

**Ecological Aspects of Irruptive Bird Migration in Northwestern
Europe**

STAFFAN ULFSTRAND

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Ecological Aspects of Irruptive Bird Migration in Northwestern Europe¹

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The object of this paper is to review recently accumulated data on irruptive bird migration in northwestern Europe and to analyze some of the relationships between this particular kind of bird migration and certain ecological factors, particularly food. A great deal of work on irruptive species has been carried out in Fennoscandia in recent years, and an additional purpose of this contribution is to draw attention to the results. The migration has been closely studied at several places for periods up to 15 or 20 years, and extensive data on annual fluctuations of the seed crop of certain trees are available.

The term *irruption* has often been used in a very loose sense; *invasion* has been used even more loosely (cf. Elton, 1958). Lack (1954:240) opposes the practice of calling any sort of mass occurrence, or any sort of occurrence outside the normal range of a bird species, an irruption or invasion. The term *irruption* has, however, been in long use as referring to a limited number of species, the migratory habits of which have been considered to differ sharply from those of other migratory birds through their irregularity. Various other properties have been thought to be diagnostic for irruptive birds, such as violent population fluctuations in the breeding area, absence of return migration, etc. The idea has been put forward that irruptions, at least of many species, recur with cyclic regularity, or that the disposal of large numbers of birds is the function of the wanderings.

The ecological significance of irruptions has recently become more fully understood, perhaps particularly because of Lack's (1954) stimulating analysis. An important step has been the realization of the many resemblances between irruptive and *regular* migration (Rudebeck, 1950:49 et seq.), and most authors now agree that no sharp limit can be drawn between irruptive birds and other migratory birds. Several authors have stressed the fact that irruptive birds seem to be more directly influenced by food factors: The fluctuating abundance of some certain kinds of food has a strong effect on the temporal and spatial course of the movements. This difference, however, is qualitative rather than quantitative. Svårdson (1957: 328) in an important discussion makes the point that irruptive migration is an adaptation to annual, rather than seasonal, fluctuations in food supply.

Restriction of the term *irruption* seems to be highly desirable. It should be used only in cases where the direct influence of fluctuating food conditions

¹ Report from Falsterbo Bird Station No. 26.

on birds' movements has been demonstrated and these fluctuations are due to variations in productivity of the food organisms.

My recommendation of a stricter use of *irruption* in no way indicates that I think that birds may be classified as *irruptive birds* and *regular migrants*. The direct influence of food on bird movements varies from species to species: In many cases, food scarcity is avoided by an early departure from the breeding grounds, so that food conditions have lost practically all importance as proximate releasers of migration; in many other cases, variations in the food supply exert a mild influence on the migratory movements; in still other cases, the whole annual pattern of movements is governed by the regionally and temporally variable food supply. Irruptive tendencies may thus be more or less expressly present in a species or a population. Yet, the term *irruptive bird* will sometimes be used in this paper instead of an awkward expression like "bird with pronounced irruptive tendencies in its migratory habits."

RAPTORIAL BIRDS

A number of raptorial birds are usually listed with the irruptive birds, for example *Nyctea scandiaca* and many other owls, *Buteo lagopus*, *Stercorarius longicaudus*, and *Lanius excubitor* (particularly the North American population of the latter species). To what extent are the movements of these birds dependent on the food supply met with during their postbreeding movements? In the first place, the spring migration of *S. longicaudus* may theoretically be influenced by the food situation but not the postbreeding movement, for the food of the species during the winter season can scarcely be supposed to bring about irruptive movements. Not even for the spring migration is the influence of food fully clear, for according to Swanberg (1946:18-19) these birds seem to return to previous breeding places every year, although they do not breed if the rodent population is poor. Thus, the migratory habits of *S. longicaudus* should not be labeled as being irruptive.

The movements of the northern European population of *Buteo lagopus* have been studied particularly by Schüz (1941-45, 1952), who was only able to obtain rather contradictory evidence as to the degree to which food conditions influence the extent of the movements of these birds. Under no circumstances is the Scandinavian population capable of wintering in the breeding area, so that the first part of the postbreeding movement is in any case performed without regard to food factors. Rosenberg and Curry-Lindahl (1959) seem to be of the opinion that the abundance of rodents exerts some influence on the location of the winter quarters, and in North America the Craigheads (1956) found that the number of birds of prey in a given area was much higher in a winter season with plenty of rodents than in one without. It is well known that the numbers of *B. lagopus* on passage migration in many districts of northwestern Europe vary from year to year, but the location of their winter quarters requires further study.

