Luonteenomaisena piirteenä teeren aamulennolle voidaan pitää sitä, että se suoritetaan varsin selväpiirteisesti kahdessa vaiheessa. Näistä ensimmäinen lentokausi sattuu n. 40—60 min. kohdalle ennen auringon nousua, siis vuorokaudenaikaan, jolloin vallitsee vielä hämärä. Toinen lentokausi on vastaavasti välittömästi auringon nousun jälkeen, aurinkoisina aamuina 10—20 min. ja pilvisinä 20—40 min. auringon noususta. Myöhäislentokausi näyttää olevan käytössä vuoden pimeimpänä aikana lokakuusta huhtikuuhun ja varhaislentokausi vastaavasti valoisimpana aikana toukokuusta syyskuuhun. Lokakuun siirtymisvaiheessa aikaisemmasta myöhäisempään lentokauteen teerien on todettu olleen liikkeellä molempina mainittuina ajanjaksoina.

Lentoajoissa todettu kaksivaiheisuus ymmärretään liittyväksi teeren elintavoissa havaittaviin vuodenaikaisiin muutoksiin. Varhaislento liittyy kesälle ominaiseen »piileskelevään» elämäntapaan ja myöhäislentovaihe talven esiintymistä luonnehtivaan »avoimeen» elämäntapaan.

Delayed departure of the swift *(Apus apus)* from Finland in the autumn of 1957.

JUKKA KOSKIMIES
(Departement of Zoology, University of Helsinki)

The bulk of the swifts usually depart from southern Finland during the two last weeks of August (KOSKIMIES 1950). In the first half of September, a few individuals are normally seen (e.g. v. HAARTMAN 1951), but their occurrence in Finland in October or November is quite exceptional.

In 1918, swifts were observed regularly in Helsinki throughout September and October and in smaller numbers until the middle of November (LEVANDER 1918, PALMGREN 1918). The latest observations were from Nov. 10th (4 indiv.), Nov. 11th (1 indiv.), and Nov. 15th (one emaciated bird caught alive). The late occurrence of swifts was also observed in Sweden (e.g. TÖRNQUIST 1918) and Central Europe (e.g. GEYR 1919).

In other autumns occasional swifts have been seen later than normally (notably 1941; cf. FRANZ 1941, MENNING 1942, also KOSKIMIES 1950). However, nothing comparable with the phenomenon observed in 1918 had been reported in North-European literature until the autumn of 1957.

Late occurrence of swifts in the autumn of 1957.

In the autumn of 1957 exceptionally late swifts were reported from various parts of Finland until the month of November. The abundant occurrence of late swifts, particularly in larger cities and towns, aroused much attention and a large number of observations were recorded.

To supplement the observations spontaneously reported by individual ornithologists and newspapers an inquiry was sent to the cooperators of the Zoological Museum of the University of Helsinki. Requests for information were also delivered through the Finnish radio and various newspapers. In all, 151 persons made available their observations about the breeding phenology and migration of the swifts in 1957. Of these, 112 were regular cooperators of the Zoological Museum. I am much indebted to all these persons, too numerous to lists, for their most cooperative attitude, without which this study would not have been possible. The most complete series of observations were delivered by Messrs. O. Hytönen, L. Lehtonen, P. Linkola, M. Rautkari, A. Reinikainen and N. Söderman.

If the observations of each person for each day on or later than Sept. 15th are counted separately, the total material from Finland consists of 316 observations. 269 of these originate from October or November, 113 from November alone. The latest swifts were seen on Nov. 12th (one individual in Helsinki and Turku), and Nov. 25th (Leppävaara, see p. 121).

In Sweden, observations of 33 persons about the late occurrence of swifts in 1957, collected as a result of an inquiry through the journal »Vår Fågelvärld» have been published by ULFSTRAND (1960).

Fig. 1 illustrates the regional distribution of the observations of late swifts in Finland. From the northern, central, and eastern parts of the country no exceptionally late swifts were reported. Occasional swifts were, it is true, seen in various localities (not indicated on the map) until the middle of September, but this is not unusual even in normal years. The observations from October and November were concentrated in the south-western corner of the country, in coastal areas in particular, although in some localities farther inland (as far north as Kuopio, 62°54′ n. lat.) swifts were seen in November.

Fig. 2 shows the numbers of swifts seen after Sept. 1st in the four separate localities with the largest numbers of observations plus the remainder of the country.

On the ornithological station Signilskär (W.-coast of Aland islands, 60°12′ n. lat., 19°22′ e. long.) swifts were observed in exceptionally large numbers in the autumn of 1957 although not very late (Fig. 2 e; P. Linkola). In the course of regular observations from Aug.

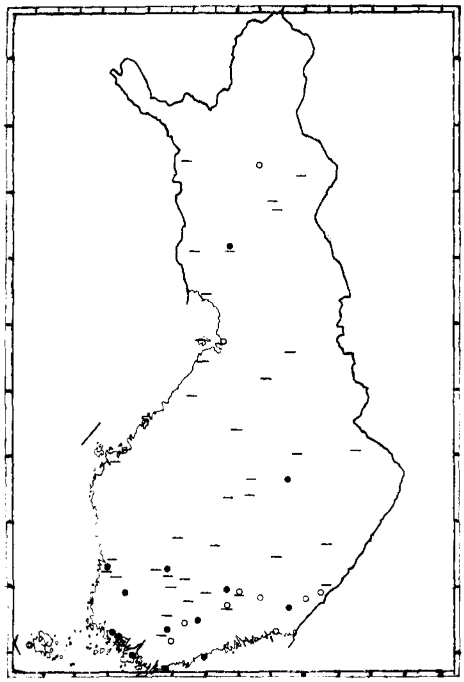

Fig. 1. Localities where swifts were observed between Sept. 15—30 (open circles) and Sept. 15—Nov. 12, 1957 (solid circles). The minus-signs indicate localities with negative observations after Sept. 15.

7th to Dec. 1st, 1957, swifts were seen during 18 days between Aug. 10th and Sept. 17th, in total ca. 435 individuals. Such large numbers of swifts, especially like those recorded between Sept. 7th and 11th, are very rare in the conditions of Signilskär. Thus observations from Aug. 18th to Sept. 29th, 1954, revaled only 6 migrating swifts (during 5 days). Similarly in 1956, only 6 swifts were seen (during 3 days) in the autumn period from Aug. 28th onwards (P. Linkola).

In Helsinki (Fig. 2 a) and Turku-Naantali (Fig. 2 b) swifts were reported fairly regularly throughout the autumn up to Nov. 12th. It seems, however, that in Helsinki at least, the numbers of swifts observed decreased after Sept. 10th only to increase again after the 20th. Mr. K. Venhe, similarly, reported that in Naantali swifts were seen until Sept. 14th, whereafter they disappeared and returned only on Oct. 19th, and were then again seen many times until Nov. 3rd.

