THE 1961 IRRUPTION OF THE CLARK'S NUTCRACKER IN CALIFORNIA

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IN a previous paper (Davis and Williams, 1957), we described five irruptions of the Clark's Nutcracker (*Nucifraga columbiana*) which had occurred in California between 1898 and 1955. In these irruptions, numbers of nutcrackers left the usual montane winter range and spent the winter in the coastal and desert regions, some remaining well into the following spring or even summer. Clark's Nutcrackers apparently depend primarily on stores of conifer seeds made in the fall to get them through the winter. The irruptions of 1935, 1950, and 1955, the only ones for which cone crop data were available, coincided with severe shortages of seed in the Sierra Nevada, whence we assumed most of the irrupting birds came. However, each of these poor seed years had been preceded by two or more years of relative seed abundance, and we hypothesized that irruptions of nutcrackers in California resulted from population increase during periods of two or more years of abundant winter food, followed by a severe decline in conifer seed crops. This pattern would result in an expanded population faced with a shortage of food to be stored for winter use, with numbers of individuals leaving the montane winter range to seek winter quarters elsewhere. In the fall and winter of 1961–62, another large-scale irruption of nutcrackers occurred in California, affording an opportunity to test our hypothesis.

TIME OF IRRUPTION

The first report of a nutcracker outside the normal range of the species in California in 1961 was of a single bird seen by Marianne Shepard at Glen Ellen, Sonoma County, on 29 September. Records continued to come throughout October and November, ranging from Glen Ellen south to San Diego. The irruption was obviously on a large scale, with reports from many coastal and desert areas. This information has been summarized by Cutler and Pugh (1962) for the northern half of the state and by Small (1962) for the southern half. The important point, however, is that the first records came in September and October. In this respect the irruption of 1961 agreed with those previously described, which supports the suggestion made in our paper of 1957, that irruptions of nutcrackers in California start when these birds begin to make their winter stores in the early fall. At this time the cones of most Sierra Nevadan conifers open and shed their seed, which is then readily available to the birds. Presumably, in years of short supply, birds seeking seeds for winter stores fail to find adequate supplies locally and

TABLE 1

CONE CROPS ON THE WEST SLOPE OF THE SIERRA NEVADA RATED ON A SCALE OF 1 (= NO CROP) TO 5 (= HEAVY CROP)

	1959[1]	1960[2]	1961[3]
Pinus ponderosa	2.11 (62)[4]	3.97 (111)	1.61 (86)
Pinus lambertiana	2.90 (50)	3.59 (88)	2.34 (84)
Pinus jeffreyi	3.19 (32)	3.51 (55)	1.51 (47)
Abies concolor	1.52 (44)	3.60 (67)	1.69 (77)
Combined mean	2.37 (188)	3.71 (321)	1.82 (294)

[1] From Forest Service records for 1959.
[2] From Schubert and Baron (1960).
[3] From Baron and Schubert (1961).
[4] Numbers in parentheses refer to numbers of reports.

wander to lower elevations in search of more. In years of widespread cone shortage, such as 1935, 1950, 1955, and 1961, such wandering may well lead a number of birds out of the normal winter range. Thus far, all of the irruptions recorded in California have started only after the seed shortages would have been evident to the birds. Lack (1954:234) noted that very large irruptions of some European species "sometimes start before the fruit crop on which the bird depends is ripe. . . ." Such a situation has not been recorded in nutcracker irruptions in California.

Nutcrackers irrupting in the fall and winter of 1961 remained at a number of coastal localities until the spring of 1962. For the first time, there were reports of nutcrackers breeding in coastal localities. However, the two reports of breeding were both of adults feeding begging young. Since feeding of full-grown begging birds, presumably females, was observed in nutcrackers on the Monterey Peninsula in 1956 (Davis and Williams, 1957:300), no report of extra-limital breeding of this species can be accepted unless confirmed by adequate photographs or, better, specimens of eggs or young.

