THE "INVASION" TYPE OF BIRD MIGRATION

By GUNNAR SVÄRDSON

INTRODUCTION

FOOD-SHORTAGE is generally assumed to be involved in those emigrations that are called "irruptions" or "invasions" (these terms of course, being applied in the areas into which the birds come). What it seemed most urgent to explain, therefore, was why the birds leave their home-range in some years but not in others.

Previous discussions have been concentrated on the stimuli that could be involved in the release of the actual irruption flight. A supposed shortage of food—or, alternatively, overpopulation by the birds—has been looked upon as the releasing stimulus. Both could be combined to mean the supply of food per individual bird, or the amount of food obtainable per unit of effort.

Lack, in a recent discussion (1954), placed the food-shortage, whether absolute or relative, as an ultimate factor, while the proximate factor, releasing the actual flight, was supposed to be a high number of birds.

continued...

In this way Lack tried to explain why some of the better-known irruption-species, viz. Crossbills*, Great Spotted Woodpeckers or Nutcrackers, begin their movement so early that food-shortage cannot yet have appeared. Lack found some support in the fact that, before large-scale invasions into Continental Europe, the Scandinavian breeding-populations of the invading species have been observed to be dense. In later sections of this paper, however, another explanation of this fact will appear.

Reinikainen (1937) discussed the normal correlation between the crop of spruce-cones and the number of breeding Crossbills in the Fenno-Scandian forests. He also stressed that the whole population of Crossbills is rather mobile after breeding and that invasions into cone-rich areas occur during the summer. This is, in fact, the general experience of Scandinavian ornithologists. Formosof (1933) pointed out that Siberian Nutcrackers also begin to move after being fledged in July.

It seems, therefore, most simple to suggest that the irruption-species start a flight every year, stimulated by the same factors as the ordinary migrants. The duration and length, however, of this flight is very variable in different years. When the flight is short the birds tend to stay within their normal breeding-range and, accordingly, no irruption or invasion (in the normal use of these words) occurs in such years.. In other years, the flight is not brought to a standstill; the birds continue and are recorded as performing an irruption or invasion.

Instead of asking ourselves why the birds start flying, it may in future be more constructive to ask: why do they stop flying in some years, to become sedentary? If they stop only when they have met with abundant food, there will often be an observable food-shortage within the "home range" of the invading birds, i.e. in the region they have just passed.

THE SEASONAL PASSAGE OF SISKINS AND WHITE WAGTAILS AT OTTENBY

Outside Fenno-Scandia it may not be widely known that hundreds of Swedish ornithologists have for some years co-operated at two famous bird-localities, counting all birds passing during the whole day. These observations have been most continuous at Ottenby, situated at the very south point of the Isle of Öland in the Baltic (see Fig. 1). Thanks to the extreme concentration of the passing birds, which follow the shore or the narrow strip of land (Svärdson, 1953), it has been possible to count almost every one, during all hours of the day, every day and for several consecutive seasons. This extremely time-consuming job was discontinued at Ottenby in the late autumn of 1956, when ten whole seasons had been ornithologically mapped. The task of analysing the enormous amount of material has yet to be begun.

*Scientific names of all bird-species discussed in the text are given in an Appendix on page 340.

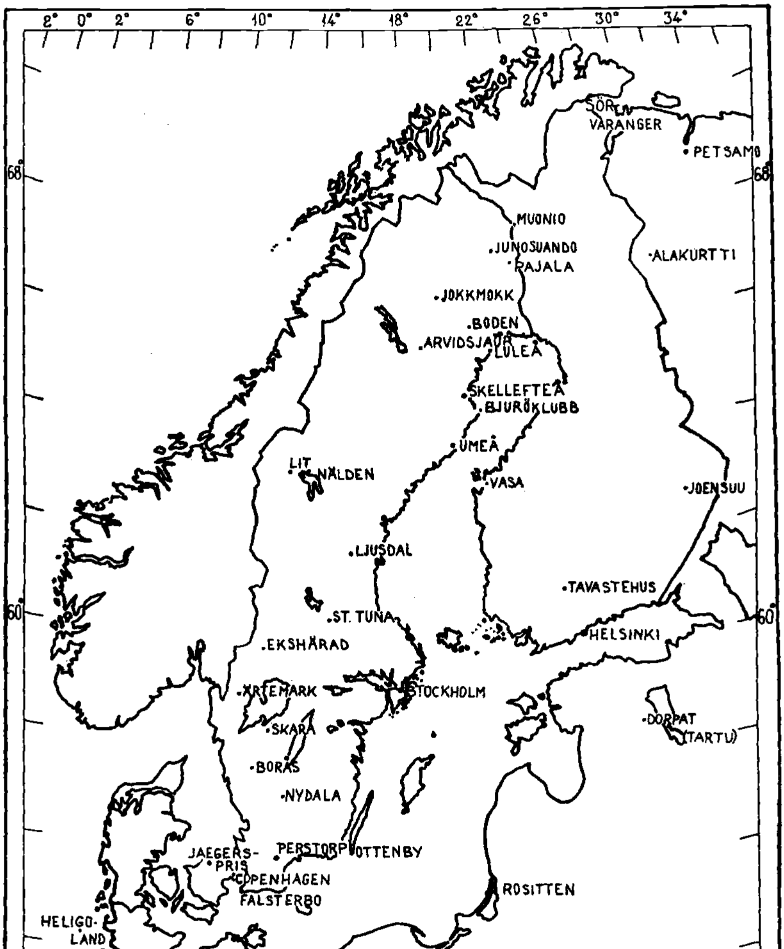

FIG. 1—MAP OF SCANDINAVIA, TO SHOW POSITIONS OF PLACE-NAMES MENTIONED IN THE TEXT

From the Ottenby diaries it is possible to divide the passage of Siskins into half-monthly periods, and so to study the fluctuations in the dates of passage in a pronounced invasion species. For comparison an ordinary migrant, which passes at the same season, has been selected, i.e. the White Wagtail. The data are found in Tables I and II.

TABLE I—PASSAGE OF SISKINS (*Carduelis spinus*) AT OTTENBY, SWEDEN, 1947-1955

Year	Birch-seed index	August 16th-31st	September 1st-15th	September 16th-30th	October 1st-15th	October 16th-31st	Season's total
		Percentage of season's total during					
1955	1.1	—	31	49	13	7	4,019
1949	1.5	3	30	37	25	5	9,752
1947	2.0	—	2	16	75	7	2,685
1952	2.0	—	—	34	52	14	4,311
1953	2.0	—	—	76	18	6	6,541
1951	2.2	—	1	37	46	16	1,233
1950	2.5	—	—	14	75	11	730
1954	2.9	—	—	3	66	31	1,030
1948	3.1	—	1	8	23	68	3,980

TABLE II—PASSAGE OF WHITE WAGTAILS (*Motacilla alba*) AT OTTENBY, SWEDEN, 1947-1955

Year	August 21st-31st	September 1st-10th	September 11th-20th	September 21st-30th	October 1st-10th	October 11th-31st	Season's total
	Percentage of season's total during						
1951	7	41	32	18	2	—	41,927
1950	6	31	35	22	6	—	36,396
1949	10	26	41	22	1	—	34,503
1952	5	38	34	21	2	—	28,327
1955	1	23	31	33	11	1	20,281
1948	5	37	43	11	4	—	20,121
1947	1	2	83	13	1	—	17,037
1954	8	16	29	42	5	—	9,659
1953	5	16	47	26	6	—	7,418

From the publications of the Institute of Experimental Forestry the fructification of birch (*Betula*) is recorded, averaged for the whole of Sweden (for details see a later section) and included in Table I. The seeds of birch and alder (*Alnus*) are the main autumn food for the Siskins. Since no information is available on the food-supply of the White Wagtails, their number was assumed to indicate the food pressure on the individual bird (Table II).

