)	18.19	<0.001
5	64.7	54% (24)	55.1 (14)	152.5 (9)	13.64	<0.001
6	48.7	0% (23)	—	21.0 (23)	—	—
7	68.2	56% (25)	68.5 (12)	110.2 (9)	0.60	0.23
8	45.9	54% (24)	71.2 (13)	182.2 (10)	4.51	0.02
9	70.4	16% (19)	43.0 (3)	24.3 (16)	—	—
All	62.8*	43.7*	65.2** (90)	104.9** (86)	7.84	0.006

* Mean for all birds.
** Excluding bird 6.

viously reported behavior of "bill-clicking" seeds (Ligon and Martin 1974) may aid the bird in selecting the most efficient hulling method.

SUBJECTS AND METHODS

Nine adult nutcrackers were housed in individual cages, in one room, and fed a mixture of mice, popcorn, sunflower (*Helianthus* spp.), and pinyon pine seeds for several months prior to our observations. Bill width (W) and depth (D) at the nostrils were measured with Vernier calipers. Culmen lengths (L) were measured with a flexible ruler after bills were clipped to correct overgrowth of upper mandibles. Bill volumes were approximated using the formula for the volume of a cone:

$$\text{Volume} = \tfrac{1}{3} \times [(W + D)/2]^2 \times L.$$

Pinyon pine seeds are relatively large ($\bar{x} = 1.3$ cm $\times$ 0.8 cm, $n = 133$), wingless, and roughly egg-shaped with a woody seed coat ($\bar{x}$ thickness = 0.35 mm, $n = 110$) enveloping an energy rich endosperm ($\bar{x} = 31.0$ kJ/g, Vander Wall and Balda 1977). Maximum length and width of seeds were measured with Vernier calipers to the nearest 0.1 mm. Seed weight was determined to the nearest 0.01 g with an electronic Mettler P163 balance. After seeds were hulled, most seed coats were collected and their thickness measured with microcalipers at three points of seed coat breakage, away from the micropile.

Each bird was observed eating approximately 24 seeds. A tray containing two seeds was inserted into the bird's cage and the bird allowed to select one seed. Two observers (L.S.J. and J.M.M.) recorded seed handling behavior and time on stopwatches. Handling time was defined as time spent between picking a seed off the tray and swallowing the endosperm. Clicking of seeds, seed opening, and separation of the endosperm from the seed coat were included in handling time. In addition to time spent bill-clicking, we also recorded the number of clicking bouts. A bout was defined as the movement of a seed from the throat to the end of the bill and back while clicking it.

We investigated the influence of seed size on handling time and clicking behavior by dividing the seeds given to each bird into three groups. Intermediate-sized seeds were within one SD of

TABLE 2. Sizes of seeds crushed (Cr) and pounded (Po). *F* and *P* values refer to one-way ANOVAs comparing sizes of seeds crushed versus pounded.

	Mean length (cm)			Mean width (cm)			Mean coat thickness (mm)		
Bird	Po (*n*)	Cr (*n*)	*F* *P*	Po (*n*)	Cr (*n*)	*F* *P*	Po (*n*)	Cr (*n*)	*F* *P*
1	1.36 (11)	1.70 (13)	1.77 0.20	0.87 (11)	0.79 (13)	4.11 0.06	0.39 (11)	0.32 (10)	8.63 0.01
3	1.32 (16)	1.26 (6)	2.13 0.16	0.84 (16)	0.74 (6)	3.46 0.08		No data	
4	1.38 (13)	1.23 (11)	9.30 0.01	0.87 (13)	0.80 (11)	5.29 0.03	0.37 (12)	0.31 (9)	6.05 0.02
5	1.36 (9)	1.30 (15)	2.71 0.11	0.87 (9)	0.81 (15)	5.35 0.03	0.40 (9)	0.36 (14)	7.57 0.01
7	1.29 (11)	1.27 (14)	0.18 0.68	0.84 (11)	0.73 (14)	6.37 0.02	0.35 (9)	0.28 (11)	12.73 <0.01
8	1.32 (11)	1.24 (13)	2.34 0.14	0.86 (10)	0.75 (13)	20.33 <0.01	0.38 (10)	0.31 (11)	5.86 0.03
All	1.34 (72)	1.27 (71)	13.83 <0.01	0.86 (71)	0.77 (71)	37.29 <0.01	0.38 (62)	0.32 (56)	34.38 <0.01

the mean size for a given measurement per bird, large and small seeds were above and below one SD of the mean of that measure, respectively. Handling times and clicking of seeds in these three groups were compared by Kruskal-Wallis one-way analyses of variance because group variances were unequal.

