THE BIOLOGY OF THE SOUTH AFRICAN CLIFF SWALLOW *HIRUNDO SPILODERA*

DISSERTATION SUBMITTED TO RHODES UNIVERSITY
FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

by

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FRONTISPIECE

The South African Cliff Swallow *Hirundo spilodera* in typical posture at the nests.

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ABSTRACT

The general biology of the South African Cliff Swallow *Hirundo spilodera* was studied over a two year period in the central Orange Free State. This species is highly colonial, nesting mostly on man-made structures such as concrete road bridges. Adult birds were usually faithful to their breeding colony and very few individuals changed colonies.

The Cliff Swallow had a surprisingly large vocal repertoire for a swallow and contact calls of the young were individually recognizable.

Three species-specific ectoparasites parasitized the Cliff Swallow but none seemed to have a noticeable negative effect on the swallows.

Breeding started earlier in larger colonies than in smaller ones and conspecific brood parasitism was a common feature in some colonies. Individual pairs made up to four breeding attempts per season.

The findings of this study are compared with the available information on other members of the Hirundinidae and the advantages and costs of Cliff Swallow coloniality are discussed.

ACKNOWLEDGEMENTS

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Lastly I would like to thank Dr. Adrian Craig for his supervision and interest which was always an encouragement.

CHAPTER 1

INTRODUCTION

The South African Cliff Swallow *Hirundo spilodera* has, despite its comonness and well known nesting colonies, never been the subject of a major study. As a starting point to comparative studies on various members of the Family Hirundinidae in the central Orange Free State, the Cliff Swallow was a natural choice for special study as it is highly colonial, but still shows various characteristics of solitary nesting swallows.

Except for information in general reference books such as Maclean (1985), there are few publications on the biology of *Hirundo spilodera*. Burgerjon (1964) studied a small, newly formed colony in Pretoria during two breeding seasons, 1958/59 and 1959/60. The data collected during that study yielded information on clutch size, incubation and nestling periods and hatching success. The retrapping of birds during this study also shed some light on the return rate of this species from its winter grounds. Nothing has been reported on its moult (Craig 1983), vocalizations, general behaviour, prey taken or intercolony movements. Except for some speculations by Burgerjon (1964) nothing is known about the timing of breeding, breeding and social behaviour, nest building and chick development.

In 1850 Sundevall described the South African Cliff Swallow *H. spilodera* from the type collected at the Valsch river east of Kroonstad in the Orange Free State (Clancey 1980). Although McLachlan & Liversidge (1978) called the South African Cliff Swallow *Petrochelidon spilodera* (Sundevall) 1850, and Brooke (in litt.) proposed *Hirundo (Petrochelidon) spilodera,* the accepted name at present is *Hirundo spilodera* Sundevall 1850 (Clancey 1980). The cliff swallows are a distinctive group in the family Hirundinidae. All species of the group except one, *H. andecola,* have pale edges to the iridescent feathers of the mantle and by the rapid abrasion of these edges a scaly effect is produced. This is a feature not found elsewhere in the Hirundinidae. Peters (1960) placed ten species in the cliff swallow group under the genus *Petrochelidon* Cabanis 1850. Brooke (1972) also made a strong case for placing the cliff swallows in this genus but later proposed *H. (P.) spilodera* (Brooke in litt.). Of the species named by Peters (1960) four were African species, three American, two Australian and one Asiatic (Figure 1-1). Hall & Moreau (1970) regarded all of these species except the sooty-brown *H. fuliginosa* of Africa and *H. nigricans* of Australia as comprising a single superspecies. These two were excluded mainly because of the atypical colour of *H. fuliginosa* and the solitary tree-hole nesting habits of *H. nigricans*. Blakers et al. (1984) placed the two Australian species in the genus *Cecropis* but all other *Cecropis* species have deeply forked tails and these two species are probably better placed with the cliff swallows. All of the species build mud nests and are usually colonial. The exception is *H. nigricans* which nests in holes in trees which it closes, if necessary, with a wall and tunnel of mud pellets (Cayley 1931).

Recently a new species of cliff swallow *H. perdita* was described as a distinctive allospecies of *H. spilodera* (Fry & Smith 1985). The description was done from a single specimen of which only the wings and tail were preserved and two photographs constitute the only record of head and trunk features. Although this specimen was found on the Red Sea it was probably a vagrant there and its breeding range is unknown. If *H. nigricans, H. fuliginosa* and *H. perdita* are included there are eleven species in the cliff swallow group. The four cliff swallow species of Africa, excluding *H. perdita* of which nothing is known, have allopatric breeding ranges (Figure 1-1) and are remarkably like the American species *H. fulva* and *H. pyrrhonota.*

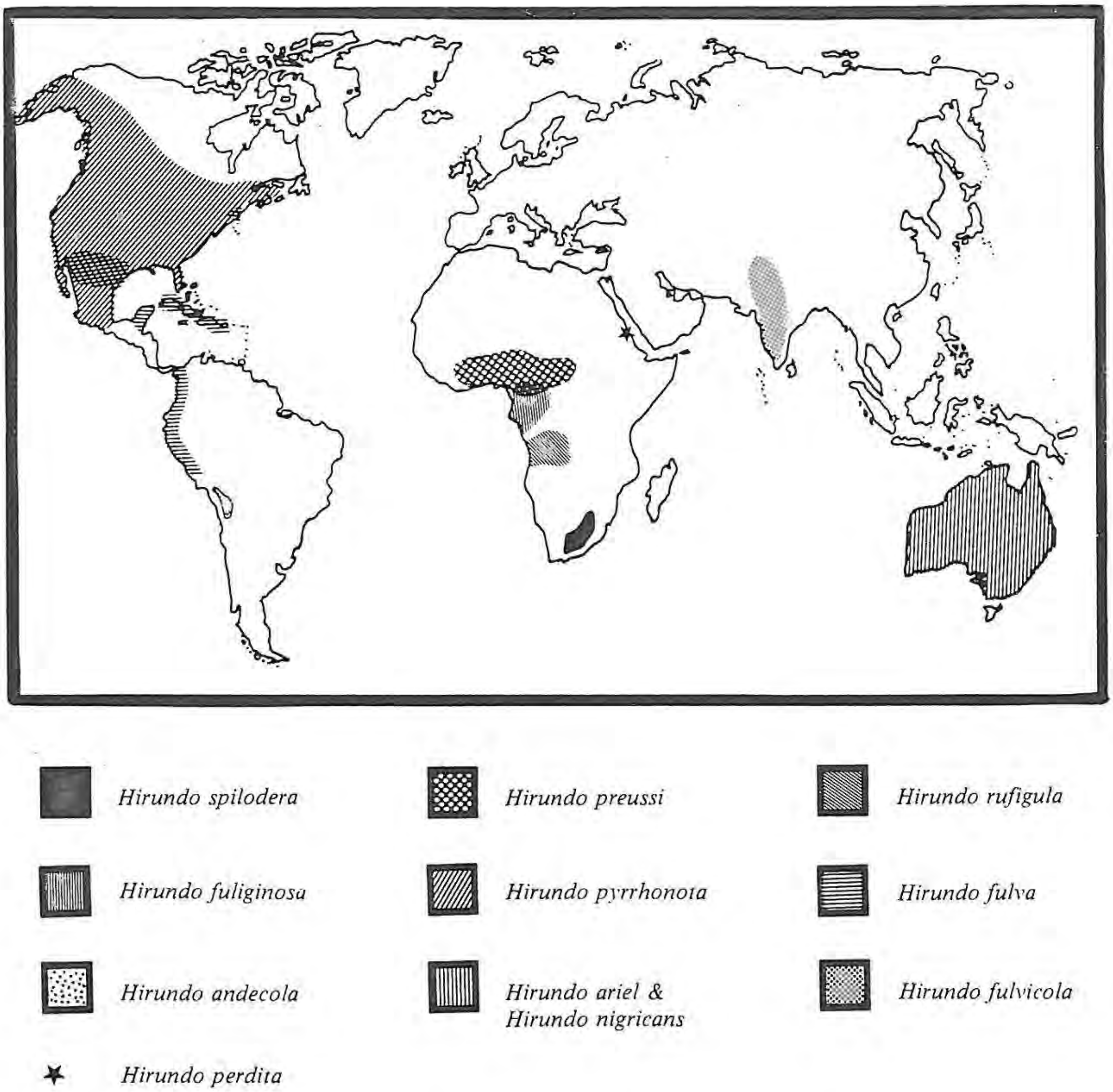


FIGURE 1-1

The distribution of species of the cliff swallow group worldwide.

Mayr & Bond (1943) pointed out that the development of coloniality in the swallow family paralleled the development of the ability to build nests. Swallows using natural holes or holes excavated by other animals such as the Greyrumped Swallow *Pseudhirundo griseopyga* and the Black Sawwing Swallow *Psalidoprogne holomelas* are solitary nesters, perhaps because of the erratic distribution of such cavities.

On the other hand, swallows which excavate their own holes, such as the Brownthroated Martin *Riparia paludicola*, or build closed mud nests, such as the Cliff Swallow *H. spilodera*, are often colony nesters. However, the Greater and Lesser Striped Swallows *H. cucullata* and *H. abyssinica* both build closed mud nests but are solitary nesters, indicating that there are more forces at work in the development of coloniality than just the ability to build nests.

Furthermore swallows which build open, cupshaped nests such as the Whitethroated Swallow *H. albigularis* and the European Swallow *H. rustica* lay eggs with various amounts of markings while closed nest breeders such as *R. paludicola* and *H. abyssinica* lay pure white eggs. The Cliff Swallow is an exception in having a closed nest but still laying coloured eggs. One tends to conclude from this that coloniality in the cliff swallow group is a recent development. However, in a colonial bird there is possibly a need for egg recognition which would not be possible if white eggs were laid.

There are no automatic or universal benefits of coloniality (Hoogland 1979) but there are some costs which are probably inevitable: increased competition (for nest sites, mates, food etc), increased transmission of diseases and ectoparasites (Alexander 1974), increased probability of misdirected parental care and increased attractiveness to predators (Hoogland & Sherman 1976). Despite all these negative factors associated with coloniality the Cliff Swallow shows no evidence that it is less successful than solitary swallows in the area and although often localised it is, by numbers, the most common.

The general biology including breeding, foraging and diet, behaviour, parasites, migration and intercolony movements of the South African Cliff Swallow was studied to gain some understanding of why this swallow species is colonial, and successful at it. This study will be followed by biological studies on other swallow species occurring in the area to be compared with results from the Cliff Swallow study. For the sake of brevity the South African Cliff Swallow *Hirundo spilodera* will be referred to as the Cliff Swallow throughout while *H. pyrrhonota* will be referred to as the American Cliff Swallow. *H. rustica* is known as the European Swallow in South Africa but as the Barn Swallow in America and will be referred to as the European Swallow throughout.

CHAPTER 2

STUDY AREA AND DESCRIPTIONS

INTRODUCTION

Fieldwork on this project started in January 1983 when the first Cliff Swallows *Hirundo spilodera* were mistnetted at a colony near Bloemfontein. This was towards the end of the breeding season and very little information was gathered except for mensural data resulting from the ringing operations.

After the Cliff Swallows had left the area in March 1983 the project was planned and another two full seasons were spent studying the birds, the first from August 1983 to March 1984 and the second from August 1984 to March 1985.

STUDY AREA

During March and April 1983 all possible nesting places within about 50 km (by road) around Bloemfontein were visited and all colonies so found plotted on a map of the area. From these a few colonies were selected for intensive studies.

Most observations were made at 20 Cliff Swallow colonies in a radius of 40 km around Bloemfontein (Figure 2-1). Observations on breeding biology were done at five colonies, Driekloof (1983/84 & 1984/85), Schoongezicht (1983/84), Meriba (1983/84), Leeukop A (1983/84 & 1984/85), Leeukop B (1983/84) and The Willows (1984/85). These colonies were selected as it was possible to reach the nests either from the ground or by standing on a stepladder. The most complete records were kept at Schoongezicht and Leeukop A & B in 1983/84 but in January 1984 the whole Leeukop B colony was destroyed by humans and only a few nests were used again in the 1984/85 season. Likewise the part of the Schoongezicht colony used for monitoring nests was destroyed in the winter of 1984 and not used again in the 1984/85 season. Early in November 1984 the Leeukop A colony was also completely destroyed, but after rains late in November most of the nests were rebuilt and breeding continued.

Except for the incidental observations done throughout the study period, general behaviour was observed mostly at the Meriba colony in 1983/84 and The Willows in 1984/85. The Willows was also used to study incubation, nest temperatures and other aspects of breeding in 1984/85. The Schoongezicht colony, The Willows and Meriba were all used to study feeding rates to the chicks, incubation and feeding ecology. All the colonies were surrounded by Karoo veld where karoo bushes such as *Chrysocoma, Pentzia* and *Senecio* dominated with a little grass and ploughed lands. Except for the colonies situated under the bridges over the major rivers such as the Glen and Krugersdrif colonies, the areas around the colonies were mostly flat and devoid of any trees.