It is seen from the Tables that there is a striking difference between the invading species (Siskin), and the ordinary migrant (White Wagtail). Both display strong numerical fluctuations in their passage-populations, but differ as regards stability of the passage-period. The Siskins pass much earlier in some years than in others. When their food is very scarce, as in 1949 and 1955, roughly a third of the population has gone by the middle of September, but in years of abundant food, as in 1948 and 1954, the first third of the population has not passed until the middle of October. Thus the bulk of Siskin-passage may vary by at least one full month. The White Wagtails, on the contrary, display very small variations in their period of passage. Five times out of nine, the peak passage was in the middle ten-day period of September.

As was observed by Haartman and Bergman (1943), Grenquist (1947), Rudebeck (1950) and Svärdson (1953), the same weather-stimulus acts on invaders as on normal migrants. This was extremely evident in the Siskin passage of 1955, when, as a result of the poor food-supply, the birds on the whole were early. In August and the first days of September, however, the weather was very warm, and no birds arrived. But when a cyclone came after a long period of anticyclonic weather, the colder air behind it caused an avalanche of Siskins at Ottenby on 9th-10th September. In two days a thousand Siskins passed, which was a quarter of the year's total. Before that only two had been seen, on 25th August.

In his review of Waxwing irruptions, Siivonen (1941) found that only the smaller flights were correlated with the food-supply. His arguments, as well as Härm's observations of Waxwings passing some local rich supplies of Rowan (*Sorbus*) berries in Dorpat, Estonia, in autumn 1931 (Schüz, 1933), have often been cited. Also, Lack (1954) is inclined to think that the invading species sometimes turn out to be "migrants", which in this case means that they overshoot regions rich in food. This unfortunately completely misses the essential character of the invading species, which is just their tendency to stay or delay further flight when they meet with a rich food-supply. As they also react to the weather stimulus, however, they might pass over locally good food-resources, when a cold air mass has just released their urge to fly.

Siivonen's results are weakened by the fact that he compares the strength of Waxwing invasions in Hungary with the fructification of the Rowan in Finland, though some invasions may have started in Russia or Siberia.

In the autumn of 1913, moreover, the Rowan, according to data available to Siivonen, had a rich crop of berries in Finland. At the same time a widespread Waxwing invasion occurred in Europe. In the foregoing winter, however, Montell (1917) found Waxwings abundant in Finnish Lapland, a result of the rich fruiting of the Rowan in the autumn of 1912. Therefore, since two good years never follow immediately after each other, Siivonen's data are probably not correct as regards northern Finland.

Summing up, there is strong evidence that invading species discontinue their flight when they meet with abundant food. On the other hand, if abundant food is not found, the wandering is continued until death.

THE SISKIN INVASION OF 1949

In an analysis of results from ringing in Belgium, Verheyen (1956) found the passage of Siskins in 1949 exceptional. Instead of wintering in Belgium or northern France, the birds of this great irruption passed through these countries, and ringed ones were recorded in southern France and Spain. This has a parallel in the records of Ottenby Bird Observatory. Of the exceptional number of Siskins passing there in 1949, some 500 were ringed and five of them were recorded in the following winter in Italy, France and Spain. The movement of Siskins in 1949 is thus similar to the greater irruptions of the Waxwings, which are built up by huge numbers of birds, start early and extend far south of the normal winter-range.

Verheyen thought the invading Siskins of 1949 came from Ural or some other eastern region. But in the spring of 1949 the breeding population of Siskins was exceptional in Sweden and therefore the birds were probably Scandinavian. It is often difficult to prove a population peak of a species which breeds regularly, but the Siskins were so numerous in 1949 that this was spontaneously reported by many ornithologists. Larsson (1952) found the Siskin abundantly breeding in south-western Sweden, near the town of Skara, in 1949. He thought they had two broods as nests were found from the latter half of April to the middle of June. They appeared in the locality (Helås) together with Redpolls which wintered. The winter was rich in spruce seeds and the autumn of 1948 also rich in other sorts of seeds (*cf.* Table I).

Large flocks of Siskins and Redpolls also wintered during 1948-1949 at the town of Borås (Rösiö, 1952) and Siskins bred there in 1949 when Crossbills were also numerous in the rich cone-supply of the forests.

In most years, Siskins do not breed in northernmost Sweden, but in 1949 the population of breeding Siskins was huge in these regions also. Blomgren (1951) found the year to be a peak one at Harads, not very far from the town of Luleå, and Brännström (1952) located some nests in the parish of Arvidsjaur, Lapland, where the birds normally do not breed.

It is well known that Siskins, as well as some other birds of the forest region of northern Sweden, have peak years when they breed much further to the north. The spring of 1949 was then such a peak year for Siskins, though 1935 may have been still better. Both springs were rich in spruce-seeds.

The rise of the population is very sudden and not due to propagation. Instead, immigration is very clearly the explanation of the peak. This immigration starts during the previous autumn, when birds are accumulating in the forests, rich in food. Therefore, the immigration in the autumn of 1948 was the ultimate cause of the high breeding-population of the spring of 1949. After breeding this population made a movement southwards in the autumn of 1949, appearing as an "irruption" in the southern part of their potential winter range, i.e. France and Spain.

Since an accumulation of Siskins in Sweden cannot occur unless birds come from the east (few breed in Norway), we must seek the explanation in an irruption of Siskins from the east.

We now begin to see how the system works in practice. The invading birds move mainly westwards (or eastwards) over their potential breeding-range, being gradually absorbed by those regions in which food is most abundant. They may or may not leave this region for a period in winter, returning in spring to breed in the region located in autumn. After breeding a new search for the next year's breeding area begins.

Verheyen may be right, when he suggests that the Siskins originated from Ural. If so, however, they arrived in Scandinavia in 1948, the year in which no invasion was noted in Sweden, though the number of Siskins (and Redpolls!) was rather high at Ottenby (Svärdson, 1949, 1950). The birds which invaded Belgium in 1949 were probably Scandinavian, and mostly Swedish. Their concentration in western Europe may have been caused by the Atlantic coast functioning as a guiding-line. We are now faced with a new problem: why did not the Siskins of 1949 start for a return flight eastwards, into the vast regions of spruce forests of Russia? We will meet this problem again related to some other invasions of recent years.

THE WAXWING AND REDPOLL INVASIONS OF 1931

There was a wide-spread irruption of Waxwings in Europe in the autumn of 1931 (Stresemann, 1932; Schüz, 1933; Tischler, 1941; Witherby *et al.*, 1938). It was also noticed in Denmark (Kjaer, 1932; Løppenthin, 1932) and in southern Sweden (Behm and Lönnberg, 1931). Even in the middle of October Waxwings were observed in central and southern Sweden. This was about six weeks earlier than is normal and their numbers were much larger than usual. Redpolls invaded northern Germany at the same time (Stresemann, 1932; Bährmann, 1932; Tischler, 1941). Both irruptions started from northern Fenno-Scandia and it is now possible to reconstruct their earlier history.

The Redpolls appeared in vast numbers in eastern Finland in October 1930. In Karelia, especially in the vicinity of Joensuu, they increased until in February 1931 they were reported almost everywhere (Pynnönen, 1934). In spring most of them disappeared from Joensuu, but some remained and bred, which is a remarkably far southern locality. Along the whole south coast of Finland, however, vast numbers of Redpolls appeared in April, from Helsinki to the Russian frontier, and later they spread to Wasa further to the north. In the latter half of April they began to disappear from southern Finland (Qvarnström, 1931) and for a short spell in the same month they also appeared in masses on the Swedish side of the Baltic, in the province of Hälsingland (Witt-Strömer, 1931).

