

Delayed autumn migration of the Swift *Apus apus* from Finland in 1986

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In the autumn of 1986 a couple of thousands of northern European Swifts did not start on migration but stayed in southern Finland and on the eastern coast of Central Sweden. Most Swifts had left Finland by the end of August, but a small number returned in mid-September, and the latest were seen in the beginning of November. In the course of the autumn no new migration could be observed.

The birds were all adults. They sank into a state reminiscent of wintering, and some individuals started moulting in October. The health of the birds deteriorated due to shortage of food, and the surviving birds perished in the beginning of November when the frost started. No decreases were observed in two closely followed breeding colonies in southern Finland in 1987, so it is suggested that the late Swifts were from central or northern Finland.

The strict time limits that the northern populations of the Swift have for breeding do not allow delayed migration caused by exceptional weather conditions as happened in the autumn of 1986. The slow moult normally commences in Africa after the autumn migration. In the autumn of 1986 the delayed departure of some individuals was due to unsuccessful accumulation of fat deposits because of adverse weather conditions. After this the birds started to winter, and, the moult commencing, it was impossible to migrate.

1. Introduction

In some autumns a part of northern European Swifts *Apus apus* does not leave for their wintering areas in Africa. Although this phenomenon is uncommon, there have been three remarkable delayed autumn migrations in Finland (in northern Europe) in the 20th century: in 1918 (Levander 1918, Palmgren 1918), in 1957 (Koskimies

1961a) and in 1986. In addition, a small number of Swifts was seen in the late autumns of 1941 (Koskimies 1961a), 1966 and 1977 (Rauhala 1980) and after the very cold summer in 1987.

The causes of the delayed migration are only partly known. Levander (1918) and Koskimies (1961a) state that the cold and rainy first half of the summer had been the main cause of the delayed departures in 1918 and 1957. At that time

the onset of breeding was delayed and it was not until August–September that the young became fledged, and, as the parent birds were in poor condition, all individuals could not migrate in autumn.

After the good breeding season in the summer of 1986 the situation was different. In southern Europe no catastrophes of equivalent scope are known to have happened, but in different parts of Central Europe Swifts have been seen late in October–November in several years (Denmark, Germany, Belgium, the British Isles; Glutz & Bauer 1980, Cramp 1985), so the phenomenon is connected with the problems of the Swift in breeding in the north.

In this paper we examine the causes of the delayed autumn migration in 1986 on one hand on the basis of breeding data, on the other hand by connecting the behaviour to the annual cycle of the Swift. Especially moult is discussed because it regulates the time Swifts spend in the breeding areas in Europe and in the wintering areas in Africa.

2. Material and methods

2.1. Breeding biology

Two colonies were closely followed: Helsinki (Käpylä school building; 60°13' N, 24°58' E) and in Virolahti (Harju Agricultural School; 60°32' N, 27°33' E). A colony of Swifts is nesting in the ventilators in the attic of Käpylä school. The size of the colony was 5–7 pairs in 1980–86 (10 nesting boxes), and 12 pairs in 1987–88 (19 nesting boxes). The Harju colony consists of 44 nesting boxes. The Swift colony nesting there (36–44 pairs yearly) has been studied closely since 1979 (Kolunen 1986). Data on breeding biology, the measurements of breeding and non-breeding adults, and definitions of the degree of moult are available especially from the summers of 1985–88, that is, before and after the catastrophe of the autumn of 1986.

2.2. Observations in the autumn of 1986

The Käpylä population was observed almost daily after the Swifts reappeared after 15 September.

On 13 October the nesting boxes and four other holes in the school attic were checked. A total of 12 Swifts were found. The nesting boxes and holes were then checked every week until the beginning of November. The birds were ringed, measured, weighed, and the age and the degree of moult were determined. Two other colonies (Lahti 61° N, 25°40' E, and Harju) were also followed in autumn, but no roosting individuals were found.

Additional data were obtained from the publications of local Finnish ornithological societies (literature searched until the autumn of 1988). The Swedish observations are based on reports in *Vår Fågelvärld*.

2.3. Weather

Weather data for 1986 come from the monthly reviews of the Finnish Meteorological Institution (Finnish Meteorol. Inst. 1987). Earlier information is based on the Meteorological Yearbooks of Finland (Finnish Meteorol. Inst. 1924, 1955, 1966).

