Mass irruption of Long-tailed Tits *Aegithalos caudatus* in Northern Europe in 1973

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In most parts of N Europe, the irruption of Long-tailed Tits in 1973 was the largest ever recorded. Data on almost 30 000 birds and from eight countries were collected. The irruption originated mainly from N Russia and extended to Lapland in the north and Poland and Germany in the south. One main stream passed through the Baltic States in a SW-S direction, and the other through Finland and Scandinavia in a W-NW, and later in a SW direction. The movement started in mid-September, reached its peak in mid-October and ended in early November. Recoveries of ringed birds (n = 142) showed that the speed of migration was 13—70, averaging 35 km a day.

The causes of eruptions are discussed. The northern populations of the species fluctuate due to variations in winter weather, previous invasions and breeding success. As a result of flock territoriality, the larger the late summer population, the heavier the autumn emigration. Abundant populations in limited areas cause minor movements, whereas population peaks occurring simultaneously over large areas result in mass eruptions. This mechanism is probably modified by food and weather conditions during September-October.

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Introduction

In Northern Europe the Long-tailed Tit *Aegithalos c. caudatus* is a typical irregular migrant, i.e. a species showing great annual fluctuations in numbers migrating. In most autumns it appears at bird stations only in small numbers, whereas in certain years mass emigrations occur (TISCHLER 1941, LINKOLA 1961, ULFSTRAND 1962a, VEROMAN 1965, BIANCHI 1967, HILDÉN 1974a, LIPSBERGS & RUTE 1975, EHRENROTH 1976). Little is known about the distances covered during these movements or about the survival and possible return attempts of the migrants. The reasons for the mass emigrations are also obscure.

The largest irruption of Long-tailed Tits ever recorded in Finland took place in 1973. In the same autumn, mass movements were reported also from many other countries of Northern Europe. The present paper documents the strength, timing and geographical course of this invasion. The speed of migration, return movements in spring and the reasons for irruptions are also discussed; some comparisons are made with earlier invasions. The weight, flock size and behaviour of migrants will be treated in another paper by E. & P. Helle.

Material and methods

Information on the 1973 irruption in

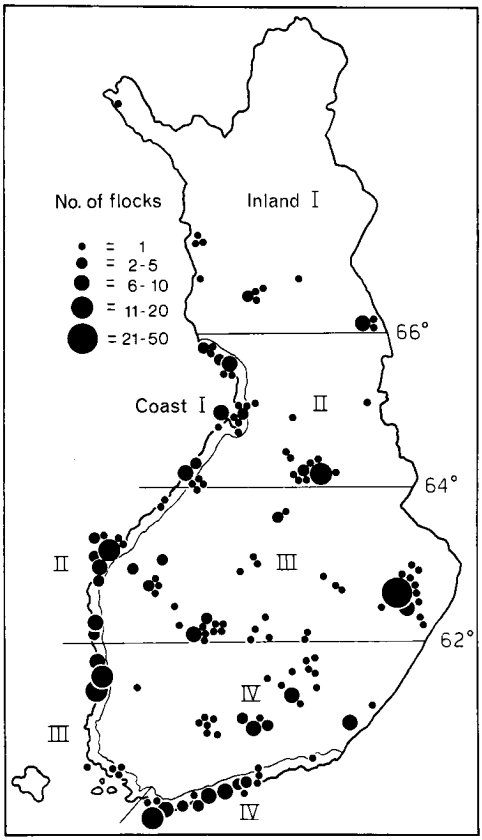

FIG. 1. The geographical distribution of reported observations of Long-tailed Tits in Finland in autumn 1973, and the division of the country into four coastal and four inland areas.

Finland was collected through questionnaires sent to private persons, local ornithological clubs and bird stations. About 180 observers and 8 bird stations sent data concerning almost 10 000 Long-tailed Tits. The data from bird stations were treated separately, because of their different character. All other localities were divided into coastal and inland, and further divided into four subareas in north-south direction according to Fig. 1. Data from these localities were discussed earlier in a Finnish article (HELLE et al. 1976).

From other countries, data on the 1973 irruption have been published from Sweden (Roos 1974, EHRENROTH 1976) and Estonia (VILBASTE 1974). Through questionnaires and personal letters I tried to get detailed information from many more countries. The 34 replies received gave a good general picture of the invasion pattern in Northern Europe. The account of the strength and timing of the irruption in different countries is based on following sources of information (see Fig. 2 for the most important observation sites):

Sweden: Ringing results from the bird stations of Hammarö (B. Ehrenroth), Hartsö-Enskär (L. Wahlén), Ottenby (L. Lindell), Torhamn (U. Lundgren) and Falsterbo (G. Roos).

Norway: Occurrences at the bird stations of Utsira (V. Ree), Revtangen (H. Holgersen), Store Faerder (J. Michaelsen), Mølen (G. Numme), Jomfruland (V. Morn), Svenner (O. W. Røstad) and Nordre Øyeren (Ø. Fritsvold), and results of mist-netting at Hareid (K. Mork).

Denmark: Occurrences at Christiansø (B. M. Sørensen), Skagen and Hanstholm (L. Braae).

Soviet Union: Occurrence on the island of Velikij in Kandalaksha (W. D. Kochanov) and ringing reports from the bird stations of Kabli in Estonia (H. Vilbaste), Pape in Latvia (J. Viksne) and Rybachi (V. D. Jefremov).

Poland: Ringing results from the bird station of Mierzeja Wiślana (P. Busse).

West Germany (FRG): Data from the Schleswig-Holstein area (R. K. Brandt, G. Schmidt), Heligoland bird station (G. Vauk), Wilhelmshaven (W. Winkler) and Baden-Württenberg (W. Gatter).

Switzerland: Ringing total at Col de Bretolet (R. Winkler).

Reports from the Netherlands (E. Osieck) and Belgium (J. C. Dambiermont) were negative. From East Germany (GDR) and Great Britain no replies were received.