TABLE 1.—DEFINITE IRRUPTIVE MIGRANTS, THEIR CRITICAL FOOD, AND SOME KEY REFERENCES

Species (Subspecies)	Critical Food	Reference
<i>Dendrocopos major</i>	<i>Picea</i> and <i>Pinus</i>	Pynnönen (1939, 1960)
<i>Loxia curvirostra</i>	<i>Picea</i>	Reinikainen (1937)
<i>L. pityopsittacus</i>	<i>Pinus</i> (and <i>Picea</i>)	Nilsson (1858:539) and later handbooks, Olsson (1960)
<i>L. leucoptera</i>	<i>Larix</i>	(No Fennoscandian food studies)
<i>Pinicola enucleator</i>	<i>Sorbus</i> (and to some extent <i>Picea</i>)	Faxén (1945), Markgren (1955:174), Markgren and Lundberg (1959:196)
<i>Turdus pilaris</i>	<i>Sorbus</i>	Nilsson (1858:362) and later handbooks
<i>Fringilla montifringilla</i>	<i>Fagus</i>	Nilsson (1858:506) and later handbooks, Granvik (1916)
<i>Nucifraga c. caryocatactes</i>	<i>Corylus</i>	Swanberg (1951, 1959)
<i>N. c. macrorhynchus</i>	<i>Pinus cembra</i>	Formosof (1933)
<i>Parus major</i>	<i>Fagus</i>	Ulfstrand (1962:27), Cramp et al. (1960)
<i>P. caeruleus</i>	<i>Fagus</i>	Ulfstrand (1962:30-32)
<i>P. ater</i>	<i>Picea</i>	Haftorn (1956:6-8)
<i>Bombycilla garrulus</i>	<i>Sorbus</i>	Nilsson (1858:241) and later handbooks, Hansson and Wallin (1958:234-235)

HERBIVOROUS SPECIES

Definitely Irruptive Migrants.—Table 1 lists those cases where critical food factors behind the irruptive tendencies have been established beyond reasonable doubt. However, not even in these species should the degree of food specialization be overrated. They may occur in numbers during months in districts where the critical food, the one about which the irruptions are centered, does not exist. Hansson and Wallin (1958) list a great number of vegetable products utilized as food by migrating flocks of *Bombycilla garrulus*. *Parus major* and *P. caeruleus* certainly are not monophagous birds (Ulfstrand, 1962), and irrupting *Loxia curvirostra* have been known to interrupt a movement for months to exploit an outbreak of *Operophtera brumata* larvae (Carlsson, 1962:10). *Loxia leucoptera* has several times successfully nested in Sweden (Sveriges Ornitologiska Förening, 1958), although *Larix* trees are scarce and restricted to parks and plantations; and *Nucifraga caryocatactes macrorhynchus* has bred once, subsisting during the previous winter largely on food supplied by man (Lundberg, 1955).

In some species, food conditions within the breeding areas exert their influence on the migratory movements, so that the birds may remain more or less stationary during years with a rich food supply. Such is probably the case in *Pinicola enucleator*, *Bombycilla garrulus*, *Nucifraga caryocatactes* (both subspecies), *Dendrocopos major*, and *Parus ater*. This statement does

not imply that all individuals of a given population remain stationary, even if the food supply is abundant. Siivonen (1941) points out that a proportion of the *Bombycilla garrulus* population moves irrespectively of the food situation. Holm (1957) states that *Pinicola enucleator* departs for a brief period in midwinter from northernmost Fennoscandia, and such is probably the situation in most species. In other species the critical food factor does not operate in the breeding areas, but the birds have to travel a longer or shorter distance before irruptive tendencies are noticeable. Such is the case in *Fringilla montifringilla*, *Turdus pilaris*, *Parus major*, and *P. caeruleus*.