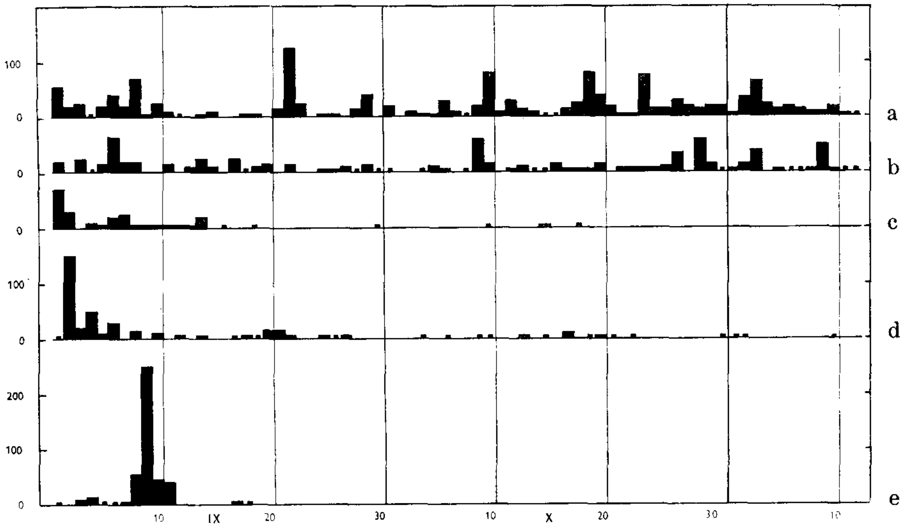

Fig. 2. Numbers of swifts observed in Helsinki (a), Turku and Naantali (b), Pori (c), the rest or continental Finland (d) and the island of Signilskär (e). The numbers of birds observed by different persons are summed for each day. The lowest broad columns = 3—7 indiv., the low narrow columns = 1—2 indiv.

In the town of Pori on the south-west coast of Finland (Fig. 2 c) migrating swifts were seen i fair numbers until the middle of September, after which date only a few occasional birds (the latest one on 18th) were observed.

In various other localities in Finland (Fig. 2 d) a distinct decrease in the numbers of observed swifts took place by the middle of September. It seems that at this time, when also considerable passage migration was observed at Signilskär, the bulk of the swifts had departed from Finland.

26 persons reporting the time of departure of the bulk of the swifts from various parts of the country in 1957 gave the following approximate dates: mid-August 7 cases, late August 11, early September 5, mid-September or later 3. The departure of the majority was thus not much later than usually.

After mid-September generally only small groups of local birds were seen. They were relatively stationary throughout the remainder of their stay.

Observations from Sweden (ULFSTRAND 1960) indicated similarly that the latest swifts remained stationary for rather long periods. The latest swifts in Sweden were observed on Nov. 12th.

From Denmark, observations of late swifts up to Nov. 7th were reported (ULFSTRAND op. c.).

In the Estonian SSR swifts were observed on the following days: Sept. 12th, 17th, 18th, 19th, Oct. 20th and Nov. 10th (Prof. E. Kumari, *in litt.).*

Swallows were also reported being late in departure: *Hirundo rustica* at: Helsinki (Sept. 29th, ca 25 indiv.; K. Malmström), Nilsiä (small downy young in mid-September; A. Kena), Oulu (two adults and two young captured from nest on Sept. 27th; A. Kumpulainen), Kemi (till Oct. 5th; T. Fräki); *Delichon urbica* at Sodankylä (nesting of the least one pair late, departure in mid-September; F. Riipinen).

Causes of the late occurrence of swifts in 1918 and 1957.

Discussing the possible causes of the late occurrence of swifts in Finland in the autumn of 1918, LEVANDER (1918) suggested that the phenomenon could have been caused by abnormal weather conditions during the late summer and autumn. Emphasizing that the rainy and cold August and particularly rainy September were followed by an unusually warm October, LEVANDER suggested that the late birds were individuals which, by the normal time of departure, were poorly developed or perhaps weak or diseased and therefore did not join the bulk of departing birds. Because of the exceptionally mild period in late autumn these birds were able to survive as long as they did.

LEVANDER's explanation seems logical and plausible, particularly in view of the information gathered since LEVANDER's days on the dependence of the life of the swift upon weather conditions (e.g. KOSKIMIES 1950). As the late occurrence of swifts in the autum of 1957 appeared basically similar to the phenomenon observed in 1918 a test of LEVANDER's hypothesis in the case of the late swifts in 1957 seemed desirable. For that purpose weather data were analysed to show whether the weather conditions of these two summers and autumns differed in their essential features in a similar way from the normal.

The breeding phenology of the swift in relation to weather conditions in 1918 and 1957.

The onset of laying in the swift is strongly dependent on weather and is commonly postponed if the weather during the proper season is cold and rainy. LACK (1956) found that under such conditions the first egg is generally laid five days after the first warm, sunny day, which indicates that the development of the ovum within the female requires five days. The second egg usually follows two or more days after the first one, and the regular incubation begins when the clutch is completed.

The incubation takes, on the average, 19—20 days but may be lengthened by 4—5 days under bad weather conditions (LACK 1956). The period of development of the young averages 40—45 days (KOSKIMIES 1950, LACK 1956), but varies within wide limits, from ca. 33 (ŽALUD 1940) or 35 (v. BOXBERGER 1941) to at least 56 days (v. BOXBERGER op. c., LACK op. c.). This variation is, likewise, primarily due to weather conditions.

The breeding season of the swift is thus very long. Under the most favourable conditions the total development from the first ovulated egg to full fledging of the clutch may take place in ca. 60—65 days, whereas in extremely bad conditions the total development may require close to 90 days, i.e. nearly one month more than in optimal conditions.

The normal time of arrival of the first swifts into southern Finland is about May 20th (v. HAARTMAN 1951) and the onset of laying normally takes place around the first half of June. An average period of 2 1/2 months for the total development of the offspring brings the fledging (and departure, which normally takes place soon afterwards) to the latter half of August (cf. p. 105).

In 1957 (Fig. 3 a), the weather conditions in late May and June were unfavourable and, on the basis of temperature records, one would expect at least a part of the swifts to have been late in their arrival. The data gathered in connection with the 1957 inquiry corroborate this idea:

Several observers reported that the arrival of swifts on the breeding grounds was exceptionally late: e.g. in Hamina (S. J. Lehtonen), Koivistonkylä (K. Antila), Lempäälä (Y. Aatinen), Tampere (A. O. Salonen), Pori (T. Tuomi), Konnevesi (O. Puttonen), Nilsiä (A. Kena), Kemi (T. Fräki), Pello (U. Pesonen).

