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Roosting in tree foliage by Common Swifts *Apus apus*

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Common Swifts *Apus apus* have occasionally been reported roosting overnight by hanging in the foliage of trees. However, roosting in foliage, which is often associated with food shortage as a result of adverse weather, appears to be an important alternative to aerial roosting. Thirty-nine observations of the behaviour have been recorded previously in Europe, some of them concerning two or more birds. Furthermore, each August from 1982 to 2000, within a restricted area of *c.* 300 × 300 m in southern Sweden, Swifts (118 total) were observed to roost in the foliage of trees or on a latticework mast, whereas others (230 total) were observed making 'fly-ins' typical of the behaviour preliminary to roosting. Of those roosting, 39 Swifts could be aged, and all but one of these were newly fledged juveniles. The Swifts perched late at dusk with maximum frequency about 30 min after sunset, but tended to perch earlier in cloudy weather and later in clear weather. Numbers of roosting Swifts were correlated with low mean temperatures in August, and appearances of roosting Swifts were correlated with low local evening temperatures. During May–July 1982–2000, within the same small area, 18 Swifts were observed to roost in this manner and 29 other Swifts made preroost fly-ins. It is concluded that the behaviour is used more frequently and is more widespread geographically than thus far published observations indicate. This applies especially to newly fledged young on their first migration. Adaptive explanations for this are suggested, with the implication that the behaviour may be widespread in swifts of the tribe Apodini.

Non-breeding Common Swifts *Apus apus* are known to roost aerially in breeding areas (for recent studies with radar and radiotracking, see Bäckman & Alerstam 2001, Tarburton & Kaiser 2001). Lockley (1970) argued that both juvenile and adult birds also use aerial roosting in Africa. If correct, they would spend about 9 months of the year continuously on the wing, whereas non-breeding birds might fly continuously for several years. Kaiser (2001) agreed with Lockley in principle. He also argued that the predominant and regular use of aerial roosting may be special for the Common Swift, and he was sceptical of the rather commonly accepted extension of the hypothesis to other swift species. However, there are very few direct observations of aerial roosting by Common Swifts in Africa (e.g. Sauer & Sauer 1960, Becker 1974 in Namibia; Herroelen 1998). Observations indicating aerial roosting in other species are also sparse, a fact that may point to the occasional, rather than regular, use of the behaviour (e.g. Snow 1962 concerning the White-collared Swift *Streptoprocne zonaris* in Trinidad; Jennings 1995 concerning the Alpine Swift *Tachymarptis melba* in Saudi Arabia; Carter 1969 concerning the Pacific Swift *Apus pacificus* in Australia). Weber (2001) saw evening ascents by the Pacific Swift in Mongolia and, after searching the literature, concluded that our knowledge about aerial roosting in the swifts is still very incomplete.

Observations of Common Swifts roosting in trees in Africa are few and uncertain. Herroelen (1998) gave a few references, and quoted Maes's (1993) observations of Common Swifts in Zaire: 'Each evening they flew towards the southeast to roost in the high trees of the marsh forests'. Considering their regular breeding in tree holes, Herroelen concluded that the possibility of roosting in trees cannot be rejected. Observations of roosting in trees in other species of the tribe Apodini are also very rare, but regular such roosting should be expected in the palm swifts *Tachornis* spp. and *Cypsiurus* spp. (presumably, foliage of palms should be the substrate most commonly used, apart from the nest). A group of African Palm Swifts *Cypsiurus parvus* was once found nesting inside clusters of leaves in a Gum Tree *Eucalyptus* sp. (Brooke 1971). There are a few further observations of swifts in connection with

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tree foliage, perhaps also hinting at roosting (e.g. Ryan & Rose 1985, Robel 2003 concerning Bradfield's Swift *Apus bradfieldi* in Namibia; Franchimont 1988, Paterson 1988 concerning the Pallid Swift *Apus pallidus* in Morocco and Spain; Newell 1930 concerning the Pacific Swift in Australia). Roosting in foliage has also been observed in swifts of the tribe Chaeturini, such as the Chimney Swift *Chaetura pelagica* in the USA (Latham 1920), and there are several observations of the White-throated Needletail *Hirundapus caudacutus* roosting in trees in Australia, sometimes in foliage (e.g. Quested 1980, Clayton 1993, Day 1993, Tarburton 1993).

The Common Swift is one of many species of bird known to use facultative hypothermia (McKechnie & Lovegrove 2002). Swifts have various adaptations (e.g. torpor, clumping on walls) to survive stressful conditions such as those caused by adverse weather and food shortage. It is known that Swifts encounter hazardous weather situations in Africa (Steyn & Brooke 1970, Bromhall 1980, Elkins 1988) and that their vulnerability to predation is increased in harsh weather (Kuhk 1948, Klass 1953).

On two occasions, in August 1978 and 1980, I happened to see a Common Swift as it perched in the foliage of a tree in a garden in Skurup, south Sweden (Holmgren 1978, 1981). This inspired a regular watch, which gave a series of observations of the behaviour (Holmgren 1986, 1987, 1993). All observations in Europe obtained by a search of the literature, requests and personal communications are listed in the Appendix. This paper reports on the observations from Skurup 1982–2000, and on analyses of a few aspects of the behaviour. The number of observations within a very restricted area, and the regularity of the behaviour, have led me to conclude that the behaviour is used much more frequently in the Common Swift than is apparent from published reports. Tree-foliage roosting appears to be an important adaptation for this species to survive adverse weather.

METHODS

The study area of *c.* 300 × 300 m is located in Skurup (55°28′N, 13°30′E), a village situated in open agricultural surroundings about 10 km from the Swedish south coast. The study area is a residential area in the southern and highest part of the village, *c.* 70 m above sea-level. Within the study area, there are several high trees of various species and a lattice-work mast *c.* 40 m high. Each year, during the main part of the summer, I kept an irregular watch for roosting Swifts. Observations increased in August, when adult and fledgling Common Swifts migrate southwards through Sweden. During the 19 years 1982–2000, I methodically spent 426 August evenings in the study area. I recorded weather, temperature (from 1984), numbers and times for Swifts making 'fly-ins' (which include practice runs and attempts at perching) or actual perching in foliage or on a mast in the study area. Time is recorded in Central European Summer Time (CEST = UTC + 2 h).