The timing of the invasion in different parts of Finland is analyzed by using weekly totals of birds recorded, to eliminate the influence of intensified observation at weekends. This method was considered appropriate even for

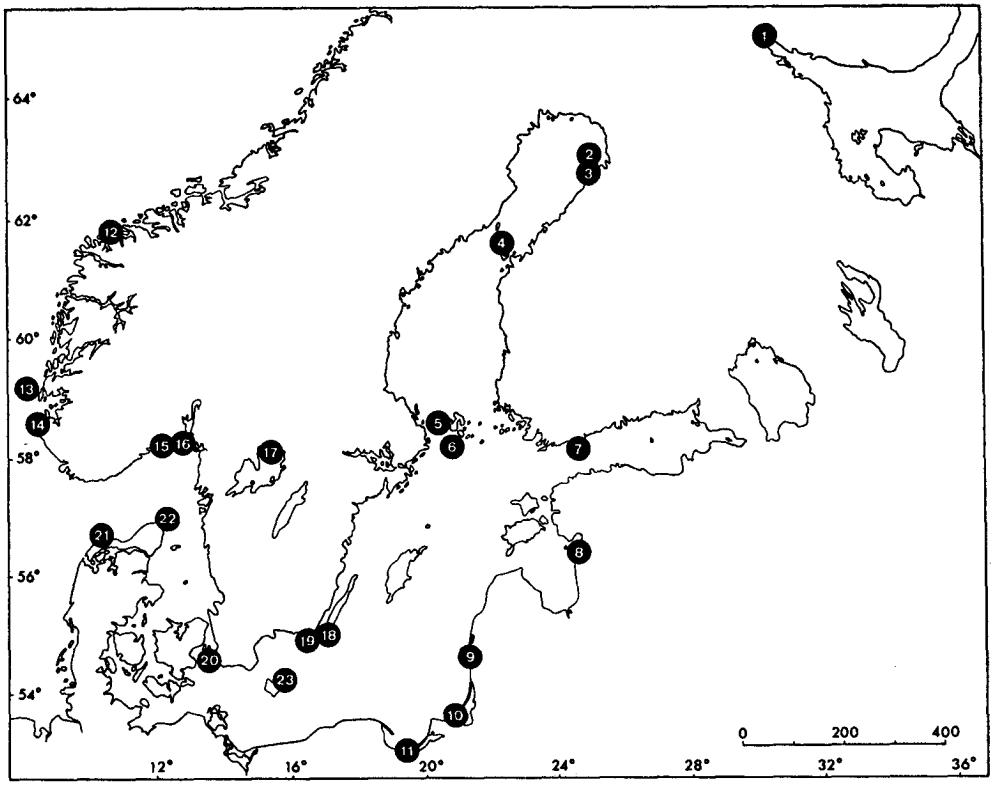

FIG. 2. The location of bird stations and other observation posts mentioned in the text.

1. Kandalaksha
2. Hailuoto
3. Tauvo
4. Valassaaret
5. Signilskär
6. Lågskär
7. Rönnskär
8. Kabli
9. Pape
10. Rybachi
11. Mierzeja Wiślana
12. Hareid
13. Utsira
14. Revtangen
15. Store Faerder
16. Mølen
17. Hammarö
18. Ottenby
19. Torhamn
20. Falsterbo
21. Hanstholm
22. Skagen
23. Christiansø

the bird stations, because Hailuoto was manned only at weekends. For those bird stations in other countries continuously in operation, pentades are used instead of weeks. Calculation of the speed of migration is based mainly on recoveries of birds ringed and controlled at the bird stations of Kabli (KASTEPÖLD 1971, 1972, 1973, 1974) and Pape (BLUMS et al. 1971, J. Viksne in litt.).

Comparison of the 1973 irruption with those of previous years

Fig. 3 shows the annual fluctuation in numbers of migrating Long-tailed Tits in various parts of Northern Europe, based on the totals of birds ringed at some permanent bird stations. Although at most of these stations there has been some annual variation in the number and effectiveness of traps used,

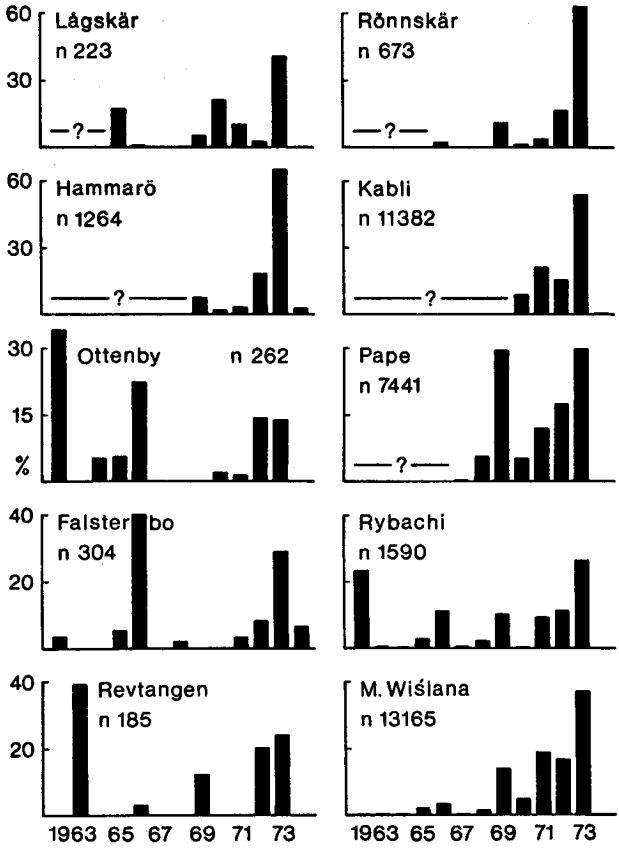

FIG. 3. Annual fluctuation in numbers of Long-tailed Tits ringed at ten bird stations in Northern Europe between 1962 and 1974.

in working methods or in operation periods, this hardly affects the general picture.

The following conclusions can be drawn from the data presented in Fig. 3. The Long-tailed Tit shows a tendency to migrate every year, although the weakest movements (e.g. those in 1963, 1964, 1967, 1974) are not recorded at all stations. In most parts of Northern Europe the 1973 irruption was by far the strongest recorded during the 1960s and 1970s, though large-scale movements also occurred in 1962, 1966, 1969, 1971 and 1972. In general, the irruptions were highly synchronized over the whole of Northern Europe. However, movements of a more local character have also been recorded. Thus, in 1963 a strong invasion was observed only in central Sweden and southern Norway (BERNHOFT-OSA 1964, EHRENROTH 1976), but not in Finland, at Rybachi or at Mierzeja Wiślana. Similarly, whereas in Finland the irruption of 1965 was considerably stronger than that of 1966 (HILDÉN 1974a), the opposite was true in both Sweden and on the eastern coast of the Baltic Sea.

Prior to the 1960s, observations were not effective enough to allow all the mass irruptions to be recorded, but at least the following are known from

Finland: 1934, 1949 and 1959 (G. BERGMAN 1951, LINKOLA 1961, HILDÉN 1974a, HELLE et al. 1976). The 1959 invasion was also recorded in the northwestern part of the Soviet Union (MESHKOV 1963, VEROMAN 1965, BIANCHI 1967) and in Sweden (EHRENROTH 1976). In East Prussia, years of especially large irruptions were 1918, 1935 and 1938 (TISCHLER 1941).

In 1973, more than 10 000 Long-tailed Tits migrated through six Finnish bird stations, and the total number passing through Finland was certainly several times larger (HELLE et al. 1976). Still greater numbers invaded the Baltic States and Poland; at the bird stations of Kabli, Pape and Mierzeja Wiślana alone, more than 13 000 were ringed! Most of these birds did not come from Finland, so the total number of Long-tailed Tits invading Northern Europe in 1973 must have been very high, probably some hundreds of thousands.

