Number of pairs, timing of egg-laying and clutch size in a subalpine Sand Martin Riparia riparia colony, 1968–1985

Sören Svensson

Svensson, S. 1986. Number of pairs, timing of egg-laying and clutch size in a subalpine Sand Martin *Riparia riparia* colony, 1968–1985. – Ornis Scand. 17: 221–229.

A Sand Martin colony in the subalpine (subarctic) birch belt at Ammarnäs, Swedish Lapland (65°N, 590 m a.s.l.), was studied from 1968 through 1985 (excl. 1970–1971). Colony size varied between 8 (1985) and 80 (1975) pairs, and the colony was deserted completely during egg-laying in 1979. Start of egg-laying varied from 3 June (1984) to 28 June (1982), and most often took place between 10 and 20 June. The start of laying was closely correlated with the date when 50% of the ground was snow-free. This date was about one month before start of egg-laying and before arrival of the Sand Martins. There was a much weaker correlation between start of egg-laying and temperature in late May and early June, indicating that the length of the snow-free period before arrival was more important. Temperature after arrival, however, modified the effects of the general advancement of spring. There was a critical temperature range (mean temperature of 5–7°C or maximum temperature of 10–12°C) below which temperatures deterred onset of laying. A temperature below this range after some pairs had started laying deterred new pairs from starting. Abundance of flying insects rather than temperature as such is likely to be the critical factor determining the start of laying, but there are no data on insect abundance during the early stages of breeding. The seasonal decline of clutch size was 0.2 eggs wk^{-1} within years, but less between years with different median dates of laying.

Sören Svensson, Dept of Ecology, Ecology Building, S-223 62 Lund, Sweden.

1. Introduction

In Scandinavia the Sand Martin *Riparia riparia* occurs as a breeding bird almost to the North Cape (Haftorn 1971). It frequently penetrates far into the mountain valleys in Lapland. In most areas artificial sites such as sand-pits harbour the majority of local populations, but natural sites along river banks are also used.

The present report contains results from a long-term investigation of the breeding biology of the Sand Martin in a colony in the subalpine (or subarctic) birch zone at Ammarnäs, Swedish Lapland. Apart from providing information about the size of the colony since 1968 the report concentrates on the effects of temperature on timing of egg-laying, and on the seasonal decline of clutch size.

The Sand Martin collects its food exclusively in the air and thus depends entirely on the occurrence of airborne invertebrates. It arrives at Ammarnäs in late May or early June, after snow-melt but before the leafing of birches and the general spring flush of vegetation and insects.

Bryant (1975) found that the onset of breeding in the House Martin *Delichon urbica*, whose feeding ecology is very similar to that of the Sand Martin, was determined by the rapid rise of insect biomass in spring. During egg-laying even single days with low temperature and/or rain were enough to cause suspension of egg-laying in the Sand Martin. One must therefore assume that amount of food determines the onset of laying also in this species. Timing of laying could then be interpreted

in terms of Perrins' (1970) assumption that, in some birds, breeding time is not determined by food abundance for the young but by food availability at the time of laying. The females wait to lay until food availability is good and stable enough, so that they no longer risk experiencing too many days without sufficient food. Turner's (1982) estimates of the number of "bad weather" days during different parts of the Sand Martin's breeding season show that in Britain such days were frequent (50%) in 1–14 May but almost zero in the latter half of May.

The Sand Martin needs at least 4–6 days for burrow excavation (Petersen 1955, Asbirk 1976). Often the excavation period is longer for birds arriving early (Asbirk 1976) or for socially inferior birds digging below other burrows (Petersen 1955). Asbirk (1976) also found that digging did not take place in bad weather, which could further extend the digging period. This was often the case at Ammarnäs but I lack precise data. Nest building takes two days (Asbirk 1976). After nest completion it takes about 5 days (0–8 days) before the first egg is laid (Asbirk 1976). Egg formation takes 5 days (the egg is laid on the 6th day after initiation; Petersen 1955).

Most studies of the Sand Martin have been carried out in areas with a much more benevolent climate and a longer summer than at Ammarnäs. At Ammarnäs it is impossible for the Sand Martin to lay two clutches, as it is for the House Martin in North Finland (Lind 1960). Two clutches are common in the Sand Martin in Britain and on the European continent (Bryant 1975) and not uncommon in South Scandinavia (Asbirk 1976).

The excavation of the burrow seems to cost much energy. Petersen (1955) found raised glucose levels during this phase which explains why the birds have to cease digging when the weather is unfavourable for their insect prey. Turner (1982) observed that even when sufficient food for energy and protein needs could be easily collected, laying might have been postponed because calcium was a limiting nutrient.

Thus, a number of factors may determine the time of laying in the Sand Martin. It is reasonable to assume that these factors are more pronounced close to the northern limit of the species' range than further south. On the other hand, the short season in the north makes it necessary for the birds to start laying as early as possible because the young of even the earliest clutches (first egg 10–15 June) will not be able to feed themselves and start migrating until early August.

Even for late first clutches the prospects are poor. In England, Sand Martin young ringed in August and September had recapture rates of 3.6 and 0% compared with 10.3 and 8.9% for young ringed in June and July (Vowley 1979). At Ammarnäs it is therefore unlikely that late broods would survive well. Thus, the females must be able to handle the trade-offs between the risk of bad weather when laying too early and a high young mortality when laying too late.