I consider roosting on the mast and roosting in foliage as, in principle, identical behaviours, because the Swifts appeared to be attracted to the mast as if it was an artificial tree. With increasing darkness, I had to move within the area to sites where Swifts were making fly-ins as preliminaries for roosting. At that time, owing to the darkness, I could cover only a minor part of the study area. The mast offered the best conditions for observing Swifts making fly-ins. Flying in the air around the mast, the Swifts remained discernible as silhouettes against the sky until it was very dark.

The fly-in behaviour was highly typical, and it could safely be interpreted as attempts to perch. Some birds had difficulty in achieving a good grasp, especially on the mast, and a bird making fly-ins towards the mast might attempt this continuously for 15–20 min. In many of these cases, the Swift eventually gave up and disappeared in the dark, perhaps perching in a tree somewhere in the neighbourhood. It was crucially important to see the act of perching, because once perched in foliage, if I had not seen precisely where it perched, a Swift was almost impossible to find even with a torch or in good light in the morning. This was much less of a problem when Swifts perched on the mast. When the daylight was bright enough in the morning, I could visually age a sample of the roosting Swifts by use of a 20× telescope.

In 1986–87, requests for observations of Common Swifts roosting in foliage of trees were published in *British Birds* (Great Britain), *Fugle* (Denmark), *Ornithologische Mitteilungen* (Germany), *Anser* and *Vår Fågelvärld* (Sweden), and *Vögel der Heimat* (Switzerland).

RESULTS

Observations in Europe

When I first saw Common Swifts roosting in foliage, I only knew of six other observations, mentioned by

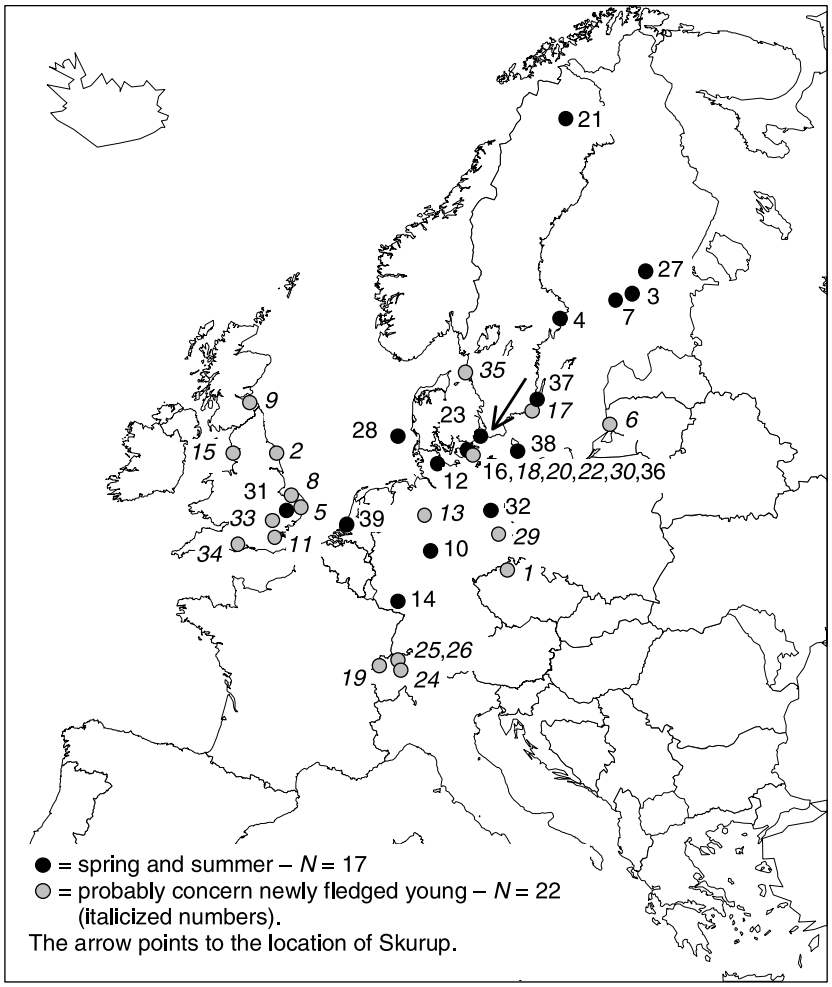

Figure 1. Observations in Europe of Common Swifts roosting in foliage or in similar situations. Numbers refer to the Appendix, where number, date, location, type of perch, short description and reference are specified for each observation.

Lack (1956, 2–5 and 7–8 in the Appendix). Requests, personal communications and a search of the literature added to the list (see Appendix), but it still has only 39 entries, although some of them concern several birds. Figure 1 shows the geographical distribution of these observations. Many of the observations are from spring and summer; 22 at most concern newly fledged young (indicated by italicized numbers and grey dots on the map). The Swifts roosted in various tree species, and a few observations of roosting on 'mast-like' structures (electric lines, poles, ship masts, outside of nestboxes) are included.

Considerable chance is certainly involved in this geographical distribution. I believe the most likely place to observe the behaviour is along coastlines, because concentrations of migrating Swifts and of Swifts performing weather movements can be observed there. However, there are ten inland observations in the Czech Republic, Germany and Switzerland. A few English reports came after my note (1993) in *British Birds*. The absence of records from southern parts of Europe may indicate a bias towards finding records from northern parts. However, because there is a correlation with low temperatures, and probably with harsh weather generally (see below), the use of the behaviour may well be less frequent in the southern parts of Europe.

The six Danish observations (Appendix nos 16, 18, 20, 22, 30 and 36) came from Hans Anker Nielsen, then lighthouse keeper at Hestehoved lighthouse, Falster, Denmark (54°50′N, 12°10′E). In addition to the listed observations, close to the lighthouse he

saw about 40 Swifts making typical fly-ins towards trees and disappearing into dark tree crowns at dusk. The recent observation in the Netherlands (Appendix no. 39) is very special. In June 2002, a Swift roosted at the same location for 19 nights, each night hanging on a net attached to scaffolding at a church tower. The bird was absent during two spells of bad weather, returning after a few days when the weather improved, which may indicate that it had been taking part in weather movements (H. Verkade pers. comm.).

In one observation of roosting in foliage (by P.G.D. Morgan, Appendix no. 31), the Swift fell to the ground when the branch was hit. It was several minutes before the bird took off, perhaps indicating that it was in a state of torpor.