The majority of analyses we report was done on an individual bird basis to underscore individual variation in handling behavior. We used parametric one-way analysis of variance and Pearson correlation analysis when Cochran's C test indicated sample variances were equal.

RESULTS

HULLING METHOD PREFERENCES

Individuals differed greatly in the proportion of the two hulling methods used (Table 1). On average, birds crushed 43.7% of their seeds. Birds 2, 6, and 9 showed such an extreme preference for one or the other hulling method that they had to be excluded from several of the following analyses. The remaining birds used the two methods about equally, crushing an average of 48% of their seeds.

HULLING METHOD AND HANDLING TIME

Handling times for crushed seeds were significantly less than handling times for pounded seeds for three of six birds and nearly so for the other three birds regularly using both methods (Table 1). It took individuals on average 2.5 times longer to hull a seed by crushing than by pounding. This difference results from the differences in time required to assess seeds and then crack the seed coat. Time spent removing the endosperm from the cracked seed was minimal and we assumed it to be equal regardless of opening method. Averaged over all birds, mean handling time for crushed seeds was 48.4 sec, whereas for pounded seeds it was 122.4 sec.

We predicted that the use of pounding should be directly related to the pounding efficiency of a given bird as measured by the time (and possibly energy) necessary to open a seed. In fact, birds which opened over 70% of their seeds by pounding (birds 3, 6, 9), spent little time handling them (Table 1), and bird 2, who rarely pounded seeds, spent an inordinate amount of time handling seeds using this technique. The overall negative correlation for the nine birds between percent of seeds pounded and handling time prior to pounding was significant ($r = -0.89$, $P < 0.01$).

EFFECT OF SEED SIZE ON HULLING METHOD

We predicted that crushed seeds would have thinner coats and be smaller than pounded seeds. Coats of crushed seeds were significantly thinner than coats of seeds pounded for all birds tested (Table 2). Crushed seeds were significantly narrower than pounded seeds for five of six birds and nearly so for the sixth bird (Table 2). Lengths of seeds crushed, however, were significantly

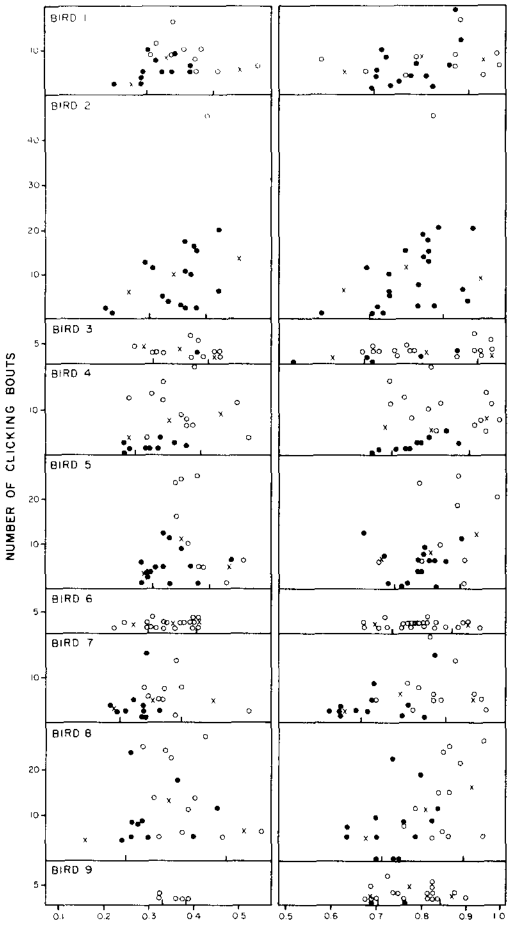

FIGURE 1. Bill-clicking of seeds with respect to seed coat thickness and seed width. Clicking of seeds that were pounded (○) versus crushed (●) is shown for individual birds. Small, intermediate, and large seeds for each individual are separated by the hash marks on the X axes. Average amount of clicking (X) in each interval shows the general clicking response of individuals to seed size.

shorter only for bird 4 (Table 2). Thus, seed coat thickness and seed width were two characteristics correlated with hulling method.