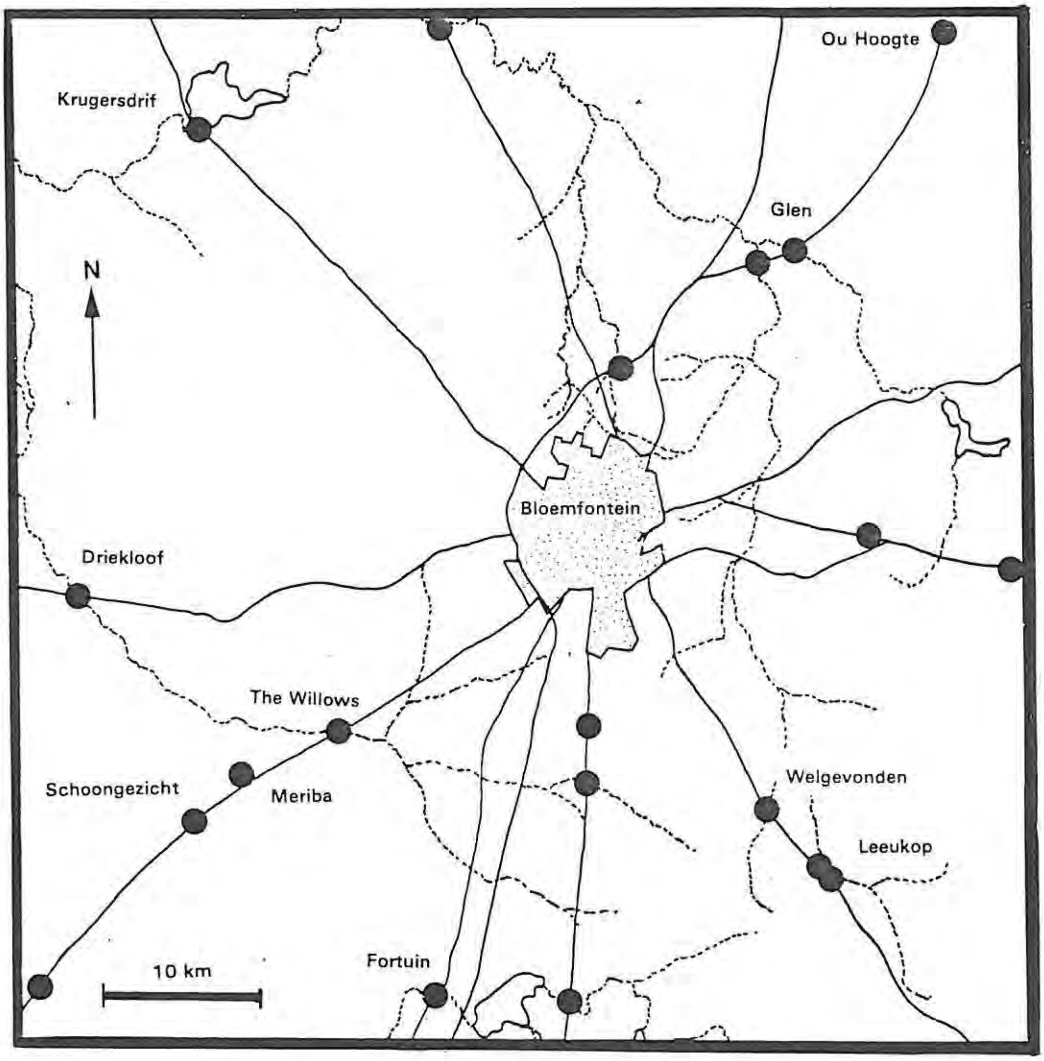


FIGURE 2-1

Map of the Bloemfontein area showing the location of *Hirundo spilodera* colonies. Unnamed colonies are not mentioned in the text.

CLIMATE OF THE STUDY AREA

It was impossible to keep a weather station in operation at each of the study colonies. It could also not be expected that the farmers closest to the colonies would keep precise records for this study. However, the owner of The Willows kept records of rainfall on his farm as shown in Figure 2-2. It was decided to use the climatic records kindly supplied by "Die Bult" observatory at the University of the Orange Free State about 15 km from The Willows colony. (Figure 2-3)

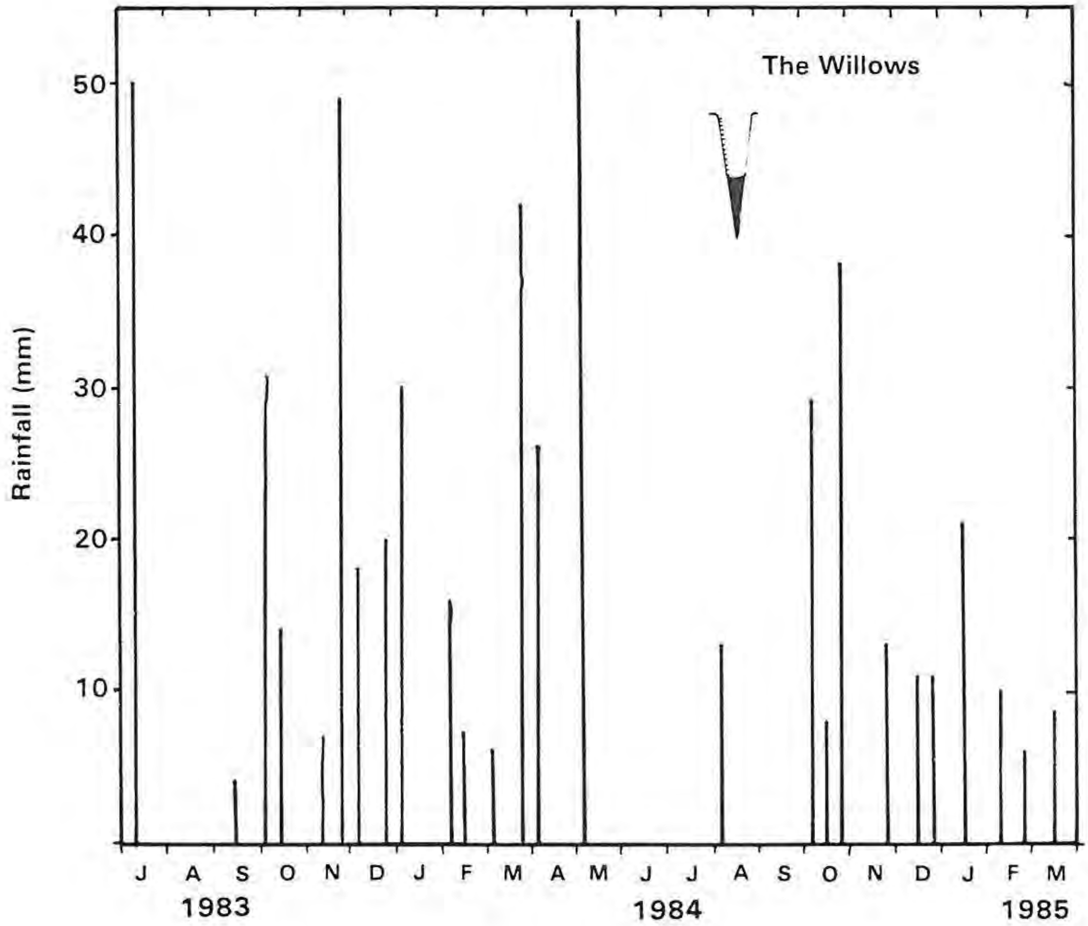


FIGURE 2-2

Rainfall recorded at the farm "The Willows" during the study period.

1. **Rainfall**

The Orange Free State has a summer rainfall regime and a dry winter. Both 1982 and 1983 were much drier than the longterm mean for the area which is about 564 mm annually. However, especially in the 1983/84 summer when rain usually occurred in short thunderstorms, the whole area did not receive the same amount of rain. On 28 November 1983 the "Die Bult" observatory at the University of the Orange Free State measured 57 mm but only 19 mm was measured at The Willows and 69 mm at Schoongezicht. The Willows and Schoongezicht are only 10 km apart. The rainfall from January 1983 to March 1985 is shown in Figure 2-3. The 1983/84 and 1984/85 seasons were exceptionally dry.

2. **Temperature**

The mean maximum and minimum temperatures as recorded at "Die Bult" are given in Figure 2-3.

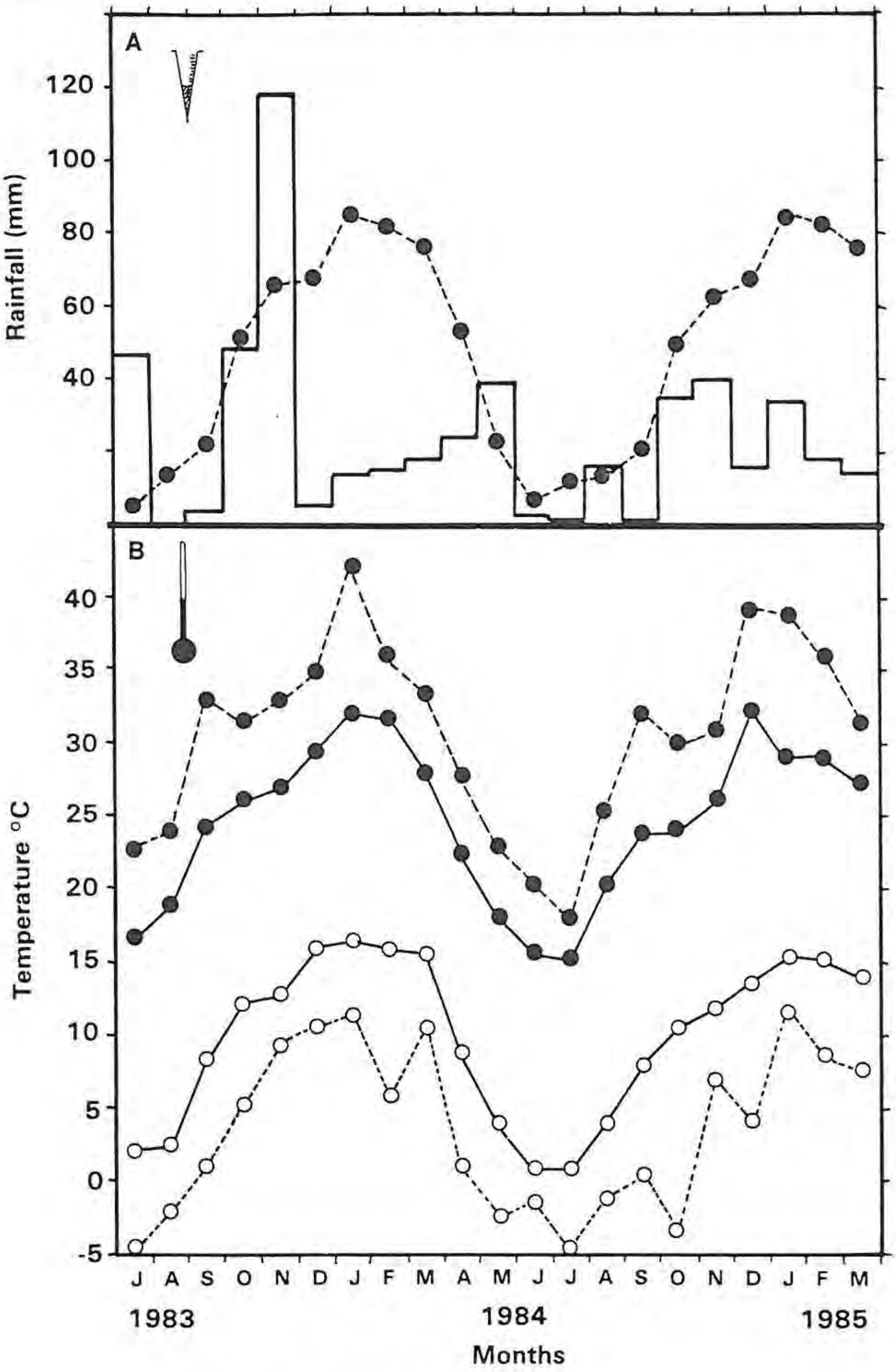


FIGURE 2-3

Climatic records as measured at "Die Bult". Observatory at the University of the Orange Free State in Bloemfontein over the study period.

A. The monthly rainfall recorded. The longterm mean is also given (-●-).

B. The mean monthly minimum (-○-) and maximum (-●-) temperatures recorded. The lowest (-○-) and highest (-●-) temperatures recorded each month are also given.

DESCRIPTION AND MEASUREMENTS

Since the brief taxonomic description of the South African Cliff Swallow by Sundevall in 1850 the Cliff Swallow has been described and figured in general texts several times recently (McLachlan & Liversidge 1978, Newman 1983, Maclean 1985). The colouration of the rufous parts as well as the amount of speckling is variable, allowing for some birds to be individually recognizable when under close observation. Maclean (1985) gives a good written description of the Cliff Swallow which is figured in a typical posture in the frontispiece.

TABLE 1

MEASUREMENTS OF A SAMPLE OF *HIRUNDO SPILODERA* MALES AND FEMALES TRAPPED DURING THE STUDY.