Geographical analysis of the irruption

The eastern origin of the irrupting Long-tailed Tits is clear both from observations of migrating flocks and from the timing of the invasion in different areas. Most of the migrants came from northern Russia, and they were joined later by the breeding populations of Fennoscandia and the Baltic States. The huge numbers of birds involved suggest that departures occurred over very large areas, since nowhere is the species known to be a numerous breeding bird. The 1959 mass irruption was supposed to have originated from the Volodga-Archangel-Komi regions, in the northwestern part of the Soviet Union (BIANCHI 1967), and these were probably the main areas of departure again in 1973. But some of the migrants may have come from areas still farther east. Irrupting Nutcrackers *Nucifraga caryocatactes* (HILDÉN 1969) and Nuthatches *Sitta europaea* (ERIKSSON 1970), for instance, have been proved to come all the way from Siberia. Unfortunately, so far we have no ringing recoveries from the eastern breeding grounds of Long-tailed Tits ringed during the invasions.

The flocks crossed Finland mainly in a W to NW direction, although topographical leading lines and wind conditions frequently caused deviations from this standard direction. The movement extended unexpectedly far to the north. Several flocks were recorded in Finnish Lapland, in spite of the very few observers there, the northernmost in Kilpisjärvi (69°03′N, 20°50′E). The directions of movement there varied from W to N. On the Russian side of Lapland, more than 100 Long-tailed Tits were observed in Kandalaksha, most of them migrating to the W. The northernmost observation was made in Norway, where two flocks were reported from Suki (70°12′N, 28°35′E) in October (RANDA 1976).

The largest concentrations of Long-tailed Tits in Finland during the 1973 irruption were seen in the central and northern parts of the country. For example, 2350 birds were counted at Hailuoto, in spite of observations only at weekends, and 1300 at Tauvo during a period of ten days. In Björköby near Valassaaret, along the main flyway over the sea to Sweden, movements of "several thousands" were estimated on 12 and 14 October. Such high numbers in central or northern Finland were unknown in earlier mass invasions. In southern Finland, on the contrary, the numbers recorded in 1973 did not significantly exceed those of earlier mass irruptions (cf. Fig. 3).

Most of the migrating Long-tailed

Tits left Finland either westwards to Sweden, round the Gulf of Bothnia, over the Quark or via Åland, or southwards to Estonia, across the mouth of the Gulf of Finland. Evidently the latter route was used by a flock, ringed on 2 October at Tauvo and controlled on 15 October at Kabli, Estonia. In Scandinavia the birds gradually changed their direction to SW and S, but comparatively small numbers were seen to cross the sea from the southern coast of the peninsula. Thus, Falsterbo bird station reported only 100 birds observed on migration and another 89 ringed, which is somewhat less than during the earlier peak years (cf. FRITZ 1966, PERSSON 1972, ULFSTRAND et al. 1974), and Christiansø 105 in total. Similarly, only small numbers reached the southernmost bird stations in Norway: rather more than 100 recorded at Mølen and 40 at Utsira, 45 ringed at Revtangen and 41 at Store Faerder. Three Norwegian stations (Nordre Øyeren, Jomfruland, Svenner) reported little or no movement. A small influx was noticed in northern Denmark, suggesting some movement from Sweden and/or Norway: in total 130 birds reached Skagen and Hanstholm.

The main stream of the invasion passed south of the Gulf of Finland, through the Baltic States, as revealed by the very high numbers of birds ringed at the bird stations there (cf. Fig. 3). Open sea forced the west- and southwestwards migrating flocks to turn more to the S, leading to a heavy concentration on the eastern coast of the Baltic Sea. This main passage along the coast southwards can be followed in detail by dozens of recoveries of birds ringed at one station and recaptured some days later at another farther south. The invasion, still at high intensity, reached the northeastern parts of Poland (Mierzeja Wiślana), but seems to have ended soon afterwards. No appreciable influx was noticed in the western parts of Poland, nor in Schleswig-Holstein or near Wilhelmshaven in West Germany. At Heligoland no movement was observed, and reports from southern Germany, the Netherlands and Belgium were also negative.

The main invasion streams on both sides of the Baltic Sea thus seem to have ended at about the same latitude, in the northern parts of Germany and Poland. The two preceding mass irruptions, in 1971 and 1972, reached further south and west. Thus, a flock of about 200 white-headed Long-tailed Tits was observed in December 1971 in the Netherlands, this being the first record of the subspecies *caudatus* in that country (VAN MARLE et al. 1973). In 1972, 201 migrating Long-tailed Tits in 20 flocks passed an observation post in Baden-Württenberg, southern Germany, and 48 were ringed at Col de Bretolet in Switzerland; about 38 % were white-headed birds of *caudatus* type (GATTER 1973). In 1973, only 10 Long-tailed Tits were ringed at Col de Bretolet, probably indicating slight local movement.

Timing of irruption

Figs. 4 (Finland) and 5 (other countries) illustrate the temporal pattern of the irruption, based on the numbers ringed or recorded at different observation posts in Northern Europe.

In Finland, the first signs of the invasion were noted in the eastern parts of the country in the beginning of September. In mid-September, or soon afterwards, observations were reported over almost the whole of Finland, and the first wave of migrants also reached western Estonia. Simultaneously the first few flocks were seen at some bird