EFFECT OF BILL SIZE ON HULLING METHOD

We predicted larger-billed birds would crush a greater proportion of their seeds because of the greater force their bills and associated muscles are able to generate. No strong relation was found between bill volume and percentage of seeds crushed when data for all nine birds were analyzed ($r = 0.21$, $P \gg 0.10$). Individual differences independent of morphology were evident. Bird 8, a small-billed bird, crushed most of its seeds and bird 9, a large-billed bird, pounded most of its seeds (Table 1). If these two individuals are removed from the analysis, bill size becomes a very accurate predictor of the percentage of seeds crushed ($r = 0.93$, $n = 7$, $P < 0.01$).

The relationship between hulling method and seed size differed among individuals. For example, bird 7 pounded relatively thin and narrow seeds compared to those pounded by other birds (Table 2, Fig. 1). Bird 5 crushed relatively thick-coated seeds, which averaged thicker than those pounded by bird 7 (Table 2, Fig. 1). These differences are not explicable by bill size because bird 5 had a smaller bill than bird 7. Nutcrackers initiated pounding on seeds with a coat thickness ranging from 0.25 mm (bird 6) to 0.42 mm (bird 2) and width ranging from 0.60 mm (bird 1) to 0.84 mm (bird 2).

BILL-CLICKING OF SEEDS

After selecting a seed, birds usually performed several bouts of bill-clicking; rapidly opening and closing the mandibles as the seed moved from the throat to the tip of the bill and back.

All birds clicked at least some seeds but the amount of clicking varied widely among birds ($\bar{x} = 6.1 \pm 3.57$ clicking bouts/seed, Table 3). The number of clicking bouts performed on a seed appeared to be related to how the seed was opened. Of the six birds for which adequate sample sizes of the two hulling methods were obtained (1, 3, 4, 5, 7, 8), all clicked seeds more often before pounding than before crushing; significantly so in three of six birds (Table 3). Individuals averaged 2.9 times as many clicking bouts on seeds pounded than seeds crushed. Overall, mean number of clicking bouts for seeds pounded by the birds listed above was 9.17 ± 8.74 bouts/seed compared to 4.29 ± 3.24 bouts/seed for seeds crushed.

Individual nutcrackers that pounded most (>50%) seeds clicked them much less than did birds that crushed most seeds ($\bar{x}$ for 4 pounders $= 3.15 \pm 3.73$ clicking bouts/seed; $\bar{x}$ for 5 crushers $= 8.37 \pm 7.31$ clicking bouts/seed; $t = -6.72$, df $= 206$, $P < 0.0001$). The three birds that pounded 70% or more of their seeds averaged only 1.83 ± 0.20 clicking bouts/seed.

BILL-CLICKING AS A SEED ASSESSMENT PROCESS

Pounding is more time consuming, and may cost more energy than crushing and distracts the feeding bird more from its environment because its eyes focus on where the bill is to strike the seed. For these reasons, it would be beneficial for nutcrackers to be able to accurately determine the most efficient hulling method. Hulling method may be assessed visually before a seed is picked up in the bill. Reliance on visual cues and tactile cues gained immediately as the seed is picked up appeared only to occur in very small seeds which were picked up and immediately crushed (birds 3, 4, 8, 9, Fig. 1). Once a seed is in the bill it may be bill-clicked to further assess hulling method. If bill-clicking is an assessment process, the amount of clicking should vary in proportion to the uncertainty a nutcracker may have in selecting an efficient hulling method.

Nutcrackers should be most uncertain about hulling method when seed characters are variable. We predicted uncertainty to be especially high when characters correlated with hulling method for a given seed indicate both methods may be appropriate. For example, thin-coated, wide seeds may provide conflicting information; thin seed coats may indicate to nutcrackers that the seed can be most easily opened by crushing, whereas width may indicate that pounding will be the most effective method.