Since there was a bad cone-winter in the spruce-forests no Redpolls were reported as breeding in southern Finland or middle Sweden, apart from Karelia. The Redpolls must have travelled farther north for breeding and this was verified by the reports from Stuart Baker and Hortling to Qvarnström (1931) that Redpolls bred numerously in the arctic part of Fenno-Scandia in the summer of 1931. Breeding of the E. Scandinavian race *C. f. holboellii* was proved, as also of the Arctic Redpoll. Nests of the latter species were found in 1931 in Petsamo by Merikallio (1934).

It is interesting that one specimen of *C. f. holboelli* was shot by Bährmann (1932) on 24th November 1931 in the province of Brandenburg in Germany. It fell from a flock of the invading Redpolls.

The evidence about the Waxwing is equally convincing. In the winter of 1930-31 Fenno-Scandia was invaded by a huge wave of Waxwings, arriving from the east. Rowan berries were extremely abundant over all the region, as was stressed in a number of published reports about the Waxwings. This abundant supply of food led to wintering in northern Fenno-Scandia by almost all the Waxwings! Their scarcity was commented upon from southern localities.

Large flocks of Waxwings appeared near Helsinki on 16th January 1931 (Hortling, 1931). At Wasa in Finland they did not arrive until the second week in February (Tegengren, 1931). On the Swedish side of the Baltic, they appeared in February-March at Luleå and remained there for the rest of the winter (Holm, 1935). In Jämtland, almost in central Sweden, the Waxwings also wintered, which has happened only once before (Nilsson, 1944). Everywhere they fed on the Rowan berries, which were so numerous that the Waxwings could eat them the whole winter. Normally the supply is soon exhausted.

Siivonen (1941) says the abundant Waxwing breeding in northern Finland and Sweden in the summer of 1931 was the result of a normal population increase. It is true that this sudden rise of the population is normal both for the Waxwing and other invading species, but it is by no means a gradual increase due to natural propagation. On the contrary, we know that the abundant breeding of 1931 was due to the fact that the invading and wintering Waxwings remained to nest. It is known that the Waxwing in spring also feeds on frozen berries from the previous autumn, notably berries of Crowberry (*Empetrum*), Bearberry (*Arctostaphylos*) and Cowberry (*Vaccinium*) (Finnila, 1914). No data exist on the abundance of these berries in 1930, but they often follow the Rowan.

Nilsson has described the breeding in some detail for Nälden in Jämtland, where in his long experience Waxwings have bred only in 1931. In April of that year flocks of 10-20 Waxwings were observed flying around in the forests, but though this was Nilsson's first observation of Waxwings in spring since the beginning of the century, he did not realize at first that they would remain and breed. But in May and June the birds were still there, and finally he located several pairs and found four nests (Nilsson, 1944). The same process was no doubt going on over vast areas. Along the Swedish coast of the northern-most Baltic, where normally no Waxwings nest, the birds bred abundantly in the summer 1931, even on small isles off the coast (Holm, 1935). Nests were found also in Pajala, in the forest region (Lönnberg, 1931).

Thus, the irruptions of Waxwings and Redpolls in the autumn of 1931 into the regions south and south-west of Fenno-Scandia were made by the abundant breeders of the summer of 1931. These, however, had arrived from the east in the late autumn of 1930.

The Waxwings returned to Fenno-Scandia to breed abundantly also in the summer of 1932 (Holm, 1935) and an "echo-flight" was observed in Europe in the winter of 1932-33 (Schüz, 1934). This second invasion was for the most part weaker than the first, except in Norway (Løvenskiold, 1947) and Hungary (Schüz). Anyhow, in the spring of 1933 the survivors must have flown to the east, as hardly any breeding was reported in Fenno-Scandia during 1933-1936.

THE CROSSBILL INVASION OF 1942

In 1942 Crossbills started a large-scale irruption westwards from a region east and north-east of Germany (Drost and Schüz, 1942). Reports from the German soldiers in Russia showed that the movement was observed as far east as the River Volchow on the southern shore of Lake Ladoga (Hornberger, 1943). Crossbills were also observed in Schleswig-Holstein (Emeis, 1942) and in the Netherlands (Bos *et al.*, 1943), and they arrived in great numbers in the British Isles.

The movement was in full swing from the latter half of May and gradually died down in late summer, as is usual with the Crossbills. At that time they had accumulated in those areas where the fructification of spruce was good. This was the case in almost the whole of central Europe as well as in parts of Finno-Scandia (Sweden). The wooded mountains of Thüringer Wald as well as Schwarzwald had a fine Crossbill winter. In 1943, breeding was proved abundantly in Germany and also in Denmark (Hornberger, 1943).

In Sweden the cone-crop of the spruce was excellent over the whole country. It was the best crop since the winter of 1931-32 and was rivalled later only by the winter of 1954-55. As regards Crossbills, however, the winter of 1942-43 was probably the richest in Sweden for a really long time, due to the rare combination of fine cone-crop *and* a great invasion from the east. In 1931-32 the Crossbills were in fact few (Rosenberg, 1935) and in 1954-55 they were only moderately numerous. The correlation found by Reinikainen (1937) therefore is not always so positive as indicated by his material.

The summer-invasion of 1942 was noted in Sweden at Falsterbo (Rudebeck, 1943) and Hälssleholm (Linder, 1942), in Ärtemark in western Sweden (Karvik, 1942) and many flocks headed west at Jokkmokk in Lapland (Bollvik, 1943). Nests were found in February-March 1943 at Harads near Luleå (Blomgren, 1944); the Crossbills were abundant near Boden (Herner, 1944) and they appeared in the province of Norrbotten in "enormous numbers"

(Holm, 1945). Ten nests were found at Lit in Jämtland in a small area (2 acres) of young spruce (Jonsson, 1949), 2 nests were located near Ljusdal (Witt-Strömer, 1950) and 4 nests were found near St. Tuna in the province of Dalarna (Frendin, 1943); Crossbills had their "richest season of breeding" at Ekshärad, Värmland (Hannerz, 1945), were numerous in Nydala, further south in Småland (Jakobson, 1945) and were often observed at Perstorp, northern Scania (Lilja, 1946). Several Crossbills nested near Copenhagen (Nielsen, 1943), the species occurred in "masses" at Jaegerspris, northern Sjaelland (Holstein, 1954), and many bred in Jutland in the conifer plantations (Poulsen, 1947).

There was also an earlier, but smaller, invasion in the summer and autumn of 1941 (Rudebeck, 1948). Some Crossbills bred in Sweden and Denmark in the spring of 1942, but further east the population seems to have been more dense, i.e. near Alakurtti, north-eastern Finland (67°N, 30°E) (Franz, 1942), at the south end of the great Lake Onega (Perttula, 1944) as well as along the River Svir (Syväri) between Lake Onega and Lake Ladoga (Klockars, 1944). The area of emigration for the 1942-invasion thus seems to have been confined to eastern Fenno-Scandia and north-western Russia, possibly also the central part of the European part of Russia.

In May 1943, after the abundant breeding from northern Sweden to southern Germany there was an exceptionally dense population of Crossbills in this western fringe of their enormous potential breeding area (Fig. 2). And what happened to them? They all returned back, eastwards! No observations of east-flying Crossbills in 1943 were published in Sweden, but in Germany, with its better guiding lines for birds flying east, things were different. Hornberger (1943) reported east-going flocks from February on, though most were later, in May, June and July, i.e. the normal annual movement-time for Crossbills. In Hanover, Mark, Rheinland and Ostpommern, birds were seen flying north-east or east. In East Prussia movement was intense from the start in February to the peak in June. On 11th June 1943 no less than 3,460 Crossbills were counted flying north-east over the Frische Nehrung, a narrow strip of sand some distance from the Baltic shore. Also, farther inland, many more were seen in Losgehnen between 22nd April and 26th June than ever before in spring time (Hornberger, 1943).