MALES

Measurement	n	Mean	S.D.	Range	Median
Mass (g)	500	20,40	1,31	16,0 - 24,2	20,5
Wing length (mm)	226	111,27	2,41	105,0 - 118,0	111,0
Tail length (mm)	172	50,50	2,79	45,0 - 56,0	50,8
Exposed culmen (mm)	47	8,11	0,38	7,4 - 9,2	8,1
Tarsus (mm)	127	13,87	1,09	11,7 - 16,8	13,7

FEMALES

Measurement	n	Mean	S.D.	Range	Median
Mass (g)	500	20,7	1,68	16,5 - 26,0	20,6
Wing length (mm)	136	111,70	2,64	105,0 - 119,0	112,0
Tail length (mm)	99	51,48	2,25	45,4 - 57,2	51,2
Exposed culmen (mm)	29	8,08	0,52	7,0 - 9,1	8,0
Tarsus (mm)	77	13,82	1,07	12,3 - 17,8	13,6

METHODS

Cliff Swallows were weighed with a 50 g capacity Pesola spring balance to the nearest 0,1 g.

Winglengths are maximum chord measured with a wingrule with a stop at the end. All other measurements were done with dividing calipers accurate to 0,05 mm. To measure tail-length calipers were pushed against the body with the bird held belly upward and the longest feather was measured. The exposed part of the culmen was measured and the tarsus was measured in a non-standard way from the ball of the foot to the dent in the tarsal joint.

RESULTS

Adult Cliff Swallows are about 14 cm in length. Other body measurements are given in Table 1. There is no statistically significant size difference between males and females, and it was only possible to sex live birds on brood patch criteria (see Chapter 3). The frequency of occurrence of different wing lengths of male, female and unsexed birds are given in Figures 2-4 and 2-5. From this it is clear that there is no difference in male and female wing lengths and that the wing lengths measured in this study had a wide range. The mean was 111 mm for both males and females while Maclean (1985) recorded a mean of 114 mm for unsexed birds. Although the weights of the Cliff Swallow fall well within the ranges given by Maclean (1985), none ever came close to 13 g and even a bird which went without food for as much as 60 hours only weighed 15,7 g after the ordeal (Earlé 1983). Birds were heavy in mid morning after their first foraging trips, and late afternoon after their final foraging trips and significantly lighter ($p < 0,005$) early in the morning before foraging (Table 2). As with the wing lengths (Figure 2-4) and weights (Figure 2-6) there was no difference between male and female tail lengths (Table 1), although males tended to have a larger proportion of shorttailed individuals (Figure 2-7).

TABLE 2

WEIGHTS OF *HIRUNDO SPILODERA* AT DIFFERENT TIMES OF THE DAY. NO DISTINCTION WAS MADE BETWEEN MALES AND FEMALES.

Time Period	n	Mean (g)	S.D.	Range (g)	Median (g)
Early morning 05h30 - 07h00	50	20,3*	0,69	18,8 - 21,7	20,3
Late morning 10h00 - 11h00	50	21,8	1,49	19,0 - 25,5	21,5
Early afternoon 12h00 - 14h00	50	21,0	1,26	18,3 - 24,4	21,0
Late afternoon 17h00 - 19h00	50	22,5*	1,24	20,0 - 25,8	22,8

* Significantly different.

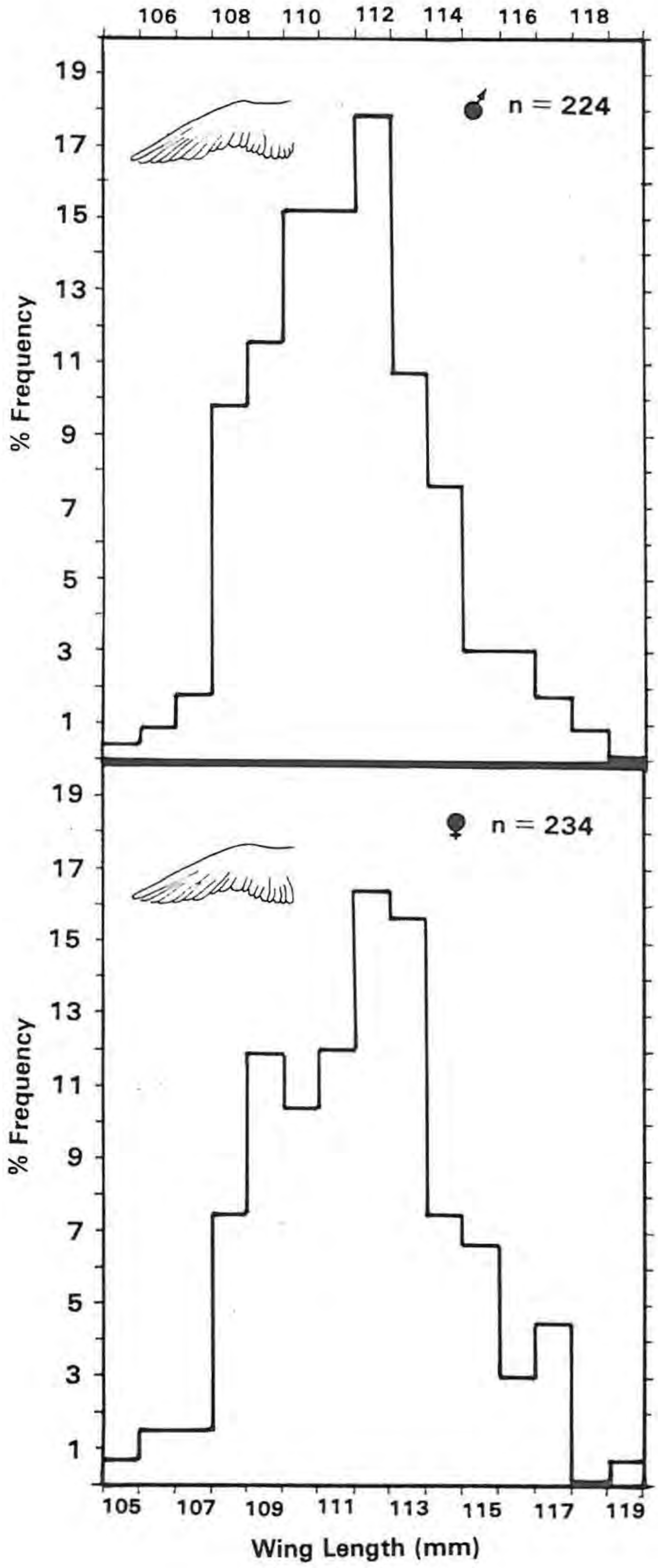


FIGURE 2-4

The frequency distribution of *Hirundo spilodera* wing lengths for adult male and female birds separately.

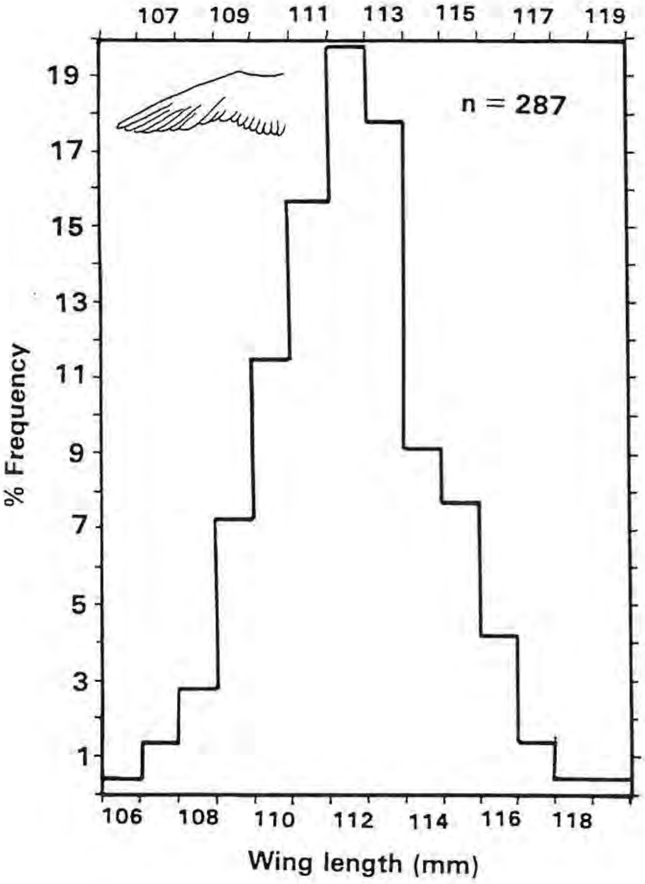


FIGURE 2-5

The frequency distribution of *Hirundo spilodera* wing lengths for unsexed adult birds.

TABLE 3
DEFORMITIES, PROBABLY THE RESULT OF INJURIES, FOUND ON *HIRUNDO SPILODERA* INDIVIDUALS HANDLED DURING RINGING OPERATIONS.

Number of deformities	**Part of body**						
	Tarso-metatarsus	**Fibula**	**Phalanx**	**Culmen**	**Carina & Clavicle**	**Skull**	**Eye**
				5	11	2	
Right	21	5	32				2
Left	16	4	28				
Total	37	9	60	5	11	2	2
% of Total deformities	29,3	7,1	47,6	4,0	8,7	1,6	1,6

A number of birds with unusual markings or slight deformities was found at all of the colonies apparently coping well. Adult birds with white markings around the face were often found and in all the cases where the individuals were ringed earlier, these were found to be first year birds which retained their fledgling facial markings (see Chapter 4). Two birds at the Driekloof colony had light grey crowns instead of sooty brown or metallic blue-black

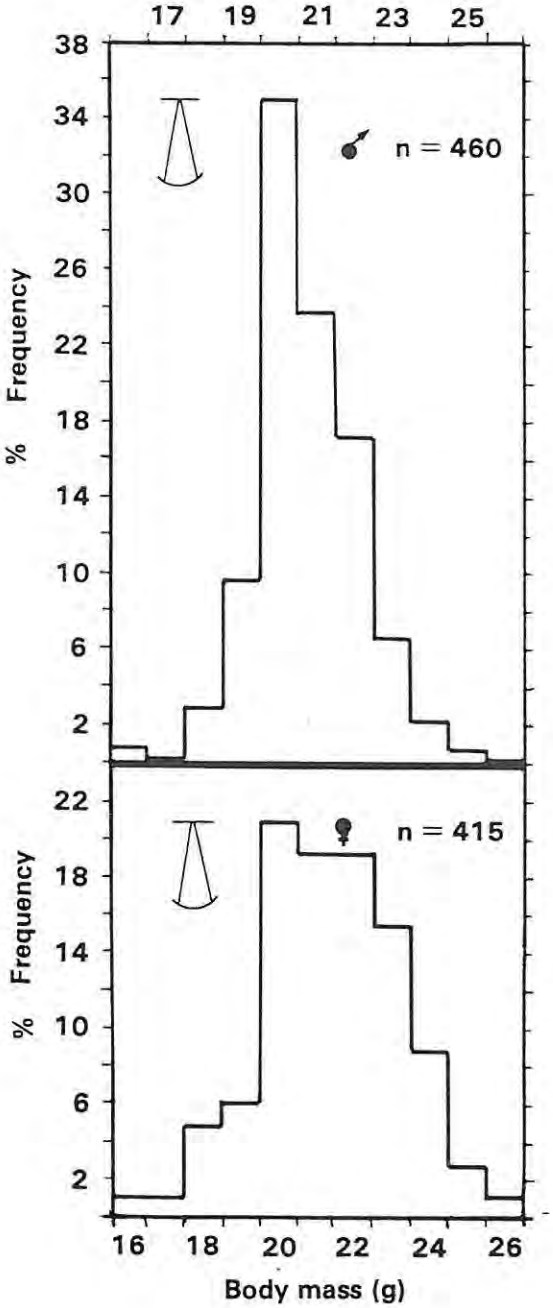


FIGURE 2-6

The frequency distribution of *Hirundo spilodera* body for adult male and female birds separately.

