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EMIGRATION BEHAVIOR OF CLARK'S NUTCRACKER

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ABSTRACT.—Eruptive movements of the Clark's Nutcracker (*Nucifraga columbiana*) were observed during the late summer and fall of 1977, 1978 and 1979 in northern Utah and adjacent states. Over 2,000 emigrating nutcrackers were seen during these periods. Eruptions began in mid to late August, about the time nutcrackers began foraging on developing conifer cones, and continued until early October. Nearly all nutcrackers traveled in small, loose flocks ($\bar{x}$ = 10.1 individuals). During 1977–1978, most emigrating nutcrackers appeared to winter in piñon-juniper woodlands of Utah and adjacent states and no nutcrackers were reported outside their normal breeding range. A northward movement of nutcrackers, presumably the same population observed emigrating southward in fall 1977, was noted in summer 1978. Evidence for breeding of nutcrackers on their wintering areas is presented. A compartmental model summarizes current knowledge on the temporal and spatial aspects of nutcracker emigration.

Clark's Nutcracker (*Nucifraga columbiana*) inhabits montane coniferous forests of western North America from Arizona and New Mexico to central British Columbia (A.O.U. Check-list 1957). At irregular intervals, nutcrackers leave their usual breeding range to winter in lowland deserts, plains and coastal areas. Davis and Williams (1957, 1964) concluded that these eruptions are caused by poor conifer seed crops, an important food for Clark's Nutcrackers during the fall, winter and breeding seasons (Mewaldt 1956, Vander Wall and Balda 1977, Giuntoli and Mewaldt 1978, Tomback 1978). Population densities of nutcrackers at the time of cone crop failure may influence the magnitude of eruptions (Davis and Williams 1957, 1964). Populations of the Eurasian Nutcracker (*N. caryocatactes*) also erupt during years of low conifer seed production (Formosof 1933).

In this paper we describe eruptions of the Clark's Nutcracker through the mountains of northern Utah and adjacent states. Specifically we: 1) describe timing of fall and summer eruptive movements; 2) contrast behavior and flock structure of emigrant versus resident nutcrackers; 3) describe probable wintering areas of the emigrants; 4) discuss conditions which may influence the decision of emigrating nutcrackers to settle in an area for the winter; and 5) present evidence for breeding of emigratory nutcrackers on their wintering areas during the spring. Based on data presented here and elsewhere (primarily Davis and Williams 1957, 1964) we construct a compartmental model relating temporal and spatial patterns of Clark's Nutcracker eruptions.

The nutcrackers seen moving through northern Utah did not originate there but from areas to the north. Resident nutcracker populations in northern Utah did not participate in the eruption. Throughout this paper, nutcrackers observed moving through Utah and adjacent states and these birds on their wintering areas are referred to as "emigrants" (i.e., we describe nutcracker movements with respect to their area of origin). Nutcrackers that did not participate in an eruption are referred to as "residents."

STUDY AREA AND METHODS

Emigrating flocks of Clark's Nutcrackers were studied at three places in northern Utah and one in eastern Nevada (Fig. 1). Most of the information on behavior and flock structure was taken at a site (elev. 2,560 m) in the Wellsville Mountains (elev. 2,850 m) in northern Utah (Fig. 1, number 1). The Wellsville Mountains are a steep, narrow range with a north-south axis. Observations were made in late summer and fall of 1977 (6, 14 and 19 August and 27 August through 25 October), 1978 (27 August, 3 and 4 September and 6 September through 20 October) and 1979 (6 September through 10 October and 12 through 17 October) from approximately 11:00 to 16:30. Additional observations at elevations of 2,560 and 2,000 m in the nearby Bear River (Fig. 1, number 2) and Promontory (Fig. 1, number 3) mountains, respectively, were made irregularly from 28 August to 15 October 1977. In 1979, emigrating flocks of nutcrackers were observed from 19 to 24 September and 4 to 11 October in the Goshute Mountains, Nevada (elev. 2,750 m; Fig. 1, number 9). In the sum-

TABLE 1. A summary of observations on emigrating flocks of Clark's Nutcrackers in northern Utah and adjacent states from fall 1977 through fall 1979.