In the late summer and autumn of 1943 all were gone from Sweden and the woods were emptied not only of Crossbills but also of cones. There was hardly any flowering of the spruce in the spring of 1943.

THE FIELDFARE INVASION OF 1937

Every third or fourth winter Scandinavia is invaded by huge masses of Fieldfares, which in some cases remain to breed in the following spring. In the winter of 1936-37 such an invasion

FIG. 2—THE BREEDING-DISTRIBUTION OF THE CROSSBILL (*Loxia c. curvirostra*)
Drawn after Dementiev and Gladkov (1954), but modified in Europe according to the spontaneous occurrence of Norway Spruce (*Picea abies*).

appeared, but it came exceptionally late. Due no doubt to the weather, a number of other bird species were also late and great "hard-weather movements" of migrants occurred at Heligoland during January 1937 (Drost, 1937).

From 28th January onwards thousands of Fieldfares appeared at Stockholm and other localities in the vicinity. Lönnberg (1937) was interested in their obvious eastern origin and asked ornithologists living in the north for information. Mr. Sune Hederström reported from Bjuröklubb, some 40 kilometres S.E. of Skellefteå on the Bothnian coast, that at least a thousand Fieldfares appeared there on 26th January. Later they flooded the town of Skellefteå and there were estimated to be "several tens of thousands". From the town of Umeå Mr. O. Holm reported large flocks of Fieldfares during the very first days of February. They were accompanied by Waxwings and both species fed on the Rowan berries, of which there was a fine crop.

This invasion had some extraordinary consequences, which were not realized until Salomonsen (1951) announced the immigration and breeding of the Fieldfare in Greenland. The reconstruction by Salomonsen, however, that the immigration followed a flight from south Norway "in the afternoon of 19 Jan. 1937" downwind to Jan Mayen and Ymer Island on N.E. Greenland seems rather improbable to the present writer. The birds recorded on 20th January probably belonged to a different wave from those recorded flying southwards in western Greenland during 27th-31st January. There is a week between the two sets of records and, moreover, the birds that were drifted to Ymer Island on the east coast of Greenland would have had to survive the week in a very severe environment. Death seems more likely to have been the fate of the birds of 20th January.

There is, however, a suggestive coincidence in the appearance of the huge masses of Fieldfares in Sweden and in western Greenland. They first occurred on 26th January in north-eastern Sweden, on 27th January on the west coast of Greenland and on 28th January at Stockholm, further south in Sweden. If they had started somewhere on the Taimyr peninsula in Siberia the distance would have been the same to Godthåbsfjord in Greenland as to Stockholm in Sweden! The distance is of the same magnitude as a transatlantic flight, which is known to be performed by some birds. The darkness of the arctic region during January may have stimulated the birds to continue flying for an exceptional distance.

The same agent that caused the sudden "winter-flights" of various birds during January 1937 may have had something to do also with the situation that led to a drift of Russian or Siberian Fieldfares out over the Arctic Ocean. There was no exceptional strength to the gale which Salomonsen thought to be responsible for driving the Fieldfares across the Atlantic Ocean. Fieldfares are probably on the move off the Norwegian coast almost every winter and the gales are there too. But the Fieldfare was new to the Nearctic fauna in 1937 and this stresses the remarkable nature of the events that led to the transatlantic colonization.

A further spread of the Fieldfare in the Nearctic seems very probable.

BREEDING AFTER INVASIONS AND THE DIRECTION OF FLIGHT

Invasions are often followed by breeding in the invaded area. This fact has been stressed by Kalela (1949) but otherwise this significant trait is often neglected in the literature. Also the dominant westerly trend is a characteristic of an invasion movement, which adds to the principal differences between invasion and ordinary migration.

In order to give further evidence of these traits, some other recorded invasions may be surveyed shortly.

The Two-barred Crossbill invades Scandinavia from Russia or Siberia in some years, chiefly during the larger movements of Crossbills. Their western trend is so pronounced that up to 1940 (Tischler, 1941) only two records were known for East Prussia. The second was in 1930, when again the species was much more abundant in Fenno-Scandia. Hortling (1931b) saw the largest flock, one of 40, but flocks were observed in that year by many ornithologists in Finland, Sweden, Norway and Denmark.

The post-invasion breeding is not related to the size of the movement but to the fructification of spruce seeds. If the crop is bad, Two-barred Crossbills do not remain in Scandinavia at all, but continue—and are almost certainly lost over the Atlantic. In other years, as in 1903, 1914 and 1926, nesting was proved after winters rich in cones.

The Siberian Nutcracker often has a marked westerly course. In the movement of 1931 many Nutcrackers were observed in Finland (Hortling, 1931a) and Sweden (Lönnberg, 1931b), but comparatively few passed through East Prussia (Tischler, 1941). As these Nutcrackers never meet with their main food, the seeds of the Arolla Pine (*Pinus cembra*), they hardly ever stop and the invasions become real death-wanderings. After the 1911 movement, however, nesting was proved in 1912 in Denmark (Jespersen, 1913) and during the 1954 movement two of these birds were fed by the lighthouse-keepers on the isle of Gotska Sandön in the Baltic. They bred in June 1955 and appeared with their young at the feeding-place (Lundberg, 1955).

The Russian or Siberian subspecies *biedermanni* of the Nuthatch has made some westerly invasions over Finland and into northernmost Sweden, especially in the winter of 1900-01 and again in 1951-52. Breeding occurred in the spring of 1952 at Junosuando (67° 30′N.) in Sweden after regular feeding at a "bird-table" (Svärdson, 1955a).

The Long-tailed Tit also invades Sweden from the east in some autumns. After some of these wanderings, the breeding population is greatly increased, as in the years 1925, 1930 and 1935

(Svärdson, 1935; Durango, 1941). It is not known what kind of food is involved in this case.

Roughly every third or fourth autumn the Bullfinch is also on the move. Its population peaks have not been recorded in Sweden, but in Denmark the subspecies *pyrrhula* was formerly known only as a winter-visitor. In the winter of 1933-34 many were observed at Jaegerspris, Sjaelland; they remained in the spring and Holstein (1935) could report at least nine pairs breeding. This certainly was due to a rich supply of spruce seeds, as the Siskins, which had been abundant winter-visitors too, also remained and bred (Holstein, 1934).

There was a big influx of Great Spotted Woodpeckers in central Europe in the late summer of 1929. In the alpine region there was an exceptionally rich crop of spruce-seeds in the spring of 1930 (Geyr von Schweppenburg, 1930). The participants of the 1929 movement which happened to find this area of rich food remained to breed. This was followed by a second invasion of young birds in August 1930 in Italy (Duse, 1932) which had not been visited in the movement of 1929. To take an example from the opposite limit of distribution of this species: after the great 1909 movement the Great Spotted Woodpecker bred in 1910 in Sør-Varanger in northermost Norway at 70°N. (Løvenskiold, 1947).

That the rodent-eating birds—owls, some raptors, skuas and shrikes—behave in just the same manner is better known. Their power of locating an area rich in food and gathering there—also for breeding—is commented upon in many books (cf. Hagen, 1952). Both the predators and the vegetarian birds therefore have one important stimulus in common: a rich supply of food depresses their mobility and releases a sedentary habit.

The direction of flight is often mainly west. But as most ornithologists live on the western fringe of the land-masses of the Old World, their opinion of the general direction of invasions is sometimes influenced by guiding-line effects on the birds. The Crossbill irruption of 1953 probably originated in the central part of European Russia, as Bubnov (1956) reported exceptionally abundant Crossbills during the winter of 1952-53 in the district of Kostroma, some 200 miles N.E. of Moscow (58°N., 41°E.). Their main direction of movement was therefore westerly. In several irruptions Crossbills ringed on Heligoland or Fair Isle later turned sharply off and were found in Italy. In this way a wrong opinion of the standard direction of the birds could easily occur. Schaanning (1948) demonstrated the strong western preference of the ringed Fieldfares from Scandinavia which were later found in France. They had taken a trip over the British Isles before reaching their wintering area, south-westwards from Scandinavia.