3. Results

3.1. Delayed autumn migration in 1986

Käpylä. After mid-August Swifts were no longer observed and they were assumed to have migrated after the breeding season as normally. Unexpectedly, about 20 Swifts appeared on 16 September 1986. They circled round the Käpylä school and even visited nesting holes. After this 2–8 individuals searching for food were observed in the surroundings from 18 September to 12 October. In the school area no Swifts were seen in daytime before 13 October, but when checking the nest-boxes in the evening 10 individuals, all unringed and adults, were found. In addition, one more adult was caught on 14 October and 23 October.

The Swifts were adults and clearly starving (mean weight 37.5 g, SD = 3.1, n = 12). During the breeding season the weights of the breeding and non-breeding individuals vary between 38 to 46 g (mean 42.9 g, SD = 2.1, n = 254, Kolunen

1986). The ten individuals caught in the evening of 13 October were indoors in the room temperature for 24 hours, and they lost weight on average 3.7 g. The birds were fed and set free on 14 October. The same individuals were observed until the beginning of November, when they had either died or disappeared (Table 1). The health of the birds deteriorated all the time even though they were searching for food in the urban area of Helsinki in the daytime (see Vasamies 1987). The dead birds weighed from 27.5 to 31.5 g (Table 1). They had lost nearly all their fat (visual estimate, see Koskimies 1961a, pp. 106), and had died in their roosting holes.

The weight of the Swifts decreased evenly. The average weight loss was 1.0 g per day

($n = 7$) on 13–16 October and 0.75 g per day ($n = 6$) on 16–22 October. Several night torporing individuals were noticed: one individual on 16 October, 4 individuals in one nesting box and one lonely individual on 21 October, and one individual on 23 October. The birds felt cold when handled, their movements were slow, and they did not try to flee. The ambient temperature was below $+10^{\circ}\text{C}$.

Finland and Sweden. The autumn migration of Swifts started after the good breeding summer of 1986 in the beginning of August. The majority of the birds disappeared from breeding sites in southern Finland by 12 August, when a long period of rain started. Notable gatherings of migrants were observed e.g. at Rönnskär bird station west of Helsinki (780 migrants on 14 August, Karlsson 1988), in Oulu (1000 individuals on 18–22 August, Heikkinen 1987), and in Porvoo (250 individuals on 23 August, Juvonen 1988). In the beginning of September there were few local Swifts around and records of the last large numbers of migrating Swifts were from Turku on 7 September (398 migrants, Klemola et al. 1987), and from Muurame on 10 September (266 migrants, Honkalahti et al. 1987). At Rönnskär bird station the last migrants (3 individuals) were seen on 4 September (Karlsson 1988). At Viikki in Helsinki even 3000 migrants, young birds among them, were counted in the best mornings in August, but only a few stayed until the beginning of September (L. Lehtonen pers. comm.).

On 14–16 September Swifts appeared in large areas in Finland and in the coastal areas of Västerbotten in Sweden (Fig. 1). In many areas Swifts had no longer been seen since August. In Hyvinkää about 300 migrants and 100 local individuals were seen on 14 September (Ahtiainen et al. 1987). The northernmost observations came from the Kemi – Tornio area in Finland (2 individuals on 16 September, Rauhala 1987) and the surroundings of Umeå in Sweden (50 individuals about on 15 September, Arnell 1987). The Swifts stayed in many areas until October (Jantunen 1987, Kontkanen & Parviainen 1987, Kuokkanen et al. 1987, Lind 1987, Moilanen 1987, Okkonen 1987, Rajala 1986, Vähämäki 1987). From northern Finland they disappeared by mid-October

Table 1. Changes in the weight (g) of the Swifts in the autumn of 1986 (Käpylä). Dead individuals are indicated by an asterisk (*). The birds were weighed in the evening after the sunset. On 24 October all holes were empty. ¹⁾ Found dead in Helsinki (5 km S). ²⁾ Found dead outside the nesting-boxes later.

Bird number	Date (October)				
	13	14	16	22	23
A-264329	40.0	34.5	36.0	29.5*	
A-264330	34.5	30.5	–		
A-264331	36.0	33.5	36.0	29.5*	
A-264332	38.0	34.5	34.0	–	
A-264333	37.5	32.5	–	27.5*	
A-264334	35.5	32.5	32.0	30.5	29.0*
A-264335	41.0	37.0	38.0	33.0	31.0
A-264336	32.0	29.5	30.0	–	
A-264337	39.0	35.0	–	–	* ¹⁾
A-264338	42.0	38.5	37.0	32.5	31.5*
A-264339	–	38.0	35.0	32.0	* ²⁾
A-339479	–	–	–	–	32.0
Mean					
Alive	37.5	33.8	34.6	32.0	31.5
Dead				28.8	30.3