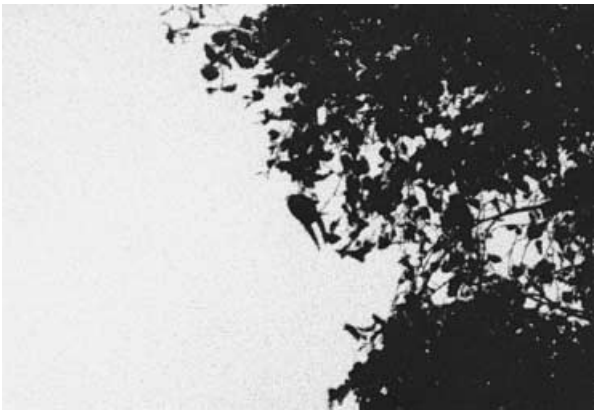

Figure 2. Juvenile Common Swift roosting in Birch in Skurup, August 1988. After several fly-ins, the Swift perched in this position at 20:50 h on 20 August. Erich Kaiser took the photograph at 05:30 h on 21 August. The young bird's whitish 'face' could clearly be seen in the field. The Swift departed at 05:35 h.

Observations in study area in August 1982–2000

Within the study area, I observed Common Swifts making fly-ins or perching on 131 evenings (31% of all study evenings), during which 118 Swifts roosted overnight (55 in trees of various species, 63 on the mast). Two-hundred and thirty other Swifts made fly-ins towards trees or the mast, probably most of them finally perching in the foliage of trees outside the small part of the study area in which I could observe in the poor light available. I could age 39 roosting Swifts. All except one, observed on 21–22 August 1992, were juvenile birds.

In attempts to age birds in the morning, I could see their mode of hanging by their feet in foliage. The birds often had some support for the body in the foliage, but sometimes the Swift was hanging freely, in a few cases apparently on just one leaf. In these cases, the bird had its back downward with wings pointing obliquely downwards (Fig. 2). In strong wind in the evening a bird could be torn loose so it had to come back for a safer grasp, and some birds were flung vigorously from side to side all night.

The numbers of Swifts using the behaviour varied greatly between years (Fig. 3). Although I watched on most evenings, no Swift was seen roosting in August 1983 and 1995, and I saw only one or two in 1984, 1996 and 1997. In these years, the local evening temperatures, registered each study evening, were mostly well above the mean temperature of all the study evenings for which I have temperature records (mean 1984–2000 = 14.5 °C (sd = ±2.44), $n = 360$). The three Augusts with the highest numbers of observations (1992, 1993, 1998) are shown in Figure 4. In 1993 and 1998, the mean temperatures of 'observation evenings' (evenings with at least one observation of a Swift roosting or making fly-ins) were significantly lower (12.9 °C (sd = ±0.57), $n = 10$ and 13.0 °C (sd = ±1.83), $n = 13$) than the mean temperature of all the study evenings. In 1992 this was not the case (mean 14.4 °C (sd = ±1.34), $n = 14$). Rain and wind were not extreme either, so conditions other than the local weather appear to have been of influence. There was a significant negative correlation between high numbers of roosting Swifts and the mean evening temperatures for August (Fig. 3; Spearman rank correlation, $r_s = -0.59$, $n = 17$, $P < 0.05$). In a few years, a relatively high monthly mean temperature, combined with a high number of roosting Swifts, may have been caused by a very warm period followed by cooler and unsettled weather. For example, such a pattern was discernible in 1992 (Fig. 4).

That the Swifts had a tendency for more frequent perching on colder evenings can also be seen in Figure 5. In this figure, the same observations are sorted per day in August, and the local temperature records are sorted into two categories: means are calculated for each day separately from 'observation evenings' and from 'non-observation evenings'. The mean temperatures for all 'observation evenings' (13.8 °C (sd = ±1.79), $n = 116$) and all 'non-observation evenings' (14.8 °C (sd = ±2.63), $n = 244$) differed significantly ($F = 2.16$, $P < 0.01$). This is reflected in the trend curves for the daily means (the trend curves of Figures 5 and 7 are least-square polynomials of power 3 or 4). The numbers of 'all Swifts'

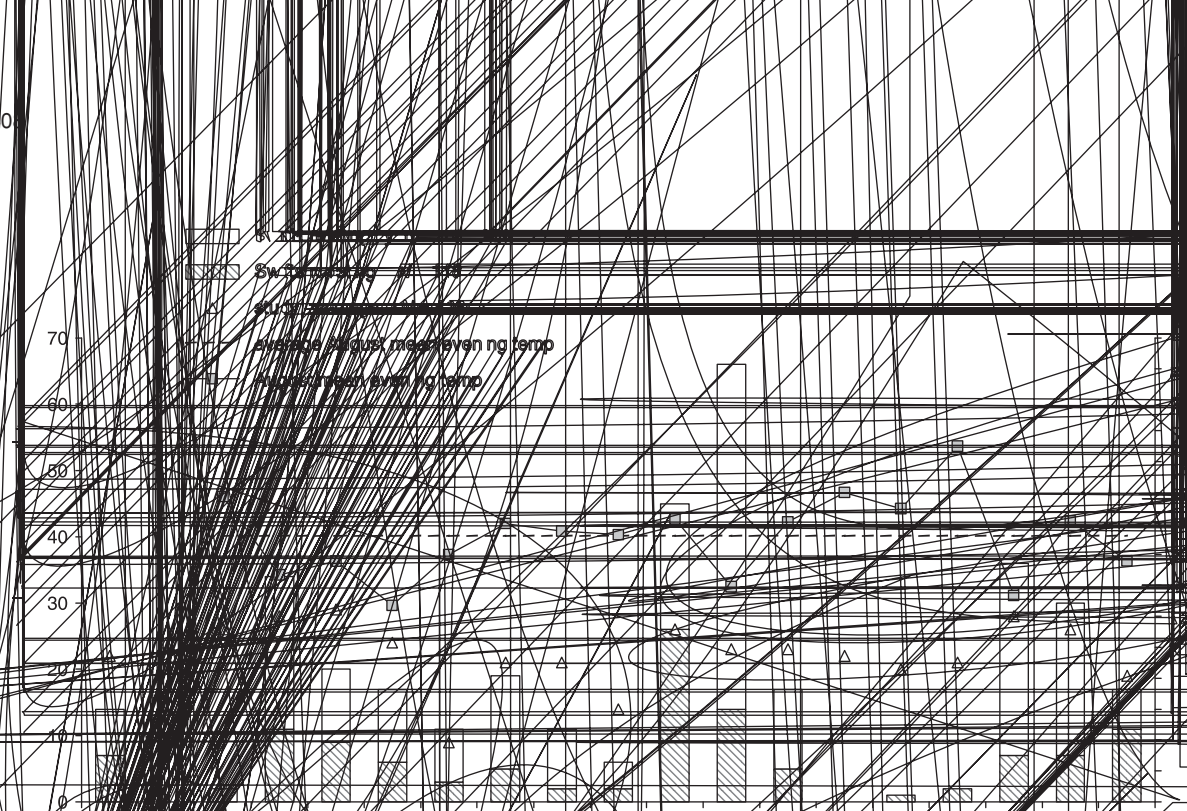

Figure 3. [illegible] observations of Swifts roosting or making fly-ins and evenings spent watching (study evenings) in August distributed per year.