THE 1961 IRRUPTION AND FOOD SUPPLY

Table 1 presents information on cone crops on the west slope of the Sierra Nevada for 1959, 1960, and 1961, for the ponderosa, sugar, and Jeffrey pines (*Pinus ponderosa, P. lambertiana,* and *P. jeffreyi*) and the white fir (*Abies concolor*). These are the four species considered in our 1957 paper; because of their relative abundance and wide distribution in the winter range of the Clark's Nutcracker in the Sierra Nevada, they must be of primary importance in providing seed for winter stores. The cone crops were rated by the foresters on a scale of 1 to 5, with 1 indicating no crop and 5 a heavy crop. For 1959, we averaged the reports of individual foresters throughout the west slope of the Sierra Nevada (U.S. Forest Service seed collection zones II, III, IV, and V) provided by Frank J. Baron from Forest Service files to

TABLE 2
CONE CROP RATINGS FOR THE SOUTHWESTERN UNITED STATES AND FORT VALLEY, ARIZONA

Year	Southwest	Fort Valley	Seeds per Acre at Fort Valley
1959	Poor	Very poor	1,040
1960	Excellent	Excellent	263,440
1961	Generally poor	Poor	4,240

bring the data into line with those furnished for 1960 and 1961 by Schubert and Baron (1960) and Baron and Schubert (1961), respectively. None of the four species did well in 1961, and the mean rating of 1.82 for all species indicates a cone crop somewhat less than "very light." Baron and Schubert (1961:1) stated: "Poor cone crops are prevalent on nearly all species of forest trees this year [1961] over most of the state." As regards southern California (U.S. Forest Service seed collection zone IX), the ratings are based on far fewer individual reports than are those for the Sierra Nevada, but they parallel the annual ratings for the latter region for 1959, 1960, and 1961. Thus, as was true of the irruptions of 1935, 1950, and 1955, the irruption of 1961 coincided with low seed production on the winter range. So far, every Californian irruption for which cone crop data are available has coincided with poor cone crops and thus with low supplies of winter food on the normal winter range.

THE 1961 IRRUPTION AND POPULATION LEVEL

The irruption (and poor cone crop) years of 1935, 1950, and 1955 were preceded by two or more years in which there were heavy cone crops in at least one of the four conifers considered (Davis and Williams, 1957:302, Tables 1 and 2). We suggested that populations of nutcrackers built up in the Sierra Nevada during these years of abundant winter food supply. Further, since single years of heavy cone production followed by poor cone crop years (1936–37, 1941–42) did not result in irruptions, we suggested that it would take at least two years of good seed crops to build nutcracker populations up appreciably, since individuals of this species do not breed until they are two years old (Mewaldt, 1952: 361). Presumably, it would take two years of abundant winter food to build the breeding population up to a level at which the entire population, including breeding adults, nonbreeding first-year birds, and young-of-the-year, would be high in the fall, coincident with a shortage of cones. This pattern, however, did not occur in the two years prior to the irruption of 1961. As can be seen from Table 1, 1959 was a poor cone year, 1960 was a good cone year, and 1961 was again a poor

year. Schubert and Baron (1959:1) stated of the 1959 cone crop, "Only a few localities in California can expect a good crop of forest tree seed in 1959." These same authors (1960:1) stated of the 1960 crop, "Prospects are favorable for a good crop of forest tree seed in 1960." Thus, the irruption of 1961 was preceded by only one year of relative seed abundance. As noted previously, there were no irruptions following the poor cone years of 1937 and 1942, although 1936 and 1941 were years of cone abundance. Since there was an irruption in the poor year of 1961 following the good year of 1960, one may wonder why no irruptions occurred in 1937 and 1942. As regards 1937, it must be remembered that an irruption had occurred in 1935, a year of very poor cone crops. Since a number of birds that irrupted in 1935 undoubtedly never found their way back to the Sierra Nevada, and since the overwintering of nonirrupting birds might have been poor in the winter of 1935–36 because of the cone shortage, it seems likely that the population was at a low level in the fall of 1936. The good cone crop of that year might have raised the level of the population somewhat, but the population faced with a cone shortage in the fall of 1937 may well have been below normal, and perhaps for this reason, despite the cone shortage, there may have been enough food for most birds and hence no irruption occurred. However, no such explanation can be adduced for the absence of an irruption in 1942. Since an irruption did occur in 1961 after a similar sequence of years, the role of population buildup and consequent overcrowding in the Californian irruptions is not clear.

IRRUPTIONS IN OTHER STATES

As we pointed out in 1957, irruptions occurred in 1935, 1950, and 1955 not only in California, but in other states as well. The same was true of the 1961 irruption. Coincident with the Californian irruption of 1961, there were reports of Clark's Nutcrackers outside their normal range in Arizona and New Mexico. In addition, nutcrackers were recorded in states lying wholly outside the normal range of the species; extralimital records were reported from Texas, Oklahoma, Kansas, and Missouri. If food is the proximate factor in irruptions in other states, as it seems to be in California, then it must be assumed that the cone crops in many parts of the total range of the species fluctuate synchronously and in the same direction. Unfortunately, no other western state keeps records of cone crops comparable to those kept in California. However, Mr. Gilbert H. Schubert of the Rocky Mountain Forest and Range Experiment Station, Flagstaff, Arizona, kindly forwarded ratings of cone crops in the Southwest for 1959, 1960, and 1961 (Table 2). It can be seen that the ratings for the Southwest in these three years agree closely with those for the same years in California. Here, then, is the first evidence,