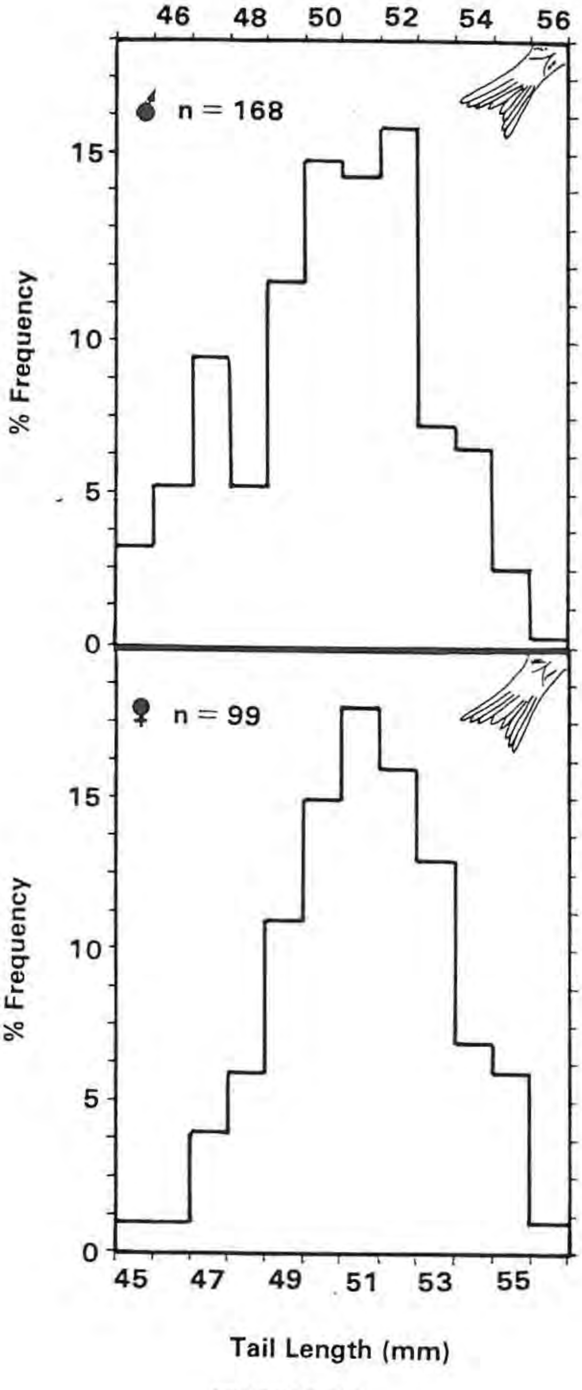


FIGURE 2-7

The frequency distribution of *Hirundo spilodera* tail lengths for adult male and female birds separately.

crowns. The occurrence of deformities, probably all the results of injuries, are given in Table 3. Markus (1964) reported on a facial anomaly in a Cliff Swallow in Pretoria where the bill of this bird was deformed. Most of the deformities in this study were on the feet and toes, although a surprisingly large percentage of injuries were to the carina and clavicle (Table 3). By far the greatest number of deformities were to the toes, which were either missing or crooked. Most of the injuries to the toes were probably caused by nesting material, especially sheep's wool, getting entangled in the toes and stopping the bloodflow, causing the toe to die off. Birds were often found with pieces of nesting material around toes or the tarso-metatarsus. Such entanglement in nesting material often resulted in death if the bird could not free itself from the nest pad (see Chapter 3). Two birds were found with one eye each totally blind and dried out and another two had parts of the skull soft and no feathers growing on those parts of the skull. Where the carina was deformed it was usually crooked and in one case the left supracoracoideus muscle was underdeveloped but the bird flew away normally. In total about 1,8% of all birds handled had some deformity.

MOULT

A total of 19 birds was found moulting the primary feathers in March 1983 and March 1985 but no birds in moult were found at the end of the 1983/84 season. The earliest date that a moulting bird was trapped was 10 March when p1 and p2 were already full grown and p3 was missing. Moulting could thus have started during the first few days of March. All other birds trapped in moult had p1 missing to about half grown and p2 missing to about a third grown. It seems as if p1 and p2 were dropped either simultaneously or within a day or two of each other, and p3 was then only dropped after p1 and p2 were fully grown. The primary coverts of the moulting primaries were all in the same growth stage as the primaries. None of the other areas of the body were found to be in moult during the season in southern Africa.

The Cliff Swallow seemed to follow the normal passerine moulting pattern described by De Bont (1962) for the European Swallow *H. rustica* in central Africa and also noted in other parts of Africa (Broekhuysen & Brown 1963, Dowsett 1966, Mendelsohn 1973) and for other swallow species such as the Purple Martin *Progne subis* (Niles 1972). No juvenile Cliff Swallows were found in moult. Mead (1975) found several swallow species starting their moult before migrating.

CHAPTER 3

DISTRIBUTION, MIGRATION AND POPULATION STRUCTURE

INTRODUCTION

The distribution and population structure is an important facet of the biology of a species. A species will only be present where suitable habitat occurs and, if nesting sites are not evenly distributed as is the case with the Cliff Swallow, the species will have a patchy distribution. A patchy distribution in turn results in heavy demands being made on the available resources in areas around such nesting sites. The population size and structure of the species will be influenced by the availability of these resources which will affect natality and mortality.

In this chapter an attempt will be made to describe the distributional range of the Cliff Swallow both during the breeding season and winter months, the size of the breeding populations and the migration and movements.

METHODS

Trapping and ringing

The trapping of Cliff Swallows has been discussed elsewhere (Earlé 1984) but I feel it necessary to repeat some of the comments here.

An important facet of this study, which is still continuing, is intercolony movement and the return rate of birds from their wintering grounds. To study these movements large numbers of birds were trapped and ringed. Initially, all birds were mistnetted by setting up nets close to the nesting bridges. However, this was found to be very time consuming, especially early or late in the season as the birds would be out foraging, and for as much as three hours at a time no birds would come near the nets

During the very dry summer of 1983/84 all the streams below the smaller bridges at The Willows, Schoongezicht, Driekloof, Ouhoogte, Fortuin and Leeukop dried up and another technique could be used to trap large numbers of these swallows in single attempts. This technique was also used by Mayhew (1958) to trap large numbers of the American Cliff Swallow *Hirundo pyrrhonota.* The open ends of the culverts or bridges where the swallows nested were sealed off at night with old fishing nets and the birds captured by hand as they left their nests and clung to the nets which blocked their exit. The nets were put into place earlier in the afternoon before the trapping operation by fastening them to the top of the bridge and sometimes to the sides as well but the entrance to the bridge was always kept open. On arrival at the colony to be trapped just after dark, the nets were dropped from the top of the bridge to seal off the entrances. Head lamps were then switched on and the swallows were usually very easily caught after leaving the nests, as they sat passively against the net or on the ground.

Because the chicks very seldom leave the nest before they are ready to do so, only adults and young already fending for themselves were trapped with this method. At three of the colonies where swallows were trapped by this method records were also kept of breeding success. No indication was found that this mass trapping had any effect on breeding success.

The swallows were kept overnight after the ringing was completed and the birds were again released at their colonies in the morning.

Sexing and Ageing

From about the first week in October to the first week of March it was easy to sex Cliff Swallow adults. Females always had a very clear brood patch while males never had the breast completely free of feathers. After the middle of March some females could be mistaken for males although the greater majority still showed a clear brood patch or the feathers of the patch were in pin.

Birds in their first breeding season could not be distinguished from older birds. For the first two months after leaving the nest young birds can be separated from adults by the

FIGURE 3-1

The tertiaries and secondary coverts of juvenile *Hirundo spilodera* showing a buff edge.

prominent yellow gape but towards the end of the season (February — March) many young birds resemble the adults except for the tertiaries showing a buff edge. (Figure 3-1).

Distributional and migration records

Distributional records were gathered from all possible sources; museum skins, literature and in the Orange Free State especially from records submitted for the Orange Free State Bird Atlas (Earlé & du Toit in prep.) while Transvaal records were from the Bird Atlas of the Transvaal (Kemp et al. 1985). Records of recoveries of Cliff Swallows ringed in South Africa were supplied by the South African Bird-Ringing Unit, who also supplied some nest record cards.

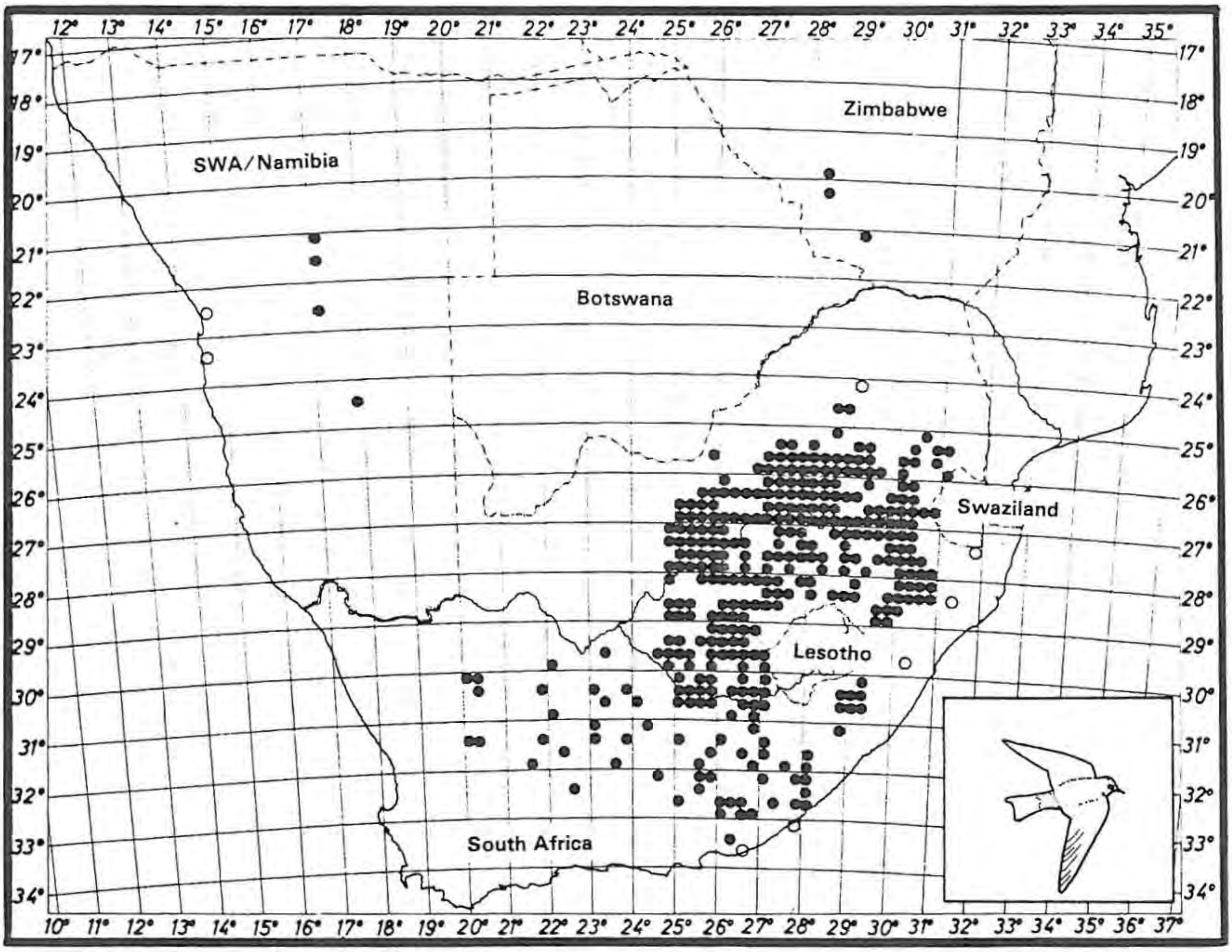


FIGURE 3-2

The distribution of *Hirundo spilodera* during the summer months of southern Africa. Open circles (○) indicate localities where this species were only sighted and not found breeding. Solid dots (●) are localities where breeding takes place or probably takes place.

RESULTS

Distribution

The Cliff Swallow occurs during the summer months (August - April) in the Karoo districts of the Cape Province, the greater part of the Orange Free State, the Natal interior and the highveld areas of the Transvaal. Occurrences was also reported from a few localities in South West Africa (Clancey 1966 & Nest record cards) and South-western Zimbabwe (Figure 3-2). The patchy distribution of this species especially the western Transvaal and South West Africa is probably the result of a lack of records from those areas but the patchy distribution in the western Orange Free State and karoo areas is probably real. The distribution of the Cliff Swallow is very much dependent on the availability of nesting sites and these are not evenly distributed, resulting in this patchy distribution.

The larger part of the population probably breed between 25 ° and 31° *S* and 24° and 31°E with some breeding colonies in the eastern Cape being used regularly. Vernon (1962) recorded a substantial northward extension of the breeding range to just north of Bulawayo in Zimbabwe (Figure 3-2). However, the colonies in this area were abandoned after a few seasons and the species probably had not bred in Zimbabwe recently (Irwin 1981). Rowan (1963) reviewed the literature on the range of the Cliff Swallow and described a major range extension in a westernly direction in the Cape Province during the summer of 1961/62 after exceptionally good rains over the whole western Karoo earlier that year. It was not possible to determine if all the colonies used when Rowan reviewed the literature are still in use but the Cliff Swallow is not common at the western extreme of its range and is probably very localized around breeding sites. Several authors (e.g. Godfrey 1943, Pike 1954, Taylor 1949, Brooke 1959, Winterbottom 1962) reported on the range extension or "unknown" occurrence of the Cliff Swallow in the Cape Province and from this it is clear that the range of this species started extending through the eastern Cape with the establishment of towns and especially the construction of large buildings and bridges. Although a large part of the drier grassveld and Karoo areas is probably suitable breeding area for this species, the shortage of nesting sites in these areas prevents the Cliff Swallow from extending its range even further.