Variability in seed characters, and thus possibly the uncertainty of nutcrackers, is related to seed size in two ways. First, variability in coat thickness of individual seeds increases with average thickness ($\bar{x}$ SD per seed of thin-coats = 0.19, $\bar{x}$ SD of intermediate-coats = 0.23, $\bar{x}$ SD of thick-coats = 0.34). Increased variability results from thick-coated seeds having a greater difference between average and minimum coat thickness ($\bar{x}$ difference for thin-coated = 0.004 mm, $\bar{x}$ difference for thick-coated = 0.035 mm;

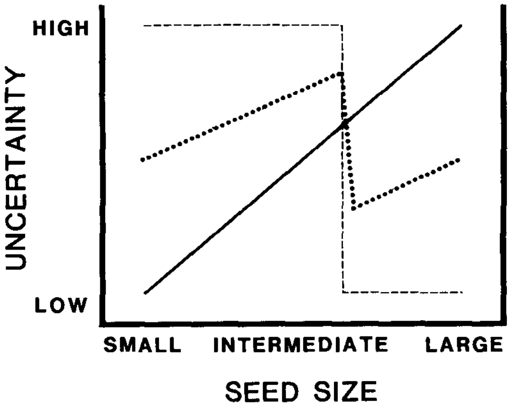

FIGURE 2. Presumed uncertainty of nutcrackers in choosing hulling method as a function of seed size. Uncertainty increases with seed size because of the variability in seed coat thickness (solid line), but is low in large seeds because measured characters of these seeds are strongly inter-correlated (dashed line). The average uncertainty if both uncertainty functions are weighted equally is highest in intermediate-sized seeds (dotted line).

Kruskal-Wallis $\chi^2 = 18.2$, $P < 0.001$). That is, thick-coated seeds commonly have thin-coated sections. Second, measured characters of large seeds are more highly inter-correlated than are the same characters of small or intermediate seeds. For example, coat thickness and seed width are correlated in very large seeds ($r = 0.41$, $n = 16$, $P = 0.057$) but only weakly correlated in small ($r = 0.25$, $n = 16$, $P = 0.18$) and intermediate-sized seeds ($r = 0.24$, $n = 75$, $P = 0.02$, note that our argument depends on the value of r, not P, because P is sensitive to n).

We have graphically shown the relationship of the uncertainty nutcrackers may have in selecting a hulling method as a function of seed size in

TABLE 3. Mean number of clicking bouts for seeds pounded and seeds crushed. Sample sizes in parentheses. F and P refer to one-way ANOVAs comparing clicking bouts before crushing and pounding seeds.

Bird	Mean clicking bouts			F	P
	All seeds	Seeds crushed	Seeds pounded		
1	6.88 (24)	5.77 (13)	8.18 (11)	1.98	0.17
2	10.59 (22)	8.70 (20)	29.50 (2)	—	—
3	2.05 (22)	0.83 (6)	2.50 (16)	6.96	0.02
4	6.67 (24)	1.64 (11)	10.23 (13)	33.99	<0.001
5	8.50 (24)	5.73 (15)	13.11 (9)	9.06	0.007
6	1.65 (23)	— (0)	1.65 (23)	—	—
7	5.29 (24)	3.85 (13)	7.00 (11)	2.53	0.13
8	10.58 (26)	7.77 (13)	14.00 (11)	3.69	0.068
9	1.79 (19)	0.00 (2)	1.75 (16)	—	—
All	6.12 (205)	5.52 (93)	7.88 (89)	5.61	0.019

TABLE 4. Characteristics of intermediate-sized seeds that were bill-clicked less than (Few) or greater than (Many) the average. Sample sizes in parentheses. *P* values derived from one-way ANOVAs comparing characters of seeds clicked few and many times.