Map number	Location (flight direction)	Elevation (m)	Date	Hours observed*	Observation		Observer(s)
					Birds	Flocks	
	Fall 1977						
1	Wellsville Mts., Utah(S)	2,560	27 Aug–29 Sept	216	894	93	the authors
2	Bear River Mts., Utah(S)	2,560	31 Aug, 18 Sept	12	56	5	S. Hoffman, L. Haggas†
3	Promontory Mts., Utah(S)	2,000	28 Aug, 21 Sept	11	58	3	the authors
4	Black Mts., Utah(S)	2,450	1, 20 Sept		48	4	S. Dunkle†
5	Davis Creek, Utah(S)	2,000	~10 Sept		~300	?	R. Edens†
6	Grouse Creek Mts., Utah(S)	1,825	1, 2 Oct		~50	3	J. Gessaman†
7	Pocatello, Idaho(S)	1,825	19 Sept		39	1	C. Trost†
8	Mt. Bross, Colorado(S)	3,500	21 Aug		35	2	Kingery (1978)
	Summer 1978						
1	Wellsville Mts., Utah(N)	2,560	1 July	8	20	1	G. Briggs†
2	Bear River Mts., Utah(N)	2,560	20–29 June		190	7	K. Smith, D. Andersen†
	Fall 1978						
1	Wellsville Mts., Utah(S)	2,560	9 Sept–7 Oct	257	62	10	the authors
1	Wellsville Mts., Utah(N)	2,560	15 Sept–8 Oct	257	133	7	the authors
	Fall 1979						
1	Wellsville Mts., Utah(S)	2,560	8–21 Sept	245	40	5	the authors
9	Goshute Mts., Nevada(S)	2,750	19 Sept–11 Oct	113	130	20	S. Hoffman, S. Werner

* Hours observed during total observation period (see Study Area).
† Personal communication.

mer of 1978 emigrating flocks of nutcrackers were studied at the Wellsville and Bear River mountain sites between 20 June and 1 July.

Nutcrackers that may have been overwintering emigrants were observed in the Raft River Mountains of northwestern Utah on several occasions from 1 September to 20 October 1977 and on the Kaiparowits Plateau and Circle Cliffs near Escalante in southcentral Utah from 13 April to 27 June 1978 (Fig. 1). These wintering areas were in piñon-juniper (*Pinus monophylla* or *P. edulis-Juniperus osteosperma* or *J. monosperma*) woodland.

Observations were made with 7 × 35 binoculars. Number of individuals per flock, direction of flight and qualitative data on flock structure were recorded. Age of flock members was determined when possible using Mewaldt's (1958) plumage criteria. Individual nutcrackers or small flocks traveling less than one minute behind large flocks were considered stragglers and counted as part of the larger flock.

To compare the relative energetic values of conifer seeds available to emigrant nutcrackers in areas where they did and did not winter, we determined foraging rates (mean number of seconds required to remove one seed from a ripe cone) of resident nutcrackers on singleleaf piñon pine and Douglas-fir (*Pseudotsuga menziesii*). Seed weights were determined by collecting, shelling and drying (60°C) samples of mature seeds from several trees. Caloric value of singleleaf piñon pine seeds was determined with a Phillipson microbomb calorimeter.

RESULTS AND DISCUSSION

TIMING OF ERUPTIONS

Eruptions of Clark's Nutcrackers through northern Utah and adjacent states continued from late August through late September or early October (Table 1). In 1977, the first flocks of emigrating nutcrackers were seen on 27 August in the Wellsville Mountains and on 28 August in the Promontory Mountains. We visited the Wellsville Mountain observation point for a total of 10.5 h on 6, 14 and 19 August but saw no nutcrackers. Nutcrackers (apparently emigrants) were observed as early as 21 August 1977 at Mt. Bross, Colorado (Kingery 1978). In 1978 and 1979, we did not record emigrating nutcrackers until 9 and 8 September, respectively. The latest observed flocks of emigrating nutcrackers were sighted in the Goshute Mountains, Nevada on 10 October 1979. In 1977, emigrating nutcrackers were observed as late as 2 October (Grouse Creek Mountains, Utah, J. Gessaman, pers. comm.) and in 1978 flocks were seen until 8 October (Wellsville Mountains). Prior to 1977 few observations of emigrating nutcrackers had been made (Presnall 1936, Webster 1947, Mewaldt 1948, Phillips et al. 1964, Fisher 1979) but these agree with our findings that eruptions occur from late August to early October.