2. Study site and methods

The study colony was found in 1968 in a sand-pit 6 km west of the village of Ammarnäs (location of colony: 65°58'N, 16°05'E, 590 m a.s.l.). The sand-pit seemed relatively new that year, but the colony may have existed before. In earlier years another colony was present about 1 km further west but the sand-bank there had deteriorated and the site was deserted. A few pairs also bred 16 km to the southeast, but this site was completely deserted during the first years of this study. A few pairs also bred, perhaps not every year, along the low river banks in the Ammarnäs delta. Thus, the study colony was an isolated one with no other colony within the maximum range of daily feeding flights.

On my first visit to the colony each year all burrows were numbered. A 5 × 5 cm piece of paper was fastened close to the entrance hole using a nail that was pushed into the sand. New numbers were added as new burrows appeared. The nests were inspected using a "ripariascope" (described in Svensson 1969), consisting of a metal rod with a mirror and a lamp. This ripariascope made it possible to determine the content of almost all the nests and to count the eggs. Only a few very curved burrows escaped inspection but most often I could determine whether they were inhabited or not.

Temperature and precipitation data were obtained from SMHI (Swedish Meteorological and Hydrological Institute). For the years 1972–1985 they refer to the weather station in the Ammarnäs village (405 m a.s.l.). For 1968 and 1969, when the Ammarnäs station had not yet opened, I used the means for two nearby stations, Hemavan 54 km WSW and Vindel-Björkheden 45 km ESE of Ammarnäs. Comparing data from three years common to all three stations I found that these figures described adequately the weather at Ammarnäs ($r = 0.95$, slope $= 1.00$). Data on snow-melt were also obtained from SMHI. Apart from snow depth at a standard site, the extent of now cover was reported. I used the first day with more than 50% snow-free ground in my comparisons with the Sand Martins' breeding time.

The date of the first visit to the colony was too late in 1974 and 1981 to allow a direct determination of the start of egg-laying for the early clutches. For these clutches I calculated laying date from hatching date. This was also done for a few very early clutches in some other years. A few very late clutches were probably missed in some years.

3. Results and discussion

3.1. Size of the colony

The number of burrows in a Sand Martin colony is usually higher than the number of breeding pairs (Kuhnen 1978). Thus, it is not possible to estimate the number of pairs by counting the number of burrows. Tab. 1 shows the number of burrows of different categories.

Tab. 1. Size of colony and number of burrows of different categories.

	1968	69	72	73	74	75	76	77	78	80	81	82	83	84	85
Nest with egg	61	23	82	79	78	97	45	53	21	21	61	25	42	19	8
Nest without egg	2	5	11	2	3	10	4	3	3	4	2	4	1	1	0
No nest, >20 cm deep	10	6	26	15	23	28	17	30	20	11	7	14	4	4	4
No nest, <20 cm deep	3	7	5	0	9	10	11	17	7	4	9	5	5	2	1
Into another burrow	4	0	1	2	4	6	5	1	1	1	2	1	0	0	0
Not inspected	1	3	0	0	0	1	1	0	0	0	0	0	0	0	0
Old nest	3	12	0	2	0	0	3	0	0	0	0	2	0	1	2
Total	84	56	125	100	117	152	86	99	52	41	81	51	52	27	15
No. of pairs	55	27	75	75	73	80	50	50	24	21	57	24	42	20	8
% of burrows	65	48	60	75	62	53	58	51	46	51	70	47	81	74	53

A rather large proportion of the burrows remained without any nest. They had full length and often a proper nest chamber. In some cases these burrows had probably been excavated by yet unmated males but in other cases I trapped males in them that were mated to a female breeding in another burrow. Thus at least some males may try to attract a second female but I have no indications of any male having succeeded in doing so. Neither do I know if any males remained unmated throughout the season.

Some burrows were shorter than about 20 cm and they always lacked a proper nesting chamber. Most often these burrows had been deserted before completion because the material was unsuitable for digging or because there was a stone preventing further digging. In a few cases one burrow entered another one. Nests remaining from the previous year were very few because most were destroyed by sand erosion or sand exploitation from one season to the next. When, exceptionally, a pair took an old burrow it removed the old nest material, dug deeper and made a new nesting chamber.

Tab. 1 shows that an average of 60% (range 46–81%) of the burrows were inhabited by breeding pairs. This figure is high compared with the corresponding figures for German colonies (Kuhnen 1975, 1978). Hence, at Ammarnäs it seems that the males do not excavate as many nests for the females to choose among as they do further south (Kuhnen 1985). This is probably because the birds are more time constrained at Ammarnäs with its more severe climate and shorter breeding season.

The number of pairs varied considerably between years (Tab. 1). In one year, 1971, I did not visit the colony so the number of pairs that year is unknown. In 1970, the colony was active, but I paid only one brief visit to it. On 16 June there were 14 burrows of which 10 were inspected: 3 were empty without a nest, 2 had nests without eggs, and 4 had 1, 4, 5, and 5 eggs. On 20 July 20 adults were ringed (Göran Högstedt, in litt) so some pairs did stay to complete breeding in that year. In only one year was the colony completely deserted. This happened in 1979 when at least four or five pairs started egg-laying on 17–20 June only to desert the colony a few days later. I was not able to determine the number of

pairs that were present before desertion so 1979 has been excluded.