		Intermediate coat thickness			Intermediate seed width	
				Mean		
Bird	No. of clicks	Seed width (mm)	Minimum coat thickness (mm)	Width—average coat thickness (mm)	Seed coat thickness (mm)	Width—coat thickness (mm)
1	Few	0.78 (6)	0.31 (6)	0.43 (6)	0.34 (12)	0.57 (2)
	Many	0.86 (3)	0.32 (3)	0.52 (3)	0.35 (4)	0.61 (1)
4	Few	0.85 (11)	0.32 (11)	0.51 (11)	0.33 (9)	0.49 (9)
	Many	0.85 (11)	0.32 (4)	0.50 (4)	0.34 (3)	0.49 (3)
5	Few	0.82 (11)**	0.34 (11)	0.45 (11)	0.36 (12)	0.46 (12)
	Many	0.90 (4)	0.36 (4)	0.53 (4)	0.38 (3)	0.49 (3)
7	Few	0.77 (13)	0.29 (13)	0.47 (13)**	0.31 (10)	0.48 (10)
	Many	0.87 (2)	0.31 (2)	0.54 (2)	0.30 (1)	0.54 (1)
8	Few	0.78 (12)***	0.32 (12)	0.44 (12)***	0.37 (8)	0.46 (8)***
	Many	0.86 (8)	0.33 (8)	0.52 (8)	0.34 (7)	0.51 (7)

** $P < 0.10$.
*** $P < 0.05$.

Figure 2. This uncertainty increases linearly with seed size because of the variation in coat-thickness within individual seeds. Uncertainty also follows a step function in relation to seed size because the inter-correlation among seed characters is high for large seeds but low for small and intermediate-sized ones. If bill-clicking is used to assess hulling method, we predicted intermediate-sized seeds would be clicked more than small or large ones because nutcrackers may be least certain of how to hull seeds where the average of the two uncertainty curves was highest (dotted line in Fig. 2). This prediction assumes that nutcrackers use both measures of uncertainty approximately equally and that seeds with uncertain hulling methods require more assessment than those with certain hulling methods.

Clicking varied with seed size in the manner we predicted for birds that frequently used both hulling methods (Fig. 1, birds 1, 4, 5, 7, 8). Thin-coated seeds were typically clicked few times and then crushed. Intermediate-sized seeds were clicked a variable but, on average, large number of times and then crushed or pounded with equal frequency. Thick-coated seeds were again clicked few times (except bird 4), but usually pounded. Only birds 1 and 7 showed a similar relationship between seed width and clicking frequency. Coat thickness thus appears to be directly assessed by bill-clicking of seeds.

Variation in clicking of intermediate-sized seeds was high. In accordance with our hypothesis that clicking is an assessment process, this variation may result from differences in assessability among intermediate-sized seeds. We predicted assessability would be most difficult when different seed characters indicated use of different hulling methods. Seeds with large differences in characters correlated with hulling method (e.g., thick-coated, narrow seeds) should therefore be clicked more than those with small differences. We examined this by comparing seeds clicked more and less than average (Table 4). Seeds with coats of intermediate thickness were clicked often if they were also wide. On average, they were 0.07 mm wider than those clicked less often. Minimum coat thickness did not differ between seeds clicked few and many times. Clicked seeds of intermediate width did not differ with respect to coat thickness. The differences in seed coat thickness and seed width were greater for intermediate seeds clicked many times than for those clicked few times (Table 4). We conclude nutcrackers have difficulty in assessing hulling method for seeds of intermediate width, especially when these seeds have atypically thick coats. This may result because width indicates nutcrackers could crush these seeds, but coat thickness indicates they must be pounded. Coat thickness appears most influential because the majority (74%, $n = 19$) of seeds clicked many times were eventually pounded.

Our sample includes four birds with idiosyncratic tendencies to specialize on one hulling method. They appear to be very certain of the hulling method they will use regardless of variability in seed characters. Three are efficient, specialized pounders (birds 3, 6, 9). We predicted these birds should spend minimal time assessing seeds, and assess small, easily crushed seeds more than intermediate or large ones. These birds spent the least amount of time assessing seeds, as predicted (Fig. 1). An inverse relationship between clicking and seed characters, however, was only evident in bird 3 with respect to seed coat thickness ($r = -0.34$, $P = 0.035$, Fig. 1). Bird 2 was a crusher, possibly because of his large bill size (Table 1). We predicted this bird should also spend minimal time assessing seeds, and assess large, potentially uncrushable seeds longer than small or intermediate seeds. As predicted, clicking in this individual increased directly with seed width ($r = 0.38$, $P = 0.04$) and thickness of the seed coat ($r = 0.48$, $P = 0.02$). Contrary to our prediction, this bird spent considerable time clicking seeds.