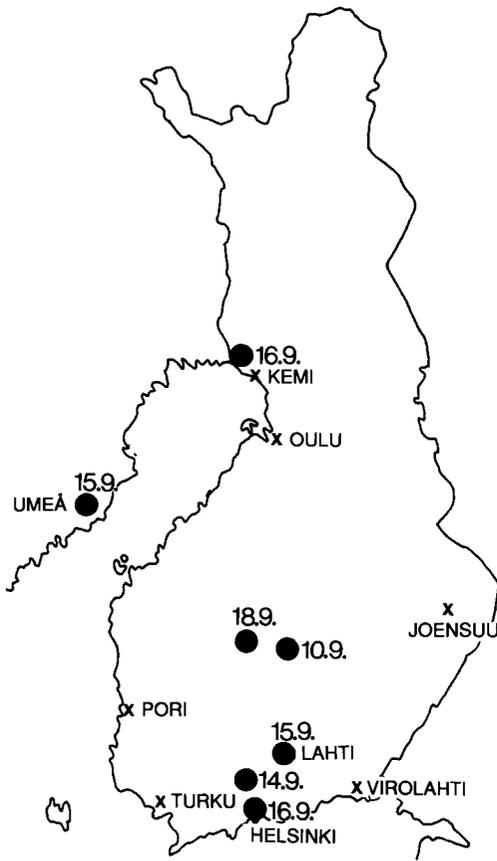


Fig. 1. The area in Southern Finland, where the Swifts reappeared in September 1986.

ber, but in Sweden the last ones were seen in the beginning of November. In central and southern Finland thousands of individuals were observed in October, in the area of Helsinki alone about 1700 Swifts (Hildén 1986, Mikkola & Hildén 1987).

In the end of October Swifts in poor condition were seen mainly in cities and towns south of the line Pori – Joensuu (Fig. 2). The number of individuals diminished as Swifts died of cold and hunger (e.g. Turku, Klemola et al. 1987; Tampere, Aro et al. 1988; Jyväskylä, Martikainen 1986; Hyvinkää, Ahtiainen et al. 1987; Porvoo, Juvonen 1988). About 150 individuals, which were starving or had just starved, were brought to the Zoological Museum in Helsinki (Vasamies 1987).

Migrating Swifts were exceptional in October; at Jurmo bird station one migrating individual was observed on 20 October. In Helsinki Swifts flew to search for food outside the city, e.g. to reedy bays, in the morning, returning in the afternoon to roost in the city (Vasamies 1987).

In the beginning of November the last individuals were seen in flight in the same places where they had stayed after mid-October (Fig. 2). The birds were at that time in a very poor condition, and several were seen benumbed or dead, e.g. one of the last ones in inland areas was an exhausted Swift seen in Heinola on 8 November (weight 27 g, A. Bosley). In Umeå, Sweden, the last individual was observed on 10 November (Ellmberg & Stenström 1987, Hirschfeld 1987). On the southern coast of Finland the last Swifts were seen in Helsinki on 12 November, in Turku and Merimasku on 13 November, in Turku on 19 November and in Kotka on 19 November (a dead bird in the street) (Vasamies 1987). It is evident that the Swifts that were alive in the beginning of November starved, mostly in their roosting sites beyond reach.

3.2. Breeding season of the summer of 1986

The weather conditions were favourable during the breeding season in the summer of 1986 (Table 2). The first young fledged in the beginning of August, the majority of them by 10 August. In the Harju population in Virolahti the number of breeding pairs was 39 (variation is 36–44 pairs

Table 2. The mean temperature ($^{\circ}\text{C}$; Helsinki, Finnish Meteorological Institute) and the long-term (1931–60) average.