tend [illegible] normal distribution peaking near the mid[illegible] and this strengthens the conclu[illegible] that the [illegible] observed birds were newly [illegible] on their first migration. In spite of [illegible] watch, roosting Swifts seen at other [illegible] during the summer were very sparse compared with the concentration in August. With more data, it would be possible to discern the arrivals of young from different populations (e.g. from Finland or [illegible]) at various times in different years, and correlate their numbers and times of arrival with weather conditions in the breeding areas. However, my data are insufficient to make such an analysis.

The reason for the general scarcity of observations of roosting Swifts may be that this behaviour [illegible] during a short period in the evening, [illegible] The [illegible] times I have [illegible] according to the degree of cloudiness, [illegible] Figure 6. In Figure 7, the same data are [illegible] 30-min intervals in relation to time of sunset. The frequency of perching peaked at 25–29 min after sunset (mean = 28.6 min [sd = ±10.51], $n = 93$, $P <$ [illegible]). A normal distribution might be expected, and the deviation from a normal curve at the right side indicated in the trend curve for all observations may have been caused by the increasing difficulty of seeing Swifts in the darkness. The frequency of Swifts perching in cloudy weather peaked at 15–24 min after sunset (mean = 19.4 [sd = ±11.46], $n = 31$, $P < 0.05$), whereas the frequency of Swifts perching in clear weather peaked at 28–34 min after sunset (mean = 30.81 [sd = ±9.33], $n = 34$, $P < 0.05$), about 12 min later than in cloudy weather. Although there is considerable overlap, the difference between these means is highly significant ($z = 4.42$, $P < 0.01$).

The morning departure times I have noted are shown in Figure 8. Most are centred on sunrise, and there appeared to be a tendency for the Swifts to leave earlier on clear days. Seven of the Swifts stayed until considerably later, from 80 min to almost 2 h after sunrise. All these cases were in connection with light rain (but other birds in rain left at a time close to sunrise). In two of these cases the weather improved, and the bird was hanging for some time in clear sunshine.

I made only one observation of Swifts roosting on the outside of a building. In light rain, two Swifts perched on gables of villas in the study area in the evening of 23 August 1988.

Observations in study area in May–July, and other miscellaneous observations

Outside

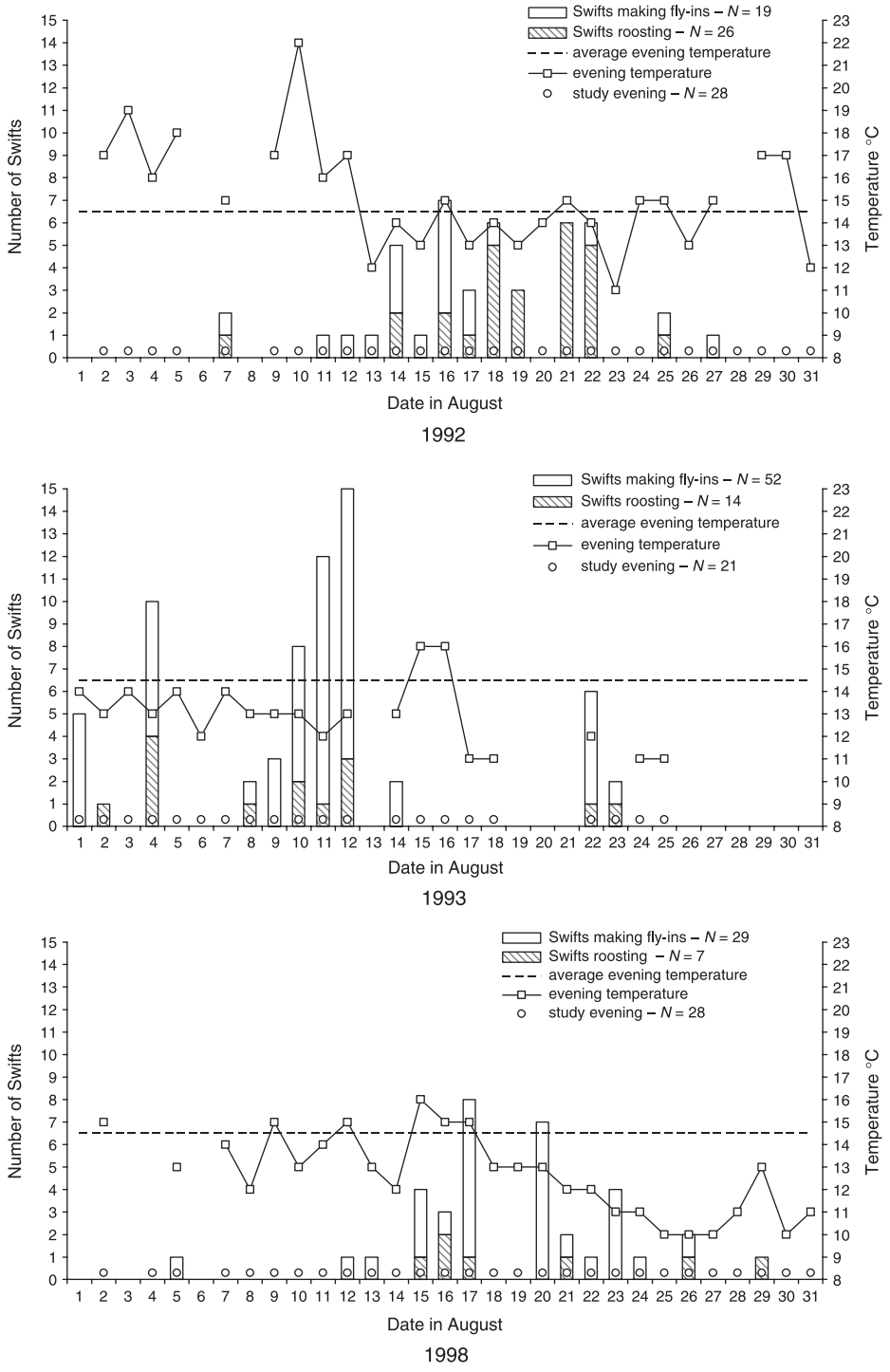

Figure 4. The three August months with the highest numbers of observations.

these in trees, 12 on the mast) and 29 observations of typical fly-ins. The two July observations are from the early half of the month; so all these observations must concern birds in at least their second calendar year. Nearly all observations are connected with harsh weather conditions, or with low evening temperatures.

