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HOW NUTCRACKERS FIND THEIR SEED STORES

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ABSTRACT.—The Clark's Nutcracker (*Nucifraga columbiana*) stores conifer seeds in the late summer and fall of each year. During winter and spring, seeds from buried caches are the major food of nutcrackers and their young. A bird must find more than a thousand seed caches each year. The alternative means by which nutcrackers may locate seed stores are (1) memory of cache site and (2) trial and error search.

While searching for stored seeds, a Clark's Nutcracker makes a series of prod holes with its bill. A hole from which a cache was recovered is usually distinguished by a pile of broken seed coats. This allows an estimate of a nutcracker's success rate in locating seed caches. Theft of seed caches by rodents and removal of intact seeds from cache sites by nutcrackers may confuse this estimate. A field technique based on deductive reasoning is presented to determine how nutcrackers recover their caches.

In the eastern Sierra Nevada I gathered field data on the success rate and nearest neighbor distances among prod holes in spring and summer of 1975. Data indicating the proportion of caches taken by rodents were obtained in 1978. Analyses of these data suggest that nutcrackers find most of their caches by means of memory. A search based on memory implies that seed stores are not communal and that nutcrackers must remain in the area where they stored seeds until the following summer.

Theft of seed stores by rodents must be an important selective pressure on nutcracker caching behavior. By caching seeds in storage areas which become covered with deep snow, nutcrackers may reduce their losses to rodents.

Many birds of the family Corvidae store food for future use. Food storage is a major event in the annual cycles of the genera *Garrulus*, *Aphelocoma*, *Gymnorhinus* and *Nucifraga* (Turček and Kelso 1968). Both species of *Nucifraga*, Clark's Nutcracker (*N. columbiana*) and the Eurasian Nutcracker (*N. caryocatactes*), store conifer seeds in late summer and fall (Bibikov 1948, Reimers 1953, Kuznetsov 1959, Vander Wall and Balda 1977, Tomback 1977a). These stores are the major food of the nutcrackers from winter to mid-summer (Kuznetsov 1959, Mezhenny 1961, Holtmeier 1966, Tomback 1977a). Both species breed in early spring, raising young almost exclusively on stored seeds (Mewaldt 1956, Swanberg 1956, Reimers 1959a).

Stores made by nutcrackers consist of many small clusters of seeds hidden in a variety of sites throughout the montane habitat (Bibikov 1948, Swanberg 1951, Reimers 1959b, Kishchinskii 1968, Tomback 1977a). I will use the term "cache" to denote one cluster of seeds; seed stores consist of many caches. The means by which a nutcracker finds these stored seeds has not been satisfactorily explained and remains an intriguing problem in animal behavior.

The most direct approach to this problem would be experimentation on captive birds under controlled conditions. R. P. Balda (in press) recently concluded a series of controlled investigations of seed recovery behavior in the Eurasian Nutcracker. His findings concur with previous field observations (Swanberg 1951, Mezhenny 1964, Crocq 1977, Mattes 1978) and also present new information. However, it is possible that the limited space and predictable stimuli of experimental enclosures can bias results. Before similar experimental work is undertaken on the Clark's Nutcracker, confirmation of laboratory findings with field data is desirable. In this paper I present the results of a field investigation of how Clark's Nutcrackers recover their seed stores.

THE NATURE OF THE PROBLEM

Vander Wall and Balda (1977) calculated that a single Clark's Nutcracker may store between 22,000 and 33,000 piñon pine seeds (*Pinus edulis*) in the late summer and fall of each year in northern Arizona. This quantity represents between 2.2 and 3.3 times the energetic requirement of the nutcracker. I calculated (Tomback 1977b, unpubl. data) that each year in the eastern Sierra Nevada one Clark's Nutcracker may store as many as 32,000 whitebark pine seeds (*P. albicaulis*) at subalpine elevations. Using methods similar to those of Vander Wall and Balda (1977), but with data obtained from the Sierra Nevada, I determined that these whitebark pine seed stores represent up to three times the energetic requirements of the individual for spring and summer, although this figure would be less for breeding birds, which use their seed stores for feeding nestlings and fledged juveniles. According to my estimate (Tomback 1977b), one nutcracker buries about 7,700 separate whitebark pine seed caches per year (each cache containing a mean of 4.4 seeds) throughout the whitebark pine forest.

Like the Clark's Nutcracker, the Eurasian species stores more seed than it requires. Bibikov (1948) reported that rodents took 20% of the seed caches hidden in forests by the Eurasian Nutcracker and 74% of the caches buried in tundra; Pivnik (1960) reported an 80% loss to rodents. As little as 6% to 33% of the seed stored by Eurasian Nutcrackers is recovered, according to the observations of Reimers (1956).