In the other 15 years the number of pairs varied between 8 and 80. There was a series of years, 1972–75, when the size of the colony was stable at about 75 pairs, but numbers then dropped to reach their lowest level in 1985, with only 8 pairs.

Sand Martins normally return to breed within 10 km of their previous breeding or hatching site (Persson 1978, Mead 1979) so the Ammarnäs colony probably had little exchange of birds with other colonies. In the years when the population was small there was plenty of room for more pairs, so the number of pairs must reflect the numbers arriving at Ammarnäs. If the size of the colony should reflect winter survival one would expect that colony size at Ammarnäs should correlate with that of more southerly populations. But this was not the case, at least not with the British population (Cowley 1979); r = −0.25, not significant.

3.2. Timing of breeding

Fig. 1 gives the date of the first egg in all nests where this date could be determined. In some years the number of dates for the first egg is higher than the number of nests with egg or the number of pairs. This is because in some nests there were more than one breeding attempt.

In most years the first egg in the colony appeared in the period 8–18 June (13 years). Two years were earlier, 5 June in 1981 and 3 June in 1984, and one year was extremely late, 28 June in 1982.

Most often the vast majority of the breedings began within about a ten days period. The most striking exception was 1981 when breedings were started at an almost equal rate at least between 9 June and 18 July (last visit on 19 July).