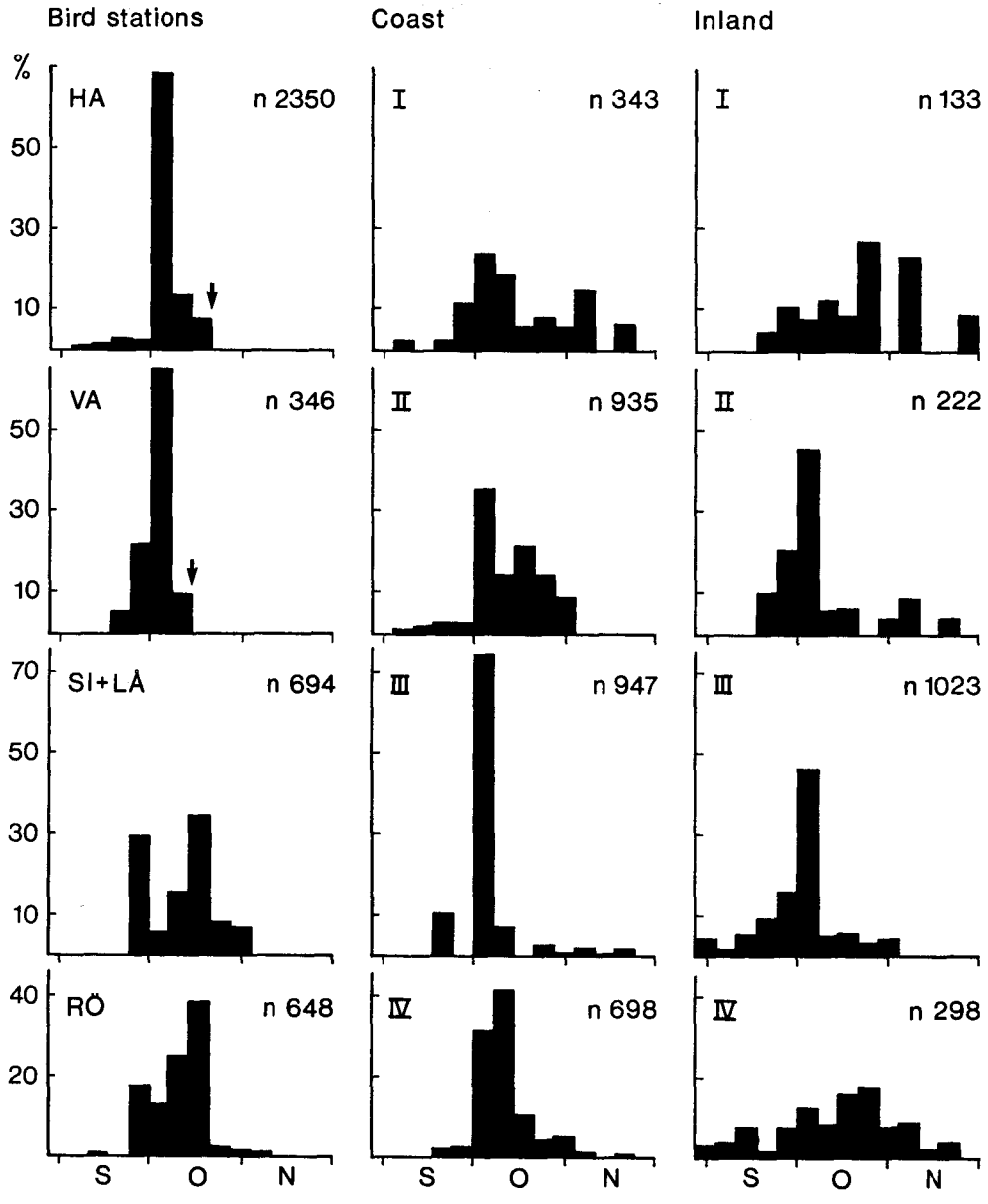

FIG. 4. Timing of the 1973 irruption of Long-tailed Tits in Finland, according to weekly totals of birds recorded in different parts of the country. Arrows indicate the end of the observation period. HA = Hailuoto, VA = Valassaaret, SI = Signilskär, LÅ = Lågskär and RÖ = Rönnskär. The four coastal and inland areas are marked in Fig. 1.

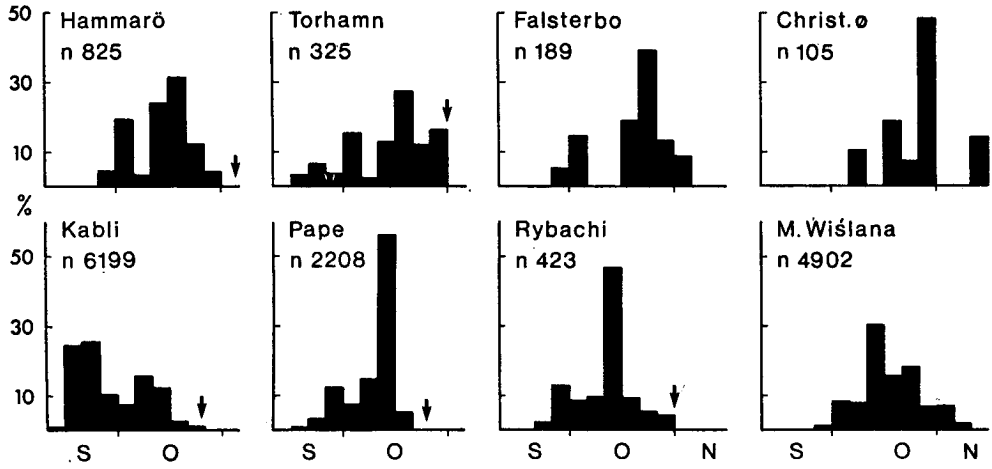

FIG. 5. Timing of the 1973 irruption of Long-tailed Tits at different bird stations in Northern Europe, according to the numbers ringed in 5-day periods (the figures from Falsterbo and Christiansø include birds recorded on migration). Arrows indicate the end of the observation period.

stations in central and southern Sweden (e.g. Hammarö, Torhamn, Ottenby) and western Norway (Hareid), but most probably these belonged to the local Scandinavian population. At the end of September the irruption extended into most parts of Northern Europe: at bird stations, for instance, the first flocks appeared in southwestern Finland (Signilskär, Lågskär, Rönnskär) and on the southeastern coast of the Baltic Sea (Pape, Rybachi, Mierzeja Wiślana), and a marked wave of invasion was recorded in Sweden. By the beginning of October the invasion had already reached the southernmost coastal regions of the Scandinavian peninsula (Utsira, Revtangen, Store Faerder, Mølen, Falsterbo, Christiansø) in the south, and Kandalaksha in the north. (Some sporadic individuals or flocks seen many days ahead of the following ones and probably belonging to the local populations are not included in the description given above.)

The earliest peak of passage was recorded in Estonia, where the daily numbers of birds ringed at Kabli began to fall as early as late September. The movement reached its highest intensity in early October in the central parts and on the west coast of Finland, around mid-October in southwestern Finland, central and southern Sweden and on the southeastern coast of the Baltic Sea, and in the second half of October in southernmost Norway, Falsterbo and Christiansø. The strength of the invasion decreased rapidly in late October, but at several stations still in operation in late autumn, some migrating flocks were recorded as late as early November. The movement seems to have ceased earlier in the north (e.g. Hailuoto) than in the south (e.g. Mierzeja Wiślana). The complete migratory period lasted about one and a half months at any one place, with the peak of passage two or three weeks after the appearance of the first wave of migrants.

Some additional general features of the temporal pattern of the 1973 irruption deserve mention. The peak was nearly two weeks earlier in the northern part of the Gulf of Bothnia (Hai-

luoto, Tauvo, Valassaaret) than in the southwestern Finnish archipelago (Signilskär, Lågskär, Rönnskär), indicating straight rapid movement across Finland to the NW but a turn later to the SW-S by part of the flocks. The data of the irruption peak at the southwestern bird stations was delayed even more compared with that at Kabli, situated only 200 km south of Rönnskär. This further supports the suggestion that most flocks crossing the sea from southwestern Finland had reached that area by a long detour. The early passage at Kabli also proves that the invasion wave moved westwards especially fast to the south of the Gulf of Finland.