Elsewhere I described how and where nutcrackers store seed (Tomback 1977a). As nutcrackers harvest conifer seed from cones, the seed is placed in the sublingual pouch—a sac extending down from the floor of the mouth and opening anterior to the base of the tongue (Bock et al. 1973). When the pouch contains from about 35 to 150 seeds ($\bar{x} = 77$, Tomback 1977a), the bird carries the seeds to a storage site. There it digs a hole with its bill tip, places several seeds from the sublingual pouch into the hole, and covers them with soil or pine needle litter. No sign is visible to indicate that a cache is present, although nutcrackers have been observed to place a few pebbles or other small objects on the cache site (Vander Wall and Balda 1977). The bird continues making caches in the same general area or flies to another area to make caches, until the sublingual pouch is empty.

Both the Clark's Nutcracker and Eurasian Nutcracker store seed in loose, gravelly soil, in forest litter, in the ground at the base of trees, rocks or logs, among the roots of dense creeping plants, among rocky rubble, and in holes, cracks, or under the bark of trees (Bibikov 1948, Swanberg 1951, Reimers 1956, Kishchinskii 1968, Tomback 1977a). In addition, the Eurasian Nutcracker hides caches under lichen and moss.

Recovery of seed stores by nutcrackers usually occurs as follows: a bird lands on the ground at a selected site and then either probes one spot at the site by thrusting its bill into the soil or forest litter or digs a hole ("prod hole") with sideswiping motions perpendicular to the long axis of the body. If seeds are located, the nutcracker digs quickly with more sideswipes of the bill and removes the cache, leaving behind any spoiled seeds. Often after recovering one cache, a bird moves to other sites nearby and uncovers several more caches. In most cases nutcrackers open the seeds at the recovery site, leaving behind a pile of seed coats (Tomback 1977a).

When a nutcracker departs from an area where it has searched for and found seed caches, it leaves behind a record of its search effort. The holes show the pattern and extent of the search, and the presence of seed coats at certain holes allows a conservative estimate of the success rate of the nutcracker. Swanberg (1951) and Mezhenny (1964) were the first to use these features in field studies of the Eurasian Nutcracker.

Even if only a fourth or less of the seed stores made by an individual Clark's or Eurasian nutcracker is recovered over the year, an individual must still be able to find more than a thousand seed caches. Sense of smell probably does not play a significant role in this ability, since olfactory lobes are poorly developed in most birds (Bang and Cobb 1968). Experiments with Eurasian Nutcrackers by Swanberg (1951) further indicate that sense of smell does not aid the finding of seed stores. How an individual finds caches is not yet fully understood.

REVIEW OF PREVIOUS WORK

Most investigators of nutcracker behavior believe that some form of memory is involved in recovering seed caches. Swanberg (1951) observed Eurasian Nutcrackers dig caches out from under as much as 45 cm of snow. Of the 351 holes dug by nutcrackers in the snow and subsequently encountered by Swanberg in his study area, 86% had seed coats near them. He suggested that the nutcrackers' ability to locate the caches was better than the 86% indicated by seed coats. He later attributed at least part of the 14% unsuccessful attempts to prior robbery of caches by mice and voles (personal communication to Richards 1958).

Mezhenny (1964), Crocq (1977), and Mattes (1978) reported seed coats near 60% to 80% of the diggings of the Eurasian Nutcracker. Mezhenny (1964) suggested that the actual ability to recover seed stores was higher than his figures indicated and attributed the difference to theft by rodents and removal of intact, recovered seed from the site by nutcrackers. According to Mezhenny (1964), nutcrackers went directly to sites where they dug for stores. This certainty of movement suggested to him that visual and locomotor memory were the means by which nutcrackers recovered their stores. Reimers (1966) and Holtmeier (1966) reported that Eurasian Nutcrackers went directly to sites where they dug through as much as 130 cm of snow and recovered seed stores. I have observed Clark's Nutcrackers recover seed stores in spring and only rarely fail to locate a cache (Tomback 1977b).

Krushinskaya (1966, 1970) surgically removed from Eurasian Nutcrackers the hippocampal regions of the brain which, according to current theory, help consolidate long-term memory. The experimental birds could relocate their stores within 15 min after making them. If more than 15 min elapsed, they were not able to find their caches and continued digging with little success throughout the aviary.

According to Turček (1966), the recovery of seed caches is, in part, trial and error. He watched Eurasian Nutcrackers as they found seed stores in forest litter or snow as deep as 20 cm. On several occasions the birds failed to find seeds after digging. Turček (1966) concluded that familiarity with terrain, experience and memory, used in conjunction with trial and error search, were the means by which the birds recovered seed caches.