Even in years with a high degree of synchronization there were almost always a few late clutches. Some of them were renestings after previous failures. However, in seasons with very extended breeding periods, like 1977 and, particularly, 1982, the late layings were by birds who had not attempted to breed earlier that year. This was clear from the continuous digging of new bur-
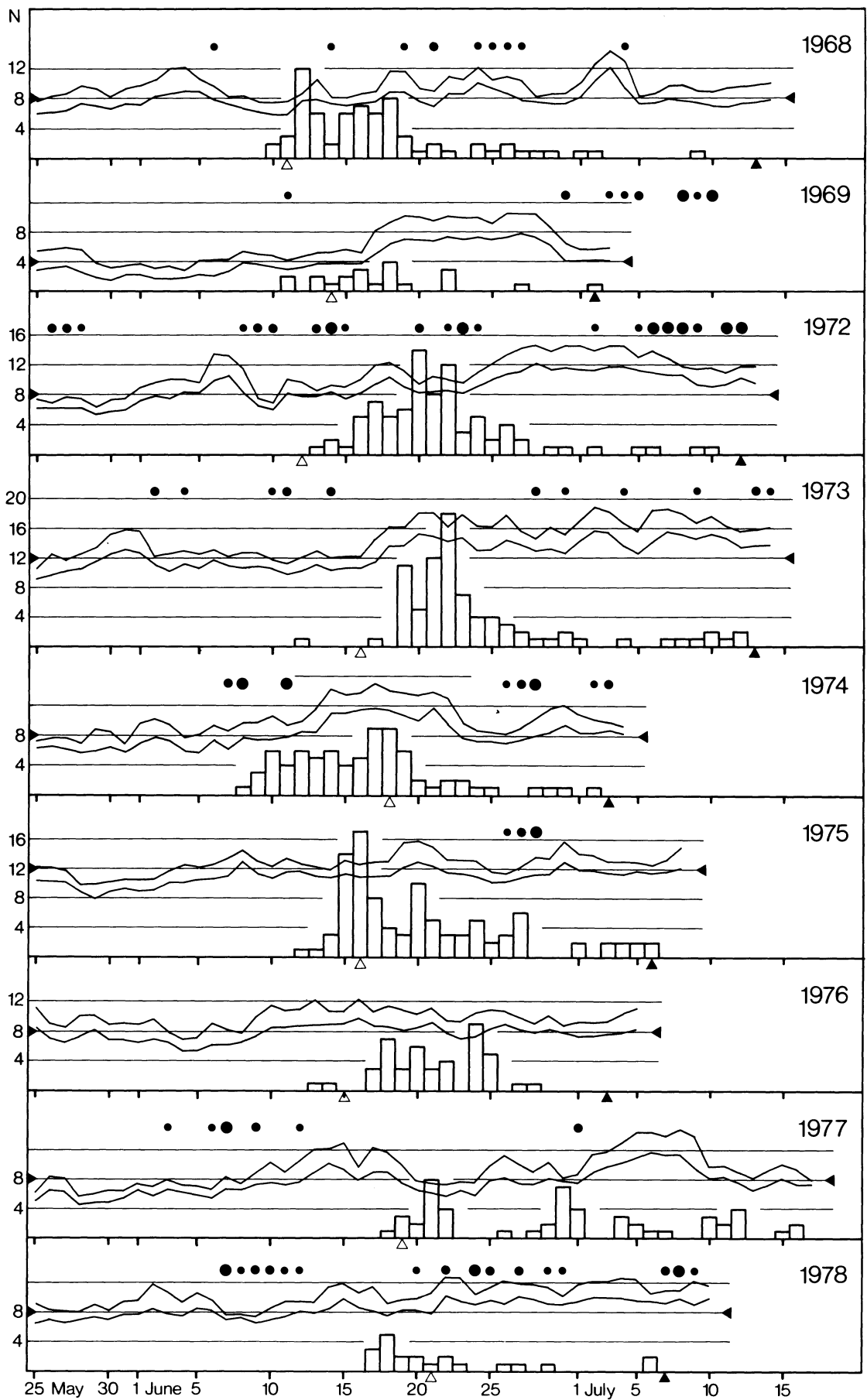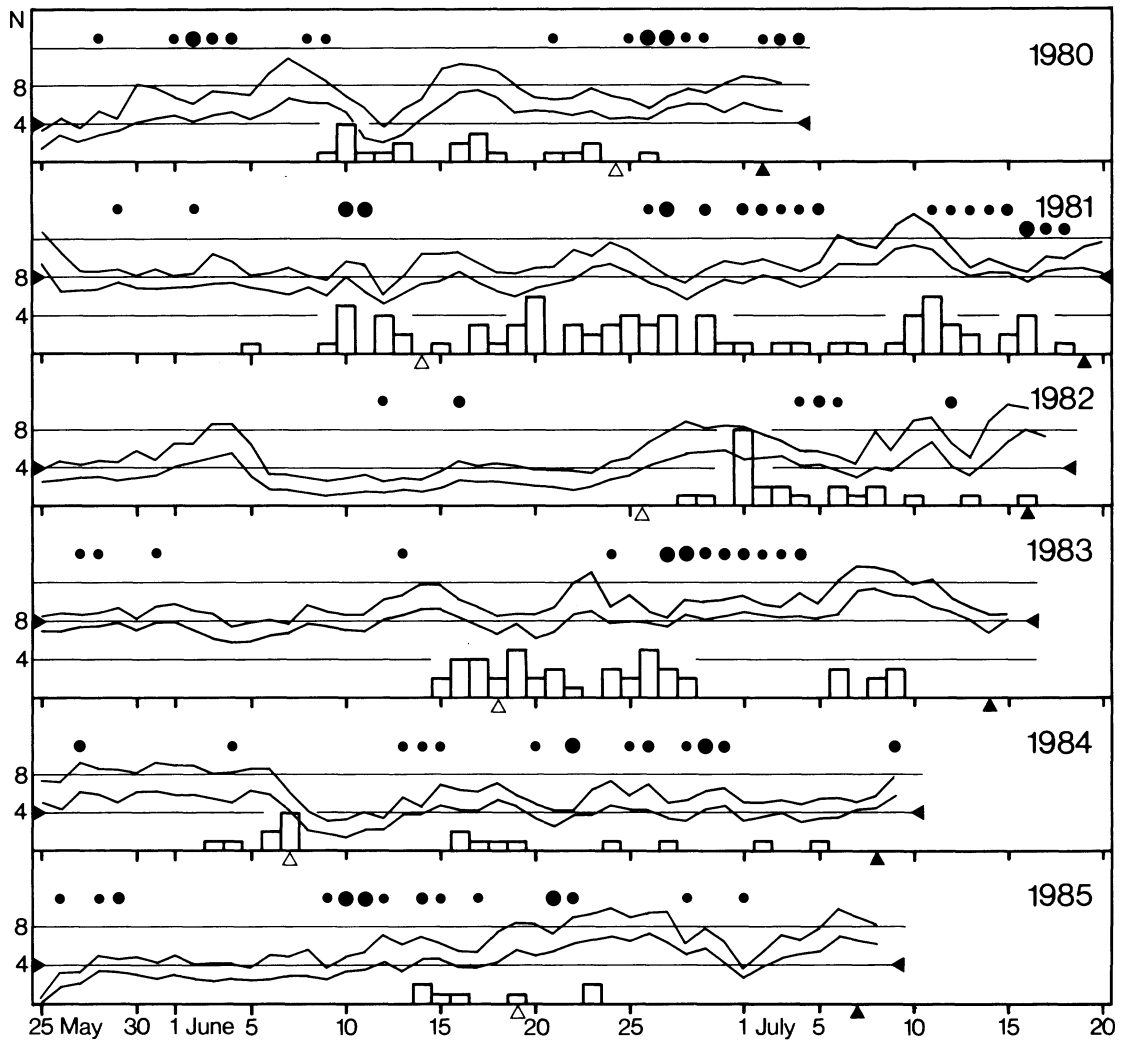
Fig. 1. Date of laying of the first egg, temperature, and amount of rain at Ammarnäs in 1968–1985. The bars give the number of clutches (N) started on each day. The two curves give maximum and mean temperatures. The lines marked with a triangle at each end show 10°C, and the other parallel lines are 10°C apart. Black dots show the amount of rain: small, medium and large dots mean 2–4.9, 5–10, and >10 mm, respectively (days with less than 2 mm not marked). Open and filled triangles below the date lines indicate my first and last visit to the colony in each season (last visit in 1977 was on 27 July).

rows by birds other than those who had already laid eggs.

In 1973, 1976, and 1981 one or two pairs started egg-laying a few days earlier than the bulk of pairs. This makes it somewhat difficult to select a certain date as representing the date of onset of laying in those years. Tab. 2 provides information on when the first egg was laid and when the first 10% and 50% (median date) of the clutches were started.