Month	1986	Mean 1931-60	Difference
May	10.3	9.3	1.0
June	17.0	14.5	2.5
July	17.3	17.8	-0.5
August	14.6	16.5	-1.9
September	8.4	11.7	-3.3
October	6.6	6.1	0.5
November	4.7	1.8	2.9

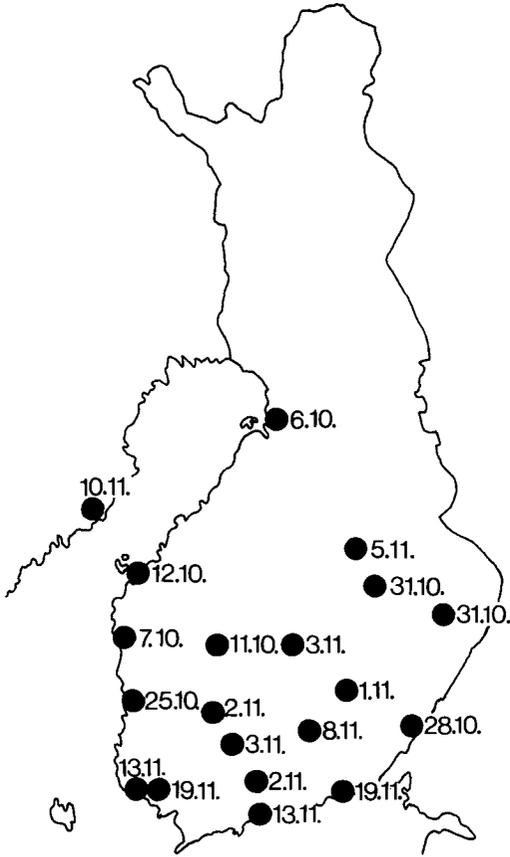


Fig. 2. The last observations of Swifts in the autumn of 1986.

yearly). The median of the start of egg-laying was 12 June, which is the same as the longterm average (Kolunen 1986).

No late clutches were observed in this colony. On 28 July 81% of the hatched young ($n = 56$) were alive, and the 2 young birds of the youngest brood weighed 54.5 g and 55.5 g (the corresponding wing lengths were 94 mm and 102 mm).

3.3. Moulting

Eight individuals (67%, Table 3) of the Swifts caught in the autumn of 1986 were in moulting. The descendent moulting started in the first primaries. There were one or two first primaries in moulting, and the replacement of the corresponding first

primary coverts started simultaneously. The food condition deteriorating, the moulting did not progress further (see Table 1). The moulting adds 20–40% of the basal metabolic rate to the energy requirements (King 1980).

We also examined the Swifts in the Zoological Museum, University of Helsinki. There are 13 adult individuals from the autumn of 1957. Of them 7 (54%) had started moulting (Table 4). From other autumns there are two late adults, neither of them moulting (6 November 1941, 11 October 1968).

3.4. Weather in the autumn of 1986

The weather type in Finland became unsettled in the end of the breeding season after 10 August. The warm and dry area of high atmospheric pressure that had prevailed all the summer moved away, and the rainy and chilly weather lasted until the beginning of September after mid-August (Table 2). The average temperature in August was $+14.6^{\circ}\text{C}$ at Kaisaniemi, Helsinki (1.9°C lower than normal) and the rainfall 160 mm, about 2.5 times more than normal. The corresponding figures in September were $+8.4^{\circ}\text{C}$ (3.3°C lower than normal) and 65 mm (approximately normal). October was warmer than usual, especially in central and northern Finland (in Helsinki $+6.5^{\circ}\text{C}$, 0.5°C higher than normal). In southern Finland precipitation exceeded the normal (Turku 141%, Tampere 115%, Jyväskylä 103% and Helsinki 121%).

The first severe frost was on the nights of 3 and 4 November, and the day temperatures went up to $+2$ to $+3^{\circ}\text{C}$. On 11–13 November the temperature was several degrees below zero also in the daytime. After this only few Swifts were observed (Fig. 2).

The Swifts appeared in Finland and Sweden in September ahead of a large area of low atmospheric pressure, which reached southern Finland in the morning of 15 September. At that time a heavy S and SW storm passed eastern Fennoscandia (Fig. 3). After the storm cold arctic air spread from NW to eastern Sweden and Finland by 17 September. After this many areas of low atmospheric pressure passed Finland and weather was variable until early October.

Table 3. The moult of the 12 individuals examined in the autumn of 1986 (Käpylä). Symbols: 0 = old, worn feather, 1–4 = growing, 5 = full-length fresh feather. Both the right (R) and the left (L) wing have examined. The primaries and primary coverts have been marked. All examined on 14 October except A-339479 (23 October).