SEARCH PATTERN PREDICTIONS

On the basis of field observations in the eastern Sierra Nevada, I see two possible means by which nutcrackers might find their caches. To maximize seed recovery efficiency, an individual should search for caches in areas where it stored seed the previous fall. Within these areas the bird should be able to recognize the general terrain where it buried seeds. Search within this terrain may be based on 1) trial and error or 2) memory. That is, the nutcracker may search for caches by seeking the same types of visual cues, i.e., micro-habitat features (Tomback 1977a), that it originally used for seed storage; or alternatively, it may have a precise memory of the position of each cache in relation to objects near or at the storage sites. In the latter case, even if nutcrackers generally used memory to recover their seed stores, they might also be able to find the stores of other nutcrackers by trial and error search.

The arrangement of unsuccessful and successful prod holes and the distances between holes may indicate the types of search patterns used by nutcrackers. However, the number of successful prod holes may be underestimated, as explained below.

Success rate. Success rate is defined as the ratio of the number of *successful* prod holes in an area to the *total* number of prod holes in the area. If a nutcracker remembers how to find its seed stores, the success rate of the search within an area should approach 100%. If a nutcracker uses trial and error, the success rate from area to area should vary from zero to low success.

Unsuccessful prod holes. If nutcrackers use memory to locate seed stores, there should be few or no unsuccessful prod holes in an area. When there are a few unsuccessful prod holes, each should occur next to a successful prod hole, indicating that a slight miscalculation in cache position had been made and corrected. If nutcrackers use trial and error, there should be many unsuccessful prod holes, and nearest neighbor distances between unsuccessful and successful prod holes should vary considerably. Some randomness in the search pattern and recovery of stores should be apparent.

Nearest neighbor distances between prod holes. When nutcrackers store a series of caches within a small area, the caches are separated by distances which fall within a range of values. If caches are found by memory, the average nearest neighbor distance between prod holes should not differ much from the average nearest neighbor distance between caches, indicating that nutcrackers go directly to the correct locations. In trial and error search, a nutcracker must make several prod holes in a site likely to contain seed caches. It would be inefficient to prod once in a likely site and, if unsuccessful, move on. Caches may be overlooked. Clusters of unsuccessful prod holes with nearest neighbor distances considerably less than the average distance between caches, i.e. successful prod holes, would indicate a trial and error method of search. In contrast, a single unsuccessful prod hole next to a successful prod hole would suggest an imperfection in location recall for that cache site.

Spring vs. summer. If seed stores are remembered, then the success rate or any category of nearest neighbor distances should differ little between spring and summer.

However, some decrease may be expected if nutcrackers "forget" the locations of caches. The observations of Mattes (1978) on the Eurasian Nutcracker suggest that this is not the case. In spring many seed caches have not yet been recovered, and there is a higher density of caches in seed storage areas in comparison to summer. If nutcrackers search by trial and error, their success rate should be higher in spring than in summer, and the nearest neighbor distances between successful prod holes should be shorter in spring than summer.

Interpretation of actual field data may be complicated by two factors. First, rodents steal seeds from nutcracker caches (Bibikov 1948, Pivnik 1960). Although some rodent species may be better than others at detecting dispersed seeds (Reichman and Oberstein 1977), both mice and sciurids find buried seeds by means of an acute olfactory sense (Cahalane 1942, Richards 1958, Howard et al. 1968). Of all rodents in the United States, the white-footed mice (*Peromyscus* spp.), particularly the deer mouse (*P. maniculatus*), are probably the most voracious predators of conifer seeds (Baker 1950, Jameson 1952, Abbott 1961). In the Sierra Nevada deer mice live in all habitats up to subalpine elevations, but are most abundant in coniferous forest (Jameson 1951, Storer and Usinger 1970). White-footed mice cache a variety of food items, especially seeds (e.g., McCabe and Blanchard 1950, Abbott and Quink 1970). In coniferous forest, white-footed mice tend to eat seeds at their cache sites, leaving seed coat fragments in place. However, the mice replace the forest litter so the substrate appears undisturbed (Abbott and Quink 1970). Abbott and Quink (1970) could not distinguish between undisturbed and emptied seed caches of white-footed mice (*P. leucopus*) by substrate appearance and, instead, used a scintillator to search for cached scandium^{46}-tagged seeds and seed coats. It is reasonable to assume that deer mice raiding nutcracker caches would also eliminate signs of substrate disturbance. Consequently, a nutcracker probing for intact seeds in a mouse-raided cache would appear to be unsuccessful. In late spring and early summer, mice may rob more caches although they eat somewhat less pine seed at this time (Jameson 1952). During spring and summer in the Sierra Nevada *Peromyscus* spp. produce young; their populations increase until mid-summer (Storer et al. 1944, Jameson 1953). An increase in cache theft may cause nutcracker field data to resemble those predicted for trial and error search, i.e. lower success rate in summer.