Migration

None of the Cliff Swallows ringed to date during this study has been recovered in its winterrange. Of the nearly 20 000 birds ringed between 1950 and 1970 in the Transvaal only 4 were recovered, in western Zaïre (Table 4). The bird recovered at Tshikapa was found only 15 days after being ringed and had thus travelled a minimum of 154 km per day. Three of the recoveries were made within the first two weeks of April when there were surely still some birds in their summer range area. It thus seems as if there is little evidence for mass departure of the Cliff Swallow and it is more likely that migrating birds can be found anywhere from their breeding colonies to the winter areas during this time. Very much the same situation probably occurs when the swallows are on their way to their breeding areas as the build up of Cliff Swallows at The Willows and Driekloof early in the 1984/85 season showed (Table 5). The recovery of the bird on 12 August (Table 4), supports this view of gradual migration

TABLE 4

RECOVERIES OF *HIRUNDO SPILODERA* FROM THEIR WINTER-RANGE AREA.

Ringing Location	Date ringed	Recovery location	Date recovered	Days elapsed	Distance moved (km)
Pretoria, Transvaal 25°45'S; 28°14'E	15.11.1953	Feshi, Zaïre 06°07'S; 18°18'E	07.04.1955	508	2 415
Rustenburg, Transvaal 25°53'S; 27°25'E	10.03.1963	Kansanza, Zaïre 06°08'S; 19°26'E	14.04.1963	35	2 317
Brits, Transvaal 25°48'S; 27°46'E	04.04.1954	Kobo, Zaïre 04°54'S; 17°09'E	12.07.1954	99	2 528
Barberspan, Transvaal 26°33'S; 25°36'E	26.03.1968	Tshikapa, Zaïre 06°26'S; 20°48'E	10.04.1968	15	2 311

Some of these recoveries were published in Ashton (1957) and Elliot & Jarvis (1970).

TABLE 5

NUMBER OF *HIRUNDO SPILODERA* PRESENT AT THE WILLOWS AND DRIEKLOOF COLONIES EARLY IN THE 1984/85 SEASON.

Colony	Date in 1984								
	08.08	10.08	12.08	16.08	20.08	25.08	28.08	01.09	Maximum*
The Willows	0	8	9	44	82	150	300	400	975
Driekloof	3	29	37	200	400	700	800	900	1 306

*Maximum is numbers trapped during ringing operation early in the season.

The only other records of the Cliff Swallow outside its breeding range are two sight records from the Mwinilunga district in the north-western part of Zambia (Figure 3-3). Dowsett (1979) recorded a single bird in November which he considered to be a late straggler. The record of Bowen (1983) on 7 August of a small flock of Cliff Swallows moving in a southward direction fits in well with the migration dates as this species arrives in South Africa in August and the area where the birds were seen was on route between Zaïre and South Africa.

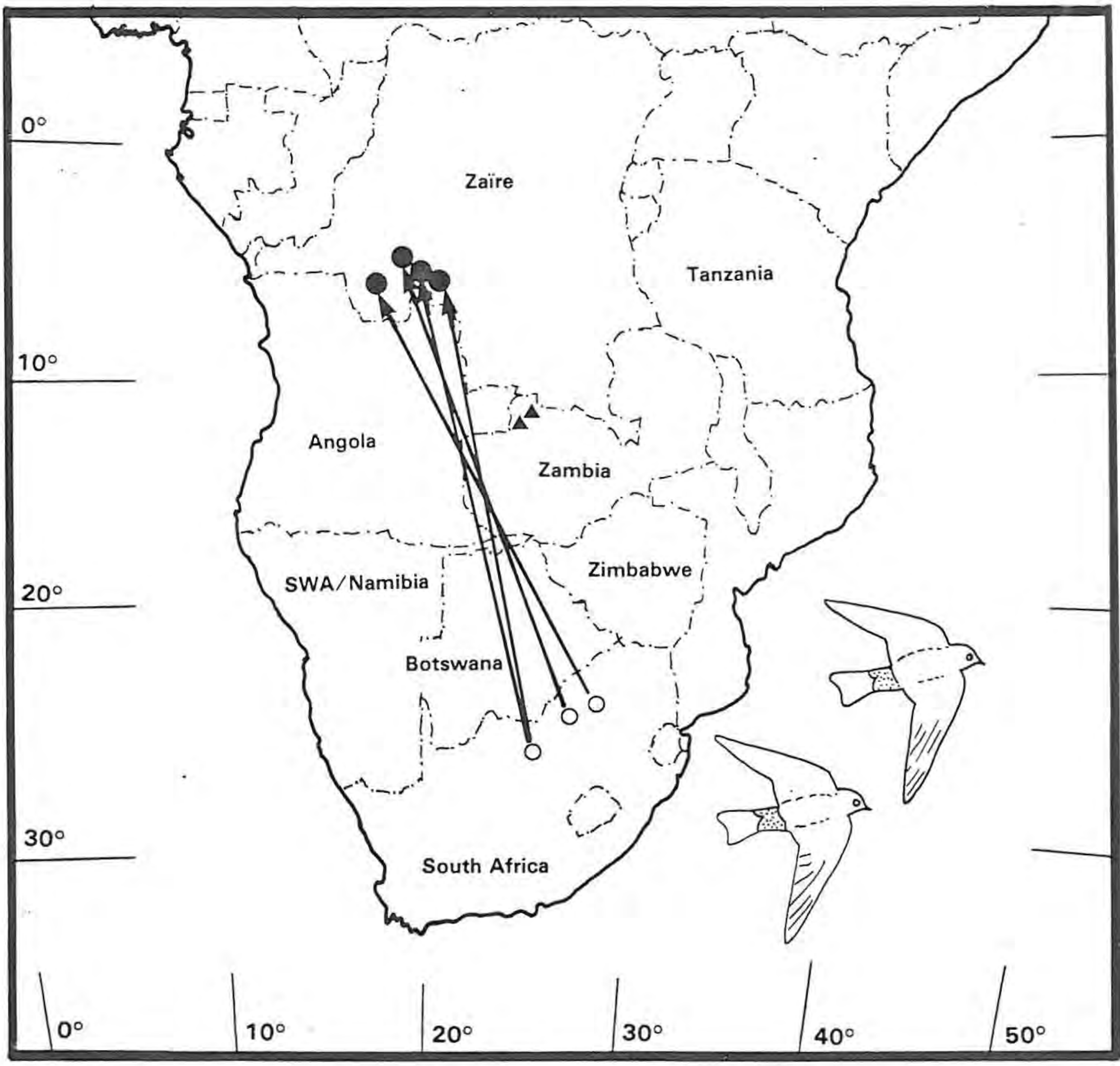


FIGURE 3-3

Ringing (o) and recovery (●) localities of four *Hirundo spilodera* individuals. The localities where Cliff Swallows were observed, probably on their migration route in Zambia, are also indicated (▲).

The arrival and departure dates of Cliff Swallows in South Africa are given in Table 6. There are no records of dates for different areas in the same year so that a comparison of arrival or departure dates is not possible. Broekhuysen (1974) summarised sight records of the Cliff Swallow over a 17-year period from 1950-1966 and, although the records were few, it seemed as if birds arrived a few days earlier in the Transvaal than in the Orange Free State. During the present study no birds were present during May, June or July but Broekhuysen (1974) recorded a flock of about 150 early in June and up to five birds during the second half of July in the Transvaal. These July birds were probably early arrivals as the first arrivals at Barberspan were also recorded in July of 1973 (Skead & Dean 1977).

TABLE 6

ARRIVAL AND DEPARTURE DATES OF *HIRUNDO SPILODERA* IN SOUTH AFRICA.

Area	Season	Arrival Date	Departure Date	Source
Pretoria	1958/59	19 November	11 April	Burgerjon (1964)
Pretoria	1959/60	2 October	± 18 March	Burgerjon (1964)
Barberspan	1971/72	7 August	-	Skead & Dean (1977)
Barberspan	1972/73	5 August	-	Skead & Dean (1977)
Barberspan	1973/74	30 July	-	Skead & Dean (1977)
Barberspan	1974/75	5 August	-	Skead & Dean (1977)
Barberspan	1975/76	19 August	-	Skead & Dean (1977)
Pretoria	1979/80	10 August	16 March	Winterton (1982)
Pretoria	1980/81	23 August	17 May	Winterton (1982)
Bronkhorstspruit	1981/82	29 October	-	Winterton (1982)
Bloemfontein	1982/83	21 August	11 April	This study
Bloemfontein	1983/84	15 August	8 April	This study
Bloemfontein	1984/85	8 August	21 April	This study
Bloemfontein	1985/86	7 August	-	This study

Homing abilities

The results of three homing experiments done in the 1983/84 season are shown in Table 7. There was no indication of how quickly the homing birds returned to their original colonies but retrapping efforts were within one month of the release. A remarkably similar percentage of birds returned to their colonies and except for the two birds which were found at different colonies (Table 7) there was no indication what happened to the birds that did not return. The birds were released as a flock and the possibility that they escaped recapture is very small as trapping success at the sites was nearly 100%. It is interesting that none of the

Schoongezicht birds released at The Willows colony was ever retrapped at that colony. There is also no indication that either males or females had a higher return rate. Of the 121 birds released in the three experiments 55 were males, 55 were females and 11 were of unknown sex. Of these 34 (61,8%) of the males and 35 (63,6%) of the females returned while 6 (54,5%) of the unsexed birds returned.

TABLE 7

HOMING ABILITY OF *HIRUNDO SPILODERA* IN SOME EXPERIMENTS IN 1983.

Colony	Release Point	Number Released	Number Retrapped	% Returned	Distance (km)
Fortuin	Bloemfontein City	21	13	62	48
Schoongezicht	Bloemfontein City	50	32*	64	35
Schoongezicht	The Willows	50	31	62	12

*This number excludes one retrapped at Meriba in the same season and one bird retrapped at The Willows in the following season.

Intercolony movements

In total 89 birds ringed during the three seasons were ever recaptured at a colony other than the original ringing colony (Table 8). This is 1,2% of all birds ringed (Table 9). However, this included 18 birds which moved from the Meriba colony to Schoongezicht and The Willows after the desertion of the colony in October 1983. If these birds were excluded only 0,93% of the birds moved between colonies. Only three birds moved more than 20 km with the longest movement that of 72 km by a female between the Leeukop and Ou Hoogte colonies (Table 9). There was no indication that one of the sexes was more inclined to move than the other with 41 males and 35 females changing colonies. There seems to be slightly more females changing colonies within a season and again more males changing colonies after the migration but differences are too small to draw any conclusions from.

Return rate after migration

The number of Cliff Swallows ringed and recaptured during three seasons are given in Table 9. Of the 541 birds trapped in 1982/83 40,1% returned in 1983/84. In 1984/85 the Schoongezicht colony was not trapped during a mass trapping operation and if this colony is excluded, 35,2% of the birds ringed in the 1983/84 season returned in the 1984/85 season.

Although the return rate of Cliff Swallows can be low, some individuals can return for quite a number of years. The oldest Cliff Swallow retrapped to date being at least 99 months old (Table 10).

TABLE 8

NUMBER OF *HIRUNDO SPILODERA* RINGED AND RECAPTURED DURING THREE SEASONS

	Season						
	1982/83	**1983/84**			**1984/85**		
	New Captures	**New Captures**	**Recaptures****		**New Captures**	**Recaptures****	
			From Ringing Colony	From Other Colonies		From Ringing Colony	From Other Colonies
Schoongezicht	171	1 434	92	3	173	30	2
The Willows	178	754	68	15	530	450	11
Driekloof	180	1 624	36	3	810	538	10
Leeukop A & B		585	-	-	88	85	0
Meriba		58		-	-	-	-
Ou Hoogte		301	-	-	30	68	1
Fortuin		297	-	-	330	105	1
Welgevonden					76	0	4
Other*	12				-	-	-
Total	541	5 053	196	21	2 037	1 276	29

*Other includes few birds trapped at Glen and Koffiefontein.

**Retraps do not include birds retrapped in the same season at the original or at another colony, but do include individuals retrapped at a colony other than the ringing colony in a later season.

TABLE 9

INTERCOLONY MOVEMENTS OF *HIRUNDO SPILODERA* DURING THREE SEASONS

A. Movements withing the 1983/84 season

Movement from-to	Distance (km)	Males	Females	Juvenile/ unsexed	Total
The Willows-Schoongezicht	10	2	4	2(u)	8
Schoongezicht-The Willows	10	1	1	0	2
Schoongezicht-Meriba	5	1	5	3(u)	9
Schoongezicht-Driekloof	16	0	1	0	1
Schoongezicht-Fortuin	23	0	0	1(j)	1
Meriba-Schoongezicht	5	8	6	3(u)	17
Meriba-The Willows	5	1	0	0	1
TOTAL		13	17	1(j) 8(u)	39

B. Movements in later seasons 1982/83 - 1983/84

Movement from-to	Distance (km)	Males	Females	Juvenile unsexed	Total
The Willows-Schoongezicht	10	10	4	1(u)	15
Schoongezicht-Meriba	5	1	0	1(u)	2
Schoongezicht-Driekloof	16	0	1	0	1
Driekloof-Schoongezicht	16	2	1	0	3
TOTAL		13	6	2(u)	21

TABLE 9 (Cont.)