Specimen	Age	Wings	Moult of the primaries										primary coverts				
			inner					outer					1	2	3		
			1	2	3	4	5	6	7	8	9	10					
A-264329	ad.	L	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0
		R	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A-264330	ad.	L=R	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A-264331	ad.	L=R	5	4	0	0	0	0	0	0	0	0	0	5	4	0	
A-264332	ad.	L	5	0	0	0	0	0	0	0	0	0	0	5	0	0	
		R	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
A-264333	ad.	L=R	5	4	0	0	0	0	0	0	0	0	0	5	4	0	
A-264334	ad.	L=R	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
A-264335	ad.	L=R	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
A-264336	ad.	L=R	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
A-264337	ad.	L	5	0	0	0	0	0	0	0	0	0	0	5	0	0	
		R	5	4	0	0	0	0	0	0	0	0	0	5	0	0	
A-264338	ad.	L	5	0	0	0	0	0	0	0	0	0	0	5	0	0	
		R	5	2	0	0	0	0	0	0	0	0	0	5	2	0	
A-264339	ad.	L=R	5	4	0	0	0	0	0	0	0	0	0	5	4	0	
A-339479	ad.	L=R	5	0	0	0	0	0	0	0	0	0	0	5	0	0	
Number of moulted feathers		L	7	3	0	0	0	0	0	0	0	0	0	8	3	0	
		R	6	5	0	0	0	0	0	0	0	0	0	6	4	0	
Moulting individuals			7	5	0	0	0	0	0	0	0	0	0	8	4	0	
%			58	42										67	33		

For the late Swifts 2–3 October were the first possible days for daytime migration. Then a sunny, mild southwestern air flow prevailed and the temperature went up to +15°C in southern

Finland. Similar weather conditions prevailed on 13–15 October, even if the temperature was lower. Later in October and especially in the beginning of November the weather conditions were unfavourable.

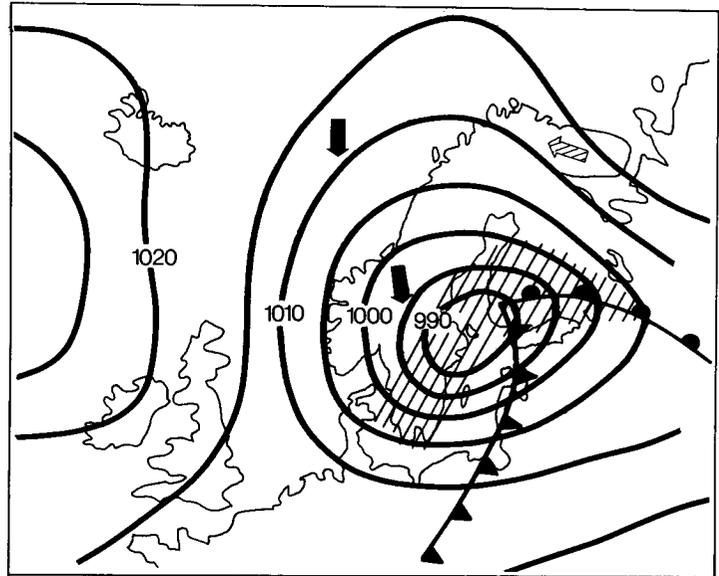


Fig. 3. General weather conditions on 15 September 1986. The warm front has just arrived to Southern Finland. The center of low atmospheric pressure is in SW Finland.

avourable for migration. The nights were cold, and in the mornings there was often fog.

engaged pairs. Death rate from 1986 to 1987 was not above average (18.9% yearly, Kolunen 1986).

3.5. Origin of the birds

Käpylä. The population nesting in the attic of Käpylä school has been observed since 1980. In 1980 there were 7 pairs, in 1981 5 pairs, in 1986 presumable 6 pairs estimated after the breeding season from the number of nests used (there were no dead young birds in the nests), in 1987 6 pairs and 6 “engaged” (non-breeding) pairs and in 1988 6 pairs and 6 engaged pairs. The many engaged pairs in 1987 and 1988 were due to the new nesting boxes added.

The number of breeding pairs of Swifts did not decrease from 1986 to 1987. Because the adults had not been ringed, this suggests that the 12 adult individuals caught from the nesting holes in the autumn of 1986 did not belong to the original breeding population in Käpylä.

Harju. The breeding population in the summer of 1987 was 40 pairs (in 1986 39 pairs and in 1988 43 pairs). Of the breeding pairs 85% (n = 34) were old, ringed individuals that had at least once bred together, and 15% (n = 6) were new

Table 4. The moult of the late Swifts in the autumn of 1957 examined from the skin collection of the Zoological Museum, University of Helsinki. Symbols: f = female, m = male, 0 = no moult (old worn feather), 1 = new 1st primaries, 2 = new 2nd primaries.