When squirrels (e.g., *Spermophilus*, *Tamiasciurus*) and chipmunks (*Eutamias*) empty their caches and those of other animals, they transport intact seeds away from cache sites. Unlike mice, they do not cover up their excavations (Abbott and Quink 1970). Sciurid holes are two to three times larger than those made by nutcrackers (Sharp 1959, Abbott and Quink 1970) and have a characteristic appearance: they slant downward away from a pile of soil or litter (Tomback, unpubl. observ.; D. C. Ure, pers. comm.). It is possible, but most unlikely, that a few of the smaller sciurid holes may be counted as unsuccessful nutcracker prod holes in field data.

A second difficulty is that nutcrackers sometimes carry off intact seeds from cache sites, so a successful recovery effort may be counted as unsuccessful. Field observations provide some information on the frequency of occurrence of this behavior pattern.

METHODS

NUTCRACKER CACHE RECOVERY

Field data were collected in the south-central region of the eastern slope of the Sierra Nevada, Inyo National Forest, Mono County, California. Details concerning the study areas are in Tomback (1977a, b). In April and May of 1975, I found groups of nutcracker prod holes in sites where snow had recently melted. I measured the success rate and nearest neighbor distances for 10 groups of prod holes found in the Jeffrey pine belt (*Pinus jeffreyi*) in the Mammoth Lakes and Casa Diablo areas, elevation about 2,200 m to 2,400 m. The term "group of prod holes" indicates that a concentration of prod holes was visually distinct and separated by a distance of several meters from another concentration of holes. For half the groups described below, no other groups or scattered prod holes occurred in the same vicinity. Prod holes with seed coats nearby were counted as successful. The seeds recovered from stores were predominantly from Jeffrey pine and a few from singleleaf piñon pine (*P. monophylla*). Distances from each prod hole to its nearest neighbor were measured to the nearest 2 cm. Forty-five nearest neighbor distances were measured, which were then separated into three categories: 1) distances between two successful prod holes, 2) distances between one successful and one unsuccessful prod hole, and 3) distances between two unsuccessful prod holes.

In the first half of July 1975, I found many groups of prod holes in the Casa Diablo and Tioga Pass areas, elevation 2,270 m and 2,980 m, respectively. To obtain an accurate record of the patterns within these groups of holes, I mapped out successful and unsuccessful prod holes for 3 m by 3 m portions of the forest floor, using a grid divided into 2-cm squares. Five grids, or 45 m^2 of forest floor, were mapped in the Casa Diablo area where Jeffrey and piñon pine seeds were stored by nutcrackers. Three separate grids, totalling 27 m^2, were mapped at Tioga Pass where nutcrackers stored whitebark pine seeds. Together, the eight grids contained a total of 195 prod holes distributed as follows: 12, 19, 20, 24, 30 for Casa Diablo, and 20, 34, 36 for Tioga Pass. I obtained 195 nearest neighbor distances, limited to 2 cm accuracy, which were treated as described above.

A nutcracker on the ground searching for seed caches initially attracted me to several of the spring and summer groups of prod holes. Between 21 and 24 April 1975, and on 6 and 7 June 1976, I observed nutcrackers from a distance as they recovered caches. Also, for several hours on 6 and 7 June at Tioga Pass, I followed a nutcracker as it went from site to site searching for caches. I noted the number of prod holes made by each nutcracker and its success rate.

CONTROL FOR RODENT THEFT OF CACHES

Four experimental sites were constructed in the Casa Diablo study area on 24 March 1978, at or near the locations of the 1975 prod hole groups. These sites, each 2 × 2 m and separated by 5 to 20 m, were initially in snow-free patches of the forest floor. Deep snow (about 0.5 m) was cleared from a fourth location. Subsequent storms covered all sites with snow for varying periods of time. Within each experimental site I buried 5 artificial "nutcracker" caches of commercially obtained Colorado piñon pine seed (*Pinus edulis*), a close relative of locally-occurring singleleaf piñon (Lanner 1974). These low cache densities are compatible with field observations of nutcrackers storing seed (Tomback 1977a). Positions of these caches in each site were determined as follows: Distances along set x and y axes were selected from a table of random numbers (Rand Corporation 1955) and recorded. One cache was buried under 2–4 cm of soil and/or forest litter at each point generated. In case nutcrackers find seed caches by trial and error, access by birds—as well as by larger mammals—was restricted at two experimental sites. Aluminum window screening was stretched across these sites and stapled to stakes, 5–10 cm off the ground. For three of the experimental sites, each cache contained three seeds. For one unscreened site, caches each contained seven seeds. Larger caches hypothetically provide rodents with stronger olfactory cues. On 24 June 1978, I dug up the experimental sites and counted the number of caches and seeds remaining.