Emigrating nutcrackers outside their normal breeding range usually have been seen considerably later than birds still within the breeding range. Davis and Williams (1957, 1964) first saw nutcrackers on the Monterey Peninsula during the eruptions of 1955 and 1961 on 7 October and 29 September, respectively. Westcott (1964) first noticed nutcrackers invading southeastern Arizona on 10 October 1961. Other observations of nut-

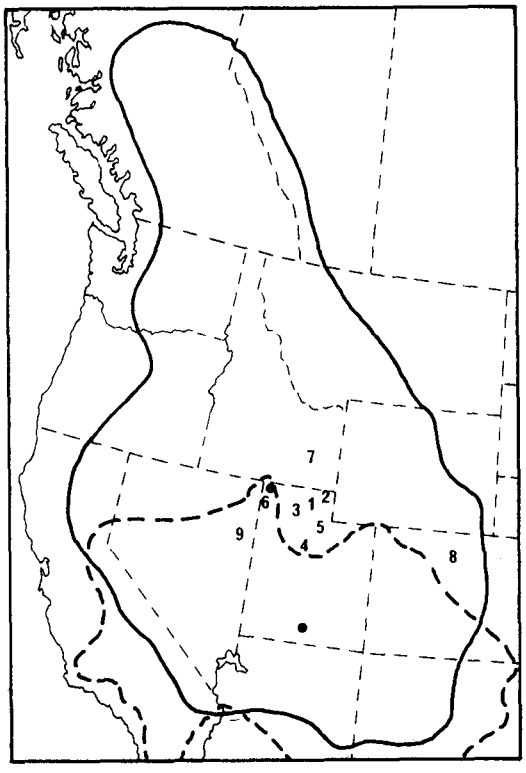

FIGURE 1. The approximate geographic distribution of Clark's Nutcracker (solid line, after A.O.U. Check-list 1957) showing the locations (numbers) where emigrating nutcrackers were observed in falls 1977 through 1979 (see Table 1 for site names and details). The Raft River Mountains (northwestern Utah) and Kaiparowits Plateau and Circle Cliffs (southcentral Utah) are areas where nutcrackers thought to be emigrants wintered in 1977–78 (closed circles). The approximate geographic distribution of piñon pine (*Pinus edulis* and *P. monophylla*) is represented with a heavy broken line (modified from Critchfield and Little 1966).

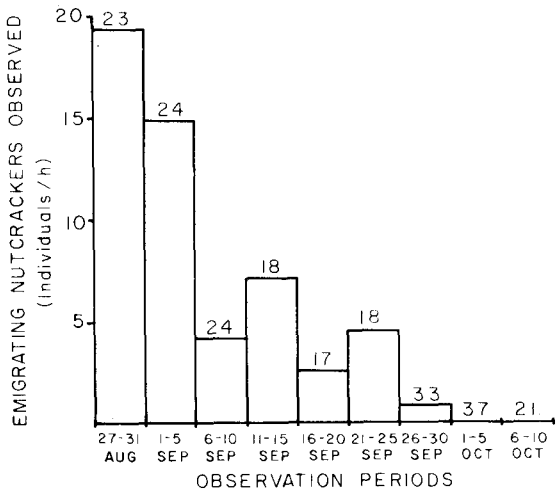

FIGURE 2. Number of emigrating nutcrackers observed per hour during fall 1977 at the Wellsville Mountain observation point. Numbers at the top of each column are the hours of observation during each observation period. Results from 6, 14 and 19 August (10.5 h, no flocks recorded) are not included.

crackers outside their normal range (cited in Davis and Williams 1957) have been in October or November, with a few sightings in mid to late September. Fisher and Myres (1980) recorded several emigrating flocks outside their normal range during August and early September but suggested that such movements occurred in conjunction with weather disturbances which may have induced nutcrackers to leave their range prematurely. These data suggest that nutcrackers may wander extensively inside their normal range and habitats, searching for suitable food sources before exploring extralimital areas.

Most nutcrackers passed through northern Utah during the early portion of the eruption period. We recorded 93 flocks containing 894 individuals during the 34-day period when emigrating nutcrackers were observed at the Wellsville Mountain site in 1977. Many other flocks, containing an estimated total of 300 to 400 nutcrackers, were seen but not counted. The majority of these birds passed the observation point between 27 August and 5 September (Fig. 2) when they were recorded at a mean rate of 15 to 19 individuals/h. From 6 to 25 September, the number of emigrating nutcrackers observed decreased to a mean of 3 to 7 individual/h and decreased further during 26 to 30 September to about one individual/h.