One could further expect that, as poor weather continued until early July (Fig. 3 a), a part of the nesters postponed the start of their breeding until about 10th of July. Alternatively, some of the clutches started at a normal date may have been destroyed during the long

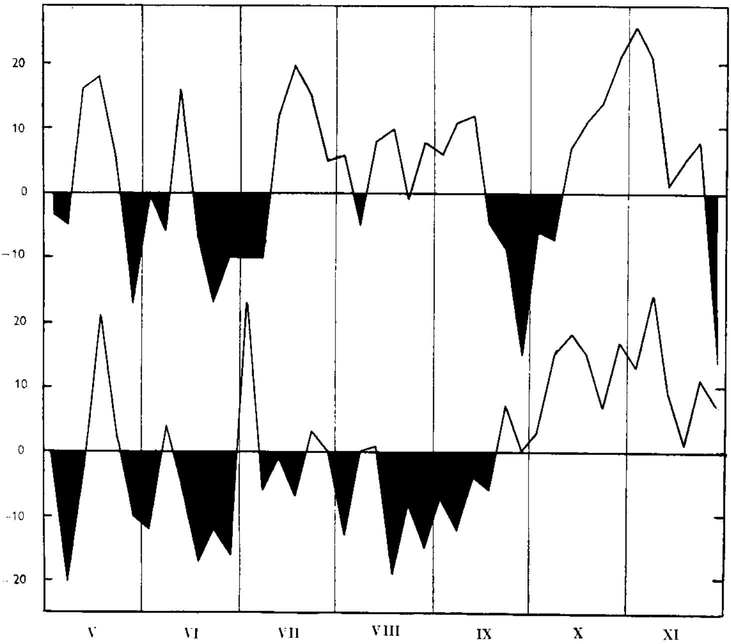

Fig. 3. The 5-day sums of deviations of the daily mean temperatures from the long-term average (0-line) at Helsinki in May-November, 1957 (above) and 1918 (below). Data of Figs. 3—6 from the Meteorological Institute, Helsinki.

cold period which followed. This again must have resulted in renewed clutches commenced on about the above date (July 10th).

Observations reported in 1957 show that the nesting was in fact late.

In some cases the bulk of the birds arrived and nesting commenced a long time after the appearance of the first individuals. In Pello, for instance, where the first birds were seen on June 5th, the main migration took place only around June 24th (U. Pesonen). Likewise, after the first observations in Kemi (June 3—5th) swifts were not seen until the 26th, when they probably also commenced nesting (T. Fräki). From Tampere (first birds on May 17th) the swifts disappeared totally in early June and were absent for days (A. O. Salonen).

The onset of nesting in 1957 was also reported as late in the following localities: Hämeenlinna (»at least two weeks later than normally»; on July 14th birds still incubating; E. Karjalainen), Ruovesi (P. Jalonen), Pihlava (A. Kaukola), Savukoski (»about two weeks late»; L. Merikallio). Further data are presented below.

The breeding population was reported smaller than usually at Oulu (A. Kumpulainen), Kemi (J. N. Jestilä), Länsi-Teisko (O. Vesa), and Lappee (A. Pohjonen).

In many cases in which late nesting was reported, the swifts had been nesting in boxes inhabited by starlings in the same spring. In several cases it was emphazied that the nestings of starlings in this spring was late and this prevented the swifts from occupying their nesting sites at a normal date or even from nesting at all.

Spontaneous reports suggesting that the allegedly late nesting of starlings in 1957 may have been a partical cause of the late nesting of swifts were obtained from the Helsinki area (L. Nupponen), Nummela (M. Laakso), Tammela (A. Huokuna), Vainikkala (A. Pohjonen), Pälkäne (H. Heinonen), Harjavalta (R. Mikola), and Oulu (O. Lahdenperä).

The weather conditions throughout the summer of 1957 were exceptionally bad (Fig. 3 a). This can be expected to have resulted in serious difficulties in the energy economy and juvenile development of the swifts. Catastrophes among nestling swifts, as a result of inclement weather, are common (see the literature mentioned in KOSKIMIES 1950, pp. 70—73). There are some observations indicating such instances from the summer of 1957:

At Oulu, after a protracted spell of bad weather around the middle of August a starved young was found in a swift's nest. The other young was in a very weak condition and left the nest as late as Sept. 3rd (O. Lahdenperä). The young from another nest left on Aug. 25th.

From Riihimäki comes an interesting series of observations: On Sept. 13th a young swift was still observed in a nesting box. On the 27th the young was seen outside the box for the first time. The birds were later seen around the nestling place taking short flights but, especially on rainy days, soon returning to the nest. On Nov. 4th the (only?) parent died, on the 8th or 9th the young died (T. Järvinen, A. Pynnönen).

Swifts were reported absent from the breeding places for many days during bad weather in Ravijoki (R. Kuokka) and Riihimäki (O. Halttunen).

A delay causing a portion of breeders to start laying around the 10th—15th of July can be calculated to have brought the bulk of the young of these late nesters into fledging condition towards the middle or early latter half of September.

Young swifts were still found in nests in late August or in September in Nummela (M. Laakso), Riihimäki (see above), Turku (R. Kehvola), Oulu (see above), and in Nynäshamn, Sweden (see ULFSTRAND 1960).

However, the middle of September, 1957 in itself nearly a month past the normal migration date, coincided with the onset of a pronounced and long period of bad weather. This probably resulted in that the fledged young and possibly their parents remained in near-starved condition even after the weather markedly improved in October. By that time conditions, although better than normal in that season, were hardly tolerable for the swifts.

In 1918, the conditions were probably very similar to those in 1957, although direct observations on the course of breeding in Finland are not available. In Germany, however, nesting of swifts in 1918 is known to have been late (GEYR 1919). One may also form a fairly good picture of the probable conditions in Finland on the basis of weather data (Fig. 3 b).

The months of May and June were roughly equally as bad as in the summer of 1957, and one would expect that a part of the birds were late in migration and a number of nesters portponed the onset of laying until the 5th of July or so. The entire remaining season was cold, particularly in August and September. Under such conditions the development of the young could not have taken place in less than average time (2 1/2 months, see p. 110). Thus the late nesters could not have had their young in a fledged condition before the middle of September, at the earliest, i.e. nearly a month later than the normal time of departure. They must also, judged by the weather conditions towards the end of their development period, have fledged in poor nutritional condition, and many may not have fledged at all. Similarly, the parent birds of such late broods, if still present, must have been undernourished.

CUTCLIFFE (1955) reported that in the extremely bad summer of 1954 all nestlings of swifts in a colony in Devon starved to death by the 17th of July. Although now without any nesting responsibilities the badly emaciated parent birds remained there for 27 more days, about two weeks beyond the normal date of departure. They finally left within a two days period only after the weather had turned »the most promising for the summer». That case is similar to those in 1918 and 1957 except that the latter years failed to develop, during the critical period, a spell of weather favourable enough to enable and stimulate the birds to depart after the normal period of migration was over.