The 1973 irruption was about two weeks earlier than the average dates of autumn movements of the Long-tailed Tit (cf. HILDÉN 1974a). This is typical for mass irruptions, which tend to occur earlier than minor invasions (EDELSTAM 1972, HILDÉN 1974a). On the whole, there are rather wide annual fluctuations in the timing and duration of invasions of this species. The onset, for instance, varies between years by 3—4 weeks (cf. LINKOLA 1961, BIANCHI 1976, EHRENROTH 1976). To some extent, however, these differences are only apparent and due to the fact that in minor invasions the small number of individuals involved move during a short period concentrated around the peak.

Northern observations of the subspecies *europaeus*

According to the above analysis, the irruption was directed at first to the W, and later to the SW and S. However, several observations of the Central European subspecies *europaeus* were made in Fennoscandia in 1973 and these seem to contradict my interpretation by indicating long movements to the N. These records were also highly surprising because *europaeus* is considered to be mainly resident, and not to undertake long movements.

In Finland, specimens with dark eye-stripes were recorded in four places from the south coast to Kuusamo in the north. All birds examined closely enough showed all the characteristics of the subspecies *europaeus* (see the photograph in HELLE et al. 1976). The observations were as follows: (1) Tauvo on 4 October one bird ringed (M. Lagerström, in litt.); (2) Kuusamo, Särkelä on 12 October a flock of 8 birds straggling to the NE (E. Nyholm, in litt.); (3) Rönnskär on 11 November a flock ringed, consisting of 5 *caudatus* and 4 *europaeus* (O. Saksela, in litt.); (4) Åland, Finström on 16 December 2 *europaeus* together with 4 *caudatus* and 3 Blue Tits *Parus caeruleus* in a reed belt (G. Andersson, in litt.). The subspecies has not been recorded previously in Finland.

In Sweden, birds showing *europaeus* characters had been observed at least 14 times up to 1971 and at present may breed regularly in the southernmost part of the country (KÄLLANDER 1971 and in litt.), but no northern records referring to 1973 have been reported to the Swedish Rarities Committee (L. Svensson, in litt.). In Norway, a total of six specimens showing characters intermediate between those of *caudatus* and *europaeus* were ringed at Hareid on the west coast during September and October 1973 (FOLKESTAD 1974).

The distribution and hybridization of the subspecies *caudatus* and *europaeus* in Europe has been considered, among others, by VAURIE (1957, 1959), ULFSTRAND (1962b), GATTER (1973) and BRANDT (1974). The borderline between the subspecies runs through Denmark, Germany, Poland and the Ukraine, from NW to SE. As a result of free interbreeding in the zone of overlap, hybrids show every gradation between the two subspecies. Specimens with almost complete *europaeus* characters may occur deep inside the range of *caudatus*, and *vice versa*. According to TISCHLER (1941), some birds with dark eye-stripes breed even in the Eastern Baltic. Hence, the records of the subspecies *europaeus* or intermediate

TABLE 1. Speed of migration (km a day) of irrupting Long-Tailed Tits, as indicated by recoveries of birds ringed and checked during the same autumn at bird stations in Northern Europe. Sources of information: A = HELLE et al. (1976), B = Viksne (in litt.), C = KASTEPÕLD (1972, 1973, 1974), D = BLUMS et al. (1971) and Viksne (in litt.), E = PAYEVSKY (1973).

Place of ringing and recapture	Distance (km)	No. of birds	Migration speed Range	Mean	Source
Tauvo—Kabli	660	3	51	51	A
Pyhäranta—Mierzeja Wiślana	700	2	70	70	A
Gumbaritzy—Pape	850	4	50	50	B
Puise—Pape	330	3	22—25	24	C
Kabli—Pape	300	19	13—43	28	C
Kabli—Neringa	360	13	14—50	28	C
Kabli—Rybachy	410	3	51	51	C
Kabli—Mierzeja Wiślana	520	44	21—65	40	C
Pape—Rybachy	120	13	13—40	29	D
Pape—Mierzeja Wiślana	230	37	17—56	30	D
Rybachi—Falsterbo	500	1	63	63	E
Total material		142	13—70	35	

forms in Fennoscandia may concern birds which originated north of the hybrid zone and so became associated with the invasion. Another possibility is that during the autumn dispersion, some *europaeus* flocks penetrated north into the area of *caudatus*, where they joined the irrupting flocks.

The northern observations of *europaeus* undoubtedly imply movements of several hundreds of kilometres to the north, against the standard direction of the irruption. As strange as this may appear, it is probably a characteristic feature of the irruptions of Long-tailed Tits. The movements of individual flocks are determined to a considerable degree by local leading lines and wind conditions, which may deflect birds long distances in "false' directions. Intensive reversed autumn migration of Long-tailed Tits, to the north, has been observed frequently on the west coast of Estonia (VILBASTE 1974), and has been confirmed also in Operation Baltic by several recoveries to the north of birds ringed some days earlier at more southerly bird stations. Due to the very strong sociability of Long-tailed Tits, *europaeus* specimens joining *caudatus* flocks may in this way wander long distances from their native areas.

Speed of migration

Large-scale trapping of irrupting Long-tailed Tits, particularly at the bird stations along the eastern coast of the Baltic Sea, has produced large numbers of recaptures. These give information on the speed of migration in this species. The birds covered 13—70, on average 35 km a day (Table 1). This is somewhat less than the average speed of typical migratory passerine species, which may fly 50—80 km a day (HILDÉN 1974a). The difference is to be expected considering the strict adherence of migrating Long-tailed Tits to topographical leading lines, their reluctance to crossing open areas, their frequent reversed movements and slow speed of flight.

A striking feature of the data in Table 1 is that the longer distances were covered at higher average speeds than the shorter ones. Thus, the aver-

age speed on distances more than 400 km long was 43 km a day (57 birds), but on distances less than 400 km long only 29 km a day (85 birds). This can hardly depend merely on a chance. One possible reason is that the average speed of migration is higher during the early phase of irruption than nearer the terminal areas. Another factor may be that three of the long distance movements with high average migration speeds (Tauvo—Kabli, Pyhäranta—Mierzeja Wiślana, Rybachi—Falsterbo) involved crossing of open sea; also, the flock that reached Rybachi from Kabli in eight days may have crossed the Gulf of Riga.

Survival of migrants and return movements in spring

LINKOLA (1961) holds the opinion that the theory of "death wanderings" of invasion birds applies well to the Long-tailed Tit. According to this theory, mass eruptions are merely a mechanism for removing a "doomed surplus", which moves out and wanders till death. It is true that mortality seems to be very high among irrupting Long-tailed Tits, and LINKOLA presents impressive examples of this. However, in spite of heavy losses, significant numbers of migrants survive the irruptions. This is documented partly by later controls of birds ringed during irruptions, and partly by return movements in spring.