Our findings on bill-clicking as a seed assessment process can be summarized as follows. First, birds which use both hulling methods click intermediate-sized seeds more than small or large ones. Second, uncertainty in hulling method for these birds is highest for intermediate-sized seeds. Third, uncertainty in hulling method is not equal among intermediate-sized seeds and nutcrackers click intermediate-sized seeds in proportion to this uncertainty. And fourth, birds specializing on one hulling method appear more certain of how to open seeds and accordingly three of four specialists clicked seeds very infrequently. We conclude nutcrackers click seeds they are uncertain of how to open more times than those with more certain hulling methods.

DISCUSSION

Optimal foraging theory assumes predators spend foraging time either searching for or handling prey (e.g., Krebs 1976). Our study concerns only handling time because we eliminated search time by presenting pine seeds directly to nutcrackers. Few studies emphasize *variation* in foraging behavior, instead *average* behavior is typically compared to behavior predicted from optimality theory (e.g., Pyke 1984). Our results emphasize three sources of variation in handling behavior. First, individual nutcrackers handle wide, thick-coated seeds differently than narrow, thin-coated seeds. They typically pound open the former and crush open the latter. Second, the method of handling similar-sized seeds differs between individuals and appears to be related to bill morphology and possibly, prior experience. And third, individuals using the same handling method, on a similar range of seed sizes, have different handling times. On average, hulling seeds by pounding took 2.5 times longer than hulling by crushing, however, individuals that relied predominantly on pounding were able to pound open seeds as fast as other birds crushed open seeds.

Variability, such as we have documented, in one component of foraging behavior has important implications for general foraging theory. This variability may allow foraging behavior to rapidly evolve as current environmental conditions change. Optimal foraging models assume such change can occur (Pyke 1984). Choice of handling method may influence a nutcracker's ability to perform other tasks, such as detection of predators and conspecifics. This is assumed not to occur in models of optimal foraging (Pyke 1984). Although we did not test this idea, it seems likely that an individual focusing on where to strike a seed held between its feet and perch will be less aware of its surroundings than it would be when crushing a seed in its bill during which time the head can be held upright. Individual variability in time spent handling similar food items suggests prey profitability is not only a function of energy gains and time expenditures, but is dependent on the individual predator. Previous studies have modified prey profitability in accordance with predator morphology (Kislalioglu and Gibson 1976) and experience (Jaeger and Rubin 1982). We suggest that this should be extended so that tests of optimal prey choice are based on profitability of prey to, and choice of prey by, individual predators. Comparing choice exhibited by a population of predators to average prey profitability may be misleading.

Pinyon Jays (*Gymnorhinus cyanocephalus*), which also rely heavily on thick-coated pine seeds for sustenance, do not open them by the crushing technique. All seeds regardless of size or shape are pounded (pers. observ. from field and laboratory). This species has a long pointed, but relatively narrow bill, which may make crushing seeds less efficient than pounding them. Crushing may allow birds to remain attentive of their surroundings, which may not be of paramount importance to a social bird with well developed sentineling behavior (Balda and Bateman 1971). Thus, selection for maintaining vigilance while opening seeds may be weak or not present in individual Pinyon Jays.

There are several possible functions for the bill-clicking of seeds. One function was suggested by Ligon and Martin (1974) for Pinyon Jays. They concluded that it would be maladaptive for birds to harvest, transport, and store aborted and inedible seeds and that a rapid and accurate method of recognizing good seeds would be favored. In experiments where birds accurately discriminated between pale, rough and aborted seeds or dark brown, edible seeds, jays primarily used the visual cues of color and texture. Weight cues, as judged by holding a seed momentarily in the bill were of secondary importance. Bill-clicking seeds was a last step in assessment. They hypothesized that bill-clicking provided auditory cues as empty seeds sounded hollow when tapped.

Bill-clicking by nutcrackers harvesting seeds from pine cones has been interpreted as a seed assessment behavior (Tomback 1978, Vander Wall and Balda 1977, 1981). Nutcrackers are known to leave pale, aborted seeds in cones (Vander Wall and Balda 1977). Birds must discriminate between viable seeds and similarly colored and weighted diseased, infected or spoiled ones. Vander Wall and Balda (1977) reported that of 400 seeds extracted by nutcrackers from cones, 18 seeds were discarded of which four were collected and found to be spoiled. Although no count was made, they state discarded seeds were "bill-clicked more extensively than the seeds that were kept" (p. 97). Of 500 seeds recovered from nutcracker pouches, all were found to be edible (Vander Wall and Balda 1981). Seeds harvested were clicked between 4 and 11 times ($\bar{x}$ = 7.3, n = 67, Vander Wall and Balda 1981). Cues for rejection or acceptance provided by bill-clicking of seeds are still unknown. In our experiments, nutcrackers were not harvesting seeds and all seeds fed to birds were dark brown and edible. No seeds were rejected. We suspect bill-clicking of seeds in our situation served a different function than assessment of seed quality.