The only vegetarian irruptive species that are dependent on the critical food factor during both the winter and breeding seasons belong to the genus *Loxia*. In this connection, attention is drawn to Olsson's (1960) estimate that a clutch of *L. pityopsittacus* devours about 70,000 *Pinus* seeds during the nesting period. The role of seeds during the breeding season is rather unclear in *Carduelis spinus* and *C. flammea*.

All the other species listed in Table 1 live on lower animals or on a mixed diet during the breeding season, and their young are fed mainly or wholly on insects. Thus, during the breeding season they are independent of the critical food factor. The statement by Svärdson (1957:320), therefore, that the irruptive birds "search for" a new breeding area during their movements is too wide a generalization; except perhaps for some of the rodent-eating raptores and for the *Loxia* species, the irruptive birds "search for" a wintering area with satisfactory food abundance. It is quite a different thing that they often remain in the area and breed, given certain circumstances.

Questionably Irruptive Migrants.—In Table 2 a number of species are listed which are more or less generally suspected of exhibiting irruptive tendencies in their migration habits but for which the critical food factor has not been convincingly demonstrated. To that list, in point of fact, several species might be added.

TABLE 2.—SPECIES OF QUESTIONABLE STATUS AS IRRUPTIVE MIGRANTS

Species (Subspecies)	Reference
<i>Sitta europaea asiatica</i>	Svärdson (1955)
<i>Aegithalos caudatus</i>	Svärdson (1935), Tischler (1941:281), Ulfstrand (1962:93 et seq.)
<i>Garrulus glandarius</i>	Putzig (1938:203, 213), Enemar (1957), Berndt and Dancker (1960), Ulfstrand (1959:148–151)
<i>Pyrrhula pyrrhula</i>	Rudebeck (1950:50), Svärdson (1957:327)
<i>Chloris chloris</i>	Rudebeck (1950:50)
<i>Emberiza citrinella</i>	Rudebeck (1950:50)
<i>Carduelis spinus</i>	Svärdson (1957:317 et seq.)
<i>C. flammea</i>	Svärdson (1957:320 et seq.), Lennerstedt and Ulfstrand (1959)

There seems to be little doubt that *Carduelis spinus* and *C. flammea* have irruptive migration habits. For the latter species, *Betula* and *Alnus* seeds make up by far the largest proportion of the winter food, and these seeds are known or likely to occur in fluctuating abundance (cf. Table 3). However, the species also takes a great many seeds of herbs. In the former species, the situation is very complicated. In his important analysis, Svårdson (1957) tries to correlate the passage of the species at Ottenby on the island of Öland in the Baltic with *Betula* seed abundance (p.317), but in another connection points to the importance of *Picea* seeds for the birds (p.319). A glance in some Scandinavian handbooks reveals that the relative importance of different seeds for *C. spinus* is poorly known. Nilsson (1858:489) mentions *Betula*, *Pinus*, *Picea*, and *Alnus* in that order; Svårdson and Durango

TABLE 3.—CHIEF MOVEMENTS OF SPECIES WITH MORE OR LESS OBVIOUS IRRUPTIVE MIGRATION HABITS (MARKED BY X) IN 1942-44^a AND 1949-61^b; WITH FRUCTIFICATION INDICES OF *Picea* AND *Betula* (WHOLE SWEDEN), *Quercus* (SOUTHERN THIRD OF SWEDEN), AND *Fagus* (SOUTHERNMOST PROVINCES ONLY)^c