RESULTS

RODENT THEFT OF SEED CACHES

After three months, only one of the 20 artificial caches remained intact, and all three seeds of this cache had germinated several weeks prior. Some seeds of two additional caches remained and were presumably "available to nutcrackers." Altogether, 85% of the caches had been completely raided. Rodents found small caches as readily as large ones (Fisher Exact Probability test, $P = .75$). Of the 80 seeds originally cached, 92.5% were taken. But, in April and May, when the spring data on nutcracker cache recovery were collected, it is likely that the percent of real nutcracker caches taken by rodents was not yet as high.

REMOVAL OF INTACT SEEDS FROM CACHE SITES BY NUTCRACKERS

My field notes provide some information on how frequently nutcrackers carry off intact seeds from cache sites. Combining my observations for April 1975 and 6 June 1976, nutcrackers opened seeds at cache sites for 12 of 16 recovered caches, or 75%. About 80% of the 21 caches located by a single individual on 6 June (not included in the above data) were hulled at the cache site. Most of these seeds were fed to begging juveniles who accompanied the adult. Balda (unpubl.) observed a captive Eurasian Nutcracker open seeds at cache sites in the aviary approximately 67% of the time. In contrast, on 7 June 1976, I watched one nutcracker recover three caches. The bird transported the intact seeds from each cache over several meters to a log, which it used as an anvil. The piles of seed coat fragments on and around the log indicated much use for this purpose. However, the field data for this study were not gathered in proximity to an anvil. It appears that nutcrackers usually carry off intact seed from 20% to 30% of the caches they uncover.

SPRING DATA

A total of 55 prod holes were surveyed in spring. The size of each group follows, with the percent of successful holes in parentheses: 1(100%), 2(50%), 3(33%), 3(67%), 3(67%), 3(100%), 7(71%), 9(89%), 9(unknown), 15 (60%). The average success rate per group was 67%, and the overall success rate among all prod holes with data available was 72%. The actual overall success rate was probably higher, since by late April rodents had probably raided some caches. This success rate, including a margin for rodent theft, is higher than one might expect from a trial and error search. It suggests that nutcrackers remember the locations of their seed caches. In spring I observed nutcrackers go directly to sites and probe for caches, with frequent success. Twice, I found an unsuccessful shallow prod within 2 cm of a successful prod hole, suggesting that a nutcracker had miscalculated in finding a cache.

The nearest neighbor distances between successful and unsuccessful spring prods varied from 2 to 242 cm (Table 1). According to my predictions, this pronounced variation suggests trial and error searching. However, maps of the prod holes show that a cluster effect did not occur. Also, a statistical comparison of nearest neighbor distances for the successful-successful and successful-unsuccessful prod pairs shows no significant difference between them (Mann-Whitney U test, $P = .20$).

SUMMER DATA

The success rate for the eight grids of prod holes mapped in summer ranged from 14% to 67%. The average success per grid was 32%, and the rate for all holes combined was 30%. This success rate appears too low to indicate memory but too high to be from trial and error search. These data were collected at the same time of year I recorded an 85% cache loss to rodents in the Casa Diablo area.

Nearest neighbor distance data support the memory hypothesis. Although distances varied greatly between successful-unsuccessful and unsuccessful-unsuccessful prod pairs (Table 1, Fig. 1), a cluster effect around successful prods did not occur. The distances of the two prod pair categories, successful-successful and unsuccessful-unsuccessful were similar ($P < .41$, Table 1). The nearest neighbor distances between unsuccessful and successful prods tended to be somewhat smaller than those in other prod pair categories ($P > .098$, Table 1). This may be a consequence of the trend toward a higher frequency of small nearest neighbor distances (4 cm and 6 cm) in the successful-unsuccessful category relative to the unsuccessful-unsuccessful category ($.10 > P > .05$, $\chi^2 = 3.6$, Fig. 1).

By following two nutcrackers as they searched for caches at Tioga Pass in June 1976, I made several observations which verify the accuracy of the summer prod hole mapping technique. One bird made 79 prod holes and located 21 caches; the other made 37 holes and found 9 caches. When searching for seed, each nutcracker went directly to sites. At each site it made only one probe for seed caches, rather than a cluster of unsuccessful prod holes. The overall success rate for both birds was 26%, which is similar to the 30% overall success rate obtained from the summer grid analysis.