In some years laying took place in several "waves" This was very prominent in 1984 when eight pairs started in the beginning of June and no new layings occurred until 16 June. In 1983 there was a late peak of laying on 6–9 July with no clutches started during the previous week.

3.3. Laying and weather

Slagsvold (1976) showed that the onset of breeding in the Great Tit *Parus major* was closely correlated with spring temperature (and with phenological events such as leafing and appearence of larvae). The period with which the best correlation was obtained was shorter and fell closer to the time of egg-laying at northern than at southern latitudes. Slagsvold contrasted the mainly resident Great Tit with a tropical migrant, the Pied Flycatcher *Ficedula hypoleuca*, in which the onset of laying was only weakly correlated with spring temperature and phenological development. High correlations were obtained only for rather brief and late periods (2–3 weaks before start of laying). In another tropical migrant, the

Tab. 2. Dates when the first egg was laid and when the first 10% and 50% (median date) of the clutches had been started. All dates counted from 1 June. No studies in 1970 and 1971. Colony deserted early in 1979.

Year	1st egg	10%	50%
1968	10	12	16
1969	11	13	17
1970	–	–	–
1971	–	–	–
1972	13	16	21
1973	12	19	22
1974	8	10	16
1975	12	15	19
1976	13	17	21
1977	18	20	30
1978	17	17	20
1979	–	–	–
1980	9	10	16
1981	5	12	26
1982	28	31	32
1983	15	16	22
1984	3	4	16
1985	14	14	16

Spotted Flycatcher *Muscicapa striata*, mainly feeding on flying insetcs, O'Connor and Morgan (1982) found that 25% of the variation in the proportion of clutches started in May could be explained by May air temperature. They also found that there was no correlation with the amount of rain in May.
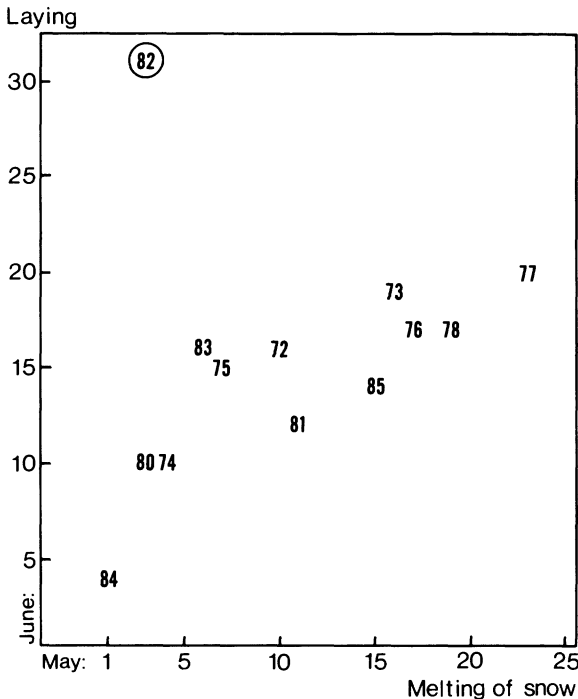

Fig. 2. Start of egg-laying (day when 10% of the clutches had been started) versus date for "half-melt" of snow, i.e. date with about 50% bare ground. The correlation coefficient, with 1982 excluded, is 0.81 (p < 0.001).

The Sand Martin is also a tropical migrant, so one would not expect any direct effects of local weather on laying time before it arrives, usually not before the end of May. Nonetheless, it is important to account also for earlier weather conditions since they will determine snow melt, the general progress of spring and the development of vegetation and insect life. In fact, the progress of snow melt is probably a very suitable "integrating" variable that could be used instead of data on birch leafing or insect abundance at arrival, which are not available for Ammarnäs.

In Fig. 2 the dates when 10% of the Sand Martin clutches had been started (Tab. 2) are plotted against the dates for the half-melt of snow (see Methods for details). Excluding 1982 (a year with such an extreme influence of a long cold period in most of June that any effects of earlier events were suppressed) there is a significant correlation $r = 0.81$, $p < 0.001$). The date when there is an appreciable amount of snow-free ground thus explains about two thirds of the annual variation in the timing of egg-laying. Insect abundance should be correlated with the general progress of spring and with vegetation development (reflected by the disappearance of snow). Thus, onset of laying in the Sand Martin is mainly determined by the weather already well before arrival.

A further examination of Fig. 1 reveals that there is no simple relation between start of egg-laying and temperature between arrival and start of egg-laying, i.e. during late May and early June. However, extreme conditions may either delay the onset of laying or suspend further starts of laying for a few days. In 1982 laying was delayed until about 1 July by an unusually extended period of low temperatures that lasted between 6 and 23 June. Apart from three days, mean temperature did not exceed 6°C and maximum temperature rose above 11°C on only two days. There was little rain so temperature must have been the predominant factor. 1982 is the year that deviates strongly in Fig. 2, and this period with low temperatures clearly was the cause. In 1984, a warm period started on 15 May and continued without interruption until 6 June (one of the earliest springs ever). The unusual combination of a very early snow melt and a long warm period allowed some pairs to start laying already on 3–7 June. On 7 and 8 June the temperature suddenly dropped about 10°C and the remaining pairs did not start laying until nine days later when temperature had risen again. Another case of suspension of new starts of egg-laying occurred on 23 June 1977 after a similar temperature drop. These cases indicate that a *mean* temperature below 5–7°C and/or a *maximum* temperature below 10–12°C prevent the start of egg-laying, thus overriding the effects of the general spring earliness.