Date	Age	Sex	Moult
18.10.	ad.	f	0
24.10.	ad.	m	0
25.10.	ad.	–	0
05.11.	ad.	–	0
06.11.	ad.	f	1.2
07.11.	ad.	–	0
09.11.	ad.	f	1
09.11.	ad.	m	1.2
09.11.	ad.	f	1
09.11.	ad.	f	1.2
10.11.	ad.	f	1.2
11.11.	ad.	f	1.2
25.11.	ad.	f	0
Total	13	moult	7 (54%)

4. Discussion

4.1. Earlier delayed departures

In the autumn of 1918 a small number of Swifts that did not start on migration were seen in Helsinki in September to November (Levander 1918, Palmgren 1918). The autumn migration had largely ended by the end of August, the last observation being from 9 September. After this there was a month's interval in the observations, for the next individuals had been seen on 19 October. The last individual was captured exhausted in a balcony of the University on 15 November 1918 (Levander 1918).

According to Levander (1918) the summer of 1918 was chilly and wet. He thought that this might have delayed the onset of the breeding of the Swifts. The development of the young was slow, which postponed the nestling period until late August. A continued rain period prevailed during the normal time of migration in mid-August and hindered the parent birds from accumulating fat deposits for migration. Levander (1918) also suspected that the delayed migrants were weak and in poor condition. The weather in the beginning of October and November was relatively warm, which, in turn, made it possible for the Swifts to survive with very little food as late as that.

The autumn migration of the Swifts was delayed in the autumn of 1957 due to the cold and rainy early summer, which postponed the onset of breeding (Koskimies 1961a). According to Koskimies most Finnish Swifts had migrated by mid-September. After this quite a number of Swifts stayed in Finland to the beginning of November. The last live individuals were seen on 12 November. In Sweden, Denmark and Estonia Swifts were also late.

The autumn of 1957 was a variant of the year 1918. From the summers analysed by Koskimies (1961a) the years 1918 and 1957 distinguish from all the other summers in the 20th century on the basis of a cold early summer with heavy rain. The weather had clearly delayed the onset of breeding and thus postponed the time the young leave the nest until September in part of the population. The migration of the Swifts was hindered by their physiological condition. Rainy

weather minimized the appearance of flying insects and there was not enough nourishment to be stored for migration. As migration instinct had slackened, the Swifts did no longer migrate in October but stayed in their breeding localities in poor condition (Koskimies 1961a).

In the autumn of 1941 Swifts were exceptionally late in Eastern Karelia after the autumn migration on 8 October (Franz 1941), and in Haapasaari, Muurola, Alakurtti and Ivalo in mid-October (Koskimies 1950). The weather conditions in the summer of 1941 were unfavourable for the Swift. Because of wartime observation was not efficient and there is no information on the number of Swifts. In 1941 Swifts were very late also in Belgium (Menning 1942).

In the autumns of 1966 and 1977 late Swifts were seen in Kemi (Rauhala 1980). In 1977 there were still 40 individuals on 28 September. About 20 individuals were found dead in October. The last ones survived until the beginning of November: on 1 November 2 individuals and on 2 November one individual. According to Rauhala (1980), as a result of late spring migration and bad summer, the birds did not have time to breed normally.

4.2. The delayed departure in the autumn of 1986

Timing of moult. A full moult in the Swift takes place after autumn migration in the wintering areas in central Africa (De Roo 1966, Stresemann & Stresemann 1966, Cramp 1985). During the breeding season no moulting individuals have been described from Europe (Glutz & Bauer 1980, Cramp 1985).

The Swifts in moult seen in Finland in the autumns of 1957 and 1986 had commenced moulting exceptionally during October as autumn migration had been interrupted during October. In De Roo's (1966) data from eastern Africa Swifts were undergoing the same stage of moulting on 19–24 August as the Finnish moulting individuals in October. Normally over 50% of the primaries have been moulted in October (De Roo 1966). The moult lasts about 6 months and ends in February (Stresemann & Stresemann 1966).

The moult of the late Swifts in 1957 and 1986 had thus also been delayed and interrupted presumably due to shortage of food.

Weather. The Swift is dependent on the prevailing weather conditions (Koskimies 1950). The food consists only of insects and spiders caught in the air (aeroplankton), the availability of which is governed by temperature and rain (Lack 1956). According to Glick (1939) the number of aeroplankton diminishes rapidly when the temperature falls below +15°C.