I have attempted to photograph Swifts hanging in foliage, but because of the darkness, or because of

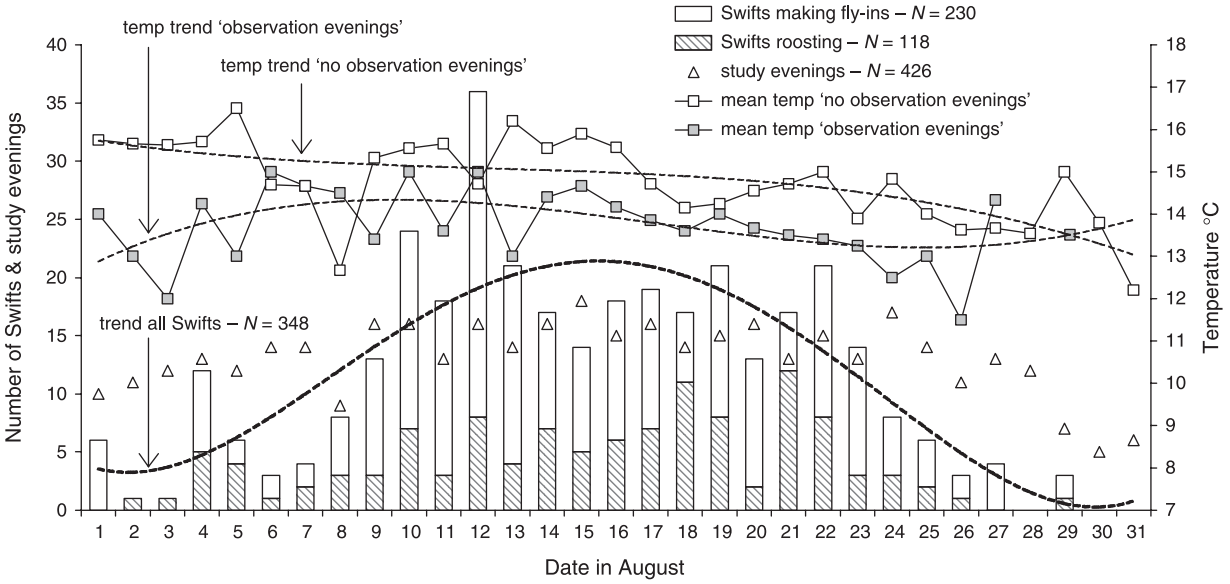

Figure 5. Observations of Swifts roosting or making fly-ins and evenings spent watching (study evenings) distributed per day in August. The trend curve fitted by MS Excel for the numbers of 'all Swifts' is: $= 0.0005\ ^{4} - 0.0321\ ^{3} + 0.5582\ ^{2} - 1.7675\ + 4.7927$. Polynomial trends are provided to aid visualization only rather than to test statistical significance etc.

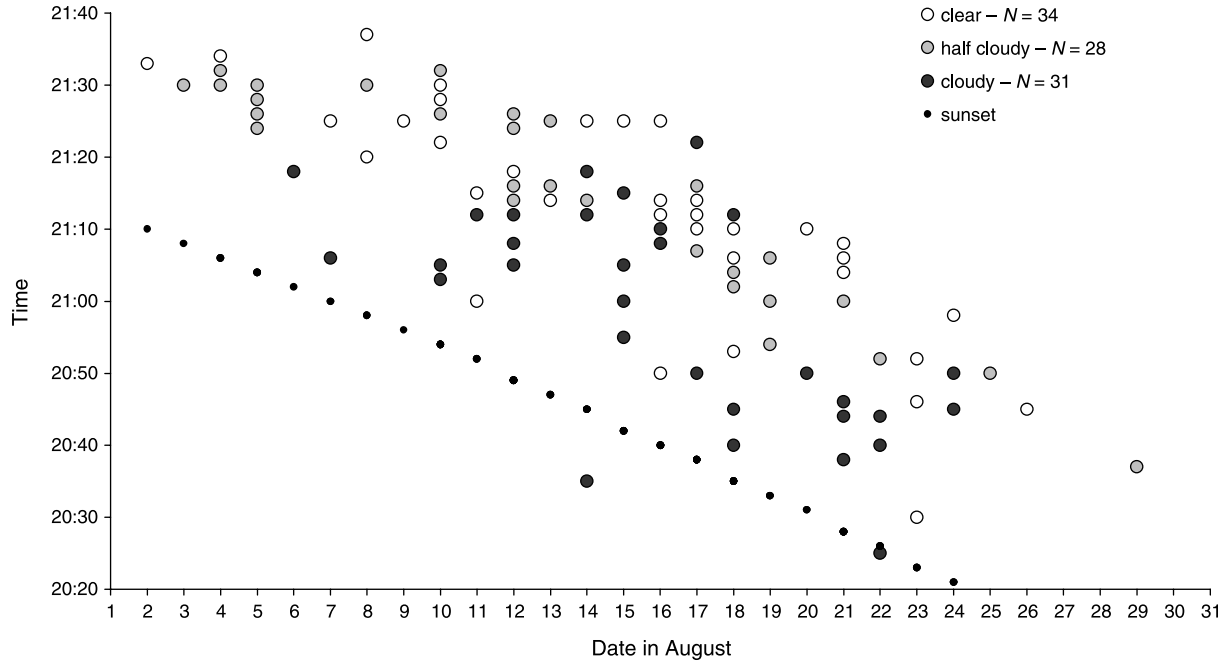

Figure 6. Perching times of Swifts roosting in study area in August. Observations are sorted into three categories: clear, half cloudy and cloudy sky.

the bird's position high up in a tree or mast, I have failed to achieve good results. Apart from a photograph from 1914 in Koskimies (1950, no. 3 in Appendix), the only existing good photograph was taken by Erich Kaiser in the present study area on the morning of 21 August 1988 (Fig. 2). In recent Augusts, I have attempted to record the behaviour on video instead, which has been slightly more successful. This film was taken in Abbekås (55°24′N, 13°36′E), a village on the south coast (Fig. 9).