There are, however, cases when temperatures almost as low as those just mentioned did not delay the onset of laying. In 1974 mean temperature stayed below 7°C from 25 May to 7 June (except on four days) without

any pronounced delay of onset of laying. The situation was rather similar in 1973 with a fortnight of rather low temperatures preceding onset of laying. Laying was 9 days later in 1973, but this difference is almost fully explained by the later snow melt in 1973 (Fig. 2). There are also examples of rather long periods with temperatures above the values of 7 and 12°C without any clutches being initiated. Thus, in 1968, 1976, 1978 and 1983 breeding started rather late in spite of mean temperatures above 7°C during most days for at least 15–20 days before laying started. This supports the conclusion that the general progress of spring is more important than temperature in late May and early June.

Turner (1982), using estimates of the energy requirements of the egg-laying female and data on how temperature affected insect abundance, calculated the critical temperature for egg-laying at about 10°C (about two degrees higher if also rainy). This calculation was based on a rather uncertain regression (her Fig. 2b), but nonetheless agrees well with my field observations.

Rain is an additional factor potentially capable of modifying the effects of temperature, but the evidence for rain being important is rather weak. There were a few cases when it seems that rains may have prevented birds from starting to lay. In 1983 eight rainy days on 27 June–4 July seem to have caused a 7 days period without any new clutches. Mean temperature was above 10°C and maximum temperature around 15°C during this period, so temperature per se could hardly have prevented the birds from beginning to lay. It is also possible that the extended breeding period of 1981 was equally due to the rainy weather from 26 June onwards as to the low temperature. In 1977, 1978 and 1980 a rainy period occurred about a week before laying started. The number of days between the end of the rainy period and onset of laying was similar to the period needed for forming an egg. But in these cases it is difficult to distinguish possible effects of rain from the effect of spring earliness.

Turner (1983), studying energy gain rates during the nestling period, found a correlation with both insect abundance and ambient temperature, but not with the amount of rain, despite insect abundance being correlated with both temperature and rainfall. Therefore it seems that rain, unless very heavy, is less important than temperature for the Sand Martins' feeding rate.

Fig. 3. Mean clutch size versus (A) annual median laying date in June, (B) calendar date in June and July, and (C) day number from first egg in the colony. In B, the leftmost data point is the mean of 9 very small clutches (8 of which laid in 1984), indicated by "84" and 23 large clutches laid in other years, indicated by "R". Likewise, the rightmost point is the mean of 20 relatively large clutches laid in 1981 ("81") and 17 small clutches laid in remaining years ("-81"). In C, the large clutches laid in 1981 deviate from the general pattern of a seasonally declining clutch size. Sample sizes for the 11 black dots in B are (from left to right): 32, 34, 35, 74, 89, 91, 88, 87, 43, 40, and 37 and sample sizes for the 10 dots in C: 57, 95, 115, 87, 83, 64, 53, 51, 25, and 20.

3.4. Clutch size and time of breeding

It is well-known in many birds that clutch size declines with the progress of the season (e.g. von Haartman 1969). This was a very prominent feature of the Pied Flycatcher's breeding biology at Ammarnäs (Svensson in press), and, as can be seen from Fig. 3, also of that of the Sand Martin.