	4 = extremely rich crop 3 = rich crop			2 = rather poor crop 1 = very poor crop			0 = practically no crop												
Species (Subspecies)	'42	'43	'44	'49	'50	'51	'52	'53	'54	'55	'56	'57	'58	'59	'60	'61			
<i>Dendrocopos major</i>	-	-	-	x	-	-	-	x	-	-	x	-	-	-	-	-			
<i>Nucifraga caryocatactes</i> ssp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x			
<i>N. c. caryocatactes</i>	-	x	-	x	-	-	-	-	-	x	-	x	-	-	-	-			
<i>N. c. macrorhynchus</i>	-	-	-	-	x	-	-	-	x	-	-	-	-	-	-	-			
<i>Garrulus glandarius</i>	-	x	-	x	-	-	-	-	-	x	-	-	-	-	-	x			
<i>Parus major</i>	-	x	-	x	-	-	-	-	-	x ^d	x ^d	x	-	x	-	x			
<i>P. caeruleus</i>	-	-	-	x	-	-	-	-	-	-	x	-	-	x	-	x			
<i>P. ater</i>	-	-	-	-	-	-	-	x	-	-	x	x	-	-	-	x			
<i>Aegithalos caudatus</i>	-	-	-	-	-	-	-	-	-	-	x ^e	x ^e	-	-	-	-			
<i>Carduelis spinus</i>	-	x	-	x	x	-	-	x	-	x	-	-	-	-	-	-			
<i>Loxia curvirostra</i>	-	-	-	-	-	-	-	x	-	-	x	-	x	-	-	-			
<i>Pyrrhula pyrrhula</i>	-	x	-	-	-	-	-	-	-	-	-	-	-	-	?	x			
<i>Picea</i>	3.1	0.5	1.6	0.8	1.3	1.6	1.3	1.5	3.7	0.4	2.1	0.8	2.0	1.4	1.8	1.2			
<i>Betula</i>	3.1	1.4	2.5	1.4	2.5	2.4	2.0	2.1	2.9	1.2	2.8	1.6	2.7	2.1	2.9	2.3			
<i>Quercus</i>	1.5	0.9	2.1	1.3	1.9	1.5	1.7	1.2	2.6	1.0	1.3	0.9	1.2	1.6	2.0	1.4			
<i>Fagus</i>	2.5	0.5	3.0	0.1	1.6	1.3	1.6	1.0	3.4	0.2	3.7	0.0	1.2	0.3	3.3	0.7			

^a Rudebeck (1950).

^b At Falsterbo, southern Sweden; taken from annual reports of Falsterbo Bird Station, published serially in *Vår Fågelvärld*, and from unpublished material in the archives of the bird station. Movements of *Pinicola enucleator* scarcely ever reach this place. *Turdus pilaris*, *Bombycilla garrulus*, and in part also *Carduelis flammea* usually occur so late in the season that they are not recorded. The figures for *Loxia curvirostra* are somewhat uncertain, for part of the movements occur so early in the season that the birds are not recorded. *L. pityopsittacus* and *L. leucoptera* are extremely rare in southernmost Sweden.

^c The figures are averages from a great number of indices, estimated by professional foresters, and published by Tirén (1942-44, 1949-50) and Fall (1951-61).

^d Cf. Ulfstrand (1962).

^e The two cases of *Aegithalos caudatus* involve relatively large-scale movements, but the status of this species as an irruptive bird in the sense of this paper is open to strong doubt.

^f In the most extensive *Fagus* districts the crop was better than indicated by this figure, which was lowered by indices from some peripheral districts with a poor crop.

(1950:182) list *Picea* and *Alnus*; and Poulsen (1959:133) enumerates *Picea*, *Pinus*, and *Betula*. The standard works by Niethammer (1937:55) and Witherby et al. (1948:62) both state that *C. spinus* takes both coniferous and deciduous seeds. Hence, the correlation between irruptive movements of this species and its food factors is very complex, and that may explain why Svårdson (1957) found one of the highest totals for passing *C. spinus* during a year with the highest "*Betula* seed index." These uncertainties have caused me to include *C. spinus* in Table 2 rather than in Table 1.

Garrulus glandarius is another species that almost certainly has a strong irruptive component in its migrations, but both Putzig (1938) and Berndt and Dancker (1960) are of the opposite opinion. However, according to my judgment, the evidence produced by these authors is not convincing. Putzig (p.203) says that the great movement through East Prussia in 1936 was contemporaneous with a heavy crop of *Fagus* and *Quercus* seeds, but points out that no information was available from the area in which the movement had its origin, namely Poland. In any case, the fact that the birds neglected an area of rich food supply is of great interest, but it certainly does not prove that food is without significance for the movements. In 1955, when the largest *Garrulus* movement in recent years took place, the *Quercus* acorn crop in southern Sweden was extremely poor, several forestry districts reporting "no crop" (Fall, 1955-61). Berndt and Dancker (1960) argue that the species must be independent of this source of food, since a considerable population lives north of the northern limit of *Quercus*. However, even if this northerly population is independent of *Quercus* acorns, the more southerly and denser populations probably are very dependent on this food. Until further studies on the ecology of this species have been made, it seems, however, better to place *Garrulus* in Table 2.