COMPARISON OF SPRING AND SUMMER DATA

There were important differences between spring and summer data. First, the success rate was greater in spring than in summer. According to my predictions, this outcome is expected if cache density decreases from spring to summer and nutcracker recovery is based on trial and error search. However, experimental data indicate a high frequency of cache loss to rodents by early summer. Second, taking the entire sample, nearest neighbor distances were significantly shorter in spring than in summer ($P < .001$, Table 1). Distances between successful prod holes were significantly shorter in spring than in summer ($P < .007$, Table 1). This suggests trial and error search and reflects a decrease in available seed caches.

TABLE 1. Nearest neighbor distances between prod holes (cm).

Prod* pairs	Mean	Standard deviation	Median	Range	N
Spring					
all	27	±42	16	2–242	45
s-s	17	±14	16	2–56	34
s-n	51	±76	25	2–242	10
n-n	—	—	—	128	1
Summer					
all	32	±23	26	4–148	195
s-s	32	±21	24	8–72	24
s-n	29	±23	26	4–124	69
n-n	33	±24	28	4–148	102

* s = success, n = no success.
Mann-Whitney U tests: summer
s-s vs. n-n, $P < .41$
s-n vs. n-n, $P = .098$, s-n shorter.
Mann-Whitney U tests: spring vs. summer
overall spring vs. overall summer, $P < .001$, spring shorter
overall spring vs. summer s-s, $P = .007$, spring shorter
overall spring vs. summer s-n, $P < .004$, spring shorter.

DISCUSSION

Using prod hole success estimates and nearest neighbor distances, I was able to determine how nutcrackers find their seed stores only when two additional factors were considered: the proportion of seed caches lost to rodents and how often birds remove intact seeds from cache sites. Data gathered in 1975 from sites where nutcrackers had searched for seed stores were analyzed by deductive reasoning in conjunction with 1978 data on the proportion of caches taken by rodents and observations of birds recovering caches.

Analysis of spring 1975 data supported the memory hypothesis. The overall prod hole success rate of 72% was too high to be a product of trial and error search. The high success rate within several of the prod hole groups further supports this conclusion. Both loss of caches to rodents and removal of intact seeds from cache sites by nutcrackers could easily account for 20% to 30% discrepancy from the predicted near-100% success rate. Nearest neighbor distances between successful prod hole pairs and between successful-unsuccessful prod hole pairs were not significantly different. The pattern of unsuccessful prods did not fulfill

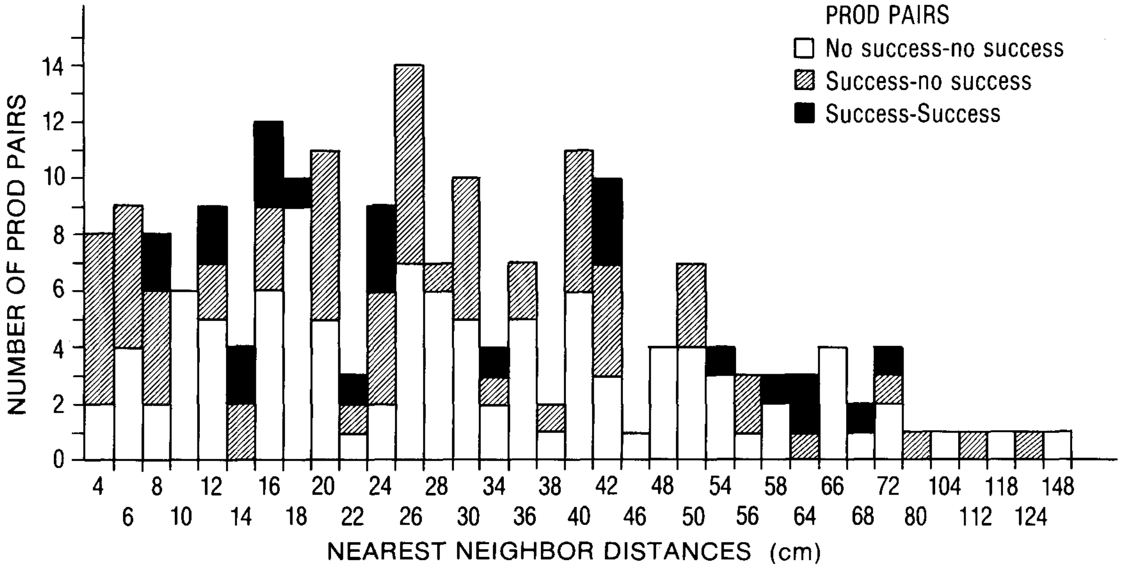

FIGURE 1. Summer nearest neighbor distances between nutcracker prod holes, showing relative distributions of the three categories of prod hole pairs.

the predictions for trial and error search; i.e., nutcrackers went directly to cache locations. It is very likely that many of the unsuccessful prod holes were actually "successful" and a consequence of rodent raids or transport of seeds away from cache sites.