It seems probable that even after the weather in late October 1918 and 1957 turned unseasonally warm, the birds were no longer able to reach a normal nutritional balance and physiological readiness for migration. In somewhat near average weather conditions they would probably have starved in a short time, whereas they now were offered possibilities for a more prolonged survival.

The final collapse of the remaining population in 1918 as in 1957 took place immediately after the period of abnormally favourable weather was over.

The exceptional character of the summers 1918 and 1957.

The weather conditions and their probable effect on the breeding of the swifts in both 1918 and 1957 conform to the general idea presented by LEVANDER (1918). A combination of long cold periods in the summer and warm late autumn, as was characteristic of these two years, can theoretically be expected to lead to the observed late appearance of swifts.

However, this explanation can be accepted only if the two summers in question were the most, or at least among the most exceptional ones in regard to weather conditions postulated to have caused the late appearance of swifts. Obviously the cold early summer is the primary factor which causes nesting to be late with subsequent delay in departure. Therefore, an analysis of the temperature conditions for the period 1930—1956 was carried out for a comparison with those in 1918 and 1957. The period analysed includes 50 days beginning at the average time of arrival in southern Finland, this being the last ten days of May, the entire month of June and the first ten days of July. The following comparisons were made:

1) The number of days with a mean temperature below the long-term (1883—1950) average (Fig. 4) and

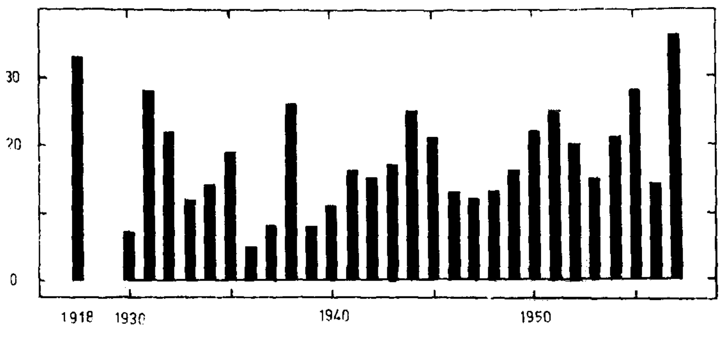

Fig. 4. The number of days with a mean temperature below the long-term average during the first 50 days after the average arrival of the swifts in South Finland (May 21—July 10) in 1918 and 1930—57.

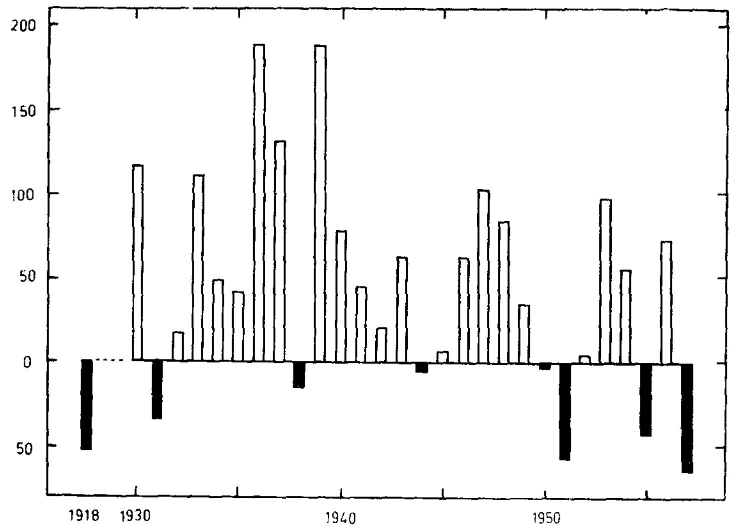

Fig. 5 The deviation of the sum of the daily mean temperatures from the long-term average (0-line) during May 21 — July 10 (see Fig. 4) in 1918 and 1930—57.

2) the deviation of the temperature sum (sum of daily mean temperatures) from the long-term (1883—1950) average for the period of the 50 days specified above (Fig. 5).

As to the numbers of days with mean temperature below normal (Fig. 4) the summers of 1918 and 1957 were clearly the two most extreme of the years analysed. Likewise, the temperature sum (Fig. 5) for 1957 was lowest, and except for one year (1951) 1918 had the lowest temperature sum after 1957.

Clearly the two summers after which the departure of the swifts was delayed had exceptionally poor temperature conditions during the early stages of the normal breeding period of the swift.

Two other summers in the 1950's (1951 and 1955) exhibited temperature conditions (low temperature sums in particular, see Fig. 5) nearly as bad as in 1918 and 1957. As these summers are not known to have led to delayed departure of the swifts, a more detailed analysis of the temperature conditions in these two summers was made.

In 1951 (Fig. 6 a) the month of June was relatively warm, so that no general postponement of onset of breeding was probable. The cold July was followed by a very favourable August (and September). Therefore the conditions prior to

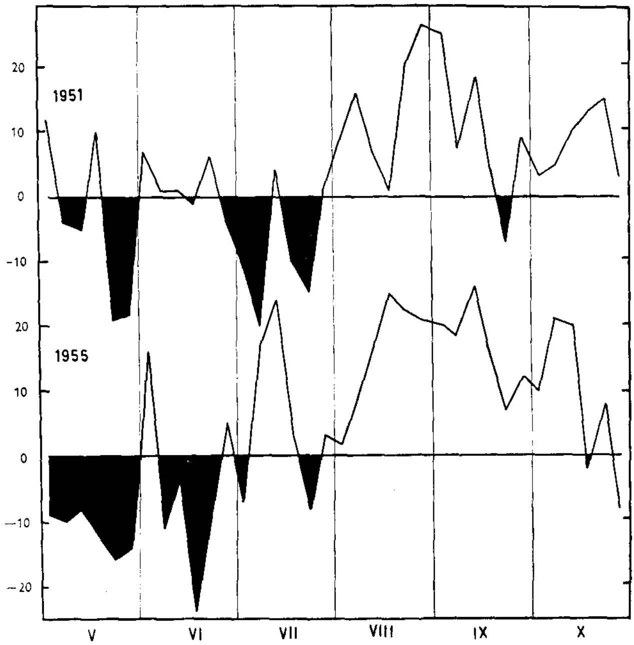

Fig. 6. The 5-day sum of deviations of daily mean temperatures from the long-term average (0-line) in May-October, 1951 and 1955.

and during the normal time of departure were probably good enough to allow normal departure.

In 1955 again, the conditions were rather similar to those in 1957 except that favourable temperature conditions started around July 10th and were maintained practically throughout a period of over three months against only two months in 1957. As three months are enough for the normal development of young swifts even under relatively adverse conditions (p. 110), but two months only in extremely good ones (what the summer of 1957 obviously did not offer), this difference probably was the cause of the diverse breeding results in these two summers.