Aegithalos caudatus is stated to be exclusively insectivorous, and therefore it seems unlikely that its movements are irruptive in the sense of this paper.

FACTORS OTHER THAN FOOD

Even if we restrict ourselves to the species listed in Table 1, food is obviously not the only factor influencing the movements. It has already been mentioned that certain populations have to travel a considerable distance before they enter the area in which the critical food exists. During the first part of their journey, they apparently are stimulated by the same factors as all other birds. Svårdson (1957) stresses the fact that the movements of several irruptive birds start very early in the season, before food shortage has become apparent. However, for *Nucifraga c. macrorhynchus*, *Loxia curvirostra*, and *Dendrocopos major*, Formozov (1960:228) points out that the new crop of seeds constitutes the chief food beginning in June or July. It seems very likely that the population density as such may act as a proxi-

mate stimulus for releasing the movements under certain circumstances. Kluijver (1951) has demonstrated this factor in *Parus major*, and Kalela (1954:7) points out that in some species the movements start at the season when the young gain independence and disperse to occupy their own territories.

Meteorological factors also play an obvious role. Low temperatures may start movements even in midwinter in *Pinicola enucleator* (Grenquist, 1947; Markgren, 1955:175–176), and midwinter movements, probably released by cold weather, have also been recorded for *Turdus pilaris* (Mathiasson, 1960: 115). Svårdson (1953:185) found that temperature drops in autumn release migration in *Carduelis flammea*, *Turdus pilaris*, and *Loxia*, as well as in more or less all other species of migrants. Climatic fluctuations have been suggested by Malmberg (1949) to play an important role in the reduced frequency and extent of the irruptive movements of *Pinicola enucleator* in the twentieth century.

As mentioned above, Putzig (1938) recorded large numbers of *Garrulus glandarius* passing through areas of abundant food supply, and the poor correlation between low *Picea* seed crop and high figures of departing *Loxia curvirostra*, *Parus ater*, and *Dendrocopos major* at Falsterbo, southwesternmost Sweden, indicates that the birds may under certain conditions pass through extensive areas of rich food supply (cf. Table 3 for the years 1953 and 1956). This provides further confirmation of the fact that food is not all-dominant but that other factors also play a role.

ANNUAL FLUCTUATIONS IN THE SEED CROP OF CERTAIN TREES

In Table 3 the annual variations in the seed crop of *Picea*, *Betula*, *Quercus*, and *Fagus* in Sweden are set forth. It is unfortunate that we do not possess corresponding data from *Alnus*, *Sorbus aucuparia*, *Corylus avellana*, and other plant species of significance for certain bird irruptions.

A weakness of the data in Table 3 is that the figures are based upon field estimates (by professional foresters) of the cone frequency and not on measurement of the number of filled seeds. However, Sarvas (1957) has shown that, in general, the rule holds that the higher the number of cones, the higher the proportion of filled seeds. Thus, the data are certainly adequate for the present purposes.

A glance at the figures in Table 3 tells us that a certain amount of seed is nearly always produced in all the trees. Particularly in *Betula* and *Quercus* the fluctuations are of only moderate extent. In the former, however, the fluctuations are partly smoothed out due to the fact that the figure given is an average for the whole country. If attention is restricted to a single sample area or to a number of adjacent areas, sharper fluctuations can be found. *Picea* shows stronger fluctuations, and *Fagus* has in a few years reached an average index of only slightly above zero. It should, however, be kept in mind that smoothing out of the figures occurs least in *Fagus*,

for this tree occurs only in the southern third of Sweden and is frequent only in the three southernmost provinces, so that the average is based only on about 10 sample districts (as contrasted to about 90 for *Picea* and *Betula* and about 25 for *Quercus*).

Striking local differences are exhibited by these phenomena. It is not unusual for two adjacent districts in the same year to report a "good crop" and "very poor crop," respectively. Thus, only very rarely are all the *Picea* forests of Sweden empty or nearly empty of seed crops in 1 year. Because of the local differences, it is not necessarily inexpedient for the birds to return to approximately the same breeding place in 2 consecutive years. Even if the same tree and probably the same woods do not carry a rich crop in both years, the birds have a considerable chance of finding a fairly rich area in the vicinity.