Conclusions from analysis of July 1975 data were not as clear-cut. The overall prod hole success rate of 30% was too high to result from trial and error search. Success rates among the eight grids varied from that predicted for trial and error search (14%) to that requiring some recall (67%). However, the high percent of cache losses to rodents recorded in June 1978, implies that many of the nutcracker prods recorded as unsuccessful were actually "successful" in regard to correct location. Also, as suggested by Balda's observations (in press), nutcrackers may have removed some caches previously and forgotten this fact. Nearest neighbor distances supported either interpretation. Distances among successful prod pairs and unsuccessful prod pairs were similar. Again, the pattern of occurrence of unsuccessful prods did not suggest trial and error search. The similar spacing of prod pairs in both categories could easily be accounted for if "unsuccessful" prod holes for the most part represented caches lost to rodents and sites where unhulled seeds were carried off by nutcrackers. The disproportionate occurrence of small nearest neighbor distances in the successful-unsuccessful prod pair category (Fig. 1) is expected if the search pattern is memory-based. These small distances may be the consequence of a nutcracker miscalculating, or assuming a miscalculation, in the location of a cache site and then shifting its position. Twice, as I gathered my data, I noticed that when two prod holes (both unsuccessful or successful-unsuccessful) occurred nearby, the unsuccessful prod was noticeably shallower than the other. My observations of nutcrackers storing seed (Tomback 1977a, b) suggest that caches are rarely made so close together. It is puzzling that these small distances have not occurred at equal frequencies in both the successful-unsuccessful and unsuccessful-unsuccessful prod pair categories.

A comparison of spring and summer data yielded mixed results. It is unreasonable to attribute the large difference in overall success rate between spring and summer to a switch in cache recovery method from memory to trial and error. Rather, the decline in success rate is better explained as a consequence of an accumulation of cache losses to rodents and possibly to a combination of recovery methods. The relative spacing patterns of the prod pair categories are similar for both spring and summer data, and they support memory as the principal means by which nutcrackers find their caches. But, all categories of nearest neighbor distances between prod pairs were on the whole longer in summer (Table 1). A likely explanation for this, with memory as the means of cache recovery, is based on my observations in spring: nutcrackers preferentially recover seed caches from terrain recently free of snow (Tomback 1977a). Only some caches may be removed from an area and the birds may return later to take other caches. This would cause a gradual increase in nearest neighbor distances among caches as the season progressed. As a consequence, after all snow is gone from an area, the remaining caches may have a scattered distribution (many of which may be taken by rodents). Allowing for losses to rodents, on the whole the field data support memory as the principal method used by Clark's Nutcrackers to find seed stores.

These conclusions correlate with the recent findings of Balda (in press) on Eurasian Nutcrackers under controlled conditions. Agreement between the results of field and aviary experimentation is a prerequisite for any future aviary research on this behavior system.

The outcome of these two investigations does not rule out the possibility that nutcrackers are able to find by trial and error search the stores made by other individuals, as well as their own, and do so under some circumstances. Which search method predominates has important implications for the behavioral ecology of the Clark's Nutcracker. If memory is the more commonly used method, as our analyses suggest, then seed stores are not communal. Because each nutcracker would know the approximate location of its own caches, the efficiency of its search would be greater than that by trial and error. For a memory-based search, a bird must remain in the areas containing its seed stores. Emigration to other regions could only occur after mid-summer, when the new cone crop is ripening and before new stores are made.

Under some circumstances it would be particularly adaptive for nutcrackers to search for the caches of other individuals by trial and error, e.g. when nutcrackers have four or more fledged young to feed (Tomback 1977b, unpubl. data) and in years when cone crops are poor. A trial and error search raises the possibility that "cheater" nutcrackers may occur in a population. The problem of cheaters evolving within a population of animals that store food is treated by Andersson and Krebs (1978). "Cheater" nutcrackers would make few stores and search for the caches made by other individuals. If a trial and error search method predominated, there would be a frequency-dependent selection for cheaters. At low frequencies cheaters would have the same success as nutcrackers that did store seed. If a memory-based search predominated, cheaters would spend more time and energy searching relative to non-cheaters; whenever the cone crops were poor, cheaters would be at a disadvantage. To circumvent these latter problems, it is possible that cheaters might use a mixed "store or steal" habit.