C. Movements in later seasons 1983/84 - 1984/85

Movement from-to	Distance (km)	Males	Females	Juvenile/ unsexed	Total
The Willows-Schoongezicht	10	0	1	0	1
The Willows-Driekloof	20	1	0	1(u)	2
Schoongezicht-Driekloof	16	4	4	0	8
Schoongezicht-The Willows	10	4	5	1(u)	10
Meriba-The Willows	5	1	0	0	1
Driekloof-Schoongezicht	16	1	0	0	1
Leeukop-The Willows	34	1	0	0	1
Leeukop-Ouhoogte	72	0	1	0	1
Leeukop-Welgevonden	2	3	1	0	4
TOTAL		15	11	2(u)	29

TABLE 10

DETAILS OF THE TEN OLDEST *HIRUNDO SPILODERA* INDIVIDUALS RINGED AND RECAPTURED IN SOUTH AFRICA UP TO DECEMBER 1984.

Ring no.	Location	Date ringed	Date last recaptured	Age (months)
5717362	Barberspan	18.12.1959	26.03.1968	99
5717462	Barberspan	22.01.1960	26.03.1968	98
5717464	Barberspan	22.01.1960	26.03.1968	98
60183196	Rustenburg	10.03.1963	08.11.1970	92
60183369	Rustenburg	10.03.1963	08.11.1970	92
58100966	Krugersdorp	31.03.1963	08.11.1970	92
5717912	Barberspan	09.02.1962	28.02.1969	85
5717799	Barberspan	09.02.1962	19.12.1968	82
5717815	Barberspan	09.02.1962	19.12.1968	82
5717890	Barberspan	09.02.1962	19.12.1968	82

Mortality

The causes of death of 77 Cliff Swallows are given in Table 11. The birds "shot for sport" and "trapped for food" were recovered in their winterquarters while all other deaths occurred in the Cliff Swallows' breeding range. In March and October 1984 when no drinkng water was available, most of the swallows were in bad condition and mortality was high. No estimation of this mortality was possible as birds not only died at the colonies where they could be found but also in the veld. Earlé (1984) gave some indication of mortality during mass ringing operations during this period.

Sex ratio

The sex ratio of the Cliff Swallow was 1:1 (Table 12). In the small Leeukop colony and some other colonies where it was possible to trap the whole colony with no birds escaping it was established that even within a colony this sex ratio is 1:1.

TABLE 11

CAUSES FOR MORTALITY OF RINGED *HIRUNDO SPILODERA* INDIVIDUALS DURING THIS STUDY AND AS RECORDED AT SAFRING UP TO MARCH 1985

Recovery method	Safring	This Study	All recoveries
Shot for sport	1		1
Trapped for food	1		1
Ringing activities	4	17	21
Collided with road vehicle		2	2
Found injured		5	5
Cause of death unknown	9	16*	25
Stuck in nest (starved?)		22	22
TOTAL	15	62	77

*11 Birds were found below the colony and 5 birds were found dead in nests.

TABLE 12

SEX RATIO OF *HIRUNDO SPILODERA* AT SOME COLONIES AS REVEALED BY SEXING BIRDS ON BROOD PATCH CRITERIA DURING MASS RINGING OPERATIONS. FIGURES GIVEN ARE FOR COLONIES WHERE TRAPPING SUCCESS WAS 100% OR VERY CLOSE TO IT.

Colony	Date	Number of males	Number of females	Ratio M : F
Leeukop A & B	19.01.84	236	234	1 : 1
The Willows	27.01.84	144	151	1 : 1
Fortuin	15.02.84	118	114	1 : 1
Ou Hoogte	08.02.84	123	120	1 : 1
TOTAL		621	619	1 : 1

DISCUSSION

The homing ability of members of the Hirundinidae has been investigated largely in northern America. There seems to be good evidence that all the species studied have a reasonable ability to home. A total of 16 Purple Martins *Progne subis* displaced by Southern (1959) at distances of 2,8 to 376 km all returned to their nests while European Swallows *Hirundo rustica* displaced at distances of 276 to 1 875 km from their nests showed a return rate of 40% (Rüppell 1934, 1936, 1937).The homing ability of the European Swallows, however, decreased steadily with increasing distance. For distances of up to 96 km, Nastase (1982) found that between 66% and 41% of released European Swallows returned. He observed that males and females had equal homing abilities, which he attributed to the important post-copulatory role played by the male eg. feeding of young and nest defence. Matthews (1955) reported a homing rate of 37% of Sand Martins *Riparia riparia* while Sargent (1962) had return percentages of between 33% and 80% depending on the displacement distance. In this study the nearly 63% birds homing is very close to the 58% obtained by Mayhew (1958) for 143 birds released at distances of 64 to 184 km.

For the Cliff Swallow there seem to be very similar return percentage, at least for the three distances tested. As there is some evidence that displaced birds can join other colonies (Table 7) it is quite possible that these "lost" birds have joined colonies where no ringing took place. No Schoongezicht birds released at The Willows colony were ever found at the release colony indicating that there is probably an "instinct" to home rather than just join any colony. This was also found to be the case with the American Cliff Swallow (Mayhew 1958). There is no apparent difference between the homing ability of males and females in the Cliff Swallow which can probably, as in the case of the European Swallow (Nastase 1982), be explained by the near equal roles played by both sexes in breeding (see Chapter 7).

The Cliff Swallows have a very high degree of fidelity to a specific breeding site and although interchange between colonies does take place, this involves only a small number of individuals while the greater majority of individuals probably breed in one colony their whole life. There are apparently no long distance intercolony movements in this species and during this study the longest distance moved between two colonies was a single 72 km movement between Ou Hoogte and Leeukop. Only 89 (1,2%) of all birds ringed were ever recaptured at a site other than the original ringing site (Table 8). Burgerjon (1964) even found that a large number of the individual Cliff Swallows returned to the exact same nest occupied the previous breeding season. It would seem as if the stability of the nesting sites of the Cliff Swallow, namely man-made bridges or natural cliffs, which are available for many years, resulted in the site tenacity of the Cliff Swallow. High breeding site tenacity was also found in several other Hirundinidae with stable nesting sites. Allen & Nice (1952) reported a return rate of 97% for adult Purple Martins to former nesting sites while Chapman (1955) found 40% of the breeding Tree Swallows *Iridoprocne bicolor* returning the next breeding season. Mayhew (1958) retrapped 48% of the American Cliff Swallows *Hirundo pyrrhonota* adults again in their original colony of ringing with 9% of the birds moving between colonies. Uchida (1932) found 46% of the European Swallow adults returning to the same area after migration. In a study examining the factors affecting nest and site fidelity in European Swallows, Shields (1984) found 40% of the ringed adults returned but only 2% of the juveniles were resighted. Most of the adult birds remained faithful to previously used colonies but all the nestlings recovered or resighted had dispersed. It also seems as if more European Swallow females than males dispersed which was not the case with the Cliff Swallow (Table 8).

The high degree of site tenacity in the Cliff Swallow is in sharp contrast to the common occurrence of intercolony movements in the Sand Martin (Freer 1979, Mead 1979). However, the nesting sites of the Sand Martin are not as stable as those of the Cliff Swallow although Stoner (1941) found certain individual Sand Martins even returned to the same section of the sandbank colony for several years if the colony did not deteriorate. Site tenacity undoubtedly has selective advantages in familiarizing the bird with its surroundings. This may serve well in avoiding predators, finding food and locating nesting sites (Freer 1979). In solitary breeders a factor favouring dispersal may be the avoidance of inbreeding but in colonial breeders such as the Cliff Swallow where colonies of fewer than 40 pairs are seldom found the possiblity of mating with a sibling, parents or offspring is very small. The very low return rate of first year birds to their hatching colony is probably an indication that this age group disperses more than adults as was shown to be the case for several other swallow species such as the American Cliff Swallow (Mayhew 1958), Tree Swallow (Low 1933, Chapman 1955), the European Swallow (Uchida 1932, Shields 1984) and the Sand Martin (Stoner 1941, Bergstrom 1951, Mead 1979). Young, first year birds are probably much less experienced in finding their way during migration and as individuals of different origins certainly associate on passage and in the wintering areas (Mead & Harrison 1979) it is possible that such associations lead to displacements. Mayhew (1958) found that as many as 43% of the first year birds produced in one colony go to other colonies to nest. However, these young birds emigrating nearly all nested in colonies in the vicinity of their colony of origin, which was not the case with the Cliff Swallow in the present study where no young of a certain colony were found in any of the other colonies where ringing was regularly performed. Only by ringing larger numbers of Cliff Swallows over a much wider geographical range will it be possible to elucidate the factors determining the very low return rate of first year Cliff Swallows to their colonies of origin. Mayhew (1958) found that a significantly greater number of female than male American Cliff Swallows move between colonies. There was no clearcut difference between sexes in the Cliff Swallow. However, the slightly higher number of male Cliff Swallows moving to other colonies can probably be explained by the intrasexual competition in finding nesting sites rather than by the avoiding of inbreeding in this manner.

Although some hirundines have been ringed in great numbers, very little consideration has been given to survival and mortality. Mead (1979), studying mortality in the Sand Martin, gives average mortality rates of 77% for birds in their first year and 65% annually thereafter. This is in good agreement with two other studies where mortality rates were based on capture-recapture data at Sand Martin colonies. Harwood & Harrison (1977) and Cowley (1979) found first year mortality of 80% and 77% and annual adult mortality of 60% and 58% respectively. These three studies thus yielded very similar results despite the different methods used to calculate the mortality rates. It was, however, clear that there were different mortality rates in different years. Botkin & Miller (1974) have also challenged the general assumption that adult birds have a constant mortality rate, mainly because of the large discrepancies noted between observed and expected longevity in many species. It would seem as if mortality of adult birds increases with age but it seems likely for most passerine species, which have a potential longevity of less than 25 years and a calculated mortality rate of more than 30%, that the old age-independent models are reasonably accurate. It thus seems reasonable to calculate Cliff Swallow mortality rates, for adults at least, from return rates of birds to the colonies as there is very little movement between colonies (Table 8).

CHAPTER 4

BEHAVIOUR AND VOCALIZATIONS

INTRODUCTION

There is no published description of the behaviour of the Cliff Swallow *Hirundo spilodera.* Winterbottom (1971) mentioned this species as following ploughs to obtain insects disturbed by this activity. The Cliff Swallow was also recorded as one of the swallow species which regularly visit fires so as to feed on fleeing insects or probably "smoke-bathing" (Bilby 1957). There have been a number of studies into the behaviour of several members of the Hirundinidae. Johnston & Hardy (1962) gave a descriptive account of reproductive, aggressive and group behaviour of Purple Martins *Progne subis* while Allen & Nice (1952) also described especially the behaviour associated with pair-bonding in this species.

The most complete description of the behaviour of any member of the Hirundinidae is that of Lind (1960) for the House Martin *Delichon urbica* and the description of social behaviour in nesting American Cliff Swallows *Hirundo pyrrhonota* (Emlen 1952). In the latter study, done on a close relative of *H. spilodera,* special attention was given to manifestations of positive and negative social responses and the balance of these in foraging, loafing and nesting activities.

Wing fluttering is an interesting occurrence, mainly found in the *Hirundo* genera of swallows. This behaviour was very commonly reported in the American race of *H. rustica,* only occasionally in the nominate European race and apparently never recorded in the Eastern race (Bilby 1957). Wing fluttering does not occur in the Cliff Swallow but is quite common in the American Cliff Swallow (Butler 1982) and was also recorded for the House Martin and the Purple Martin (Bilby 1957).

Most species of swallows are poor singers and the vocalizations have thus attracted little attention. Hardy (1982) however, has produced a record with the song of the Purple Martin, one of the best known hirundinid singers.

In testing the suggestion by Marler (1957) that colonial species of birds have smaller vocabularies than their noncolonial relatives, Samuel (1971a) found that where European Swallows and American Cliff Swallows occurred sympatrically, the non-colonial European Swallow had a larger repertoire than the colonial American Cliff Swallow. The vocalizations of two other swallow species have been studied in detail. Brown (1983) studied the Violet-green Swallow *Tachycineta thalassina* while Prodon (1982) recorded the vocalizations of the Redrumped Swallow *H. rufula* in France.

Although swallows are not very good songsters, they do depend to a large extent on vocalizations for recognition. The study of Beecher & Beecher (1983) suggested that in Sand Martins *Riparia riparia* sibling recognition may be a mechanism promoting location of the home burrow and that it requires a period in which the calls of siblings are learned. In other experimental work Stoddard & Beecher (1983) found that in the American Cliff Swallow the parents of chicks could locate their chicks in a colony by the signature calls of the chicks alone. Some American Cliff Swallow chicks do however also have distinctive facial markings which probably aid the parents in recognizing individuals in the nest. Brown (1983) also found that Violet-green Swallow parents could locate newly fledged young by calls alone. It thus seems as if members of the Hirundinidae rely more on calls for communication than has been realized till now.

METHODS

General observations

Observations on the general and social behaviour of the Cliff Swallow were made opportunistically but some full day observations from a hide mounted on a platform 1,2 m high set up about 8 m from the Meriba colony were also made in 1983/84. Most of the individuals at the Meriba colony were either paint-marked or colourringed and thus individually recognizable. Individual Cliff Swallows were paint-marked by applying an acetone based paint to the outer four primaries of the wing (Figure 4-1)(Samuel 1970) or to the outer two rectrices or any combination of these. Five colours were used, white, yellow, green, red and blue. Being acetone based, the paint dried very quickly and about 10 minutes after painting the swallow was ready to fly again. The individual primaries were kept apart during painting. A number of birds were also colourringed at the Meriba colony. Two colourrings on one leg in combination with a metal ring on the other leg was used. Nine colours were available: white, yellow, dark blue, light blue, green, mauve, black, red and pink.