In 1972, a total of 3046 Long-tailed Tits were ringed at the bird stations of Kabli and Pape. During the same autumn, 28 of these were recaptured at other bird stations along the eastern coast of the Baltic Sea. During the irruption in 1973, 5 additional birds were recovered, one in Finland (Hailuoto on 30 Sept.), one in Sweden (Hammarö on 23 Oct.), two in Poland (Mierzeja Wiślana on 20 and 23 Oct.) and one at the place of ringing. Considering the strong dispersion of these birds, which naturally reduces the chances of recoveries, and the small proportion of adult birds participating in irruptions (e.g. only 13 of the 423 birds ringed at Rybachi in 1973 were aged as adults), these figures suggest a rather high survival rate among the migrants. Corresponding data concerning the 1973 irruption are not available, because hardly any Long-tailed Tits visited the bird stations in 1974.

Spring movements of Long-tailed Tits have been considered very weak, at least in Finland, and this has been put forward as further evidence of high mortality among the migrants. Thus, v. HAARTMAN et al. (1963—72) mention only three spring observations from the Finnish bird stations and conclude that returning across the sea seems to be very rare. In the 1970s, however, quite a few new records have been reported, particularly in spring 1974 following the mass eruption in the preceding autumn. Thus, altogether 31 birds, including three single individuals and six groups of 3—7 birds, were recorded at Signilskär, Lågskär and Rönnskär (HILDÉN 1975). I do not have data on spring movements from bird stations in other countries.

It seems evident that the few spring observations of migrating Long-tailed Tits at bird stations do not give a complete picture of the survival of the invaders. As pointed out by HILDÉN (1974a), irregular migrants often return along different routes than those which they used in the preceding autumn, and some may remain to nest in the areas they invaded; in addition, the location of Finnish bird stations with respect to concentrations of migrants is not as favourable in the spring

as in the autumn. Most probably these considerations apply to the Long-tailed Tit as well as to other species and explain the small numbers seen at our bird stations in spring. In the surroundings of Helsinki, large migrating flocks have been seen during April in certain years. Perhaps most of the birds surviving the irruption and the following winter return by a more easterly route and thus follow a loop migration, as in the Great Spotted Woodpecker *Dendrocopos major* and the Nutcracker *Nucifraga caryocatactes* (cf. HILDÉN 1969). Some of the invaders also stay to breed in the new areas, as has been known for a long time (e.g. DURANGO 1941, SVÄRDSON 1957, HAFTORN 1971).

Indirect evidence against the idea of "death wanderings" is provided also by the occurrence of large-scale irruptions in the consecutive years 1971, 1972 and 1973. All these invasions were of such large size that they must have originated from extensive regions and involved significant parts of the populations, so new eruptions could hardly have arisen if most of the emigrants had succumbed each year.

Causes of irruption

Ultimate and proximate causes. "What causes eruptions" is one of the main questions raised by bird invasions. Most authors agree that the ultimate cause of mass emigration is to avoid food shortage, but there is some controversy regarding the releasing or proximate factors: whether overpopulation or poor food supply or both (e.g. KALELA 1954a, b, LACK 1954, SVÄRDSON 1957, ULFSTRAND 1963, NEWTON 1970, 1972, BOCK & LEPTHIEN 1976). Evidently, both these factors are important, the combined effect of them deciding the strength of the emigration, but their relative significance must vary from species to species depending on how specialized they are in their feeding ecologies (HILDÉN 1974b). Thus, for the Coal Tit *Parus ater,* which specialize on spruce seed, the size of the spruce cone crop seems to be decisive (e.g. FORMOSOV 1965), whereas in other tits of the genus *Parus,* which consume more varied foods, the strength of the movements is determined to a greater extent by the numbers present in autumn (e.g. KLUIJVER 1951, ULFSTRAND 1962a, CRAMP 1963, BERNDT & HENSS 1963, 1967, HILDÉN 1968, 1974b). In the following sections, I consider some important factors which are likely to contribute to the development of eruptive movements in the Long-tailed Tit.

Winter food. The Long-tailed Tit is rather specialized in its diet between autumn and spring, feeding mainly on eggs of plant lice (PATOMÄKI 1967). It is known that the abundance of plant lice fluctuates greatly from year to year, so here might be one factor underlying the unpredictable character of the species' autumn movements. Unfortunately, this hypothesis cannot be tested so far, as no statistics of the abundance of plant lice eggs are available in any region, and certainly not in the areas from which the irruptions were thought to originate.

Winter weather. The Long-tailed Tit is known for its highly unstable breeding populations in Northern Europe. In Finland, for instance, it can be almost absent as a breeding bird in trough years but fairly common, although never numerous, in peak years (v. HAARTMAN et al. 1963—72). The most important reason for these fluctuations is the species' poor tolerance of severe winters, which may destroy almost the entire population over large areas (e.g. S. BERGMAN 1944, LACK 1954, HILDÉN & KOSKIMIES 1969,

v. HAARTMAN et al. 1963—72, SAMMALISTO 1974). Correspondingly, mild winters are favourable for the Long-tailed Tit, and its high potential reproductive rate (large clutches, frequent renesting and the common habit of extra birds assisting the parent pair in rearing the young) enables a rapid growth of the population. Hence, if high numbers are the main proximate factor releasing eruptions in the Long-tailed Tit, mild winters are expected to start the chain of events leading to large-scale emigrations. This hypothesis fits well the 1973 mass eruption. The preceding three winters were mild in Northern Europe, the winter of 1972/73 exceptionally mild, resulting in steadily growing populations of the Long-tailed Tit, as well as of other tits, the Goldcrest *Regulus regulus* and the Treecreeper *Certhia familiaris*. All these species reached very high numbers in Finland in 1973, and they all performed unprecedently heavy eruptions that autumn (HILDÉN 1974b).

Unfortunately, data on the population trend of Long-tailed Tits in the beginning of the 1970s are sparse. The best material is provided by the Finnish winter bird censuses (see SAMMALISTO 1974). Since 1966, a second count is taken in late winter, at the end of February and beginning of March, and the results probably give a fairly good idea of the status of our Long-tailed Tit population in successive springs. After several years of low population level, a very high peak was reached in 1972—73 (Fig. 6). The number of nest record-cards sent annually to the Finnish Society of Sciences is another method which can be used to estimate roughly fluctuations in a species' breeding population (v. HAARTMAN 1974). Although the sample of the Long-tailed Tit is small, it nevertheless suggests a clear peak in 1972—73:

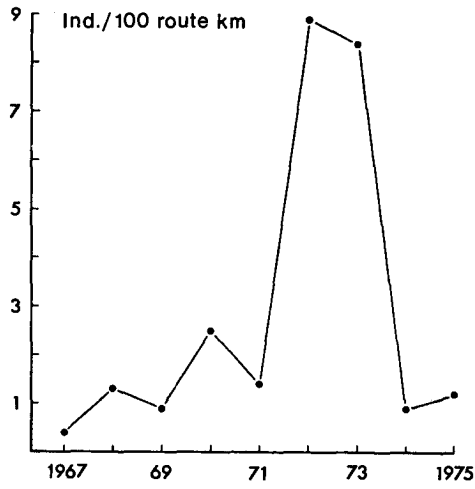

FIG. 6. Density of the Long-tailed Tit, expressed as individuals per 100 km of route, in the Finnish late winter counts of 1967—75.