In addition to low temperatures, high cloudiness and a large amount of rain were also characteristic of the summer of 1957 (comparable values of 1918 are not available). Since 1935, from which year values of relative cloudiness in Helsinki have been published, the average of the mean cloudiness values for the three summer months (June-August) reached its highest value (6.4) in 1957. Similarly, since 1930, the year 1957 was the only one in which the amount of rain in southern Finland in *each* of the six months of the summer half of the year (May—October) was higher than normal.

Notes on behaviour, especially hypothermic sleep, of the late swifts.

In October and November, 1957, swifts were seen primarily in the larger coastal cities of southern and southwestern Finland (see p. 107) and Sweden (ULFSTRAND 1960). This does not necessarily mean that a delay in nesting occurred in these areas moreso than elsewhere. It is rather likely, that in late autumn the conditions in the larger cities were more favourable for the swifts than in rural areas and therefore the swifts survived there longer than elsewhere. Particularly, it is probable that the warm roosting sites (ventilation openings of large heated buildings) were an important factor in this respect.

The late swifts generally behaved in a characteristic manner: they flew silently with slack wing beats, low between trees and buildings, hunting for insects in the lowest air layers. Insect food was probably scant at this time and the stomachs of half a dozen swifts found dead were empty. However, the gizzard of one accidentally killed swift contained a relatively large amount of Diptera remains.

In October and November, swifts were observed throughout the daylight hours (Fig. 7), but with a distinct concentration of observations in the morning (9—11 a.m.) and afternoon (3—5 p.m.). Most records in the morning originated from the period 1—4 hours after sunrise. Only very rarely (8 cases) were these birds seen flying earlier than 1 hour after sunrise; in one case only before sunrise. This is in striking contrast with the conditions in midsummer, when the activity at the latitude of Helsinki normally begins 1—1 1/2 hours before sunrise (v. HAARTMAN 1940). One individual caught alive on the ground on Nov 1st, at 6.30 a.m. (over 1 hour before sunrise) was still torpid (see p. 120), unable to fly, and died the following evening.

The swifts remained active until dusk and in most cases disappeared to roost shortly before sunset. The 7 records of actual time of entering the roosting hole (Fig. 7) coincided within +7 (Sept. 26), +15 (Oct. 5), —22 (Oct. 25, two observations), —6 (Oct. 29), —12 (Nov. 6), and —53 (Nov. 7) minutes of the time of sunset.

The period of daily activity grew shorter with the seasonal decrease of daylength. The period between the earliest and latest observation

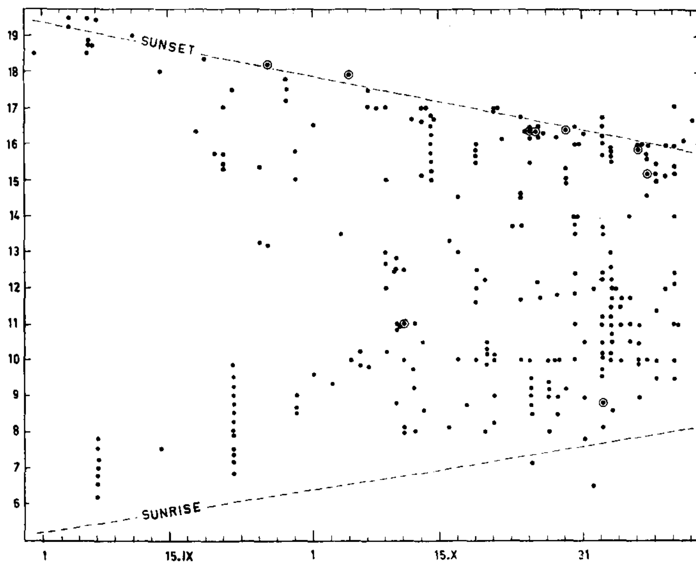

Fig. 7. The time of day of observations of swifts in the cities of Helsinki and Turku in the autumn of 1957. The dots with a circle indicate observations on birds entering a roosting hole.

for each day may be taken to indicate the minimum length of daily activity of the population in each day. On Sept. 7th the daily activity thus lasted for at least 13 1/2 hours, on Sept. 14th 11 1/2 hours, on Sept. 22nd 10 3/4 hours, whereas after Oct. 1st the minimum periods of daily activity thus computed varied (in 15 cases) between 7 and 9 hours, only once exceeding the latter value. In November the average length of the activity period was slightly over 7 hours.

The general pattern of daily activity in the cities was roughly similar to that observed in the summertime (e.g. v. HAARTMAN 1940, 1949). In the conditions of the autumn of 1957 the smaller number of observations from early afternoon hardly indicates a decreased activity (see also v. HAARTMAN 1949), as also the daily rhythm of body temperature (see p. 119) suggests. Rather is it probable that the concentration of the observations in the cities to the mornings and afternoons results from the fact that the birds spent most of the day hunting some distance from the city proper and only returned there to roost.

Mr. M. Soikkeli, in fact, reported that in early October swifts were seen in considerable numbers (up to 35 individuals) above the city of Turku throughout the day, but as the season progressed they were rarely seen in the city except when leaving or entering their roosting holes. They were observed feeding in flocks of up to 40 birds (Nov. 9th) above the large coastal islands about 7—8 km. south-west of the city.

However, in one case at least (Oct. 11st), a bird was seen to enter its regular roosting hole in a building at 11 a.m. and remain there. Similarly, on Nov. 2nd at 8.50 a.m., two birds were seen in Turku fighting against a strong south-westerly wind (temperature +8°C). After 3—4 minutes they flew into their regular roosting place in a ventilation opening.

On two occasions in which the roosting sites (ventilation openings) could be reached from inside, three and one swift were caught, respectively, all in deep hypothermic torpor. In the latter case the bird had been seen to enter the opening at 3 p.m. and was caught at 6.30 p.m. In both cases the birds were transported by car, still in uninterrupted torpor, to a laboratory for further observation. The body temperature of the single bird measured immediately after arrival at the laboratory (7.15 p.m.) was 26.6°C. The three birds from one nest aroused spontaneously the following morning and two of them underwent 1—2 further cycles of reversible nightly torpor before dying of starvation (final weights 23.9, 24.7, 27.2 g.). The one bird which had flown to the roosting hole in apparently full condition in the afternoon and caught the same evening died during the following night, apparently from starvation (final weight 26.8 g.). The observations on the torpidity of these swifts and some experiments carried out with them are described in more detail elsewhere (KOSKIMIES 1961).

There are no observations to indicate the prevalence of the nightly hypothermic torpor in natural conditions during the autumn of 1957, but it is to be assumed that it was a normal part of the daily life cycle of the late swifts in Helsinki, at least in November. We also lack any direct information about the relative roles of environmental conditions and the nutritional status of the birds in inducing the hypothermic behaviour in field conditions. Experimental results (KOSKIMIES 1961), however, indicate that birds weighing less than 30 g. resorted entirely to torpor regardless of the environmental temperature.