Observations made were either written down or recorded on a small casette tape recorder and later transcribed. Zeiss 10 x 40 dialyt binoculars were used for observations.

Vocalizations

Vocalizations of the Cliff Swallow were recorded on a Uher 4000 monitor tape recorder at a speed of 19 cm/sec. The vocalizations of chicks were recorded whenever the opportunity arose. In the 1984/85 season when several chicks were hand reared the calls of these chicks were recorded at regular intervals. The recordings of adult vocalizations were made from a hide with a Canon unidirectional microphone and a parabolic reflector. The sonograms were done using a voice Identification Instrument 7000, wide-band filter and flat shaping.

FIGURE 4-1

The primaries of a *Hirundo spilodera* individual painted with a quick-drying acetone based paint for individual recognition in behavioural studies.

RESULTS

SOCIAL BEHAVIOUR

The Cliff Swallow was a highly social animal and most of its activities were performed as part of a group, except foraging, which was mostly done individually.

Sociality at nesting sites

During the greater part of the breeding season, when most pairs had chicks to feed or were incubating eggs, there was a constant flow of individuals to and from the nests. Although the actions of these birds flying to and fro were probably quite independent of each other, certain events triggered more social activity patterns. Disturbance at the colonies, such as by man, caused all individuals present to fly from the nest with many giving the alarm call. If the disturbance continued for some time e.g. when I checked the nests which took 30-45 minutes, the whole colony of birds would circle above the nests in a close group, usually rising very high until they were almost out of sight. The contact calls given by members of this flying group always attracted attention to such a group, even when they were mere specks in the sky. The alarm call mostly had the effect that the flying group moved closer together. The stimulus for this close flying was not always apparent, but it probably had some social function as it could be observed quite often, especially at the larger colonies. A small number of birds were often seen circling above the colony and when one started giving the contact call, all would join and within seconds other individuals from all sides were observed to join this group which circled higher and higher until almost out of sight.

Before breeding started in any season the birds would, after the early morning quarrels over nesting sites, leave the colonies to forage. The colony would then be deserted for up to four hours, before the contact calls of individual swallows circling almost out of sight above the colony were heard again. Individuals could then be seen joining this group from all sides, as the group descended to the colony. The group, which would now be almost the entire colony, would eventually enter the nests and after about five minutes, only single birds would be seen flying around the colony searching for an empty nest to roost. At The Willows colony where this colonial roosting was observed on five consecutive days in September 1983, the birds arrived at the nests between 11h00 and 11h30 and left only between 15h00 and 16h00 on each of the days.

Rain was also a social stimilus and apart from the bathing, it induced the birds to chase each other excitedly.

Sociality while nest building

During nestbuilding the gathering of mud and soft materials for the nest pad was a major acitivity in the colony. Mud gathering was a highly social activity and at a peak period of nestbuilding, eg. after rain, almost the whole colony would participate during such a nestbuilding spell. All the birds collecting mud at a site, would do so from a very small area along the edge of the water. A maximum of about 40 birds would be sitting at such a site at any one time, but there was always a stream of swallows collecting mud that would move to and from this site. If the mud collectors were disturbed at the site, eg. by man, they would circle around and usually go back to the same site when the danger had moved away. If the danger did not move away it would take some time before one individual would alight on another site which would be the spark for the rest of the colony to follow, and all individuals would then again start collecting mud from this newly selected site.

When a few mud gatherers were sitting on a spot, a new arrival would usually try to alight as close as possible to them, often in the middle of the group. When an individual landed on a mud gathering site too far from the middle of the group, or too far from suitable mud, the bird would walk by placing one foot in front of the other to get to a better position.

The sociality of the mud gathering acitivity was most clearly seen during the breeding season when most pairs already had young or were incubating eggs. The mud gathering at that stage of the breeding cycle was centered mainly upon nest repairs, but as soon as one bird started collecting mud, most followed suit even only to collect one or two pellets which were added to the spouts of completed nests. After about 30 minutes only the few pairs which were really repairing nests persisted in collecting mud, but most of the colony had at least collected a few pellets of mud.

The collection of material for the lining of the nest was less social, but in some cases, eg. at newly established colonies the majority of the individual could also at some stage be seen collecting lining material. The material was collected while hovering above the flowerheads of the Compositae species and by pecking bills full of the seed plumes. Large numbers of the birds, spread over a wide area, could be seen collecting plantdown in such a manner at the same time. Feathers were collected when encountered in flight, while sheep's wool was taken from the barbed wire fence where pieces were stuck. Feathers were often brought to the nest long after incubation had started and even when chicks were already present. It thus seems as if feathers are added to the nest whenever the opportunity arises, which in turn would indicate that collecting certain nestpad materials would be a social activity.

Social foraging

Although most of the Cliff Swallows foraged individually, several instances of social foraging were observed. On several occasions at the Schoongezicht colony, groups of 10-50 birds could be seen foraging as a closely knit group close to the ground. This behaviour could have been the result of a super-abundance of arthropods in a small area. However, no evidence for the greater abundance of food was found. This behaviour was interpreted as social foraging. Several such groups could be seen at any one stage in the area around the colony, with very few other swallows feeding individually. This might be a "learning" ground for newly fledged young, as the incidence of this social foraging was far more frequent after the first young had left the nest. Ground foraging by most members of a colony was also observed after three days of rain and drizzle, when large numbers of Harvester termites *Hodotermes mozambicus* were out near The Willows colony.

Social play

Several actions by groups of Cliff Swallows were interpreted as social play, but might have had some other function which was not apparent.

Early in the season, before nestbuilding started, swallows encountering objects such as feathers and leaves in the air would grab them repeatedly. An excited bird would soon attract several other individuals which would all try to get hold of the object. When such objects were on the surface of the water, such as in the quarry at Meriba, several individuals would attempt to pick up the object from the water surface. As soon as one succeeded in picking the object from the surface, all would start playing as described above.

GENERAL BEHAVIOUR

Some behavioural aspects of the Cliff Swallow were not directly associated with social behaviour or breeding behaviour. However, these behaviour patterns might have had as social or other signalling function and thus have a bearing on the daily activities of the birds.

Locomotion

(a) Aerial

The Cliff Swallow spent the major part of the daylight hours on the wing. The flight is straight and fast with continuous wing beats when e.g. carrying mud to the nest site or the wing beats are interspersed with short periods of gliding when foraging. During the characteristic hovering of the Cliff Swallow at the nest site, the wing beats are fast but shallow, and considerable manoeuvrability was attained by using the tail.

(b) Terrestrial

When on the ground such as at mud gathering sites the Cliff Swallow proceeded by walking. Walking was also the only way of terrestrial locomotion observed in the hand reared individuals.

Comfort movements

McKinney (1965) described comfort activities for the Anatidae in great detail and the terminology used here follows that author except where the terminology was not suitable for describing the comfort activities of the Cliff Swallow. Sleeping postures and bathing are also included here.

Stretching movements

Most of the observations on stretching were made on the hand reared individuals. Stretching was usually seen after the captive birds were taken from their nesting boxes and placed on the side of the box and after they have been fed. At the colonies stretching was performed at the loafing sites on telephone wires and barbed wire fences.

(i) Wing-stretch: This was the first stretch movement performed by the captive individuals. Only one wing at a time is stretched while the head is usually held low. The wing is extended slightly backwards.

(ii) Wing-and-leg-stretch: The action is very much the same as the wing-stretch except that the leg is also extended slightly backward together with the wing and the rectrices on the stretching side were fanned.

(iii) Both-wing-stretch: The wings, with the carpal joints flexed, are both extended above the back while the head is held very low. This both-wings-stretch commonly followed the wing- or wing-and-leg-stretch.

(iv) Jaw-stretch: Jaw-stretch was observed regularly in the captive Cliff Swallows and was usually accompanied by the partial closing of the eyes. This jaw-stretch movement only lasted for about one second and was probably often overlooked. Jaw-stretching was not observed to precede regurgitation as mentioned by Kemp (1976) for the *Tockus* spp. hornbills.

Scratching

Scratching in the Cliff Swallow is direct. The leg is brought up between the body and the wing to scratch the head while the head is slightly tilted towards the scratching leg.

Preening

Preening was done at two sites. The most obvious preening sites were the loafing perches on fences or telephone wires. At each of the colonies there were particular sections of these wires where the majority of the colony members would sit to loaf and preen. Why these sections of the wires were selected was not at all clear, but certain areas were so consistently used throughout the season that there must have been some reason for not using the rest of the fence for loafing as well. These loafing sites were always close to the nesting colony, except at The Willows colony where one loafing site was nearly 500 m from the bridge.

Preening was also done by individuals while loafing and hanging at the nest openings. In the heat of the day most of the individuals returned to the nests and while one of a pair was incubating or brooding the chicks, the other would hang at the nest opening, preening.

Most of the observations on preening were done on the Cliff Swallows which were hand reared and where behaviour patterns could be observed closely. Preening was first observed when the chicks were only 14 days old. The actions at this stage were still very uncoordinated and only by day 20 were the preening actions well developed.

Nibbling preening was done on all regions of the body except the head, upper neck and the abdomen. The abdomen was devoid of feathers. The remiges were preened from the ventral side of the wing and only occasionally from the dorsal side. This preening of the primaries from the ventral side of the wing gave rise to the characteristic "arch winged" posture. When preening the tail the rectrices were held to one side and slightly fanned. Preening was usually accompanied by wing and tail shaking.

Shaking movements

Two types of shaking movements were recorded for the Cliff Swallow.

(a) Wing-and-tail shake: This shake accompanied preening and always followed after the bird has preened some part of the body but especially the wings or tail and it lasted for as much as three seconds.

(b) Bumble bee shake: This shaking action of the whole body was often seen in individuals who have just left the nest after a long period in it e.g. when they leave the nest in the morning. This action was performed while on the wing. The bird appeared to "puff" its body feathers, thus resembling a bumble bee. The whole body is then shaken with a very characteristic "wirr" sound. When the whole colony leaves the nests together these shakes could be heard and seen in as many as 30% of the individuals in the flock at any one time.

Bill cleaning

Because of the "clean" way of feeding in the Cliff Swallow, and for that matter aerial feeding birds in general, there is seldom a need for bill cleaning. It was only observed in some of the hand reared individuals when fed with messy food such as grated cooked chicken egg. Only the tip of the bill was wiped. The food stuck in the gape was not removed by bill wiping but often by scratching. Mud which collected on the bill during nestbuilding often stayed on the bill for several days. There was no direct effort to remove this mud.

Bathing

Two ways of bathing were observed. The most frequent method, was by flying low over the water and then "falling" into the water with the breast before flying out of the water again to repeat the process. Several House Martins *Delichon urbica* were also seen to bath in this manner. After a few "falls" the bird would fly to a perch, usually a barbed wire fence or telephone line to preen. As soon as one individual started bathing in this way, a large number of the other colony members would follow suit and soon most of the colony members would be participating.

The second method of bathing was during rain when large numbers of the birds would perch on wires and continuously shuffle and preen their feathers. It was interesting that on 18 October 1983, seven House Martins which were perched amongst the Cliff Swallows, did not preen and shuffle and were obviously not bathing.

COURTSHIP, MATING AND AGGRESSIVE BEHAVIOUR

Judging by the number of pairs of the Cliff Swallow, which defend nests by the first few days upon arrival from their winter quarters, it seems as if the courtship and pairbonding period can be very short. The acquisition of a nest site by a male is evidently the first and most important step in forming a pairbond. As the old, existing nests were the first ones occupied in a new season, this was where the first pairs were formed. It was impossible to establish the exact sequence of events leading to the formation of a pair bond in these old nests, but a few definite actions could be seen in cases where males occupied half completed nests or sites where new nests were to be built.