The Swifts of the autumn of 1986 appeared ahead of a deep depression along with a warm air flow in southern and central Finland and Västerbotten, Sweden (Fig. 3). The phenomenon resembles weather movements that appear during the breeding season, when breeding and non-breeding individuals may move far away, over 1000 km away from their nesting sites (Koskimies 1950). In August 1986, however, depressions followed each other so frequently that the food supply must have been poor (heavy rain in southern Finland after mid-August, the temperature continuously below +15°C). In these conditions many thousands of individuals were driven back along with a warm southern air flow (Fig. 3).

Effect on the breeding population in 1987. The Käpylä population was not smaller in 1987 than in 1986. This suggests that the individuals perishing in the autumn of 1986 were not from the local breeding population. The adult death rate in the Harju population in 1986–87 was 18% (n = 73, the longterm mean in 1972–80 was 18.9%, n = 243; Kolunen 1986). The proportion of new individuals was 18% (n = 14), which does not deviate from the number of first breeders in 1980–86 (14.3–34.9%; Kolunen 1986).

In Kangasala (61°30' N, 24° E) 4 ringed pairs nested in 1986 (P. Rassi, pers. comm.). A ringed pair returned in mid-September in 1986 and roosted in their own nesting box. In 1987 there were 3 breeding pairs but only one was a pair from the preceding summer. It was not, however, the pair observed in the autumn of 1986.

Origin of the birds. The populations studied (Harju and Käpylä) did not show any decrease in the number of adults in the summer of 1987 following the catastrophe. The observations sug-

gest that the Swifts destroyed in Finland in the autumn of 1986 were from central and northern Finland. Unfortunately, there is no other information available on the ringed population from these areas other than Kangasala.

Hypothermy. According to Koskimies (1950) an adult Swift is able to survive 4–5 days without food and a nestling on the average 9 days. This fasting ability is uncommon in insectivorous birds and is related to the total dependence of the Swift on the food caught in the air. During the breeding season the young may sink into torpor during rainy and cold weather, but adult Swifts move away from their breeding localities (Koskimies 1950). When night temperatures fell near 0°C, torpid Swifts were seen in Käpylä. At that time the weights of the Swifts had already decreased, so the birds were in poor condition (see Koskimies 1950), but signs of migration could no longer be observed. In the Nightjar *Caprimulgus europaeus* migratory restlessness hinders night torpor in autumn (Peiponen 1966).

Why delayed autumn migration? The delayed autumn migration of the Swift in 1986 differed from the autumns of 1918 and 1957 (Koskimies 1961a). The summer of 1986 was warmer than the average and had little rain, and the breeding of the Swifts succeeded well. Hildén (1987) and Vasamies (1987) think that the catastrophe in the autumn of 1986 was caused by the poor condition of the inexperienced first breeders that bred too late, and additionally by the poor condition of the individuals possibly suffering from parasites just before the rain period started in August. That is why the fat deposits required for migration of the Swifts were no longer sufficient and some birds were unable to migrate and perished.

K. Mikkola suggested in 1986 in his presentation at a meeting of the Finnish Ornithological Society that the adult birds were delayed because of the bad weather after 12 August 1986.

Elmberg and Stenström (1987) state that the late appearance of Swifts was a consequence of disturbances in the hormonal regulation of the annual cycle of the Swift due to radioactive radiation of the Chernobyl nuclear accident (in the spring of 1986). No evidence, however, supports this hypothesis (Lehikoinen & Lindström 1988).

Neither is it easy to relate the thinning of the ozone layer, suggested to be the cause of the deterred migration by Svensson (1987), with the biology of the Swift.

4.3. The annual cycle of the Swift

The spring migration of northern European populations cannot commence until the end of moult in Africa in March or April. Before migration the birds have to accumulate fat deposits, which is also important for the start of egg-laying as soon as possible in the breeding areas in Europe (O'Connor 1979). The individuals captured at the breeding sites during May weigh more than later in June (Gladwin & Nau 1964). In some individuals (10–30%, Kolonen 1986) the moult lasts too long and is interrupted so that spring migration can start.

After their arrival in Finland in the end of May or in the beginning of June the Swifts start breeding immediately (von Haartman 1951, Kolonen 1986). In favourable conditions the fledged young leave the nest in late July or early August. If the onset of breeding is delayed due to unfavourable weather, the time the young leave the nest will be delayed (Kolonen 1986). During a normal summer the young fledge by mid-August, when the adult individuals migrate. Non-breeding pairs, pairs having failed in breeding and young engaged pairs migrate earlier than breeding adults (Kolonen 1986).