We saw a northward movement of nutcrackers in summer 1978 (Table 1), presumably the same population that emigrated south in fall 1977. This suggests that nutcrackers may return to the region from which they emigrate. Most sightings were made in the Bear River Mountains, 45 km northeast of the Wellsville Mountains. A total of 8 flocks containing 210 individuals passed through between 20 June and 1 July. Approximately 200 nutcrackers seen at Bozeman, Montana on 25 June (Rogers 1978) may have been part of this same northward movement. Emigratory nutcrackers have been sighted frequently in extralimital areas in May and June but rarely in July (Davis and Williams 1957, Phillips et al. 1964, Westcott 1964).

BEHAVIOR AND FLOCK STRUCTURE

The behavior and flock structure of emigrating nutcrackers were strikingly different from those of resident birds. At the Wellsville Mountain site most emigrating nutcrackers were flying due south, parallel to

TABLE 2. Flock structure of emigrating Clark's Nutcrackers observed in northern Utah in fall 1977.

Flock size	Number of flocks	Percent flocks	Percent individuals
1–5	35	33.3	7.8
6–10	28	26.7	20.1
11–15	22	21.0	27.5
16–20	7	6.7	12.3
21–25	7	6.7	14.7
>25	6	5.8	17.7

and usually within 10 to 50 m of the ridge crest. Most individuals flew with slow regular wingbeats and appeared to gain lift from winds and updrafts. Flight speed was estimated at 45 km/h and birds seldom stopped to rest or forage. Their sublingual pouches (Bock et al. 1973) were not distended, indicating that they were not transporting conifer seeds (see Vander Wall and Balda 1977, Tomback 1978). No vocalizations were heard. In the Wellsville and Bear River mountains we watched resident nutcrackers from early August to late September collecting, transporting and storing seeds of Douglas-fir. Resident nutcrackers frequently made short flights up and down slopes and along ridges between foraging and caching areas. Unlike emigrating nutcrackers, residents often had distended sublingual pouches and called frequently.

Nearly all emigrating nutcrackers traveled in loose flocks. Estimated nearest neighbor distances within flocks varied from several to more than 100 m. Flock size in fall 1977 ranged from 1 to 42 ($\bar{x}$ = 10.1, SD = 8.2, n = 105) with over 72% of the individuals in flocks of 11 birds or more (Table 2). Flock sizes in 1978 ($\bar{x}$ = 11. 5 individuals, SD = 8.9, n = 17) and 1979 ($\bar{x}$ = 6.8, SD = 2.7, n = 25) were not significantly different from flock size in 1977 ($F_{2,142}$ = 2.38; α = 0.05). Flocks in summer 1978 (northbound) were similar to fall flocks in all respects except that they were significantly larger ($\bar{x}$ = 26.3, SD = 31.1, n = 8, $P < 0.01$, t-test). Flock size of resident nutcrackers ($\bar{x}$ = 3.3, SD = 2.9, range = 1 to 14, n = 43) was significantly smaller ($P < 0.01$, t-test) than emigrating flocks.

In the falls of 1977 and 1979, all nutcracker flocks observed were moving south. At the Wellsville Mountain site in fall 1978, however, 31.8% of the nutcrackers (62 individuals, 10 flocks) were seen moving south while 68.2% (133 individuals, 7 flocks) were moving north. Some of these flocks probably passed each other traveling in opposite directions along the ridge. It is unclear why flocks of nutcrackers should emigrate in opposite directions. One possibility is that two areas within the nutcrackers' range may have experienced cone crop failure, one north and the other south of the Wellsville Mountains. Nutcrackers leaving these areas in search of areas of conifer seeds may have been passing each other in northern Utah. Whatever the reason, these findings suggest that eruptive movements may be complex phenomena and difficult to interpret without data from many observation points.

No mixing of the two populations of nutcrackers (resident and emigrant) was apparent while the emigrants were moving. Resident nutcrackers frequently foraged on the slopes while emigrating nutcrackers moved southward along the ridge. Several individuals, apparently emigrants, were observed pausing to forage in stands of Douglas-fir. Their foraging behavior was similar to that of residents but we did not see them collecting seeds for storage.

Most emigrating nutcrackers in fall 1977 appeared to be adults. Of 26 individuals observed at close range and good light conditions, 23 were adults and 3 were juveniles. These results contrast with Lack's (1954) review of data on Eurasian Nutcrackers and finding that juveniles usually greatly outnumbered adults during eruptions. Davis and Williams (1957) examined specimens of Clark's Nutcrackers collected during eruptions and found individuals of both age groups.

We found flocks of emigrating nutcrackers in mountainous areas from 1,825 to 3,500 m elevation; over 90% of the flocks were above 2,500 m. Base elevation in northern Utah is ≈1,250 to 1,350 m. High elevations and relatively inaccessible areas through which nutcrackers emigrate may explain why so few sightings have been reported previously.