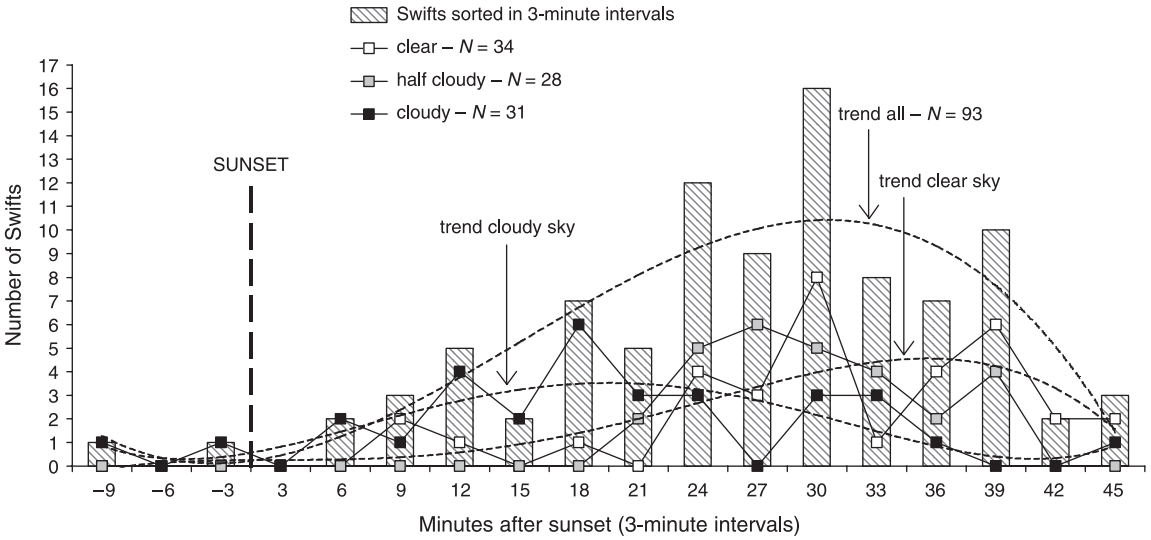

Figure 7. Roosting Swifts distributed according to their perching time in relation to time of sunset, sorted into 3-min intervals and three categories: clear, half cloudy and cloudy sky. Bars show sum of perching Swifts in each 3-min interval.

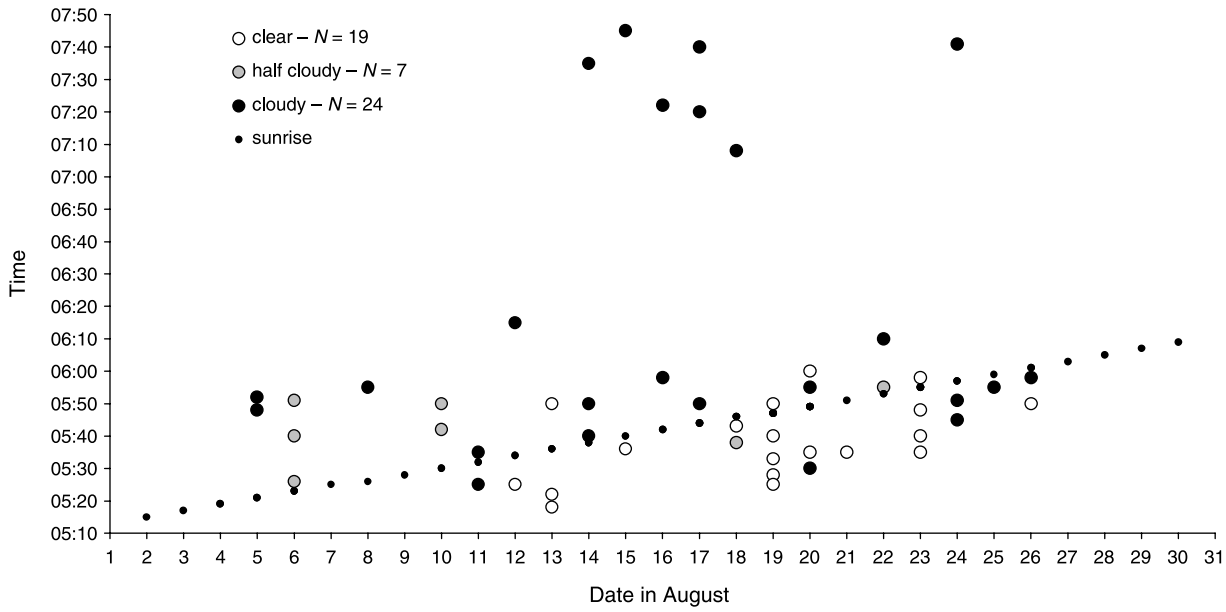

Figure 8. Morning departure times of Swifts roosting in study area in August. Observations are sorted into three categories: clear, half cloudy and cloudy sky.

During summer, on certain days with poor weather, large numbers of Swifts can be seen moving along the Swedish south coast. In August, Swifts move more regularly westwards along the coast, and I have found Abbekås to be a more dependable place to observe roosting in foliage than Skurup, although this is not quantifiable. I have seen at least 70 Swifts perching in poplars in Abbekås, and many have been making fly-ins, probably most of them perching outside the area that I could watch.

The repeated fly-ins towards various trees, before the birds perch, may have the function of bewildering birds of prey. In Abbekås, Eurasian Sparrowhawks *Accipiter nisus* are often present in the area. On 27 August 1988, one Swift made many fly-ins to different trees. Suddenly, at 20:30 h, a Sparrowhawk

Figure 9. Common Swift roosting about 10 m above ground in a Poplar in Abbekås, filmed in the morning of 23 August 2003. In the preceding evening, in cloudy and windy weather, the bird perched in this position at 20:55 h. It was awake about 20 min before it departed at 06:13 h. The Swift was capable of turning its head almost full circle, and the white 'face' clearly showed that the bird was juvenile. The bird stretched its wings and defecated shortly before it left. In the videoclip, when the Swift departs, one can see that it was grasping just one leaf. At least four other Swifts also roosted in this row of Poplars. One bird roosting a few metres from the filmed bird left at 05:48 h. At that time, several other Swifts were moving westwards at treetop level.

almost succeeded in catching it. It was dark, so the birds could only be seen as silhouettes against the sky. The Swift fluttered and tried to avoid the hawk for a short moment. Then, it flew straight away, going steeply upwards, soon disappearing in the darkening sky. The Swifts may perch late at dusk in order to avoid attacks from birds of prey. Kaiser (1984) found that fledglings usually depart in the evening, on average *c.* 70 min after sunset, perhaps for predator avoidance.