The young leaving the nest have adapted themselves to an immediate migration. The weight of the fledged young (mean 41.4 g, Glutz & Bauer 1980) is sufficient for a long continuous flight. The young do not return to the nesting hole once they have left it (Lack 1956, Weitnauer 1980, Kaiser 1984). In Central Europe migration already takes place from mid-July when aeroplankton is abundant (Koskimies 1950, Weitnauer 1980). The interval between the end of breeding and the start of migration depends on the prevailing weather conditions. In England in cold and rainy summers the parent birds stayed for an average of 11 days after their brood had gone; in years of rather poor weather the average interval was 8 days and in fine and warm years only 2–3.5 days (Lack 1956). In Switzerland the parent birds often start on migration on the same day as their young (Weitnauer 1980). In Eng-

land the parents with late broods migrate immediately after their young (Lack 1956).

In Finland the nesting period is the latest of the European populations and therefore the breeding Swifts have a tight schedule. The flight from northern Finland to the wintering areas is also the longest, so there is not much time to accumulate fat deposits. An adult Swift can put on weight many grams in a couple of days during the breeding season (Kolonen 1986). After breeding it is possible to accumulate fat deposits quickly only in good conditions.

4.4. Conclusion

We suggest that the physiological timetable of the Swifts that had stayed in Finland in the autumns of 1957 and 1986 had broken down because they failed to prepare for the autumn migration. Unfavourable weather first hindered the accumulation of fat deposits required for migration and then the whole migration. The Swifts cannot postpone their moult, the long duration of which affects on the timing of the spring migration and thus their future breeding success. The catastrophes could no longer be prevented by other factors, such as the ability of torpor, as the migration instinct had slackened and Swifts had stayed to "winter".

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Selostus: Tervapääskyn myöhästynyt syysmuutto Suomesta 1986

Syksyllä 1986 osa Pohjois-Euroopan tervapääskyistä ei lähtenyt syysmuutolle vaan jäi Etelä-Suomeen ja Keski-Ruotsin itärannikolle. Lintujen määräksi arvioitiin muutamia tuhansia, mikä on vain murto-osa Suomen pesivästä kannasta. Tervapääskyt olivat pääosin poistuneet Suomesta elokuun loppuun mennessä, mutta pieni osa palasi takaisin syyskuun puolivälissä ja niitä tavattiin aina marraskuun alkuun saakka. Syksyn kuluessa ei voitu todeta uudelleen alkanutta muuttoa.

Linnut, jotka kaikki olivat aikuisia, asettuivat talvehtimista muistuttavaan tilaan ja osalla yksilöitä käynnistyi sulkasato lokakuussa (Taulukko 3). Lintujen kunto heikkeni kuitenkin ravinnon vähyyden vuoksi, kunnes marraskuun alussa alkaneet pakkaset tappoivat kaikki yksilöt.

Ilmiön selittämiseksi tutkittiin kahden tarkoin seuratun tervapääsky-yhdyskunnan pesiviä emolintuja (Virolahti, Harju 40 ja Helsinki, Käpylä 12 paria). Syksyllä 1986 tuhoutuneiden yksilöiden ei todettu olleen näistä eteläsuomalaisista yhdyskunnista. Lintujen alkuperäksi oletetaan Keski- ja Pohjois-Suomen populaatioita.

Mikään aikaisempi hypoteesi (syksyt 1918 ja 1957) ei selitä syksyn 1986 viivästyistä. Käsityksemme mukaan tervapääskyn pohjoisten populaatioiden hyvin tiukat aikarajat pesimisessä, poikasten pesästä lähdössä ja pesivien emolintujen valmistautumisessa syysmuutolle eivät salli poikkeuksellisten sääolosuhteiden aiheuttamaa viivästyistä kuten syksyllä 1986 tapahtui. Sulkasato, mikä tällä lajilla on poikkeuksellisen pitkäaikainen, alkaa talvehtimisalueilla Afrikassa välittömästi syysmuuton päätyttyä. Syksyllä 1986 osalla yksilöitä muuton viivästyminen johtui rasvavarastojen keruun epäonnistuttua sääolojen estettyä tehokkaan ravinnon saannin. Tämän jälkeen linnut alkoivat "talvehtia" ja sulkasadon alkaessa mahdollisuudet muuttaa olivat kokonaan menneet. Luonnonvalinta karsi liian myöhään pesinnästä vapautuneita tervapääskyjä, jotka eivät voineet enää saavuttaa muuttoon vaadittavaa fysiologista tilaa.

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