PROXIMATE CAUSE OF ERUPTIONS

The 1977 eruption probably began in mid August, several days before the first observations of nutcracker flocks in Utah. This is the time when nutcrackers usually begin foraging on cones (Vander Wall, unpubl. data). In northern Utah, for example, nutcrackers begin examining limber pine (*Pinus flexilis*) cones when they are small and green in late July. Intensive foraging begins in mid August and seed storage commences by late August. Intensive foraging on whitebark pine (*Pinus albicaulis*) in western Wyoming also begins in mid August (H. Hutchins, pers. comm.). The coincidence of

initiation of emigration and intensive foraging in mid August suggests that the absence of green cones may be the proximate factor triggering eruptions. Green piñon pine cones are proximate cues causing behavioral and physiological responses in the ecologically similar Piñon Jay (*Gymnorhinus cyanocephalus*; Ligon 1974, 1978). The importance of green cones in triggering emigratory behavior may explain why eruptions occur several months prior to actual food shortage (Lack 1954, Svärdson 1957). An early response by nutcrackers to ensuing food shortage would allow them to seek out areas where food is available before the seed harvest is completed.

Davis and Williams (1957, 1964) suggested that the proximate cue for nutcracker eruptions was the lack of cones but stated that food shortage became evident to nutcrackers when they began foraging on cones in mid September. This explanation agreed well with the arrival of nutcrackers in coastal area during late September and early October. Emigration dates and initiation of foraging on cones are now known to occur much earlier.

WINTERING AREAS

We attempted to find populations of emigrant nutcrackers during the winter of 1977–78. Our results suggest that nutcrackers may have wintered in piñon-juniper woodlands in Utah and adjacent states. Piñon pine produced a medium to heavy crop of seeds throughout much of its range during fall 1977 (U.S. Forest Service unpubl. report), providing a large, suitable food supply (see Vander Wall and Balda 1977). Large numbers of nutcrackers were present at two sites visited during fall 1977 and spring 1978. In the Raft River Mountains, Utah, where nutcrackers were observed from July to October of 1975, 1977, 1978 and 1979, the nutcracker density was approximately two to three times higher in 1977 than in other years even though a cone crop was produced each year. Some of these nutcrackers were considerably underweight. Of 12 nutcrackers caught in mist nets during September and early October 1977, three individuals weighed 116 (juv.), 119 (ad.) and 120 g (ad.). Typical weights of adult nutcrackers are 134 ± 8.7 g for females and 149 ± 7.0 g for males (Giuntoli and Mewaldt 1978). One of the underweight individuals was emaciated and it nearly died. The other nine nutcrackers had weights within the normal range. The presence of underweight individuals is surprising at a time when resident nutcrackers had been foraging on the abundant and nutritious seeds of piñon pine for four to eight weeks. Giuntoli and Mewaldt (1978) found nutcrackers significantly underweight during times of food shortage in Montana. We suggest that the underweight nutcrackers we found were emigrating individuals who had recently settled in the area.

The second site we visited was the Kaiparowits Plateau and Circle Cliffs of south-central Utah, where nutcrackers were studied in piñon-juniper woodlands from April to June 1978. The high density of nutcrackers observed in this habitat during the breeding season was unusual. The nearest typical nutcracker breeding habitat (i.e., montane coniferous forest) is 20 to 30 km away. Although observations were continued in this area until September 1978, nutcrackers were rarely seen after mid June.

In an attempt to find other areas where nutcrackers may have wintered, we checked several sources of avian distributional information (e.g., *American Birds*) for unusual occurrences and numbers of nutcrackers in the western United States. No extralimital sightings of nutcrackers were reported in winter 1977–78, suggesting that the emigrating nutcrackers remained in the southern half of their breeding range. The fall 1978 eruption also went unreported outside the nutcrackers' normal breeding range.

After emigrating nutcrackers settle to winter in areas within their normal breeding range, they mix (to some extent) with the resident populations of nutcrackers, which are actively harvesting and transporting seeds to higher elevations (see Vander Wall and Balda 1977). At this time it is very difficult to distinguish emigrants from residents so we could not determine whether wintering emigrants collect and store conifer seeds in the same manner as resident nutcrackers. However, storing of food by nutcrackers wintering on the Monterey Peninsula was reported by Davis and Williams (1957).