scanty though it may be, that fluctuations in the fall supply of seeds to be stored for winter use may be the proximate cause of coincident irruptions in many parts of the range of the Clark's Nutcracker. The synchronous and similar fluctuations in cone crops in such diverse montane areas as the west slope of the Sierra Nevada and the southern Rocky Mountains are obviously dependent on some widespread environmental factor or factors. Tirén (1935; reference not seen by us, but cited extensively by Svärdson, 1957) has shown that certain climatic factors are responsible for heavy cone crops in the Norway spruce (*Picea abies*), and that rhythmic fluctuations in the cone crops of that tree are the result of interaction between these climatic correlates and the physiological state of the individual tree after coning. Something of the same sort is undoubtedly involved here.

IRRUPTION OR INVASION TYPE OF MIGRATION?

Svärdson (1957) has advanced the idea that the presumed irruptions or invasions of certain European species are, in reality, migrations, the proximate factors for which are identical to those for ordinary migration. According to this hypothesis, irrupting species such as Red Crossbills (*Loxia curvirostra*), Nutcrackers (*Nucifraga caryocatactes*), Fieldfares (*Turdus pilaris*), and others, are normally migratory in response to "hormonal change, acting through metabolism, anchored by photoperiodism" (op. cit.:330) in exactly the same fashion as ordinary migrants. The primary distinction between "invasion migrants" and ordinary migrants is that abundant food supplies have a very strong retarding effect on the migrations of the former, and a very slight effect on migrations of the latter. Thus, invasion migrants will migrate only as far as they have to in order to find adequate supplies of winter food. If winter food is abundant on the breeding grounds, the migration will be scarcely evident; if the nearest adequate supplies of winter food are far from the normal range of the species, a long migration occurs, with numbers of birds reported from extralimital localities. Such a long migration results in what observers term an irruption or invasion. The question as regards the Californian irruptions of the Clark's Nutcracker is whether this species is normally migratory, setting out on a migration each year in response to the same physiological factors controlling onset of migration in ordinary migrants, but modifying the extent of the migration according to the location of adequate supplies of winter food, or whether the species should be thought of as nonmigratory, irrupting in some years because of poor supplies of food on the normal winter range, with food thus the proximate factor behind such population dislocations.

Svärdson lists the characteristics of invasion migrations (loc. cit.), so that it is possible, where we have the information, to see how many of these

characteristics the Californian irruptions of the Clark's Nutcracker possess. The *ultimate factor* behind invasion migrations is "escape from food shortage during a certain *year*" (as opposed to escape from food shortage during a certain *season* for ordinary migrants). This is certainly true of irruptions of the Clark's Nutcracker. The *participants* include "the whole population or only part, particularly the young or females." Since Svärdson states (loc. cit.) that *all* the invaders in Nutcracker invasions in Europe are young birds, there is an obvious difference here. As we pointed out previously (Davis and Williams, 1957:298), of 21 specimens of Clark's Nutcracker collected in extralimital localities during North American irruptions, 11 were adults and 10 were first-year birds. Although the sample is small, it is sufficient to indicate that by no means all of the participating nutcrackers were young birds. As regards the *retarding stimulus of abundant food*, the effect is "*very strong.*" Not enough is known about irruptions of Clark's Nutcrackers to come to any conclusion on this point. The *tendency to return to the home or winter range of last year* is "very *weak.*" Again, not enough is known about nutcracker irruptions in this country. In the invasion of 1955, we noted (op. cit.:298) that there were many records of nutcrackers on the Monterey Peninsula throughout the fall and winter, but that the birds were seen at only two localities on the peninsula after March. It is intriguing to speculate that this abrupt dropoff in numbers at about the time of the onset of the breeding season may have resulted from numbers of irrupting birds trying to find their way back to the breeding range in the Sierra Nevada. The *performance of movement* in invasion migrations is "*irregular* in time and space." As we have seen, the onset of irruptions has been irregular as regards year of irruption, but the actual onset of the different irruptions has been remarkably constant in that all irruptions have started in California in late September and October. The Californian irruptions have been regular in space in that nearly all records during irruptions come from coastal and desert regions, especially from localities in the Coast Ranges or on the coast proper. However, this would be expected, because the next great concentrations of conifers west of the Sierra Nevada are found in the Coast Ranges and on the coast. Beyond the coastal coniferous forests lies the Pacific Ocean. There are records of irrupting nutcrackers on Santa Cruz Island and on shipboard off Los Angeles, but if any great numbers of nutcrackers flew out to sea during past irruptions in California, they would be lost as far as ornithologists are concerned. The apparent regularity of Californian irruptions in space may thus be imposed in part by the nature of the terrain over which the birds would be passing, and in part by the distribution of observers in the state. However, we must conclude that the Californian irruptions are regular in time as regards actual onset of irruption, and that they are probably regular in space as well. The