In any case, the nightly hypothermy of the swifts obviously is an important adaptation of definite survival value not only to the nestlings, as has been shown earlier (KOSKIMIES 1948, 1950), but also to the independent swifts. The rare capacity of the swifts to greatly lower the energy expenditure during the periods of inactivity by hypothermic torpidity may also have been a major factor responsible for their prolonged survival in the autumn of 1957.

The condition of the late swifts.

Without knowing the efficiency of the swifts in maintaining their daytime nutritional balance under the conditions of their delayed stay, it is not possible to conclude whether the final collapse of the population in November was inescapable even without the drop in temperature that took place during the second week of the month. The long hypothermic sleep with lowered metabolic rate might have compensated for the shortness of the daylight feeding period. However, the food supply was probably already limited so that even continuous hunting did not produce enough to cover the existing energy demands.

As a result of their weak condition, a large number of swifts were caught alive with bare hands or found dead. All were in badly emaciated condition. The following list covers the finds known to the author. Specimens preserved at the Zoological Museum of the University of Helsinki are marked with an asterisk.

Date	*Sex*	*Weight*	*Locality*	*Circumstances*	*Reported by*
*18. X	♀	28	Helsinki		H. Ahlquist
*24. X	♂	24	—»—		A. Venetsalo
*25. X	♂	28.5	—»—		—»—
1. XI		28	—»—	torpid, died	A. Pohjolainen/ J. Koskimies.
4. XI		29	—»—	weak, died	P. Voipio
5. XI			—»—	dead	Uusi Suomi (6. XI)
* 5. XI			—»—		J. Jansson/H. Ahlquist
* 6. XI	♀	24	—»—	flew in through window, died	L. Sammalisto
* 7. XI		25.5	Leppävaara		
9. XI			Otaniemi	starved, caught alive	F. Stenman/Hufvudstadsbladet (10. XI)
9. XI			Helsinki	tired, weak	M. Ingerttilä
* 9. XI	♀	25	—»—		Aurora hospital
* 9. XI	♂	23	—»—		—»—
* 9. XI	♂	24	—»—		A. Venetsalo
* 9. XI	♀	24	—»—		—»—
9. XI			Riihimäki	caught alive, died	A. Pynnönen

10. XI			Helsinki	dead	K. Sundbäck
10. XI			Turku	on ground, died	N. Fritzén
*10. XI	♂	29	Helsinki	dead	A. Niemi
11. XI		28	—»—	on ground, died	M. Oksanen/ J. Koskimies
*11. XI	♂	26	—»—		Police forces
*ca 25. XI	♀	22	Leppävaara		

The average weight at death of 15 swifts in October—November, 1957, was 25.9 with a standard deviation of ± 0.5 g. (limits 22—29 g.). The average of 19 »hunger weights» of adults swifts previously reported by KLEINER (1940), KUHK (1948) and TAAPKEN (1955) is 28.8 ± 0.6 g. (limits 20.5—32.4 g.) whereas the starving weights produced in experimental birds varied between 25.1 and 28.3 g. (average 26.1 g.; KOSKIMIES 1950). The average hunger weight recorded in 1957 is about 61 % of the normal adult weight in breeding time (42—43 g.; KOSKIMIES 1950, LACK 1956) and 48 % of the weight characteristic of autumn migrants in good condition (54 g.; LACK 1956).

Three birds caught alive from their roosting place in Helsinki on Nov. 5th (see p. 119) weighed 31, 29, and 28 g., one caught similarly on Nov. 9th (see p. 119) weighed 27 g. The latter was heavily infested by cestodes. One bird which died accidentally on Nov. 9th weighed 32 g. and was also heavily parasitized by cestodes.

These five birds thus weighed 10—15 g. (24—36 %) less than a normal adult and 22—27 g. (41—50 %) less than a migrant in good condition and had only an average margin of 1—6 grams to reach the starvation weight.

The relevance of the case to the problem of the stimulus for migration.

The phenomenon described above presents a unique natural experiment with interesting implications to the problem of the annual stimulus for migration. The layout and the results of this experiment are clear enough. Individuals of a bird species known as one of the most specialized and distinctive »instinct» migrants (*sensu* WEIGOLD 1924) of the northern Palaearctic failed to develop normal migrational behaviour with a result curiously inconsistent with the concept of adaptiveness of instinctive behaviour. It remained to reveal the »treatments» applied to produce this result, towards which end the previous chapters of this paper have been an attempt, and to coordinate the results with the existing knowledge of the factors responsible for the release of migration in autumn.

FARNER (1955) has reviewed the information available about the annual stimulus for migration. It is apparent that the release of the autumn migration cannot be explained on a common basis with regard to all species of migrants. A basic difference in this respect seems to exist between the migrants of the »instinct» and the »weather» type. The seasonal movements of the latter are largely governed by current environmental conditions. They seem to possess the capacity of responding by directed movements to relevant changes in weather, at least throughout the autumn, winter and spring seasons (see e.g. VLEUGEL 1948, SCHÜZ 1952). Many representatives of this group are also known to develop non-migrant partial populations, which tend to remain stationary on breeding areas, if the weather and food conditions permit.

In contrast to the relatively flexible and facultative behaviour of the »weather» migrants, the »instinct» type seems to have evolved more schematic, anticipatory responses to certain proximate releasers, and their behaviour is little or not at all susceptible to modification by other currently existing environmental conditions affecting their survival.

The failure of the swifts to exhibit normal migrational behaviour can be interpreted in terms of the hypothesis formulated by FARNER (1955), which reflects much of the thinking of GROEBBELS (1928, 1932) and other earlier workers.

It is generally agreed among students of migrational physiology, that »true migratory movements are always preceded by the gradual development of a distinctive metabolic state — *Zugdisposition*» (FARNER 1955, p. 121). This physiological condition is characterized by a favourable nutritional balance, as a result of which excess energy is available for migration. The timing mechanism of the development of the autumnal Zugdisposition still remains obscure, much more so than that of spring migration. Regardless of whether it normally appears in direct response to seasonal changes in environment or merely as a stage in the sequence of other annually recurring physiological events like reproduction, moult etc., it is normally reached at a relatively fixed season. Its realization, however, is dependent on the environmental possibilities for developing the required positive nutritional balance. Although the most apparent aspects of Zugdisposition include such features as a characteristic metabolic condition and development of fat deposits, this condition obviously must be thought to involve changes in the function (reactiveness) of the sensory organs and the central nervous system. The theory postulating the existence of a Zugdisposition as a prerequisite to overt migratory behaviour viz. implies that only a bird in Zugdisposition is sensitive to stimuli which subsequently may release the migration.