Previously, eruptions were recognized only when nutcrackers were seen outside their normal breeding range. Major eruptions have occurred at irregular intervals of about 5 to 15 years (Davis and Williams 1957, 1964; Phillips et al. 1964). The data presented here suggest that minor eruptions may occur very frequently but remain unnoticed because the birds find suitable wintering areas within their normal breeding range and habitat. Bock and Lepthien (1976) found that populations of conifer-

seed-eating birds in the western United States usually did not erupt in synchrony with those inhabiting northern boreal forests. They suggested that this may be due to less synchrony of cone production between regions or plant species in the West. Our data are circumstantial evidence supporting their hypothesis.

BREEDING OF EMIGRANTS IN WINTERING AREAS

Our data from the Kaiparowits Plateau and Circle Cliffs indicate that nutcrackers bred in piñon-juniper woodland during April and May 1978. One fledgling barely able to fly was observed on 25 May in the Circle Cliffs area, over 24 km from Boulder Mountain, the nearest known montane coniferous forest where nutcrackers usually breed. On 19 May, fledglings were heard begging and three adults scolded the observer (S. H.). One of these adults carried a small lizard in its bill. Willard (1916) reported similar evidence of breeding for apparently emigrant nutcrackers (but see Phillips et al. 1964). Emigrant Eurasian Nutcrackers have also been observed breeding in their wintering areas in Denmark and Sweden (Svärdson 1957).

Data presented here are consistent with the hypothesis that emigrant nutcrackers may breed in their wintering areas. Early spring breeding could have resulted in full-grown, nearly independent young by early to mid June (Mewaldt 1956). In mid June, when nearly all nutcrackers left the Kaiparowits Plateau and Circle Cliffs areas, nutcracker family groups and flocks may have begun moving northward. By late June, nutcracker flocks were noted moving through northern Utah, returning to the northern portion of their range.

THE SETTLING RESPONSE

Here we examine the food supply of the wintering area to determine its effect on causing a settling response in emigrating nutcrackers. More specifically, we ask: why did emigrant nutcrackers winter in piñon-juniper woodland of southern and northwestern Utah but not in the montane coniferous forests of northeastern Utah?

In the Bear River and Wellsville mountains of northern Utah, limber pine and Douglas-fir are the most important conifer species used by resident nutcrackers (Vander Wall, unpubl. data). Limber pine produced few cones in fall 1977 but Douglas-fir produced a large crop of cones, which resident nutcrackers used extensively. In the Raft River Mountains of northwestern Utah, limber pine, piñon pine and Douglas-fir are the most important seed sources for nutcrackers (Vander Wall, unpubl. data). Again, limber pine produced few cones but piñon pine and Douglas-fir both produced large cone crops. Nutcrackers ignored the Douglas-fir and foraged extensively on piñon pine cones. Thus, in these two areas of the state, nutcrackers foraged on the cones of different conifers.

Both seed size and foraging rates differ for Douglas-fir and piñon pine. Nutcrackers collect Douglas-fir at the rate of 24.3 s/seed (n = 231 seeds). The mean dry weight of the edible portion of mature Douglas-fir seeds is 12.0 mg (SD = 1.5, n = 48). Nutcrackers must, therefore, invest approximately 2,025 s to extract one gram (dry weight) of edible Douglas-fir seed material. The caloric value of Douglas-fir seeds is 25.1 kJ/g (calculated from Long 1934). For singleleaf piñon, mean extraction time is 16.3 s/seed (n = 335) and mean mature seed dry weight is 270.5 mg (SD = 74.2, n = 99). For singleleaf piñon pine, nutcrackers must invest 60.3 s to extract one gram (dry weight) of edible seed material. The caloric value of mature singleleaf piñon pine seeds is 31.2 kJ/g. Assuming that energy invested is proportional to time invested, nutcrackers are 41.8 times more efficient (energy harvested/energy invested) when foraging on singleleaf piñon pine than on Douglas-fir. These data indicate that piñon pine seeds are a much more attractive food source for nutcrackers than are Douglas-fir seeds. This greater attractiveness may have caused emigrating nutcrackers to settle in piñon-juniper woodland and bypass Douglas-fir forests in the Bear River and Wellsville mountains.