Obviously, however, invasions cannot always have a westerly course. We have already met with eastern movements of Waxwings (in 1933) and of Crossbills (in 1943) back into the vast taiga zone of Russia. Some ornithologists (Svante Wendel, Harry Lundin) have kindly reported summer observations of Crossbills leaving the Swedish Baltic coast to fly eastwards, and in Finland a concentrated east-going movement of Crossbills was observed near Tavastehus, Finland on 2nd and 3rd July 1948 (Nuorteva, 1952). Johansen (1944) found some vagrant Parrot Crossbills at Novosibirsk in 1935, a year of great westerly movements of Crossbills in Europe. He says that either there are isolated, unknown colonies of Parrot Crossbills in Siberia, or one is prompted to suggest that invasions from Europe may reach Siberia in certain years.

As already pointed out, most ornithologists live on the western fringe of the great Eurasian land-mass and they would, of course, observe only invasions to the west. The east-going movements—which one deduces occur more frequently than has actually been shown—could be observed only by Russian ornithologists.

INVASION AS AN ADAPTATION

"Well-developed homing behaviour is a necessary concomitant of territorial behaviour and hence shares the advantages of the latter—even spreading of the population, assurance of food supply, segregation during courtship, etc. Intraspecific competition is reduced by the avoidance of what might seem to be a natural tendency to settle in the first favourable area encountered on migration. Indeed, without homing all regular migration would break down."—(Matthews, 1955).

Intraspecific competition is no less in the winter-quarters and hence natural selection tends to make allopatric populations allohiemic, i.e. they have different winter-ranges (Salomonsen, 1955). The habit of homing both to the summer- and to the winter-areas tends to break up many bird populations into smaller, elementary populations (Isakov, cited by Salomonsen).

There is one important supposition, however, in this evolutionary thinking about the direction of natural selection. If birds return to their last breeding- or winter-area only to find it less rich in food than other areas, they are not favoured by natural selection. Those individuals on the contrary, which performed a less precise homing but could locate areas rich in food and remained there, would in fact be the most probable survivors.

It follows that ordinary migration, with its homing and seasonal stability, is an adaptation to a *seasonal* food shortage, while the *annual* differences between the food-supply of corresponding seasons are slight and insignificant from an evolutionary point of view.

Invasion is, on the contrary, an adaptation to annual differences between seasons. In its most developed form, in the Crossbills, the whole population moves once a year, in summer, from one breeding-area to the next. The shift is performed during those months in which there is a natural minimum of spruce seeds in the cones, as the new crop begins to ripen in August. At that time the new breeding-area is normally found.

Invasion tendencies are differently evolved in different species, according to the average food variations. The Siskin has to move in such a way as to meet seasonal as well as annual food differences. It behaves in autumn more or less like a migrant, but has a varying winter-range and a very varying breeding-range.

The Brambling has evolved the capacity of locating areas of rich crops of beechmast in winter. It is mainly known as a winter invader into different parts of Europe. Its invasion tendencies in summer are much less evolved, because of its insect diet at this time of the year. Nevertheless, it has repeatedly bred south of its range, and cold springs have been put forward as the cause. As suggested by Kalela (1949), however, these southern breeding records come after winter invasions, which are probably more responsible than any cold weather.

In many species of birds there is a delicate balance of three selective forces, that which results in ordinary migration, that which leads to invasion and finally that which results in completely sedentary habits. Related species may behave differently and, moreover, subspecies may differ, as in the Nuthatch. Northern subspecies may often be more irruptive than southern ones, as is indicated by many of the distribution maps in Dementiev and Gladkov (1954) which give wide east-west ranges to the northernmost races.

It is not possible to put every Swedish bird into mainly one category or another, but some 40 species have displayed invasion tendencies. This proves that the habit is common and the selection behind it rather intense.

In recent years the navigating ability of birds has been widely discussed. Irruption species seem to have an extra ability, that of locating food. How they find these regions is at present not at all understood, but, since a faculty for the rapid finding of food must be of survival value in the species, they have probably evolved a special sensitivity to sign-stimuli: perhaps, for example, the birds react to slight colour-differences in the woods, caused by the frequency of cones and seeds, as well as to the appearance of vegetation damaged by rodents. In this way Crossbills, Redpolls, Waxwings and Fieldfares, which move along fairly high in the air, could direct their further flight according to sign-stimuli reaching them from perhaps almost as far as the horizon. Their search would thus be a random one, but not a search like that of a foraging party of tits, working its way through the trees; instead it would be an optical search over a really wide range.

Those invasion birds which might find food somewhere within the taiga zone all year round have no encouragement to fly south or south-west. Their chances of finding food are greatest if they fly due west *or* due east. But a population of Crossbills, or the young of Great Spotted Woodpeckers or Nutcrackers, cannot, of course, fly west every year. The species would then soon become extinct. Some sort of pendulum flight must occur, where invasions of subsequent years tend to go in different main directions. This would be possible if the old birds, after breeding, returned in the opposite direction to that in which they had travelled the previous year as young birds. For Crossbills and Waxwings such a system would approximately work, but the partial invasion species, such as Great Spotted Woodpeckers and Nutcrackers, where all the invaders are young birds, seem more complicated. The navigation skill and standard direction of invasion birds is a fascinating problem!

To save space, an outline comparison of invasion and ordinary migration is made below:

Subject of comparison	*Invasion*	*Ordinary migration*
Ultimate factor	Escape from food shortage during a certain *year*	Escape from food shortage during a certain *season*
Proximate factors, releasing the flight	1. Hormonal change, acting through metabolism, anchored by photoperiodism 2. Temperature, visibility, stability of air, time of day	1. Hormonal change, acting through metabolism, anchored by photoperiodism 2. Temperature, visibility, stability of air, time of day
Participants	The whole population or only part, particularly the young or females	The whole population or only part, particularly the young or females
Retarding stimulus of abundant food	Effect *very strong*	Effect *slight*
Tendency to return to the home or winter range of last year	Very *weak*	*Strong*
Performance of movement	*Irregular* in time and space	*Regular* in time and space
Breeding range	*Fluctuating*	*Constant*
Distribution of population	*Accumulation in areas rich in food*	*Population evenly spread*
Aim of navigation	*Location of food*	*Homing*
Clutches	*Variable* in numbers and size	*Less variable*
Subspeciation	*Less* rapid	*More* rapid
Peak performance	Crossbills: the whole population moves *once a year*, in *summer*, *west*wards *or east*wards	Terns, Swallows: the whole population moves *twice a year*, *spring* and *autumn*, *north*wards *and south*wards

THE RHYTHM OF SPRUCE-FRUCTIFICATION AND ITS CONSEQUENCES

The economic importance of spruce and pine has led to records of their seed production in Sweden being kept for a number of years. The whole country was divided into about one hundred small districts, from which the local forestry staff estimated the cone-crops every autumn and reported it as falling into one of the following five categories:

0	1	2	3	4
none	very few	not good	good	rich supply

This system has its obvious shortcomings. But some of the errors in judgement by the local supervisor are later revised as the reports are gathered and commented upon by those working on a regional level. Eventually all reports are given over to the Institute of Experimental Forestry, which annually publishes a pamphlet about the fructification (and flowering) of some selected species.

Tirén (1935) summarized the conclusions from the recorded fluctuations of spruce-fructification between 1895 and 1934. Through the courtesy of Professor Tirén later data have been available to the present writer. The material now covers 60 years.

The reports have been grouped into three regions, showing the combined values of the autumn cone crop in southern, central and northern Sweden (Fig. 3). Every figure is based on roughly 30 local reports.