One important factor in the ecology of the nutcracker suggested by this study is the effect of rodents on nutcracker seed stores. Data indicate that a large percentage of the caches may be stolen by rodents. The loss of a high proportion of caches to rodents should be an important selection pressure on nutcrackers in relation to seed storage and/or recovery behavior. In fact, "expectation" of high cache losses may explain why nutcrackers store several times more seed than they appear to require (Vander Wall and Balda 1977). They may be gambling that a percentage of their stores will be overlooked and/or inaccessible to rodents.

Nutcrackers store seeds in two kinds of areas: *convergent* vs. *divergent.* In the first case, all the nutcrackers in a region select a steep, south-facing slope in which to store seed. They usually use that part of the slope which is open and exposed—i.e. not heavily forested—and, consequently, accumulates little snow cover (Vander Wall and Balda 1977, Tomback 1977a). Divergent storage areas are other kinds of terrain, near the trees where seeds were harvested (Tomback 1977a). The same features which make convergent seed stores readily available to nutcrackers in winter may also attract rodents and result in a high percent loss. However, caches in the divergent storage areas are usually buried under deep snow, which may prevent access by rodents (Mezhenny 1961). The Eurasian Nutcracker, and no doubt the Clark's Nutcracker, is capable of finding caches covered by snow less than 2 m deep (Reimers 1966, Holtmeier 1966, Crocq 1977, Mattes 1978). The preference of Clark's Nutcrackers for caches in sites newly exposed by snow melt-off or under little snow may minimize the energy required for, and discomfort experienced from, digging out caches in deep snow. But, the birds are also removing those caches which have become accessible to rodents. By burying seeds in divergent storage areas, nutcrackers may reduce seed loss to rodents.

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RECENT PUBLICATIONS

The Mitigation Symposium: A national workshop on mitigating losses of fish and wildlife habitats.—Gustav A. Swanson, technical coordinator. 1979. General Technical Report RM-65, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. 696 p. Paper cover. Fish and wildlife conservationists have long been disturbed about the losses of habitat which result from changing land and water use, particularly from federal development projects. A symposium to examine this problem was held in July 1979 and these are its proceedings, published with admirable promptness. The 133 papers deal with coastal zone wetlands; inland wetlands; economic considerations; mining, oil, and gas; planning, evaluation, and inventory; surveys; power projects; terrestrial management; aquatic management; legal and political considerations; transportation systems; and state perspectives. Few of the papers are specifically about birds. Illustrations and references; no discussion or index. This volume will be of value chiefly to the symposium participants and others who are working to preserve natural habitats. Nevertheless, its general findings and recommendations deserve to be widely known.

Endangered Birds: Management Techniques for Preserving Threatened Species.—Stanley A. Temple, ed. 1978. University of Wisconsin Press, Madison. 466 p. $9.50. Manipulative techniques for rescuing a species from imminent extinction have mostly been applied during the past 15 years. A symposium to examine this new subdiscipline of applied ecology was held at the University of Wisconsin in August, 1977 and its proceedings comprise this book. The 51 papers (including a summary) deal with the concept of managing threatened species, the various approaches and their integration, genetic aspects, and the reintroduction of endangered birds to the wild. Since threatened species are currently of much concern and their management is sometimes controversial, this overview of the state of the art/science merits wide attention.

The Amateur and North American Ornithology.—Donald A. McCrimmon, Jr. and Alexander Sprunt, IV. 1979. National Audubon Society and the Cornell Laboratory of Ornithology, Ithaca, New York. 80 p. Paper cover. $2.50. Available: Laboratory of Ornithology, 159 Sapsucker Woods Road, Ithaca, NY 14850. "There is no better way to amass immense amounts of significant ornithological information than to develop effective plans for the coordinated use of the energy and enthusiasm of amateurs." A conference to examine the role of amateurs in North American ornithology was held at Ithaca in Febrary, 1978 and its proceedings form this book. The first part consists of 22 papers about organizations that currently involve amateurs. The second part is an edited transcript of workshop discussions on the coordination of amateurs and professionals in advancing ornithology. Appendixes provide supplementary material, including remarks by Max Nicholson about the B.T.O. While this is all interesting reading, its value is far surpassed by the momentum raised by the conference, itself.

Conservation of Marine Birds of Northern North America.—James C. Bartonek and David N. Nettleship, eds. 1979. Wildlife Research Report 11, U.S. Dept. Int., Fish and Wildlife Service, Washington, DC. 319 p. Paper cover. This is a collection of 22 papers from a symposium held in 1975. They deal with aspects of the environment, status, biology, and conservation of marine birds. The scope exceeds the title in that three papers concern New Zealand, Greenland, and Scandinavia. No discussion is given but the symposium is summarized by I. C. T. Nisbet. Graphs and maps. Each paper has its own references. A benchmark volume, not just for researchers, but also for those who are concerned about actual or potential conflicts between the conservation of marine birds and the uses of other resources.