1960	61	62	63	64	65	66	67
—	—	—	2	2	4	1	—

1968	69	70	71	72	73	74
—	—	—	—	6	7	1

Finally, my own observations, personal information from many ornithologists and faunistic short notes in ornithological periodicals, both in Finland and Sweden, also show convincingly the high population level in 1972—73 in Fennoscandia. As mild winters prevailed in the whole of Northern Europe in the beginning of the 1970s, the same increasing trend most probably was also true of the Russian population.

How does the idea of mild winters and high numbers fit the earlier eruptions? The large-scale movements in Finland in 1949 and 1965 were clearly connected with preceding unusually mild winters and concomitant population peaks (cf. P. Linkola's data on population fluctuations in the province of Häme: v. HAARTMAN et al. 1963—72). On the other hand, the 1959 mass eruption coincided with a very low popula-

tion in Finland. Similarly, the eruption in 1966 followed the severe winter of 1965/66, which drastically reduced the Finnish population (cf. HILDÉN & KOSKIMIES 1969); and the 1969 eruption was preceded by four consecutive cold winters and a very low level of the Finnish population (cf. Fig. 6). Consequently, there is not always a clear correlation between the mildness of preceding winters and the occurrence of eruptions. In fact, EHRENROTH's (1976) data on the numbers of irrupting Long-tailed Tits at Hammarö do not show any connection with preceding winter temperatures.

In my opinion, those emigrations which occurred in years with low breeding populations in Fennoscandia originated from areas further east, where the populations had survived better. Most relevant to the occurrence of mass eruptions is the population trend in northern Russia, the nucleus of the species' range in Europe, and this need not run parallel with the situation in Fennoscandia. No data are available on recent changes in the Russian population of the Long-tailed Tit, but the mass irruptions in Northern Europe correlate fairly well with preceding mild winters in Russia (data from WORLD WEATHER RECORDS and MONTHLY CLIMATIC DATA FOR THE WORLD). Thus, several large movements occurred in the 1930s (TISCHLER 1941), and this decade was characterized by a succession of mild winters. Also, the 1959 and 1962 eruptions were preceded by two or three consecutive mild winters. However, the eruptions in 1966 and 1969 remain puzzling, as the winters in the late 1960s were very cold in northern Russia also (the mean temperature of January in Vologda, for example, was —17.7° in 1966 and —19.6° in 1969, 6.4° and 8.3° below average). Although low temperatures in a dry continental climate are not as fatal for birds as in a humid climate (cf. ERIKSSON 1970), it is difficult to understand how large numbers of Long-tailed Tits could survive these hard winters in Russia.

Preceding movements. The incomplete correlation between winter temperatures and occurrence of eruptions in the Long-tailed Tit is partly due to two other factors, which also affect the breeding populations. First, the abundance of the species in a given area, e.g. in Finland, is dependent not only on the severity of the previous winter but also on preceding movements. Irrupting flocks passing through an area may induce the local population to join the movement and thus almost empty the area of Long-tailed Tits. This happened in the mass irruption of 1973, after which the species was almost absent from Finland during the following summer and autumn, in spite of the very mild winter of 1973/74. In other years, on the contrary, irrupting flocks may remain to nest in the areas invaded, thus producing a strong increase in the numbers present. Good examples of this are mentioned by DURANGO (1941). In central Sweden, the breeding population suddenly reached a very high peak in 1935, although it was still weak in the preceding summer. A strong increase took place in autumn 1934, after which the species was common in the region throughout the winter and remained to breed there. DURANGO considered an influx from the east probable, even though he did not know about the heavy migration across the sea from Finland to Sweden recorded at Signilskär in October 1934 (p. 51), which proves the eastern origins of the invasion convincingly. The same happened again in autumn 1940, after which the species was a common breeding bird in 1941, although the preced-

ing extremely cold winter had destroyed almost completely the Swedish population. A corresponding influx may take place also during the return movements in spring.

Breeding success. Second, the size of the autumn population within a given area is also determined by the breeding success. This, in turn, is dependent on the weather conditions during the breeding season and, above all, on the abundance of nest predators. Nest losses are usually very high in the Long-tailed Tit (e.g. DURANGO 1941, LACK & LACK 1958, RIEHM 1970, NAKAMURA 1972, 1976, GASTON 1973), and one of the worst nest-robbers is the Squirrel *Sciurus vulgaris.* This species is known for its wide fluctuations in numbers, and the varying predation pressure from it may affect considerably the breeding success of the Long-tailed Tit. In the summers of 1972 and 1973, the Squirrel population of southern and central Finland, within the normal range of the Long-tailed Tit, was average or below average according to the data from the Finnish Game Research Institute. The same summers were exceptionally warm and dry in Northern Europe, which may have contributed to a good breeding success of Long-tailed Tits.

Determination of eruptions. To summarize my opinion, the determinants of eruptive movements in the Long-tailed Tit are as follows. The northern populations of the species fluctuate sharply in response to variations in winter weather, previous invasions and breeding success. Local differences in these factors often result in population peaks and troughs occurring in different years in the different parts of the species' range, whereas in certain years the fluctuations run parallel in the whole of Northern Europe. In general, the larger the late summer population, the heavier the autumn emigration. Abundant populations in limited areas cause minor or local movements, whereas simultaneous population peaks over large areas result in mass eruptions. This mechanism is probably modified by food, i.e. the abundance of plant lice eggs in autumn, and the weather conditions during September-October. The extremely cold weather in autumn 1973, for instance, probably contributed to mass eruptions of the Long-tailed Tit, as well as of other tits, the Goldcrest and the Treecreeper, by making insect food suddenly less available (cf. HILDÉN 1974b, 1975).

The way in which high numbers cause emigrations is probably through flock territoriality. As shown by NAKAMURA (1969, 1972, 1976) and GASTON (1973), each flock of Long-tailed Tits has a home-range, which is defended against other flocks, and this behaviour regulates the size of local populations. The higher the population density, the more frequent are the conflicts between flocks; this leads the birds into an excited condition, which in turn through hormonal processes gives rise to eruptive movements. A similar mechanism, but operating through inter-individual aggressive behaviour, has been proposed by KALELA (1954a, b) and BERNDT & HENSS (1967) regarding the rise of eruptions in certain species.