The spruce seed ripens in autumn and falls out from the cone during spring, mostly in April-May. The data given in Fig. 3 for a certain autumn therefore mean that the supply of seeds the following winter was the same as for the autumn. It can be seen that the winters 1913-14, 1915-16, 1921-22, 1928-29, 1931-32, 1934-35, 1942-43, 1954-55 were rich in spruce cones over the whole of Sweden.

The conclusion, drawn already by Tirén (1935), that winters rich in cones come more often in southern than in northern Sweden is confirmed in the more recent observations. It may be difficult to find a regular rhythm in northern Sweden, but in southern Sweden it is quite clear that a *rich cone-winter comes every third* or fourth year. It is also obvious from Fig. 3 that the better the crop of cones is in one winter, the worse it must be the following winter. It may be pointed out here that Formosof (1933) reported a similar rhythm of fructification of the Arolla Pine (*Pinus cembra*).

Tirén pointed out that the rhythm was the result of two factors which determine the richness of flowering in spruce. High temperature during a sensitive period of the summer (June , early July) causes many buds to become flower-buds, instead of purely vegetation buds, giving rise to shoots. This results in rich flowering in the following spring, and many cones in the autumn. Secondly, after coning the trees become "tired", which means that they need an interval of some few years to be able to react again to the temperature. This also means that, for reaction, a gradually lower temperature stimulus is needed after a longer interval. These factors give the recorded rhythm to the tree. Nutrition is certainly

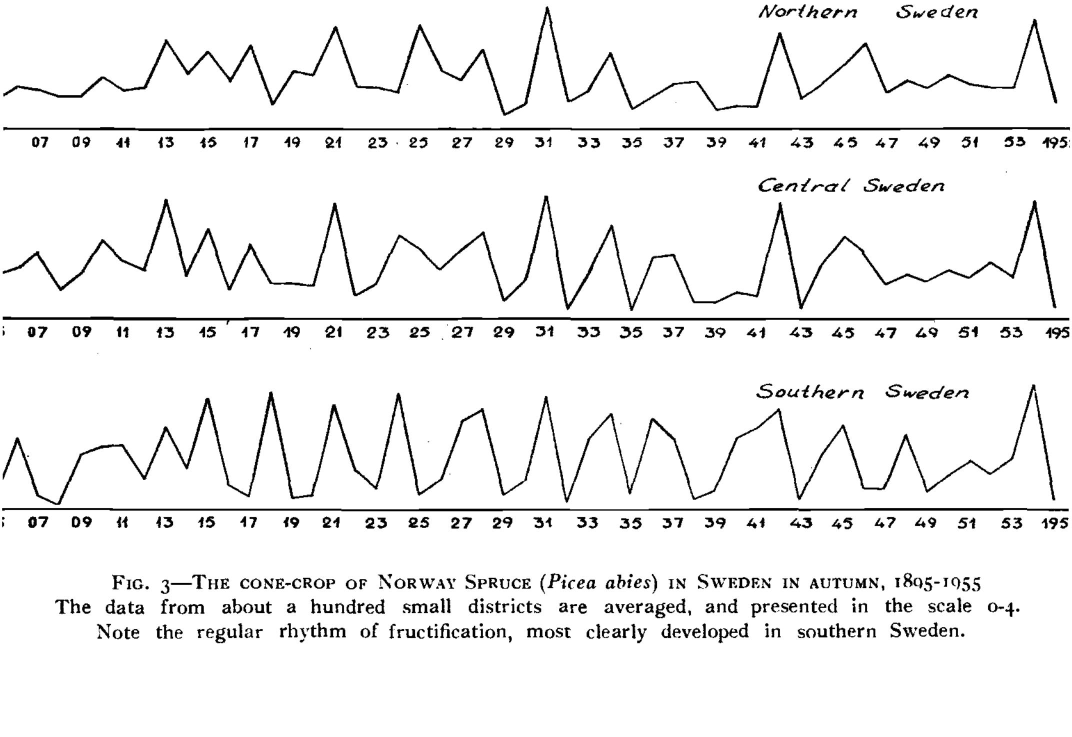

FIG. 3—THE CONE-CROP OF NORWAY SPRUCE (*Picea abies*) IN SWEDEN IN AUTUMN, 1895-1955
The data from about a hundred small districts are averaged, and presented in the scale 0-4. Note the regular rhythm of fructification, most clearly developed in southern Sweden.

involved as well, since isolated trees have more cones than trees in the forests.

The spruce seeds are eaten by a lot of birds in winter. During the winter of 1954-55 the writer observed Nuthatches and Marsh Tits, among other birds, feeding on the cones.

The Crossbills, Redpolls and Siskins all feed spruce seeds to their young. The March breeding of the Crossbills has in seed years a counterpart in the extremely early breeding of the Redpolls. In March-April 1955 some Redpoll nests were found containing eggs and young when the ground was covered by eighteen inches of snow and the temperature was −20°C. (Witt-Strömer and Ingritz, 1956). The spring of 1932 was also rich in spruce seeds (*cf.* Fig. 3). In that spring Swanberg (1939) found Redpolls nesting in March within the coniferous region and again in late June in the Salix region of the high mountains in Lapland. Young birds accompanied the breeding females in the mountains. The second brood is raised on insects and there is probably only this one brood in a year when the spruce has few seeds. The Siskin also has bred early in seed-rich years (G. von Schweppenburg, 1930; Hederström, 1944). The latter author found a young Siskin, just fledged, at Skellefteå, at the very northern limit of the species, on 1st May 1943. The species is probably double-brooded in such years. There are few observation on Crossbills having second broods, but Hallberg (*in litt.*) has seen cases where young birds were associated with, and being fed by, males or females that had nests with eggs. These were in May.

Not only birds, however, follow the rhythm of the spruce. The Red Squirrel (*Sciurus vulgaris*) (Vartio, 1946; Lampio, 1948) feeds predominantly on flower-buds and spruce-seeds and, therefore, after a warm bud-forming summer, this mammal experiences two rich winters in succession, first one of buds and a second of seeds. The squirrel then has larger and more litters and a population peak follows, probably mostly because of the lower winter mortality. Afterwards, however, there is a population crash. In the autumn of 1943, at the same time as there was a big emigration of several bird-species from Scandinavia, the squirrel population was locally in some few months reduced to 1/450th of its former size (Lampio, 1948).

Emigrations of squirrels have been observed on several occasions at times of population crashes. In the autumn of 1914, after a population-peak due to the fine seed-winter of 1913-14 (*cf.* Fig. 3), emigrations were recorded in several localities. In one place 150 squirrels were shot in one single garden into which they had come to feed on apples; and 70 were watched when they swam over a narrow part of the Lake Hjälmaren, 220 yards wide. At the same time several were seen swimming over lakes in northern Sweden (Olofsson, 1916).