The numerous fly-ins to the mast appeared rather dangerous. On a few occasions, in very strong wind, a Swift collided with the mast and appeared to fall, only gaining control just above the ground. On 10 August 1993, after many fly-ins by several Swifts, two of these Swifts perched at the top of the mast, the last one at 21:30 h. At 21:40 h, a Tawny Owl *Strix aluco* flew up, silhouetted against the sky, and perched on a bar, probably catching one of the Swifts. Instantly, the other Swift left the mast. The owl stayed for 30–40 s and then left, soon disappearing in the dark. Presumably the owl noticed the Swifts making fly-ins, and waited until they had perched.

In the evening, Swifts often arrived in small flocks, and certain interactions took place. On several occasions, when one Swift had perched on the mast, another tried to cling to it, with the result that both birds were back in the air again. On two occasions, I saw fly-ins in the morning. In the morning of 10 August 1989, one Swift made repeated fly-ins into an Ash *Fraxinus excelsior* tree, where another Swift was still perched in the foliage of the tree. That bird, however, did not leave the tree until 10 min after the first Swift had left. On the morning of 19 August 1992, one Swift left the mast, and it directly made a few fly-ins towards the mast, apparently attempting to attract its companion. The remaining bird, however, stayed until 15 min later.

In three mornings in 1992, loose flocks of Swifts gathered at the time the roosting Swifts that I had been observing had left their perch (15 August: 50 Swifts, 18 August: 30 Swifts, 22 August: 50 Swifts). On the morning of 12 August 1993, one Swift left a Birch *Betula* sp. and immediately joined five other Swifts. They moved around slowly, until they disappeared 10 min later. All these birds appeared at a low level, before any Swifts had been observed at higher altitudes, indicating that none of these Swifts had roosted aerially. Most of them had probably roosted in foliage.

DISCUSSION

Assuming that Skurup has no special attraction for Swifts, it is reasonable to assume that the behaviour witnessed here is widespread and might be verified by similar studies elsewhere.

Although the observations of Common Swifts roosting in the foliage of trees in Skurup establishes that the behaviour is used regularly, this does not deny the fact that Common Swifts also regularly roost aerially. However, correlations between numbers of Swifts roosting in foliage and low local temperatures suggest that this behaviour is used in crisis situations, when the birds are in danger of exhaustion. This might be a frequent predicament for Swifts, because they rely entirely on 'aerial plankton' for food. However, the correlation with low temperatures is not perfect. Other factors that might cause fatigue in many birds should be considered, for example unfavourable weather conditions during the breeding season causing low fledgling weights, adverse weather conditions earlier along the migration route, or infections or parasites affecting a bird's present health status. It would have been interesting

to record body weights and condition measures, but I have not been able to catch any of the roosting birds.

Nearly all the birds that I could age were young, and the concentration of roosting birds in August suggests that young Swifts roost in foliage much more frequently than adults. Perhaps the combined stresses of migrating and finding food, relying on inborn programming that has only recently been put to work, exhausts young birds, whereas experienced birds might be less susceptible to such stresses.

However, evolutionary explanations might also be hypothesized. For example, the behaviour of roosting in foliage might be of ancient origin. Prehistoric Europe was widely covered by forest, and at that time Swifts must have nested in crevices in cliffs or in woodpecker holes, as they still do in parts of their breeding range. In areas lacking cliffs, therefore, roosting in tree holes or in foliage were their only alternatives to aerial roosting.

This argument might be based even deeper in evolutionary time. It has often been claimed that the Common Swift has all its toes pointing forwards, and that this is an adaptation for clinging to vertical rough surfaces. However, clinging in such a manner is associated much more with the Spine-tailed and Needle-tailed swifts, in the tribe Chaeturini (originally inside hollow tree trunks, today often in chimneys etc.). A more obvious adaptation in this group is seen in their stiff tails (like woodpeckers) rather than in the feet, which have remained essentially 'passerine' (anisodactyl), with the hind toe pointing backwards. By contrast, the swifts of the tribe Apodini have no obvious change in the tails, but a very special foot, with the toes orientated in two opposite pairs, grasping sideways like a pair of pincers (Collins 1983; Fig. 10). Because this structure is most obvious in the Palm Swifts, which can be said regularly to 'hang in foliage', it is reasonable to suppose that this is what their feet are adapted for (Holmgren 1998). So, hanging in foliage might be a very ancient behaviour for the Common Swift, as in other swifts of the tribe Apodini.

As human constructions became common, Swifts found alternative nest sites. Their gradual change in nesting habits hints at a certain behavioural flexibility rather than a specific genetic change (Koskimies 1956). The new habits may essentially be sustained socially. Under this hypothesis, when not roosting aerially, it would seem natural then for the young birds to roost in foliage during their first migration, their first stay in the winter quarters, and their first migration back. On their return to the breeding areas, they will find most colonies in buildings, and soon learn to cling to walls, enter holes in buildings, etc. As adults, they may therefore prefer such sites, while retaining the option to hang in foliage in case they cannot find a suitable building in an emergency.

Figure 10. This photo shows the right foot of a young Common Swift (age 23 days) grasping a wooden stick (diameter 4 mm). The somewhat smaller toe is the hindtoe (toe I), which is reversed inwards–forwards. One can see that the sharp tips of the claws in this position tend to penetrate the substrate. This foot structure, with opposing pairs of toes of almost similar lengths, appears ideal for hanging in thin twigs or leaves, and perhaps it can be locked like this when the bird is asleep or in torpor.

Swifts are often exposed to the danger of starvation, and they have several complex adaptations for survival, e.g. weather movements for avoiding harsh weather, clinging together in clumps for energy conservation, and lowering of the body temperature, even into torpor. Roosting in foliage seems to have potential to save lives in acute crisis situations. I suggest that the behaviour may have played an important role in the evolution of the species, still being effectual for survival and reproductive success.

The late Richard K. Brooke gave encouragement and advice at the start of this study. The late Emil Weitnauer helped with a request and observations in Switzerland. I am grateful to the bird magazines (see text) that published requests for observations, to the persons (see Appendix) who sent reports, and to Kenneth Bengtsson, David Griffin, Walther Thiede and Ulrich Tigges, who sent references for observations that otherwise would have remained unknown to me. My warm thanks to Charles T. Collins, Michael K. Tarburton and Andrew G. Gosler, who all helped with important corrections and improvements.