breeding range of invasion migrant species is "*fluctuating.*" At present, there is no reliable record of nutcrackers breeding extralimitally anywhere in North America, and we must regard the breeding range of the Clark's Nutcracker as stable at this time. The remaining characteristics of invasion migrations listed by Svärdson either are not germane to a discussion of this particular species or represent points on which we have no information.

One possible source of evidence supporting Svärdson's hypothesis lies in the fact that wandering movements, either locally, or to great distances by small numbers of birds, occur frequently in nutcrackers in the Pacific states even in noninvasion years. Thus, Farner (1952) noted that at Crater Lake National Park, Oregon, there was an influx of nutcrackers into the higher parts of the park throughout the summer, and a gradual decline in numbers from September to December in these higher parts of the area. However, the same is also true, for example, of the Rufous-sided Towhee (*Pipilo erythrophthalmus*), definitely a nonirruptive species, in the montane parts of its range in California. As stated by Grinnell and Miller (1944:470), *Pipilo erythrophthalmus falcinellus* is "in general, resident; there is some altitudinal movement up mountain slopes after nesting and descent from higher parts of breeding range in winter, but no migration is known that carries birds outside of limits of breeding range." Such local movements may be common in montane birds, and the time of year at which they occur does not suggest that they are triggered by the same factors that are responsible for the onset of migration in ordinary migrants. Again, Grinnell and Miller (op. cit.:298) state of the Clark's Nutcracker in California that "there are frequent though irregular wanderings which carry individual birds or small companies in late summer and autumn far and wide, to lowest altitudes and farthest confines of state." It seems possible that these minor population movements, involving few birds, may be explained solely in terms of food supply: that is, that they result from restricted, local shortages of food, and that it is such local shortages that constitute the proximate factor involved.

It seems to us, then, that because of the particular characteristics of the irruptions of the Clark's Nutcracker, and because of the obvious correlation between these irruptions and food supply, it is best to think of food as the proximate factor behind them. There seems at present no reason to think of them as constituting migrations of any sort, in the absence of physiological evidence indicating that nutcracker populations achieve a premigratory state of some sort. Indeed, the extremely protracted molt period demonstrated by Mewaldt (1958) for the Clark's Nutcracker in Montana suggests that the physiology of this species differs rather considerably from that of "ordinary" migrants and that the hormonal picture in ordinary migrants and Clark's Nutcrackers may be quite different in the fall and winter.

The role of population levels in these irruptions is not clear. Nor can we explain why irruptions do not occur in some years of cone shortage. Clearly, the picture of these movements is largly incomplete. This is primarily because few ornithologists are active in the montane range of this species in the critical times of year, namely, the fall and winter periods. Thus, we have virtually no information on population levels prior to irruption, and we have no idea of movements within the montane winter range. At the present time, we can say only that these irruptions occur in relation to winter food supply, and that winter food supply seems to be affected in the same way over large areas within the range of the Clark's Nutcracker.

SUMMARY

The irruption of the Clark's Nutcracker in California in the fall and winter of 1961 is discussed. The irruption coincided with low cone crops in the montane regions of California.

An irruption of the species in Arizona also coincided with low cone crops in that state. It appears as if cone crops may vary synchronously over much of the range of the nutcracker.

It is concluded that food is the proximate factor underlying irruptions of the Clark's Nutcracker and that these irruptions are not invasion migrations triggered by the same proximate factors which trigger ordinary migrations.

ACKNOWLEDGMENTS

Frank J. Baron and Gilbert H. Schubert were most helpful in supplying cone crop data for 1959, 1960, and 1961. Many observers forwarded records of irrupting nutcrackers to us. It would be impossible to list them all here, but we should like to acknowledge especially the help of Dorothy B. Hunt, Donald M. Falconer, Ebon B. McGregor, Roger G. Simpson, Richard F. Johnston, Ralph J. Raitt, Eleanor A. Pugh, Marianne Shepard, Frances Williams, Frank A. Pitelka, and George Peyton.

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