Squirrels are taken by Buzzards and Goshawks, and in large numbers by the Pine Marten (*Martes martes*). This last predator

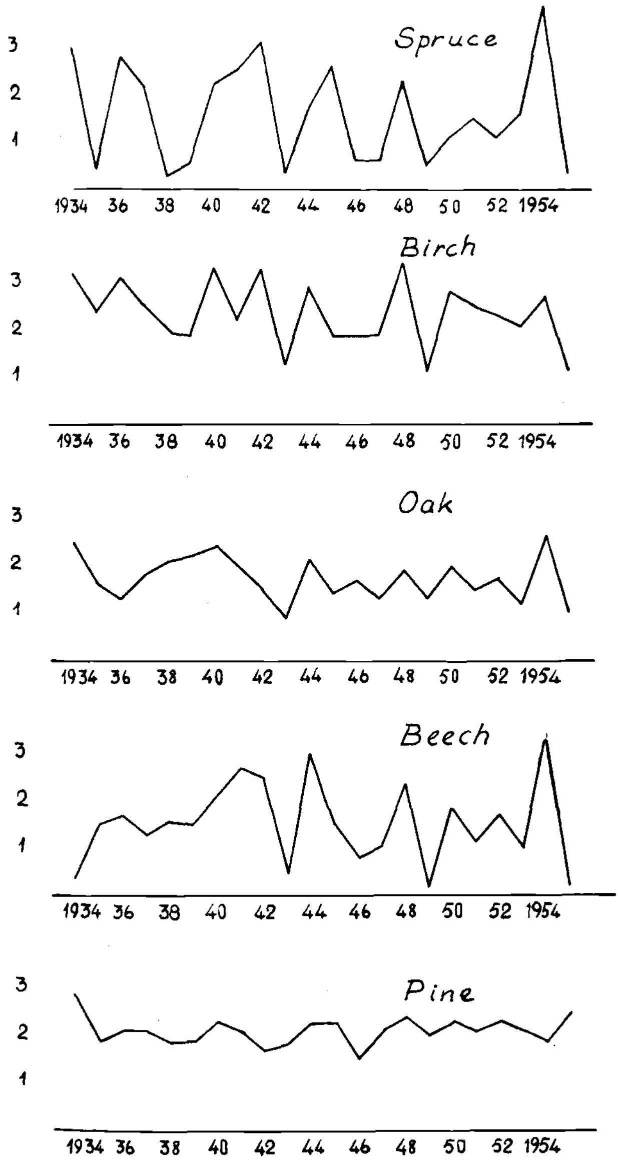

FIG. 4—THE FRUITING OF SPRUCE (*Picea*), BIRCH (*Betula*), OAK (*Quercus*), BEECH (*Fagus*)AND PINE (*Pinus*) IN SOUTHERN SWEDEN, 1934-1954

The data from about thirty small districts are averaged, and presented in the scale 0-4. The rhythms of these trees are mostly synchronous, except for pine, the cones of which take a second year to mature, so that they are out of step with the rest.

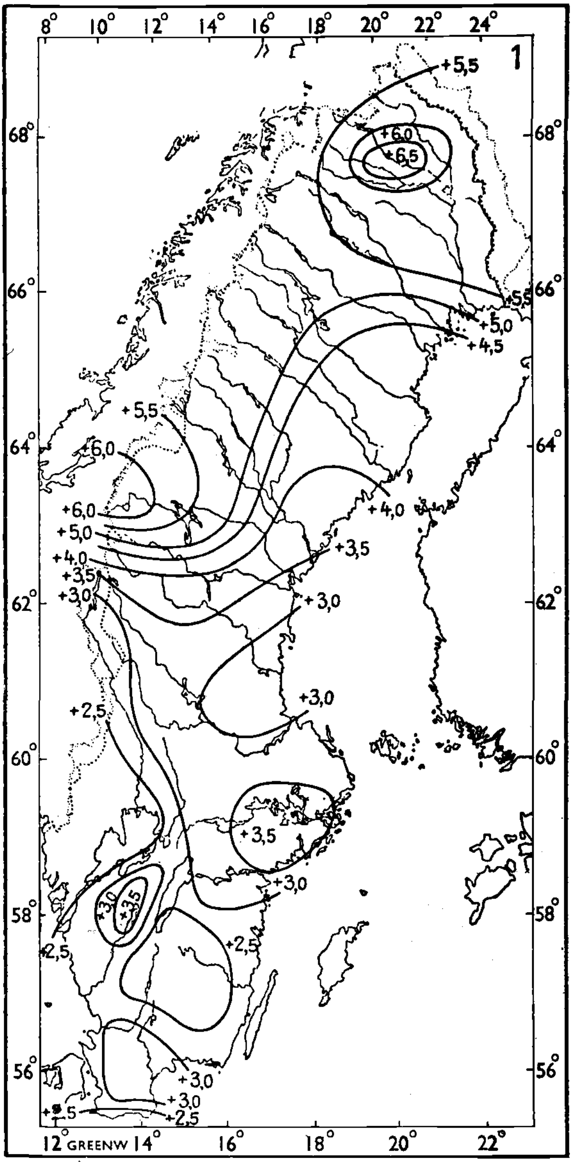

FIG. 5—THE DEVIATION FROM THE MEAN OF THE JUNE-TEMPERATURES (CENTIGRADE) IN SWEDEN IN 1953

The map is taken from the year-book of the Swedish Institute of Meteorology and Hydrology. This warm month caused a "bud-winter" in 1953-54 and a "seed-winter" in 1954-55. Population-peaks of game-birds (Galliformes) and Red Squirrels (*Sciurus vulgaris*), as well as emigrations of birds, e.g. Jays (*Garrulus glandarius*) in autumn 1955, were among its consequences.

fluctuates according to the number of squirrels (Lampio, 1948). There is thus a proved food-chain running like this: spruce rhythm—squirrels—martens.

When the spruce seed falls to the ground, it is an important food for some ground-living rodents (*Myopus schisticolor, Microtus agrestis, Apodemus sylvaticus and A. flavicollis*). *Myopus,* the Wood-Lemming, had population peaks in central Sweden in 1895, 1935 and 1945. All the recorded peaks followed winters in which the crops of spruce seeds were locally rich. The numbers of *Microtus* and *Apodemus* have also several times been recorded as reaching peaks in years of excellent spruce crops, notably in 1943.

In 1943 southern Sweden was invaded by owls (Hawk Owl, Short-eared Owl and Tengmalm's Owl) feeding on the abundant rodent population. Thus a further food-chain is established: spruce rhythm—ground rodents—owls.

This section may be summarized as follows. There is a rhythm in the seed production of the spruce and peak crops occur every 3-4 years in southern Sweden (but more seldom in northern Sweden). Some rodents have population peaks at the same time and emigration phenomena may occur in squirrels and Wood-Lemmings. Predators, like martens and owls, form population peaks as tertiary links in the food-chain.

GENERAL RHYTHM OF PERENNIAL PLANTS

The Swedish Institute of Experimental Forestry also publishes data on the fructification of pine (*Pinus*), birch (*Betula*), oak (*Quercus*) and beech (*Fagus*). In Fig. 4 it is demonstrated that these trees all tend to have synchronous fluctuations, with the exception of the pine. The pine is not synchronous because its cones are not ripe (and are therefore not reported to the Institute) until the second autumn after flowering. They are thus one year older than the fruits of all the other trees and serve in the figure as "controls". The co-variation of spruce, birch, oak and beech is statistically significant.

The factor causing the extremely rich flowering and fructification of many trees in 1954 was the high average temperature of June 1953 (Fig. 5). The deviation from the 1901-30 mean was in places as high as 6°C. (= 10.8°F.). It is of much interest that the synchronization of the rhythms of several tree species was strengthened by that warm month, as was also the spruce rhythm in different parts of Sweden (Fig. 3). In the prehistory of really great synchronous bird irruptions such an abnormal temperature is probably often involved.

With a view to supporting the suggestion, given earlier in this paper, that the 1953 irruption of Crossbills started from central Russia, the Swedish meteorological authorities were asked for details of the temperature there during June and the first half of July 1951. The temperature was said to have been more than

1 °C. above average for the whole region of central Russia and western Siberia.

It could easily be foreseen that there would be a bad crop of all trees in 1955 as a consequence of the rich fruiting in 1954. The writer therefore forecast in February that there would be emigrations of certain named Swedish birds (Särdson, 1955b) and most of them did, in fact, occur in autumn and were recorded at the Ottenby and Falsterbo bird observatories. Most numerous were the Jays, which appeared in very large flocks.