THE "PENDULUM" THEORY

Svärdson (1957) is of the opinion that the movement patterns of the more extreme irruptive birds are totally different from those found in other north-west European birds. He assumes that these birds start their postbreeding movements in alternate directions in different years. In short, his idea is that the birds move west in 1 year, breed, move back toward the east, breed again, and so forth. According to this "pendulum" theory, Scandinavia would receive large quantities of birds from the east in some years, while corresponding quantities would depart from the area toward the east in other years. Westbound movements are much easier to observe, according to Svärdson, because of the influence of the guiding-line systems of western Europe.

In my opinion, however, this theory has a great weakness, viz. that the evidence for eastbound movements of irruptive species from Scandinavia is virtually nonexistent. Extensive studies of visible migration have in the last 20 years or so been conducted in Sweden at two places: Ottenby on the island of Öland, off the Swedish southeast coast, and Falsterbo, situated in the extreme southwestern corner of the province of Skåne (Scania) and of Scandinavia. Data from these places have been published in *Vår Fågelvärld* (seriatim) in the form of annual activity reports; see also Rudebeck (1950) for Falsterbo and Svärdson (1953) for Ottenby. It has been repeatedly demonstrated that birds flying in a southeasterly direction are proportionately more numerous at Ottenby, those in a southwesterly direction at Falsterbo. It is, therefore, highly significant that large numbers of irruptive birds have practically never been recorded at Ottenby. Recently, extensive observations have been made at another place in southeastern Sweden, at the sound between the island of Öland and the mainland. No irruptive species have been recorded in numbers (Edberg, 1960, 1961). Finally, some less regular studies have been made at the extreme southeastern corner of the Swedish mainland in the province of Blekinge, and Carlsson (1962)

reports fairly high numbers of *Carduelis flammea* and certain other birds mentioned in Tables 1 and 2. The high number of *C. flammea* recorded during the autumn of 1958 agrees well with the finding by Lennerstedt and Ulfstrand (1959) that the midwinter population was much denser in southeastern than in southwestern Sweden. Further observations at this place seem highly desirable, but so far no proof of southeastbound movements has been obtained. Linkola (1960) states that a low number of *Pinicola enucleator* flocks moved toward the southeast at Signilskär, Åland, in 1956. However, his data on the movements of *Parus* spp. at the same locality indicate that the migratory pattern is very peculiar there. Many tits were seen flying east and southeast, but ringing recoveries showed that the direction of the movement was south-southwest and west-southwest (Linkola, 1961).

Observations from the northeastern part of Sweden, at the northernmost part of the Bothnian bay, would be of extremely great value in the present context. However, regular observations of visible migration have not been made in that region. In a discussion between P. Linkola and G. Markgren (Linkola, 1960), the reactions of irruptive migrants and particularly of *Pinicola enucleator* at encountering the open sea were debated. Markgren, in spite of many years' field work on the Bothnian coast, was able to cite only an isolated case of birds departing out over the sea and that was in the spring. There remains the possibility that movements of, say, *Pinicola*, *Bombycilla*, and *Loxia* spp. take place north of the Bothnian bay. This route, however, is unthinkable in species with less northerly distribution, such as *Parus ater*, *Dendrocopos major*, *Carduelis spinus*, and, of course, *Nucifraga c. caryocatactes* (for distribution, see Sveriges Ornitologiska Förening, 1958).

The conclusion drawn from this discussion is that east-west movements are not a general feature in Fennoscandian irruptive birds, not even in the species inhabiting the coniferous forests (the taiga), and that their existence has not been proved in any single case. The support for eastbound irruptive movements, presented by Svärdson (1957), consists of (1) a few observations of traveling *Loxia* and (2) the observation that the Scandinavian breeding population of *Bombycilla garrulus* had dropped sharply from one year to the next without any departure over southern Sweden having been noted.

SPRING MOVEMENTS

Many irruptive migrants occur in much smaller numbers in spring than in autumn in southern Sweden. The numerous local breeding populations of, for example, *Parus major* and *P. caeruleus*, contribute to rendering the spring passage inconspicuous. Such birds as *Dendrocopos major*, *Nucifraga caryocatactes*, and *Bombycilla garrulus*, on the other hand, are unlikely to be overlooked for such reasons. Low numbers in the spring may be due to a heavy winter mortality, but there is also the possibility that many birds

return by a different route. A certain confirmation of this idea is found in Tischler's (1941) data concerning the passage through East Prussia where, for example, *Bombycilla garrulus* is obviously not scarce in spring. Return movements are often remarkably late, as reported for *Garrulus glandarius* by Berndt and Dancker (1960) and for *Bombycilla* by Tischler (1941).