Other factors influencing the settling response may be the presence or absence of resident nutcrackers and differences in seed dispersal in the conifer species. In the Bear River and Wellsville mountains, resident nutcrackers harvested a sizable portion of the seed crop before the emigrants arrived. In addition, the wind-dispersed seed of Douglas-fir were shed soon after their arrival. Emigrants probably could not store enough food to insure their survival in winter under these conditions. During a good piñon pine cone crop year, the presence of resident nutcrackers would probably have little effect. By early September, only a small portion of the seed crop has been harvested (Vander Wall, unpubl. data) and the undefendable nature of the seed crop would

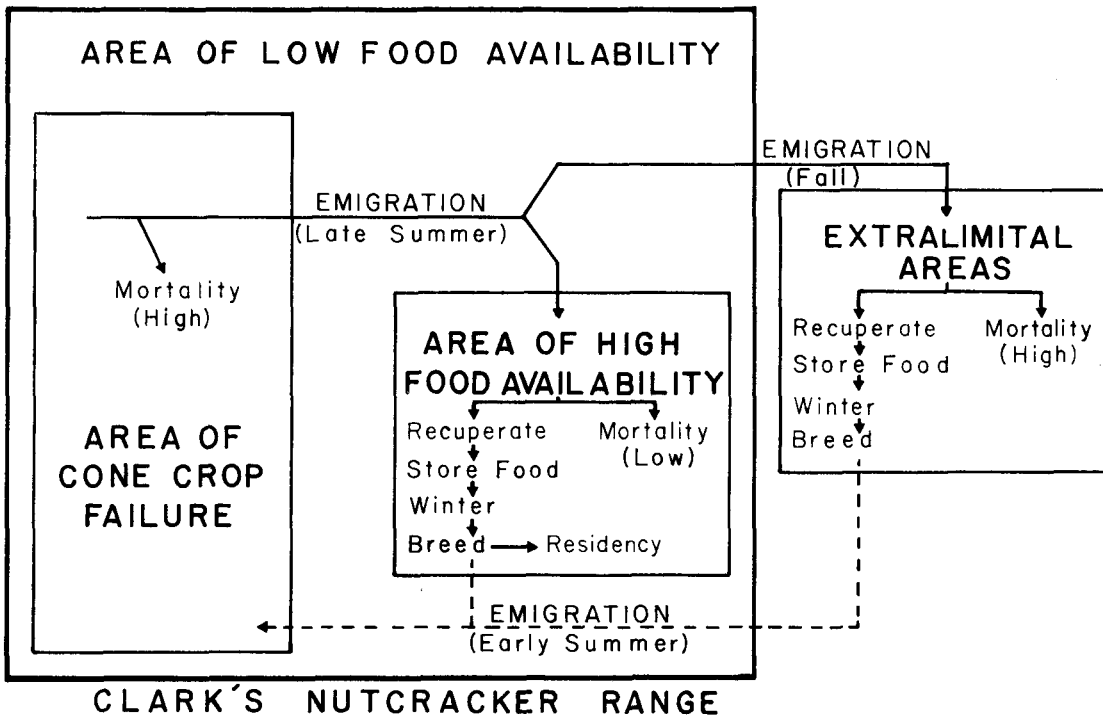

FIGURE 3. A compartmental model demonstrating some of the courses that a nutcracker eruption may take depending on the types of food resources available. Nutcrackers leaving an area of cone crop failure are represented by a solid line. Two types of wintering areas are shown, one within the nutcrackers' usual breeding range and the other in extralimital areas. Nutcrackers recuperating and wintering in an area may also store food and breed. Nutcrackers returning to their area of origin are represented by a broken line. See text for further details.

allow emigrants to effectively compete with residents. When cones open in mid September, the seeds are not shed but remain in the cones and are efficiently harvested (Vander Wall and Balda 1977). These conditions may allow emigrant nutcrackers to store sufficient seeds to survive the winter.

Nutcrackers may require a certain threshold of energy availability before settling in an area for the winter. Energy availability depends not only on the size of the cone crop but also the rate at which energy can be extracted from those cones and the potential impact of residents on that food source. In fall 1977, the amount of food energy available in the Bear River and Wellsville mountains apparently was below the threshold value required to elicit a settling response in emigrating nutcrackers, whereas in the Raft River Mountains, Kaiparowits Plateau and Circle Cliffs it was above the threshold value.

Emigrating birds have been observed bypassing areas of apparent food abundance (Lack 1954, Svärdson 1957). We suspect that in many cases a thorough investigation of the quality of food resources and foraging efficiencies of the emigrating species would indicate that these resources do not provide energy at an adequate rate to cause a settling response.