Since there is at least some annual synchronization of the fructification rhythms, the total output of food for birds and mammals may vary enormously. To take spruce seeds alone, the difference between good and bad years may be of the order 100:1 according to Professor Tirén. It is not known certainly at present if the rhythms of the berries, *Vaccinium, Empetrum,* and *Arctostaphylos* run parallel to those of the trees, but at least locally a very fine crop of berries was reported in 1954. There are in fact possibilities, which will have to be examined by the botanists, that the amounts of most flower buds, berries or seeds are largely synchronous, so that the whole question becomes of paramount importance for all vegetarian animals. It should be added that the Lemming lives in the *Salix-Betula* region of the mountains and that it may also be dependent on a rhythm of these or some other plants. It seems probable that the rhythm of flowering is accompanied by fluctuating amounts of important nutrients in the roots and shoots. In this way also root-feeding rodents could be affected. Johnsen (1928) and Hustich (1939) have both pointed out that there seems to be some coincidence between peak lemming years and the rich flowering of the pine.

Several game-birds have parallel population peaks, though they have different vegetable foods (Siivonen, 1948; Mackenzie, 1952). It is well known that the game-birds feed heavily on flower-buds and berries. Nordhagen (1928) thought the population peaks of Black and Willow Grouse and Ptarmigan had something to do with the peak years of berries, as there was a coincidence between the export from Norway of game-birds and of berries. Nordhagen thought the birds fed on the berries as long as these were not covered by snow in autumn and again in spring. The tannic acids in the berries, moreover, could have a curative effect upon grouse suffering from coccidiosis.

Since there are Finnish data indicating that game-birds have larger clutches in peak years (Siivonen 1954), an improved food supply during the previous winter seems probable. In the spring of 1948 the Finnish game-birds had larger clutches, according to Siivonen, and at least in Sweden the winter of 1947-48 was a rich "bud-winter", followed by the "seed-winter" of 1948-49 discussed earlier (*cf.* Figs. 3 and 4). The high temperature in the early summer of 1947 was the bud-forming factor.

Höglund (1956) proved the sensitivity to temperature of the young game-birds, which suffer from cold or rainy weather. It is interesting, therefore, that after the warm June of 1953 the game-bird population was high in autumn. But the number of birch and aspen flower-buds, also as a consequence of the June temperature, was very great and thus the birds had a rich supply of winter food. Possibly the quality of the food, too, was superior. In the spring of 1954 the population was still high and after a normal breeding it reached a peak in the autumn of 1954. The following autumn the population was lower and during the early summer of 1956 there was a widespread loss of downy chicks. In the autumn of 1956 the population consisted mainly of adult birds (up to 90%). The population crash in 1956 occurred in Norway, northern Sweden and Finland, and was less severe in southern Sweden. These are the opinions held by the hunters' association and their officers. No exact figures are available.

Summing up, it seems to the present writer rather probable that the much discussed problem of cycles in rodents and game-birds might be simpler than hitherto supposed. It has often been stressed that the population peaks of the predators form no major theoretical problem as they are dependent on the fluctuations of their food supply. Rodents and game-birds, however, have been supposed to have the same amount of vegetable food available every year. This is certainly wrong. They often eat buds or seeds and this is just the kind of vegetable food that is known to vary. The further study of cycles, therefore, seems to be partly a task for the botanists.

It is suggestive to look upon the high temperature during a sensitive period and the "tiredness" of the perennial plants as proximate factors only. The ultimate factor could be an adaptation, by means of which the plants minimize the damage done to them by the specialized seed-eaters. In the off-years, these seed-eaters are driven to emigration (some mammals and birds) or death (most rodents). As the plants have a longer span of life, the total number of seeds that result in seedlings might be higher if the fructification is concentrated in certain peaks, coming at intervals of some years.

In an early publication (1924) Elton gave details of a rodent population peak and a subsequent crash after exceptional fructification of beech. He also suggested that the proved better survival of the beech seedlings after the rodent crash could be an adaptation.

For the performance of pollination mutual adaptations in flowers and insects are known as one important ecological complex. Natural selection to save the seeds from destruction would be of the same strength. It might prove fertile to view fruiting rhythms, animal cycles and the invasion type of bird migration as one great ecological complex of mutual adaptation.

ADDENDUM

The months of July and August 1955 were very hot in Sweden. As a result the flowering of the Rowan was exceptional in the spring of 1956 and the crop of its red berries was really amazing in the winter of 1956-57. Fieldfares and Waxwings invaded Sweden in numbers from December 1956 onwards. In early February 1957 the numbers of Waxwings at Umeå were larger than experienced observers had ever seen before; the same thing was reported from the province of Jämtland and the Hudiksvall district. In Stockholm Waxwings arrived in numbers during the last days of February and in two weeks they took all the berries that the Fieldfares had left. It seems probable that Waxwings will breed abundantly in Fenno-Scandia during 1957 and, since the Rowan will certainly give an inferior crop of berries in the autumn of 1957, because of "tiredness", there may then be a large-scale Waxwing movement outside Scandinavia.*

SUMMARY

1. It is suggested that invasions start annually, like ordinary migration, and that they are released by the same proximate factors. The movement is halted, however, early in some years, while it proceeds in others, the reason being that a rich food supply brings the flight to a stop. Seasonal passage figures for Siskins and White Wagtails at Ottenby, Sweden, demonstrate the difference between an invasion species and an ordinary migrant.

2. The Scandinavian literature on the invasions of Siskins in 1949, Waxwings and Redpolls in 1931, Crossbills in 1942 and Fieldfares in 1937 is reviewed. The last movement resulted in colonization of the Nearctic region.

3. Invasion is contrasted to ordinary migration in a number of respects which are discussed. The main difference is that while migration is an adaptation to a *seasonal food shortage,* invasion is a corresponding adaptation to *annual* food fluctuations.

4. The fructification of spruce in Sweden during 60 years is described and discussed. Some consequences are listed. Some other trees have synchronous rhythms.

5. It is suggested that the rhythm of fructification of some perennial plants, animal cycles and the invasion type of bird migration form one great ecological complex of mutual adaptation.

*The second half of February and the beginning of March 1957 produced a sizeable invasion of Waxwings in the eastern counties of Scotland and England, the largest numbers to reach the British Isles since 1947 and 1949. This was an unusual time of year for these birds to arrive, but the invasion was evidently just the overflow from a far larger immigration into Scandinavia where plenty of food was available to halt the movement. It will be interesting to see if Dr. Svärdson's forecast of another invasion in the late autumn of 1957 will be proved correct.—EDS.

APPENDIX—SCIENTIFIC NAMES OF BIRD-SPECIES DEALT WITH IN THE TEXT

raptors (Falconidae)
Buzzard (*Buteo buteo*)
Goshawk (*Accipiter gentilis*)
Willow Grouse (*Lagopus lagopus*)
Ptarmigan (*Lagopus mutus*)
Black Grouse (*Lyrurus tetrix*)
skuas (Stercorariidae)
owls (Strigidae)
Hawk Owl (*Surnia ulula*)
Short-eared Owl (*Asio flammeus*)
Tengmalm's Owl (*Aegolius funereus*)
Great Spotted Woodpecker (*Dendrocopos major*)
Nutcracker (*Nucifraga caryocatactes*)
Jay (*Garrulus glandarius*)
Marsh Tit (*Parus palustris*)
Long-tailed Tit (*Aegithalos caudatus*)
Nuthatch (*Sitta europaea*)
Fieldfare (*Turdus pilaris*)
White Wagtail (*Motacilla alba*)
Waxwing (*Bombycilla garrulus*)
shrikes (Laniidae)
Siskin (*Carduelis spinus*)
Redpoll (*Carduelis flammea*)
Arctic Redpoll (*Carduelis hornemanni*)
Bullfinch (*Pyrrhula pyrrhula*)
Crossbill (*Loxia curvirostra*)
Parrot Crossbill (*Loxia pityopsittacus*)
Two-barred Crossbill (*Loxia leucoptera*)
Brambling (*Fringilla montifringilla*)

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