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APPENDIX

Observations in Europe of Common Swifts roosting in foliage or in similar situations

Specified for each observation: No. (italicized numbers = probably concern newly fledged young). Date. Location. Kind of perch. Short description of the observation. Reference.

1. 1 August 1893. Povrly (Pömmerle), Czech Republic. Poplar *Populus* sp. One Swift perched in the evening, but left again. Hauptvogel (1893).

2. 2 September 1897. Scarborough, England. Ash *Fraxinus excelsior*. Two Swifts made fly-ins. One of them perched 'vertically suspended like a great hawk-moth'. Gyngell (1897).

3. Summer 1914. Kirkkonummi, Finland. Pine *Pinus* sp. One Swift, photo taken by M. Savolin. Koskimies (1950).

4. 17 June 1917. Värmdö, near Stockholm, Sweden. Pine. One Swift. Hanström (1944).

5. 12 September 1930. Hickling, Norfolk, England. Willow *Salix* sp. One Swift, also observed next morning. Turner (1930).

6. Summers of 1934 and 1935. Windenburger Ecke, Lithuania. Many, mostly newly fledged Swifts landed on a mast for wind warning. A kind of 'basket' (Korbballon) could be lowered, so the 'sleeping' Swifts could be ringed. Krätzig (1939).

7. 18 June 1948. Tammisari, Finland. Tree. One Swift. Observation by Olavi Hildén. Koskimies (1950).

8. 26 July 1953. Cromer, Norfolk, England. Sycamore *Acer pseudoplatanus*. One Swift. Cox (1953).

9. 10 August 1954. Berwick-on-Tweed, Scotland. Sycamore. One Swift. On 13 August 'several Swifts attempted to alight on outermost twigs of the tree'. Church (1956).

10. May 1955. Kassel, Germany. Spruce *Picea* sp. One Swift. Böhr (1956).

11. 1 August 1956. West Ewell, England. Elm *Ulmus* sp. One Swift. *Birds of the London area*, *1956*.

12. 19 May 1959. Kitzeberg, near Kiel, Germany. Beech *Fagus sylvatica*. One Swift perched, two other Swifts made fly-ins. Schmidt (1959).

13. Autumn. Steinhuder Meer, Germany. Pine. A flock of Swifts roosted. Sturhan (1959).

14. 6 May 1962. Roxheim, Germany. Line for lighting. One Swift. Matthes (1966).

15. 4 September 1965. Walney Island, Lancashire, England. Flag- and telegraph-poles. Two Swifts. Tickle (1966).

16. 25 May 1971. Stubbekøbing, Falster, Denmark. Oak *Quercus* sp. Two Swifts made fly-ins, one of them perched, also observed next morning. Hans Anker Nielsen (pers. comm.).

17. 18 August 1972. Ottenby, Öland, Sweden. Tree. Many Swifts roosted on the walls of a lighthouse. A few Swifts were observed to leave trees in the morning. Törnlund (1979).

18. 10 September 1974. Hestehoved, Falster, Denmark. Beech. 5–6 Swifts made fly-ins, one of them perched, also observed next morning. Hans Anker Nielsen (pers. comm.).

19. 17 August 1975. Sorvilier, Switzerland. Spruce. One Swift. Observation by Roland Eggler, received from Emil Weitnauer.

20. 24 August 1975. Hestehoved, Falster, Denmark. Beech. Two Swifts made fly-ins, one of them perched, also observed next morning. Hans Anker Nielsen (pers. comm.).

21. 13 July 1977. Dokkas, Lapland, Sweden. Pine. One Swift. Leidgren (1985).

22. 9 September 1978. Hestehoved, Falster, Denmark. Beech. Five Swifts made fly-ins, one of them perched, also observed next morning. Hans Anker Nielsen (pers. comm.).

23. 1 July 1979. Falsterbo, Sweden. Birch, pine. Several Swifts in harsh weather. Hansson *et al*. (1981).

24. ?. Sempach, Switzerland. Tree. One Swift. Weitnauer (1980).

25. ?. Kölliken, Switzerland. Spruce. One Swift. Weitnauer (1980).

26. ?. Oltingen, Switzerland. Spruce. One Swift. Weitnauer (1980).

27. July 1981. Nastola, Finland. Birch. Two observations by A.O. Orlimo, one Swift each. Heikki Kolunen (pers. comm.).

28. 27 April 1983. Outside the Danish west coast. One Swift on ship mast. Lambert (1983).

29. 6 August 1983. Restloch Seese-West, Germany. Pine. Two Swifts made fly-ins, one of them perched. Observation by Rolf Striegler. Detlef Robel (pers. comm.).

30. 4 September 1983. Hestehoved, Falster, Denmark. Beech. 8–10 Swifts disappeared into tree crowns, one of them could be seen hanging in silhouette, also observed next morning. Hans Anker Nielsen (pers. comm.).

31. 21 May 1984. Norfolk, England. Willow. One Swift. When the branch was knocked, the Swift fell to the ground. After some minutes, it could fly normally. Observation by Paul G.D. Morgan, with Alan Hinchliffe and Peter Webb, received from *British Birds*.

32. 8 and 19 July 1985. Berlin, Germany. Walnut *Juglans regia*. Two observations; one Swift each. Wunderlich (1986).

33. 6 August 1985. Bedfordshire, England. Lime *Tilia* sp. One Swift. Observation by Peter E. Newbery, received from *British Birds*.

34. 27 July 1986. Salisbury Plain, Wiltshire, England. Ash. One Swift. Observation by Ian Grier, received from *British Birds*.

35. 22 August 1986. Mölndal, near Gothenburg, Sweden. Birch. Two Swifts perched at the entrance hole on the outside of nestboxes for tits. One of them stayed for the night. Björn Berglund (pers. comm.).

36. 16 June 1987. Hestehoved, Falster, Denmark. Beech. One Swift, also observed next morning. Hans Anker Nielsen (pers. comm.).

37. Mid July 199?. Össby, Öland, Sweden. Ash. About 25 Swifts perched in one tree. Lundberg (1998).

38. 15 June 1998. Dueodde, Bornholm, Denmark. Pine. 'Weather catastrophe'. Many roosting Swifts, most on lighthouse. Lou (1998).

39. 1–27 June 2002. Noordwijk-Binnen, the Netherlands. One Swift roosted 19 nights on scaffolding net on church tower. Hein Verkade (pers. comm.).

Erratum concerning Appendix page 415:
Incorrect use of italics was used in some of the entries to indicate 'newly fledged young'.
Observations nos. 3, 4, 7, 10, 12, 14, 16, 21 and 23 should not have been in italics.