If the above view is correct, then one would hardly expect any regular intervals between irruptions. However, EHRENROTH (1976) has shown that Long-tailed Tits irrupted with great regularity at Hammarö, with peaks at intervals of 3—4 years. If such a cycle really exists, then the Long-tailed Tit would differ from most Palaearctic irruptive species. LACK (1954:228) concluded in his review that invasions "come at irregular, not regular, intervals" and that "the only species known to irrupt at regular intervals are the

hawks and owls which prey on cyclic rodents". Recently, some regularity has been shown also in the eruption patterns of certain boreal seed-eating bird species (BOCK & LEPTHIEN 1976).

A glance at Fig. 3 shows that the irruptions of Long-tailed Tits in Northern Europe have not followed as regular a cyclical pattern as the local material from Hammarö seems to reveal. Although more or less pronounced peaks have occurred in 1962, 1966, 1969 and 1973, i.e. at intervals of 3—4 years, big irruptions took place even in the intervening years of 1971 and 1972, and local peaks were recorded in 1963 (Sweden and Norway) and 1965 (Finland). Even less regularity can be found in the occurrence of invasions into East Prussia, listed by TISCHLER (1941); there were both gaps of 5 to 8 years without any marked movements and big irruptions in subsequent autumns. Hence, the present material does not support the idea of cyclical irruptions in the Long-tailed Tit.

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Selostus: **Pyrstötiaisen suurvaellus 1973 Pohjois-Euroopassa**

1. Pyrstötiaisen suurvaellusta 1973 on aikaisemmin käsitelty suomenkielisessä artikkelissa (HELLE ym. 1976, Lintumies 11:1—12), jossa pääpaino oli kotimaisessa aineistossa (kuva 1). Tässä kirjoituksessa selvitellään vaellusta koko Pohjois-Euroopassa lähes 30 000 yksilöstä kootun aineiston perusteella. Pääosa tiedoista koskee lintuasemilla (kuva 2) rengastettuja yksilöitä.

2. Kuva 3 esittää vuosittain rengastettujen pyrstötiaisten määriä 10:llä säännöllisesti toimivalla lintuasemalla 1962—74. Liikehtelyä tapahtuu joka syksy, joskaan heikoimpia vaelluksia (esim. 1967, 1974) ei todeta kaikilla asemilla; suurvaelluksia ovat olleet 1962, 1966, 1969, 1971, 1972 ja 1973. Yleensä vaellukset ovat samanaikaisia koko Pohjois-Euroopassa, mutta myös paikallisia vaelluksia on todettu.

3. Syksyn 1973 vaellus oli lähtöisin pääosaksi Pohjois-Venäjältä ja ulottui pohjoisessa Lappiin, etelässä Puolan ja Saksan pohjoisosiin. Valtavirta kulki Suomenlahden eteläpuolitse Baltian kautta SW—S-suuntaan, toinen pääreitti ylitti Suomen W—NW-suuntaan ja edelleen Pohjanlahden ympäri, Merenkurkun poikki ja Ahvenanmaan kautta Skandinaviaan, missä vaellus kääntyi lounaaseen.

4. Vaelluksen ajoitus on esitetty kuvissa 4 (Suomi: havaittuja yksilöitä viikottain) ja 5 (muut maat: rengastettuja yksilöitä 5 päivän jaksoina). Liikehtely alkoi syyskuun alun (Itä-Suomi) ja lokakuun alun (Etelä-Skandinavia) välillä, huippu saavutettiin useimmissa havaintopaikoissa lokakuun keskivaiheilla, ja vaellus päättyi marraskuun alkupuolella. Erikoinen piirre ajoituksessa oli muuton myöhäinen huippu lounaissaaristossamme; n. 2 viikkoa myöhäisempi kuin Perämeren rannikolla ja 3—4 viikkoa myöhäisempi kuin Virossa. Ilmeisesti parvet saapuivat lounaissaaristoon pitkää kiertotietä pohjoisesta.

5. Neljällä taholla Suomea, pohjoisinna Kuusamossa asti, tavattiin eteläisen *europaeus*-rodun yksilöitä. Norjan länsiosissa rengastettiin samana syksynä 6 *caudatus*- ja *europaeus*-rotujen välimuotoa. Näiden yksilöiden otaksutaan kulkeutuneen kauas asuinalueiltaan liityttyään *caudatus*-parviin, jotka johtolinjojen ja tuuliolojen vuoksi olivat harhautuneet pohjoiseen vaelluksen vakiosuunnasta.

6. Rengastettujen pyrstötiaisten myöhemmät kontrollit samana syksynä toisilla lintuasemilla (n = 142) osoittavat muuttonopeudeksi 13—70, keskimäärin 35 km päivässä (taul. 1), mikä on jonkin verran vähemmän kuin tyypillisillä muuttolinnuilla. Keskinopeus oli suurin pisimmillä matkoilla, mikä ainakin osaksi johtunee näihin sisältyneistä meren ylityksistä.

7. Pyrstötiaisten invaasioita on usein pidetty tyypillisinä "kuolonvaelluksina". Suhteellisen monet rengaslintujen löydöt seuraavana vuonna, havainnot paluuvaelluksesta keväällä sekä peräkkäisinä syksyinä tapahtuneet suurvaellukset osoittavat kuitenkin, ettei vaeltajien kuolleisuus voi olla niin suuri kuin yleisesti on luultu. Pääosa eloon jääneistä palannee keväällä itäisempää reittiä, minkä takia niitä nähdään esim. Suomen lintuasemilla varsin vähän.

8. Vaellusten syistä kirjoittajan käsitys on seuraava. Kolmen päätekijän, talvien ankaruuden, edeltäneiden vaellusten ja pesintätuloksen, yhteisvaikutuksesta pyrstötiaiskannat vaihtelevat vuosittain jyrkästi. Näiden tekijöiden paikalliset erot aiheuttavat välillä huippujen ja aallonpohjien eriaikaisuutta asuinalueen eri osissa, välillä taas vaihtelut ovat yhdenmukaisia koko Pohjois-Euroopassa. Kukin parvi puolustaa omaa aluettaan muita parvia vastaan, mikä säätelee paikallisten kantojen suuruutta. Mitä runsaampi kanta syksyllä, sitä yleisempiä parvien väliset kiistat ja sitä voimakkaampaa vaellus näiden seurauksena. Suppea-alaiset runsaat kannat aiheuttavat pienehköjä tai paikallisia vaelluksia, huippukantojen osuessa yksiin laajoilla alueilla on tuloksena suurvaellus. Tätä mekanismia säädellee vielä syksyinen ravintotilanne ja sää.

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