Our observations indicate that bill-clicking of seeds may also function as a rapid and accurate means for determining the most efficient seed hulling technique. Birds could thereby check for weak areas in the hull to determine if the seed could be crushed. Birds should be able to visually and tactilely determine hulling method for small seeds which are easily crushed and indeed, these seeds are clicked significantly fewer times than intermediate and large seeds. Likewise, very large seeds are rapidly assessed with few clicks, and then pounded. Birds with large bills able to crush many seeds need only to assess very large seeds for the possibility of pounding, as shown by bird 2. Birds that rarely vary hulling methods should not perform much assessment. This was seen in birds 3, 6, and 9. The hulling method assessment hypothesis is further supported by the fact that wild nutcrackers foraging on seeds of *Pinus flexilis* and *P. strombiformis* were not observed clicking seeds and were found to hull all seeds by pounding (Benkman et al. 1984). *Pinus flexilis* and *P. strombiformis* have relatively thicker seed coats ($\bar{x}$ coat thicknesses of 0.47 mm and 0.62 mm, respectively [Benkman 1982] than does *P. edulis* ($\bar{x}$ coat thickness of 0.36 mm [this study]). If bill-clicking does function in determining hulling method, we would not expect seeds of these species to be clicked because their coats are apparently too thick to crush. Tomback (1978) found nutcrackers clicking and using both hulling methods on *Pinus albicaulis.* The coat thickness of this species is not known but is suspected to be within the range of pinyon seed coat thickness. Pinyon Jays, Steller's Jays (*Cyanocitta stelleri*) and Scrub Jays (*Aphelocoma coerulescens*), all of which normally eat pinyon seeds in the wild, have smaller, narrower bills than nutcrackers and hull seeds only by pounding (pers. observ.). Ligon and Martin (1974) observed Pinyon Jays clicking seeds one to seven times in the laboratory and we have occasionally seen the same, however, we have never observed either of the other two species clicking pinyon seeds.

A third hypothesis for the function of bill-clicking is that a clicking bout simply represents an attempt to crack the seed coat. Numerous bouts of clicking before seeds are pounded is consistent with this hypothesis, however, reduced clicking of very wide or very thick-coated seeds is not. Our observations and those of Tomback (pers. comm.) suggest that bill-clicking is a separate movement from seed coat cracking. Seeds are cracked very near the base of the bill, but clicking occurs at the distal end of the bill where it is unlikely that enough pressure could be exerted to crush seeds. Furthermore, because clicking occurs so rapidly, it is doubtful that the bird has time to exert enough pressure to crack the coat.

The act of rapidly opening and closing the mandibles is commonly used by many species of seed eaters to open thin-coated seeds (e.g., Evening Grosbeak, *Coccothraustes vespertinus,* Pine Siskin, *Carduelis pinus,* White-crowned Sparrow, *Zonotrichia leucophrys,* etc.). Birds that specialize on harvesting, caching, and recovering seeds when other foods are scarce or nonexistent use this general and possibly widespread behavior for a specialized and important function: the efficient assessment of seeds at harvest, and the determination of hulling method at the time of eating. These are specialized adaptations derived from a very general behavioral act. This is consistent with a number of other such traits in seed-caching birds discussed by Vander Wall and Balda (1981).

The ability to select an efficient seed opening technique based on seed characters may be adaptive for nutcrackers because they exploit a wide size range of conifer seeds. Flexibility in opening technique within individuals should allow rapid response to changing seed availabilities. Biases in opening method, such as those we observed, may develop in response to an individual's prior experience with food resources. Variation in opening technique among individuals may provide a means for evolutionary adjustment of food-handling behavior by nutcracker populations coevolving with seed populations.

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