A MODEL OF CLARK'S NUTCRACKER EMIGRATION BEHAVIOR

Some of the patterns in nutcracker emigrations suggested by our data and those of others (e.g., Davis and Williams 1957, 1964) are illustrated in the form of a compartmental model (Fig. 3). Although the patterns are consistent with the available data, the model should be considered tentative as several aspects of it lack sufficient documentation. We hope that by organizing the present information into a formal model, future observations on nutcracker eruptions may be more easily integrated with the existing body of knowledge and the model revised to more accurately reflect reality.

Nutcrackers apparently leave an area of cone crop failure (Fig. 3) because they are more likely to survive than if they remain (Davis and Williams 1957). Few resident nutcrackers appear to emigrate from areas where conifer seeds are available at low to moderate levels (Areas of Low Food Availability; Fig. 3). Presumably, the costs and uncertainties of emigration outweigh the potential benefits to nutcrackers in areas of

moderate seed production. Yet these areas appear unsuitable for emigrating nutcrackers. Once the advantages of residency (e.g., site-related dominance, familiarity with local terrain, food sources and predators) have been lost, the level of food availability necessary to cause a nutcracker to settle appears to be quite high. Because conifer crops in the western mountains are patchily distributed in space and time (U.S.D.A. Forest Service 1974), nutcrackers traveling through areas of low food availability should benefit by continuing to search, because the probability of finding an area of good cone production (Area of High Food Availability; Fig. 3) is, in most years, high. If areas of good cone production do not exist or are not encountered, emigrating nutcrackers will eventually wander from their normal breeding range in search of food in extralimital areas (Fig. 3).

Emigrant nutcrackers wintering within their normal breeding range in areas of high food availability probably experience relatively low mortality. Even though the areas may be unfamiliar, the types of foods on which they forage (conifer seeds) and the physiognomy of the vegetation and terrain are similar to their area of origin. In these areas, most nutcrackers probably recuperate quickly and food storage, although undocumented, probably is an important fall activity. Those individuals who winter successfully may breed and return to the region from which they emigrated by early summer or, possibly, remain in the area as residents.

Emigrant nutcrackers wintering outside the normal breeding range usually do so in areas of low food availability. In addition, the type of foods available, physiognomy of the vegetation and terrain and types of predators present, may be largely unfamiliar. For these and other reasons, mortality may be high compared to individuals wintering within their normal breeding range. Those birds who recuperate probably store little food because cachable food items may be unavailable. Because of a lack of stored food, breeding probably is infrequent and less successful than that of emigrant nutcrackers who remain within their usual breeding range and habitats. Movements back to montane coniferous forest probably occur in early summer.

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RECENT PUBLICATIONS

The Audubon Society Encyclopedia of North American Birds.—John K. Terres. 1980. Alfred A. Knopf, New York. 1,130 p. $60.00. This massive book is a one-volume library on North American birds and ornithology. Arranged alphabetically, it contains biographies of 847 species, 625 major articles about bird life and bird biology, definitions of 770 ornithological terms, and short biographies of 126 naturalists and explorers whose names are associated with North American birds. The entries are crammed with information, yet written in a clear, non-technical style. They are linked by a system of cross-references and documented with citations from an enormous bibliography of the scientific and general literature. The work is generously and instructively illustrated with drawings, diagrams, maps, and color photographs. Although this encyclopedia is intended chiefly for lay students of birds, professional ornithologists will also find it highly useful as a reliable and comprehensive reference.

Taxonomy and Geographical Distribution of the Furnariidae (Aves, Passeriformes).—Charles Vaurie. 1980. Bulletin of the American Museum of Natural History, Volume 166, Article 1. New York. 357 p. Paper cover. $24.70. "This monograph brings together for the first time a great deal of previously scattered information about the taxonomy, geographical distribution, general behavior, habitat preferences, nesting behavior, and morphological variation of the 34 genera and 214 species of the Neotropical family Furnariidae." Vaurie's classification of the ovenbirds into genera and three subfamilies was based in large part on his assessment of differences in the structure of their nests. The manuscript for this work was virtually complete at the time of the author's sudden death in 1975. Recognizing its potential value, François Vuilleumier finished and polished it, taking scrupulous care to distinguish his comments from Vaurie's own writing. Three appendices were added in order to enhance the usefulness of the monograph. This is an exceptionally complete and well-produced work, for in addition to the text it contains many keys, tables of measurements, distribution maps, and ten color plates. It is an important contribution to taxonomy and an outstanding demonstration of evolutionary radiation and convergence. Ornithologists should be grateful to Dr. Vuilleumier and his colleagues for bringing the work to completion.