PATTERNS OF MOVEMENT AND THE ECOLOGICAL BACKGROUND

The following statements seem to be based on satisfactory evidence:

1) There is no evidence for eastbound movements of irruptive birds from Scandinavia.

2) The density of the breeding population of *Bombycilla garrulus*, *Loxia curvirostra*, *Dendrocopos major*, and probably several other species in Scandinavia is very variable and generally low after an irruptive movement (Svårdson, 1957, and sources quoted by him).

3) The wintering range of irruptive birds is very variable, the breeding range much less so. Even the most extremely irruptive birds rarely or never breed south and west of certain limits.

4) Population-density variations cannot be explained by changes in productivity or by accumulated production of a stationary population. In point of fact, among all the species listed in Table 1 only *Parus major* and *P. caeruleus* have particularly large clutches. The sudden increases in population density in northern Sweden which undoubtedly do occur must therefore be caused by immigration. Thus, the population dynamics of these birds are quite different from those of the small rodents (*Lemmus*, *Clethrionomys* spp., etc.) in which the population fluctuations depend on changes in productivity and mortality and not on long-distance movements.

5) Among all the vegetarian irruptive birds, the three species of the genus *Loxia* differ from the rest in their extreme food specialization and—still more important—their dependency on the critical food factor also during the breeding season.

Many authors have assumed that irruptive movements have a fairly wide angle of spreading, particularly in their initial stages, and Svårdson (1957) states that they have a more distinctly westerly course (as opposed to a southwesterly) than most other migrants in the northwestern Palearctic. This seems to be true. In Scandinavia and western Europe, the westerly direction is changed to a more southerly one, which at least largely depends on the influence of macrotopography. Such a change in primary direction occurs in many other species, sometimes due to the effect of guiding-line systems, sometimes to other factors.

The extent of travel and the position of the winter quarters vary strongly. Thus, in some years great flocks of *Bombycilla garrulus* and *Turdus pilaris* winter even in the northern part of Sweden, in other years practically all the birds have left Scandinavia by midwinter. In some years vast quantities of *Fringilla montifringilla*, *Parus major*, and *P. caeruleus* spend the winter in

the south Swedish *Fagus* woods, in other years the former is almost absent and the density of the two latter very much lower. The Swedish population of *Nucifraga c. caryocatactes* is usually completely stationary, but sometimes the birds move hundreds of kilometers to the southwest.

It follows that in some years such birds as *Bombycilla garrulus*, *Turdus pilaris*, and *Dendrocopos major* find suitable winter quarters and remain within the normal breeding area of the respective population, even if far from the previous breeding localities or the birthplaces of the individuals. In other years, on the other hand, large numbers of birds winter 20° or 30° south or southwest of the breeding range. The sudden increases in the breeding population of, for example, *Bombycilla garrulus* in Sweden no doubt are due to the fact that the birds remain and breed in the wintering area. Birds that have traveled far to the south, on the other hand, obviously have to perform a prebreeding movement.

With regard to the preceding discussion, I conclude that the "pendulum" pattern becomes an unnecessary hypothesis. It seems to be possible to explain the movements of irruptive birds without demanding special navigational or other faculties on the part of the participating birds. Let us assume that a given population in a given year occupies a breeding range with an easterly center, for example in the taiga of the eastern part of the European U.S.S.R. After completion of their breeding, the birds start moving westward like most other northwest Palearctic birds. When they reach an area with a rich supply of the critical food, the movement is brought to a standstill. If such a suitable wintering area is found within the normal breeding area of the species, for example in northern Fennoscandia, the birds remain and start a new breeding cycle in the following spring. Next autumn, if the critical food is scarce, a new movement is started toward the west; the course later becomes more or less southerly because of the large guiding lines of western Europe, and the winter quarters are situated in western Europe. In the following spring, the birds find themselves far south of normal breeding latitudes. Then a prebreeding movement is released, probably by the same general stimuli as in other migratory birds, and an eastbound or north-eastbound movement is performed. It may be that the return movement keeps a rather strictly easterly course: Spring and autumn primary directions are very often opposite to each other, and the Baltic Sea might contribute to leading the birds eastward via north-central Europe rather than via Scandinavia.