Fig. 3A shows that the decline is evident when annual mean clutch size is plotted against median laying date, but there is a considerable spread for similar dates. Among the early years there is a difference of about 0.4 eggs and between the two very late years of 0.5 eggs.
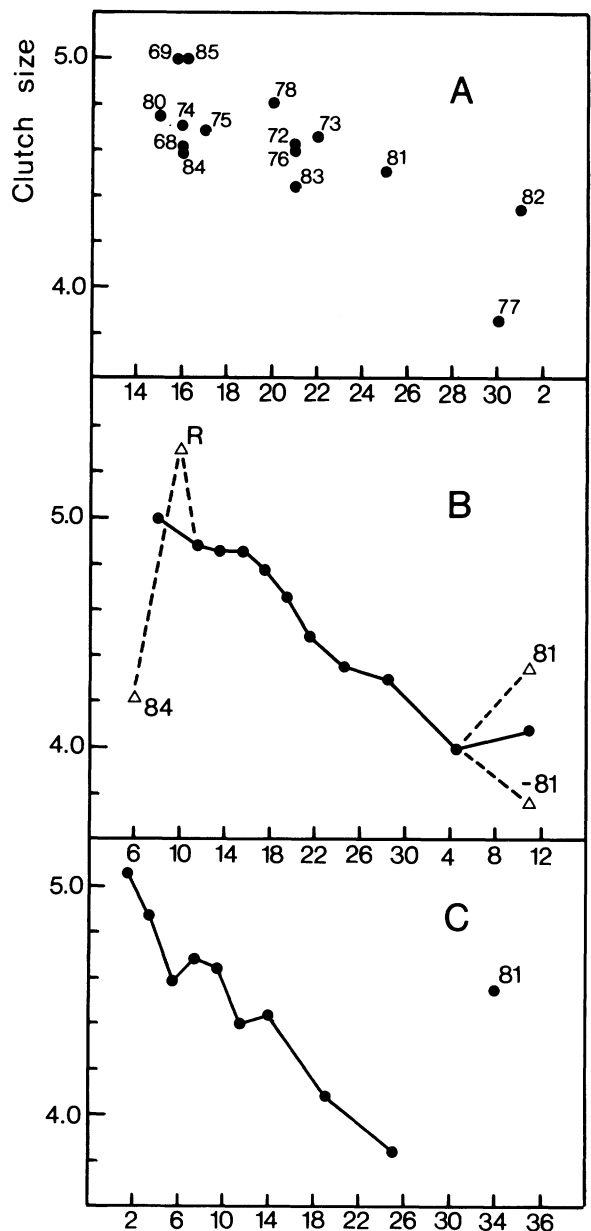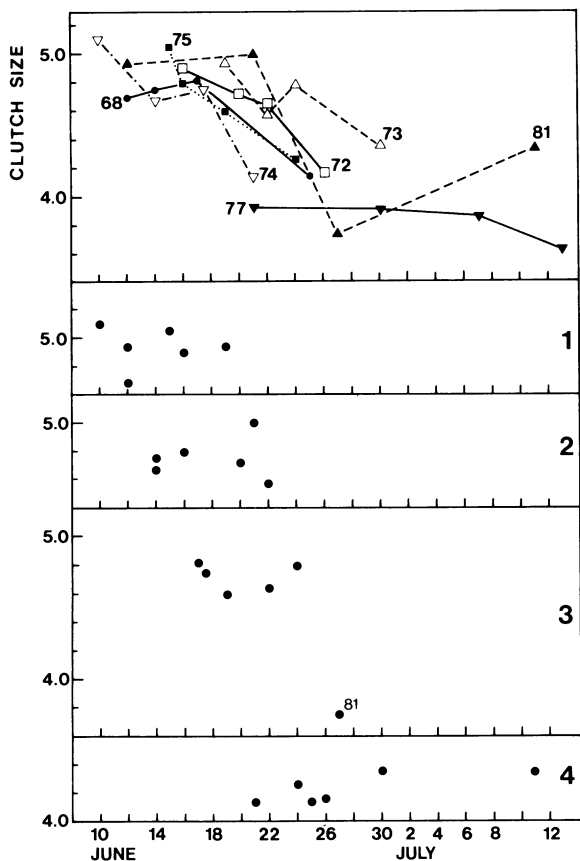
Fig. 4. Clutch size versus laying date. In the uppermost part of the figure mean clutch size is plotted against median laying date within each of the four quartiles of the laying season for those six years with sufficient number of clutches to allow this partition (1968, 72, 73, 74, 75, and 81). Corresponding data for 1977 are also shown because this year deviated from other years in having no or little seasonal decline in clutch size. The lower parts of the figure show clutch size in each quartile separately for the same six years. The data indicate that the seasonal decline in clutch size is mainly an intra-year phenomenon. Only the value for 1981 in the third quartile deviates from this pattern.

Excluding the aberrant year 1977, the slope is only 0.028 eggs d^{-1} or 0.2 eggs wk^{-1}.

Clutch size plotted against calendar date or day from the first clutch each year shows a much steeper decline (Fig. 3 A, B). From 8 June to 4 July clutch size declines almost linearly from 5 to 4 eggs. The slope of the regression line is 0.039 eggs d^{-1} or 0.28 eggs wk^{-1} ($r = -0.99$, $p < 0.001$). From the first to the twenty-fourth day clutch size declined from 5.05 to 3.85 eggs, i.e. 0.034 eggs d^{-1} or 0.43 wk^{-1} ($r = -0.97$, $p < 0.001$).

There are some noteworthy deviations from the general pattern. In 1977 (Fig. 4) there was no decline at all from the early to the late clutches (over a period of about four weeks; Fig. 1). In 1981 clutch size increased during the late "wave" of new clutches laid between 9 and 18 July (Fig. 4). In the very early year of 1984,

clutch size was considerably smaller (4.2) in the very early than in the late group of breeders (only 8 pairs, however; cf. Fig. 1). This is interesting because in some species the very early clutches are smaller than those laid a few days later (Klomp 1970). But the material is far too small to tell whether the Sand Martin belongs to the category of species with a continuously declining clutch size or to the smaller category with a convex clutch size curve.

There are few data on clutch size decline in the Sand Martin, due to the difficulty of establishing clutch size without a ripariascope. Petersen (1955) found that 104 clutches from before 15 June contained 5.0 eggs while 21 clutches from after the same date had 4.0 eggs. Among first clutches of the House Martin, Bryant (1975) found a decline of 0.16 eggs wk^{-1} which should be compared with 0.28 in the present study.

For the seven years with the greatest number of Sand Martins it is possible to analyse the seasonal decline for each year separately (Fig. 4). For each year the clutches were divided into four groups of about the same size. The aberrant year of 1977 and the large clutches late in 1981 have already been mentioned. But the rest of the data show an interesting feature, namely that if each one of the four quartiles are considered there is no tendency of a clutch size decline. This means, excluding the third quartile of 1981, that the annual curves are simply parallel images of a common decline pattern that is shifted between early and late dates in different years. If the decline pattern is interpreted from these six seasons, the decline is exclusively an intra-annual property. It would be of great interest to obtain a very early and a very late year with a large enough number of pairs and with the same degree of synchronization among the pairs as in 1968 and 1972–1975.