The case of the late swifts nicely fits into this pattern of reasoning and emphasizes the importance of a favourable metabolic state before the release of migration becomes possible. In the conditions existing in the two autumns in question, the swifts were probably unable to develop the favourable nutritional balance characteristic of Zugdisposition. Whatever the stimuli normally releasing the departure in this species, they now remained inneffective because of the lack of Zugdisposition. It is well possible that in distinctive early migrants like the swifts the persistence of Zugdisposition per se, without a specific external stimulus, is normally sufficient to release the migration (see FARNER 1955), although the influence of weather conditions has also been suggested (see KOSKIMIES 1950, LACK 1956).

The behaviour of the late swifts can also be explained in terms applicable to releasing mechanism of general instinctive behaviour. The case of the swifts indicates that their migrational behaviour possesses the characteristics of general instinctive behaviour in that it is susceptible to curiously non-adaptive misreactions in situations characterized by biologically improbable, non-average conditions. The inability of the swifts to sensefully cope with the situation in the autum of 1957 by retreating, even if belated, towards their normal wintering grounds was striking. It can thus be compared with the most extreme cases of natural or experimentally produced »errors» of more simple instinctive behaviour (see e.g. TINBERGEN 1951).

The theory of TINBERGEN and his school explains that the release of instinctive behaviour takes place as a result of summation of various internal and external stimuli. Generally an »internal motivation» for a specific behaviour (in this case migration) is assumed to be required in order that the external stimuli normally releasing that behaviour pattern be effective. The internal motivation basically involves preparatory central nervous processes rendering the animal sensitive to specific external stimuli. The internal motivation per se, without additional external stimuli may be sufficient to release the behaviour »in vacuo».

The analogy with the metabolic hypothesis of migrational stimulus is obvious. It may be thought that the internal motivation for migration, in itself a state or function of the nervous mechanisms, may have a metabolic basis, in a similar way as the internal motivation for feeding, for example. Thus the two explanations are mutually consistent. In fact, considering the present lack of precise physiological information in both fields concerned, I feel that the differences between the two alternative explanations presented above are basically terminologic.

Summary.

A considerably number of swifts were greatly delayed in their departure in the autumn of 1957. Late swifts were seen both in Finland and in Sweden regularly till Nov. 12th, i.e. over two months beyond the normal time of departure (Fig. 1—2). Late swifts were also reported from the Estonian SSR, and Denmark.

A greatly similar phenomenon was observed in Finland in the autumn of 1918, and a comparison of the weather conditions of these two summers and autumns revealed striking similarities (Fig. 3). In both years a cold and rainy early summer was followed by a similarly unfavourable late summer and early autumn. As a result the swifts were late in their nesting and the development of the young was slowed down to such an extent that at the end of the normal period of autumn migration a number of swifts had not yet reached the stage necessary for departure. These late swifts remained in poor nutritional condition and failed to develop the migratory urge. Their long survival was rendered possible by an exceptionally mild period lasting in both years in question until about the 10th of November.

The observations from Finland agree with the above hypothetical explanation based on examination of weather data. A number of reports were obtained indicating delayed arrival and onset of breeding. Cases of destruction of broods as a result of inclement weather were also reported, and exceptionally late broods were common.

Of 29 years analysed (1918 and 1930—1957) the years 1918 and 1957 exhibited the greatest numbers of days with mean temperature below average during the period of 50 days immediately following the average spring arrival of the swift in South Finland (May 21—

July 10; cf. Fig. 4). Similarly, the temperature sum for the same period (Fig. 5) was lowest in 1957, and, except for one year, the 1918 value was next lowest.

For 23 years analysed (1935—1957) the mean cloudiness of the summer reached a record high value in 1957. At least since 1930, this year was the only one with a higher-than-average monthly amount of rainfall in every single one of the six months of the summer half of the year (May—October).

Clearly, the summers 1918 and 1957 were very exceptional and very similar in their weather conditions.

Swifts were most frequently observed in the cities of Helsinki and Turku about 1—4 hrs. after sunrise and 1 hr. before sunset (Fig. 7). It seems probable that the swifts often spent the day hunting outside the cities and only returned to roost in the warm ventilation holes of large heated buildings. Their period of daily activity lasted about 10—14 hrs. in September, 7—9 hrs. in October and slightly over 7 hrs. in November (Fig. 7).

Swifts roosting in ventilation holes in Helsinki spent the night in hypothermic torpor thus considerably lowering their energy expenditure during the period of inactivity.

A number of swifts were found dead or caught alive with bare hands in badly emaciated condition. The average weight at death of 15 swifts was 25.9 ±0.5 g. Five individuals still normally active weighed 32, 31, 29, 28, and 27 grams (Nov. 5—9).

The relevance of the case to the problem of stimulus for autumnal migration is discussed.

Literature: BOXBERGER, L. v., 1941, Zum Brutgeschäft des Mauerseglers. Beitr. Fortpfl.-biol. Vögel 17: 211—212. — CUTCLIFFE, A. S., 1955, Further notes on the swift, 1944—1954. Brit. Birds 48: 193—203. — FARNER, D. S., 1955, The annual stimulus for migration: experimental and physiologic aspects. *In* Recent studies in avian biology, pp. 198—237. Urbana, Ill. — GROEBBELS, F., 1928, Zur Physiologie des Vogelzuges. Verh. Ornith. Ges. Bayern. 18: 44—74. — 1932, Der Vogel, 1. Atmungswelt und Nahrungswelt. Berlin. — HAARTMAN, L. v., 1940, Über den Tagesrhythmus des Mauerseglers, Apus a. apus (L.). Ornis Fenn. 17: 7—11. — 1949, Neue Studien über den Tagesrhythmus des Mauerseglers, Apus apus (L.). Ibid 26: 16—24. — 1951, Die Ankunftzeiten des Mauerseglers, Apus apus (L.), und ihre Beziehung zur Temperatur. Comm. Biol. Soc. Scient. Fenn. 11,2: 1—21. — KLEINER, A., 1940, Mauersegler-Katastrophe in Ungarn. Der Vogelzug 11: 127. — KOSKIMIES, J., 1948, On temperature regulation and metabolism in the swift, Micropus a. apus (L.), during fasting. Experientia 4: 274—276. — 1950, The life of the swift, Micropus apus (L.), in relation to the weather. Ann. Acad. Scient. Fenn. A, IV. Biol., 15: 1—151. — 1961, Fakultative Kältelethargie beim Mauersegler, Apus apus, im Spätherbst. Die Vogelwarte 21. — KUHK, R., 1948, Wirkung der Regen- und Kälteperiode 1948 auf den Mauersegler, Micropus apus (L.). Ibid. 1: 28—30. — LACK, D., 1956, Swifts in a tower. London. — LEVANDER, K. M., 1918, Tervapääskysen muutto syksyllä 1918. Luonnon Ystävä 22: 155—161. — PALMGREN, R., 1918, Tervapääskysen muutto syksyllä 1918. Ibid. 22: 154—155. — SCHÜZ, E., 1952, Vom Vogelzug. Frankfurt a. Main. — TAAPKEN, J., 1955, Catastrophale sterfte van Apus apus (L.), Hirundo rustica (L.) en Delichon urbica (L.) gedurende de periode van eind Mei tot begin Juni 1953, veroorsakt door abnormale lage temperaturen en voedselgebrek. Ardea 43: 275—283. — TINBERGEN, N., 1951. The study of instinct. Oxford. — TÖRNQUIST, N., 1918, Sen höstflyttning för tornsvalan. Fauna o. Flora 1918: 286. — ULFSTRAND, S., 1960, Sena iakttagelser av tornsvala (Apus apus) hösten 1957. Vår Fågelvärld 19: 55—58. — VLEUGEL, D. A., 1948, Enkele waarnemingen over »vorstvlucht» end »randtrek» in het Sloe-Schengengebied tijdens de winters van 1935/1936 en 1936/1937. Ardea 36: 143—162. — WEIGOLD, H., 1924, Das Wetter und der Herbstzug der Waldschnepfe. Journ. Ornithol. 72. — ŽALUD, J., 1940, Ueber den Brutverlauf des Mauerseglers. Sylvia 5: 10—12.

