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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 pinon-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-

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

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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