4. Conclusions

There were very strong fluctuations in population size of the Ammarnäs colony. These fluctuations did not agree with those found for the same species in Great Britain. The strong decline of the Sand Martin population in 1969 in Britain has been tentatively explained by droughts in the African winter quarters, as has the decline in the same year of some other tropical migrants, e.g. Whitethroat *Sylvia communis* (Winstanley et al. 1974). But Cowley (1979) pointed out that there was a strong increase from 1965 to 1968, so this explanation is questionable. At Ammarnäs there was certainly a decline in 1969 but the colony recovered and remained at a high level in 1972–1975 when population size in Britain instead remained at a low level. Little can be concluded about the causes of population change at Ammarnäs, since production of young was not determined.

Onset of breeding at Ammarnäs was determined by weather conditions before the Sand Martins arrived. There is probably a causative link between the time when the melting of snow occurs and insect prey abun-

dance about a month later when the Sand Martins are about to start egg-laying. The timing determined in this way can then be modified by low temperatures between arrival and the potential date of laying. In most years the degree of modification was difficult to quantify but it was quite evident that when the period of cold weather was long, as in 1982, laying dates were shifted appreciably. There is strong evidence that there is a critical temperature range (5–7°C daily mean temperature and/or 10–12°C daily maximum temperature) below which females are unable to start laying. This fits well with Turner's (1982) estimates based on energetic considerations.

This study shows that in the Sand Martin there is a seasonal clutch size decline of the same kind as has been found in many other species. This decline was mainly a within-year phenomenon. Early and late clutches in different years were of about the same size even if they were laid on different dates.

References

Asbirk, S. 1976. Studies on the breeding biology of the Sand Martin *Riparia riparia* (L.) (Aves) in artificial nest sites. – Vidensk. Medd. Dansk Naturh. Foren. 139: 147–177.

Bryant, D. M. 1975. Breeding biology of House Martins *Delichon urbica* in relation to aerial insect abundance. – Ibis 117: 180–216.

Cowley, E. 1979. Sand Martin population trends in Britain. – Bird Study 26: 113–116.

Haartman, L. von 1969. The nesting habits of Finnish birds. I. Passeriformes. – Comm. Biol. Soc. Scient. Fennica 32: 1–187.

Haftorn, S. 1971. Norges fugler. – Universitetsforlaget, Oslo.

Klomp, H. 1970. The determination of clutch-size in birds. A review. – Ardea 58: 1–124.

Kuhnen, K. 1975. Bestandsentwicklung, Verbreitung, Biotop, und Siedlungsdichte der Uferschwalbe *(Riparia riparia)* 1966–1973 am Niederrhein. – Charadrius 11: 1–24.

– 1978. Zur Methodik der Erfassung von Uferschwalben *(Riparia riparia)* – Populationen. – Vogelwelt 99: 161–184.

– 1985. Zur Paarbildung der Uferschwalbe *(Riparia riparia)*. – J. Orn. 126: 1–13.

Lind, E. A. 1960. Zur Ethologie und Ökologie der Mehlschwalbe, *Delichon u. urbica* (L.). – Ann Zool. Soc. 'Vanamo' 21 (2): 1–123.

Mead, C. J. 1979. Colony fidelity and interchange in the Sand Martin. – Bird Study 26: 99–106.

O'Connor, R. J. and Morgan, R. A. 1982. Some effects of weather conditions on the breeding of the Spotted Flycatcher *Muscicapa striata* in Britain. – Bird Study 29: 41–48.

Perrins, C. M. 1970. The timing of birds' laying seasons. – Ibis 112: 242–255.

Persson, C. 1978. Dispersion of sand martins *Riparia riparia* in Skåne, South Sweden. – Proc. 1st Nord. Congr. Orn., 1977. Anser, Suppl. 3: 199–212. (In Swedish with summary in English.)

Petersen, A. J. 1955. The breeding cycle in the Bank Swallow. – Wilson Bull. 67: 235–286.

Slagsvold, T. 1976. Annual and geographical variation in the time of breeding of the Great Tit *Parus major* and the Pied Flycatcher *Ficedula hypoleuca* in relation to environmental phenology and spring temperature. – Ornis Scand. 7: 127–145.

Svensson, S. 1969. Studies on the breeding biology of the sand martin *Riparia riparia* in a colony in southern Lapland 1968. – Vår Fågelv. 28: 236–240. (In Swedish with summary in English.)

– in press. Nesting density and breeding performance of the Pied Flycatcher *Ficedula hypoleuca* near the tree line in Swedish Lapland. – Proc. 5th Nordic Congr. Orn.

Turner, A. K. 1982. Timing of laying by Swallows *(Hirundo rustica)* and Sand Martins *(Riparia riparia)*. – J. Anim. Ecol. 51: 29–46.

– 1983. Time and energy constraints on the brood size of swallows, *Hirundo rustica,* and sand martins, *Riparia riparia*. – Oecologia 59: 331–338.

Winstanley, D., Spencer, R. and Williamson, K. 1974. Where have all the Whitethroats gone? – Bird Study 21: 1–14.