Selostus: **Tervapääskyn myöhästynyt syysmuutto v. 1957.**

Melkoinen määrä tervapääskyjä myöhästyi suuresti syysmuutossaan v. 1957. Tervapääskyjä nähtiin eri puolilla Suomea sekä myös Ruotsissa säännöllisesti marraskuun 12. päivään saakka, ts. vielä yli kaksi kuukautta normaalin poismuuttoajan jälkeen (kuvat 1—2).

Hyvin samanlainen ilmiö havaittiin Suomessa syksyllä 1918. Vuosien 1918 ja 1957 alkukesän ja syksyn sääsuhteet olivat hyvin samankaltaiset (kuva 3). Kumpanakin vuonna alkukesä oli kylmä ja sateinen ja myös alkusyksyksi sattui selvä epäedullisen sään kausi. Myöhäissyksy sen sijaan oli kumpanakin vuonna poikkeuksellisen lämmin.

Kylmän alkukesän seurauksena osa tervapääskyistä myöhästyi pesimisessään. Poikasten kehitys hidastui siinä määrin, että vielä normaalin muuttokauden päättyessäkään nämä tervapääskyt eivät luultavasti olleet saavuttaneet muuttoonlähdön edellyttämää fysiologista valmiustilaa. Myöhäiset tervapääskyt pysyivät jatkuvasti huonokuntoisina ja niiden säilyminen hengissä pitkälle marraskuuhun saakka johtui vain siitä, että syksy oli poikkeuksellisen lämmin. Lämmin kausi päättyi kumpanakin vuonna marraskuun 10. päivän vaiheilla, jolloin myös tervapääskyt hävisivät lopullisesti.

29:stä sääsuhteiltaan analysoidusta vuodesta (1918 sekä 1930—1957) vuosina 1918 ja 1957 havaittiin suurin määrä keskimääräistä (1883—1950) kylmempiä päiviä 50 ensimmäisen päivän aikana välittömästi tervapääskyn keskimääräisen Etelä-Suomeen saapumisen jälkeen (toukok. 21—heinäk. 10 p.; ks. kuvaa 4). Samoin oli mainitun kauden lämpösumma (päivittäisten keskilämpöjen summa) alhaisin v. 1957 ja yhtä vuotta lukuunottamatta lähinnä alhaisin v. 1918 (kuva 5). Myös kesän pilvisyys oli v. 1957 suurin 23 analysoidusta vuodesta

(1935—1957). Ainakin vuodesta 1930 lähtien v. 1957 oli lisäksi ainoa, jolloin kuukautinen sademäärä *jokaisena* kuukautena toukokuusta lokakuuhun oli keskimääräistä korkeampi.

Vuodet 1918 ja 1957 olivat sääsuhteiltaan selvästi erittäin poikkeukselliset ja hyvin samantapaiset.

Helsingissä ja Turussa havaittiin tervapääskyjä runsaimmin n. 1—4 t. auringonnousun jälkeen sekä 0—1 t. ennen auringonlaskua (kuva 7). Näyttää luultavalta, että tervapääskyt yleensä viettivät päivät saalistusmatkoilla kaupunkien ulkopuolella ja palasivat kaupunkeihin vain yöpyäkseen suurten kivirakennusten lämpimissä tuuletuskanavissa yms. Niiden päivittäinen liikkeelläoloaika syyskuussa kesti n. 10—14 t., lokakuussa n. 7—9 t. ja marraskuussa vähän yli 7 t.

Helsingissä tuuletuskanavissa yöpyneet tervapääskyt olivat yön ajan syvässä horrostilassa. Täten niiden energiankulutus pieneni toimettomuuden aikana.

Joukko tervapääskyjä tavattiin kuolleina tai saatiin kiinni hyvin heikossa kunnossa. 15 yksilön keskimääräinen paino kuollessa oli 25.9 ± 0.5 g eli n. 60 % normaalista aikuispainosta. Viisi vielä marraskuun 5—9 pnä normaalia elämää viettänyttä yksilöä painoi tällöin 32, 31, 29, 28 ja 27 g.

Lopuksi tarkastellaan syksyisen muuttovireen saavuttamiseen johtavia tekijöitä linnuilla yleensä, sekä niitä syitä, jotka johtivat siihen, että syksyn 1957 myöhäiset tervapääskyt eivät lainkaan tulleet muuttovireeseen.

Zur Kenntnis der Wanderungen finnischer Meisenvögel.

PENTTI LINKOLA

Dass die Wanderungen der sogen. Invasionsvögel in mancher Hinsicht so mangelhaft bekannt sind, beruht in erster Linie auf Schwierigkeiten der Feldbeobachtung: die wandernden Bestände bilden oft nur einen kleineren Teil der Population, und die Zugbewegungen werden dort leicht übersehen, wo die betr. Arten auch stationär vorkommen. Dies gilt ganz besonders für die Meisenvögel.

Die Anregung zu dem vorliegenden Aufsatz gab die interessante und vielseitige Arbeit von LEHTONEN (1958) über die Bewegungen der Meisenschwärme. Die längeren zugartigen Wanderungen werden von ihm jedoch nur in aller Kürze und z.T. in einer Weise berührt, die vielleicht zu Missverständnissen führen kann.

Die nachfolgende Übersicht über Fernwanderungen verschiedener finnischer Meisenvögel soll Material liefern zur Kenntnis einzelner Invasionen unter Berücksichtigung der Individuenzahl, Zugperioden im