In this pattern no extraordinary abilities are demanded of the birds, for it is only a modification of the general pattern among northwest Palearctic birds. In point of fact, it demands less than is known to exist in the "ordinary" migrants, for the birds may lack or have only poorly developed homing ability (*Ortstreue*). On the other hand, this pattern of more or less circular movements would confer distinct advantages to the birds. Thus, the amount of time spent traveling is reduced because of the lack of prebreeding move-

ments in most years and to the abbreviation of the postbreeding movements, in comparison with birds having a fixed wintering range. And yet the birds are able to spend most winters in areas with a rich supply of critical food.

Several populations are probably able to survive within the taiga zone for a number of years in succession, and departure from this area becomes necessary only at irregular intervals. No regular periodicity has been demonstrated in the species discussed in this paper (cf. Lack, 1954).

The circular pattern outlined above certainly does not exist in all the species listed in Table 1. Every species has many ecological characteristics of its own, and adaptive changes are unlikely to produce identical ecological patterns in different species. Irruptive-migration habits are, of course, acted upon by selection, and it is according to expectation that we find all transitions from extreme dependence on annually fluctuating food supplies, such as the seeds of several trees in the North Temperate Zone, to nearly complete independence of this kind of factor. Most extreme are the food specializations of the *Loxia* species. These may have approached the "pendulum" pattern, as suggested by Svårdson (1957), although this is not proved. Less extreme is the ecology of, for example, *Dendrocopos major*, *Parus ater*, *Bombycilla garrulus*, and *Pinicola enucleator*, which are dependent on a limited variety of vegetable foods in winter and autumn but which subsist on other foods for the rest of the year. In these birds, the circular pattern seems to have reached a higher or lower degree of development. With regard to the rudimentary *Ortstreue* of all these species, their movements are called nomadic by Kalela (1949). Some evolutionary consequences of nomadic habits are briefly discussed by Salomonsen (1955:19) and Svårdson (1957).

A different pattern is present in a number of species with rather strictly fixed breeding ranges but variable winter quarters. These birds are obviously much more similar to the nonirruptive migrants. They always perform two annual movements. The border line between this group and the nonirruptive birds is very diffuse, and many birds show irruptive tendencies insofar as they sometimes discontinue their migration in the presence of particularly rich food sources. A gradual transition between stationary and migratory habits has been demonstrated in recent years, and it seems that the same gradual series is present between irruptive movements, directly and strongly influenced by the food situation, and nonirruptive movements, the course and extent of which are governed by factors other than food. The ultimate factor behind both kinds of movements is the fluctuating food supply in the Temperate Zone.

SUMMARY

A restriction of the term *irruption* is advocated. Closer examination of the migratory habits of certain raptorial birds is necessary before their status as possible irruptive migrants may be established. A list of undoubted irruptive

migrants is presented (Table 1) and discussed. Many types of evidence exist that not even in these species is food the exclusive factor governing the movements. In several irruptive species the postbreeding movement starts irrespective of food conditions, although the latter influence the timing and extent of the movements.

Some questionable cases of irruptive migration are discussed, and population density and meteorological factors as releasers of movements in irruptive migrants are briefly touched upon.

Annual and regional fluctuations in the seed crop of certain trees are reviewed on the basis of a large body of data from Sweden (Table 3) and are correlated with movements observed at Falsterbo bird station in southernmost Sweden. Some cases where agreement was lacking between poor crop and heavy migration are discussed. Svärdson's "pendulum" theory is criticized chiefly on the ground that there is practically no evidence for east-bound postbreeding movements in Scandinavia. An alternative pattern in irruptive movements is suggested. Irruptive migration is considered as an adaptation to reducing the movements as far as possible, and it is put forward that in more fully developed cases irruptive migrants have a multi-annual migratory cycle. The considerable differences between different irruptive species are stressed, and the flexibility of the pattern is pointed out as a possible advantage with regard to the variable winter conditions within cold temperate regions.

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