At new sites where there were no existing nests, individual birds were repeatedly observed clinging to the same spot against the vertical wall of the bridge. This spot was then defended against all other birds within pecking range. A threatening, or probably luring posture was also directed towards any birds flying past the bird squatted against the wall. The squatting bird would fly off every now and again and then come back to settle on the same spot. These squatting birds, which were all found to be males in the few cases where the sex was known, were continuously harrassed by other birds which hovered close to them or even alighted on their backs. As soon as the squatting birds were stimulated enough, e.g. after rain or when most other birds in the colony were participating, they started building a mud ledge on their squatting sites (Figure 4-2). Soon after the squatters started building, pairbonds were probably formed because when about 20-50 pellets had been packed by one individual, two birds started to build at the same site. There were no definite stages in formation of the pair bond and it seemed as if it was only a case of the squatting bird tolerating the presence of the second bird, which was invariably found to be a female, at the selected nest site. Most birds who attempted to alight on or close to the squatting bird were chased away, but instead of chasing some others away, the squatted bird started quivering its wings as a bird alighted. The selected mate could be recognized by the squatter, as all other birds were still being

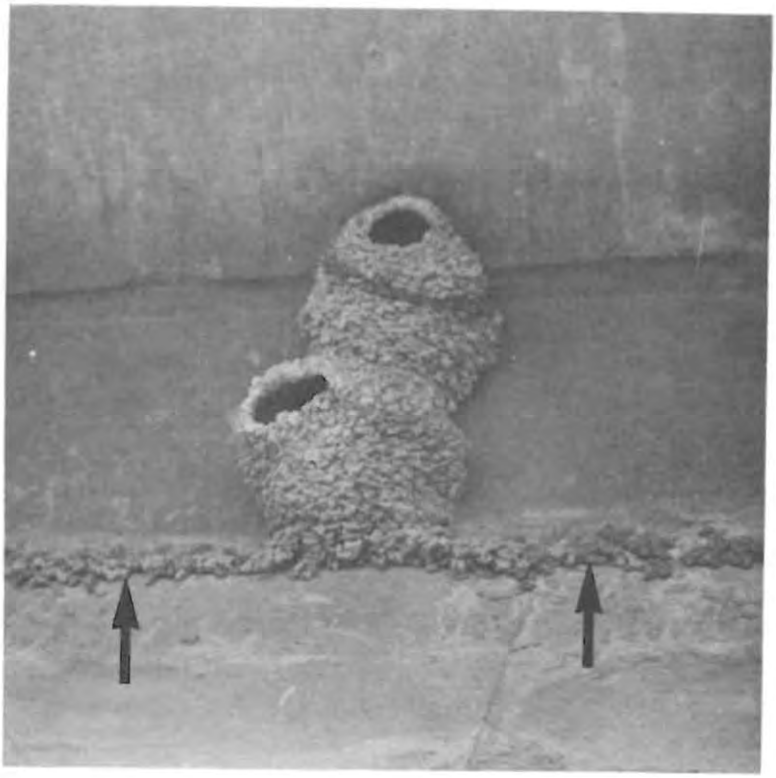


FIGURE 4-2

A ledge of mud built by *Hirundo spilodera* at the new nest site at "The Willows" colony. This ledge is used as the foundation on which nests are then built and a colony established.

FIGURE 4-3

New nests were often started on top of the spouts of other nests.

chased away from the site, but the mate was allowed to settle. It would seems as if the squatter could recognize its mate by vocalization, even at some distance, as squatters were often observed to start calling as soon as their mates approached the colony, calling.

The only easily recognizable action by unmated birds in attracting a mate, was by individuals occupying half completed nests. These individuals would sit on the half cup and sing at each swallow flying past the cup. This was done while the singing bird was crouched low, with the neck touching the rim of the half cup. Some birds flying past were obviously attracted to the singing bird as several birds, after passing the singing bird, would turn around and come to the nest of the singing bird, hovering in front of the nest. As soon as the singing bird had succeeded in attracting an individual flying past to alight on the rim of the halfcup, the singing individual would turn its tail end towards the possible mate and while still crouched, start quivering its wings. If the prospective mate did not make an attempt to get into the nest within 15-90 seconds, it was usually chased off by the nest owner and the process of attracting a mate was repeated. Once again it seems as if tolerance of the bird attracted with this luring towards the halfcup in the end leads to the formation of the pairbond. One bird would repeatedly alight on the nestcup rim of the luring bird and although it would be chased away several times it would come back, and eventually succeed in getting into the nest cup with the owner of the nest cup. When both birds sat on the nest cup they both crouched low while quivering their wings. At one nest at the Meriba colony, nestbuilding started immediately after both birds sat in their halfcup for about 15 minutes. One interesting observation, the significance of which was not known, was that when a nest owner went into a nest, a second bird, which was not its mate, would try to follow closely and also attempt to enter the nest. This was observed often and is probably either related to the tolerance of a nest owner towards a strange bird, thus determining the breeding status of the nestowner, or to conspecific parasitism. Cliff Swallows are not cooperative breeders and this behaviour could thus not be explained by cooperative behaviour theories.

No mating was ever observed in the open and the only two matings observed were in half completed nests at The Willows. As far as could be judged, matings took place in the completed nests, or at least on the nest site.

Although there is always some chasing among individuals when circling above the colony, the only really aggressive behaviour between individual Cliff Swallows was observed at the nest or as a result of earlier fights at the nests. On four occasions actual contact between birds chasing each other was observed. All of these pursuits started at the nests and when the pursuing bird caught up, the fleeing bird was grabbed on the rump. After a pairbond was established, the nest site was defended by both of the partners and it was no different from defence of the original site chosen by the squatter. The size of the territory defended was apparently determined by the reach of the bill from the nest rim. Threatening postures were adopted by one or both individuals of a pair when other swallows flew past too close, but such individuals were only attacked when they alighted within reach. As the nests were completed, neighbouring pairs were out of reach from each other as birds defended only the area which was within pecking distance from the nest opening. Defence of the nest opening could not be directed upward towards the upper rim of the nest opening and often a newly formed pair would start building a nest on top of the spout of a completed nest. (Figure 4-3).

There was no clearcut difference in the defence pattern or intensity of defence of the nest between males and females. Some males were more aggressive than others and at the Meriba colony, five of the seven physical attacks witnessed during an observation period, were made by the same bird. The threatening posture could be clearly seen to have four phases which followed each other and when threatening to the full, all the phases could be seen at once.

1. The first phase was the raising of the crown feathers when the possible intruder was sighted.
2. During the second phase, as the intruder came nearer, the bill was opened and with this open bill the bird started giving the "threat" call.
3. If the intruder alighted the defending bird would start quivering its wings, and
4. If the intruder was close enough the defending bird would peck towards it, or if it was too far away would fly towards it to chase it off.

This chain of events in defence of a nest rarely led to a physical battle between two individuals. The intruder nearly always retreated and flew away before the attacker could reach it. Of the total of 46 physical battles witnessed at the Meriba colony during the 1983/84 season, only 9 were as a result of the intruder not flying away quickly enough from the area which was defended by another bird. All the other attacks were by nest owners both male and female returning to their sites and finding an intruder there. The territory owner would in such a case, fly directly towards the intruder, striking it at the nape or head with its bill and clinging to its back with its feet. At the Meriba colony, where there was sand below the nests, both birds would then fall onto the sand. The attacker would then usually try to mate with the victim while on the surface. The intruder would continuously give an alarm call which then attracted several other swallows which would all join in the "rape" attempts. During one fight on the sand at the Meriba colony, a bird attracted to the fight was also "raped" by another "onlooker". As many as four birds would attack the fighting pair. The longest battle timed lasted nearly five minutes before the attacker flew away leaving the intruder exhausted on the sand. Although during most of these attacks there was only an attempt at mating with the attacked bird, on at least two occasions mating apparently took place, although there was no evidence of sperm transfer.

All attackers of known sex which made mating attempts were found to be males. None of the victims were sexed. As far as could be established they were unmarked birds, probably from other colonies seeking mates.

When nest owners were inside the nest and strange individuals landed at the nest entrance, they were attacked from inside the nest by pecking at their feet or head and often these intruders could be seen hanging from the nest opening while the owner would still be gripping a toe or other part of the body in its bill. When an intruder succeeded in entering a nest where the owner was inside, a fight usually followed inside the nest and after a few seconds, the intruder would be forced out of the nest often with the nest owner following closely. The longest fight inside a nest continued for more than 30 minutes before one bird flew from the nest. Birds of both sexes were often found stuck in nest openings sometimes still alive and most of these were believed to be the result of fights in the nests (see Table 11). At one nest at the Meriba colony a dead bird found stuck in a nest opening, was unringed while the female owner of the nest was still alive inside the nest.

Pairs with adjacent nests showed very little aggression towards each other, and often a whole group of territory holders would show aggression towards an intruder, and even simultaneously attack such an intruder.

The Cliff Swallow never showed any aggression towards any other bird species and even the House Sparrow *Passer domesticus* which usurped most of the nests at the Meriba colony in the 1983/84 season, was never attacked or even threatened. The House Sparrow as well as the Cape Sparrow *P. melanurus* was aggressive towards the swallows. On several occasions, when the sparrows alighted at the colonies, they tried to attack the swallows, which were much too agile and never did I see a sparrow succeeding in striking a Cliff Swallow.

The hand reared Cliff Swallows were often very aggressive towards each other especially over space. When two individuals would sit next to each other on a perch and a third individual was placed between them, both would attack this "intruder" by pecking at it. If the "intruder" was placed about 5 cm away the typical threatening posture, described earlier, whereby the feathers of the crown is raised and the bill opened, was shown.

VOCALIZATIONS

The Cliff Swallow had a relative large vocal repetoire considering that the family Hirundinidae are not good singers. Eight very distinctive calls were recognized. No song of long duration occurred which is characteristic of more solitary nesting swallows such as the European Swallow *Hirundo rustica* (Samuel 1969) or Larger Striped Swallows *H. cucullata* (Schmidt 1962).

Adult vocalizations

(a) **Chatter call** (Figure 4-4(a))

The chatter call consisted of a series of warbling notes given by several individuals simultaneously and could be heard throughout the day. This call probably served the purpose of announcing the presence of an individual at a specific site and it might thus be interpreted as a "mild" territorial song. The duration of the call sequence was about 0,4 - 0,5 s at a frequency of 1 - 6kHz.

(b) **Threat call** (Figure 4-4(b))

The threat call had very much the same structure than that of the chatter call but the warbles were in quicker succession and harsher. This was the call uttered when birds defended the nest or a site where nest building will start. This call was only given in real threat situations and usually accompanied by the raising of the crown feathers and the open bill display. (*see Coutship, Mating and Aggressive Behaviour).* The call was often repeated and each warble sequence could last up to 1,2 s at a frequency of 1-5 kHz.

(c) **Nest relief warble** (Figure 4-4(c))

This warble was given by both males and females on leaving the nest after being relieved by its mate. This was usually given on the wing but in a few cases a bird clinging to a nest entrance would give the call. The call comprised by two simultaneous warbles with one part at a frequency of 2 kHz and a higher part at 4 kHz. The warble is repeated between 5 and 10 times each having a duration of 0,4 - 0,5 s.

(d) **Low intensity alarm call** (Figure 4-4(d))

This alarm call is given by any individual first spotting danger such as the observer moving closer to the colony. It is usually a double "chick" sound each of very short duration (0,05 s) and is sometimes followed by the high intensity alarm call. The "chick" calls had a frequency of 2-3 or 3-4 kHz and comprised of two simultaneous "chick" calls probably produced by opposite sides of the birds syrinx.

(e) **High intensity alarm call** (Figure 4-4(e))

This call consisted of a single high pitched note of about 0,025 s duration and with a frequency of 4-5 kHz. This note is often, but not always, preceded and followed by another single note of similar duration but with a frequency of 3 kHz. This call is given in intense alarm situations such as when the observer stood at the colony. A flying bird would give this call and all birds in nests would respond by leaving the nests.

(f) **Distress call** (Figure 4-4(f))

The distress call was uttered by both adults and juvenile birds although juvenile distress calls were not often heard. The call comprised of two simultaneous harsh notes, one with a frequency of 3 kHz and the other higher note with a frequency of about 5,5 kHz. The call was uttered continuously by certain individuals when distressed such as when being handled during ringing operations. Each call had a duration of about 0,15 s with 0,25 s between successive calls.

(g) **Contact call** (Figure 4-4(g))

Adult and chick contact calls had the same structure indicating that the adult contact calls develop from the chick food soliciting and contact calls. Two or three contact calls were usually given in quick succession before a longer pause and a repeat of the calls. The individual calls were of short duration (0,05 s) with about 0,1 s between calls. Contact calls were individually recognizable, often even to the human ear and certain behaviour patterns indicated that breeding mates could recognize each other on calls alone. Contact calls were given at a frequency of 2-3 kHz.

Vocalizations of the young

(a) **Food soliciting call** (Figure 4-4(h))

The food soliciting call of the young Cliff Swallows exhibited gradual change throughout development. It appeared within the first 24h after hatching but was very weak at this stage. It was uttered in the early stages with a characteristic open gape held vertically upward. At about day 8-10 the call was very raspy with no musical tone to it. After the chicks were 10 days old the call started loosing its harshness and started developing into the contact call. The food soliciting call was given as single harsh notes of about 0,14 s when the chick was eight days old and at a frequency of 2-4 kHz.

(b) **Chick contact call** (Figure 4-5(a) - (d))

Although the chick contact calls all had the same structure each call was different from the next making it individually recognizable. The raspy component gradually disappeared from the calls but only in the adult contact calls were the calls free of any raspiness. This call was given both by chicks in the nest and young already on the wing. The call was probably only well developed when the chicks were 20 days and older although some chicks had well developed calls even at 15 days (Figure 4-6(d)). Eleven whole broods of 18 - 21 day-old chicks were displaced in the Schoongezicht colony for distances up to 3 m and in all cases the parent birds could find the chicks indicating that the calls were individually recognizable. Each call consisted of one or two whistle notes between 2-4 kHz with a duration of about 0,12 s. The call consisted of 3-7 of these whistles repeated in less than 1 s before a pause of a few seconds.

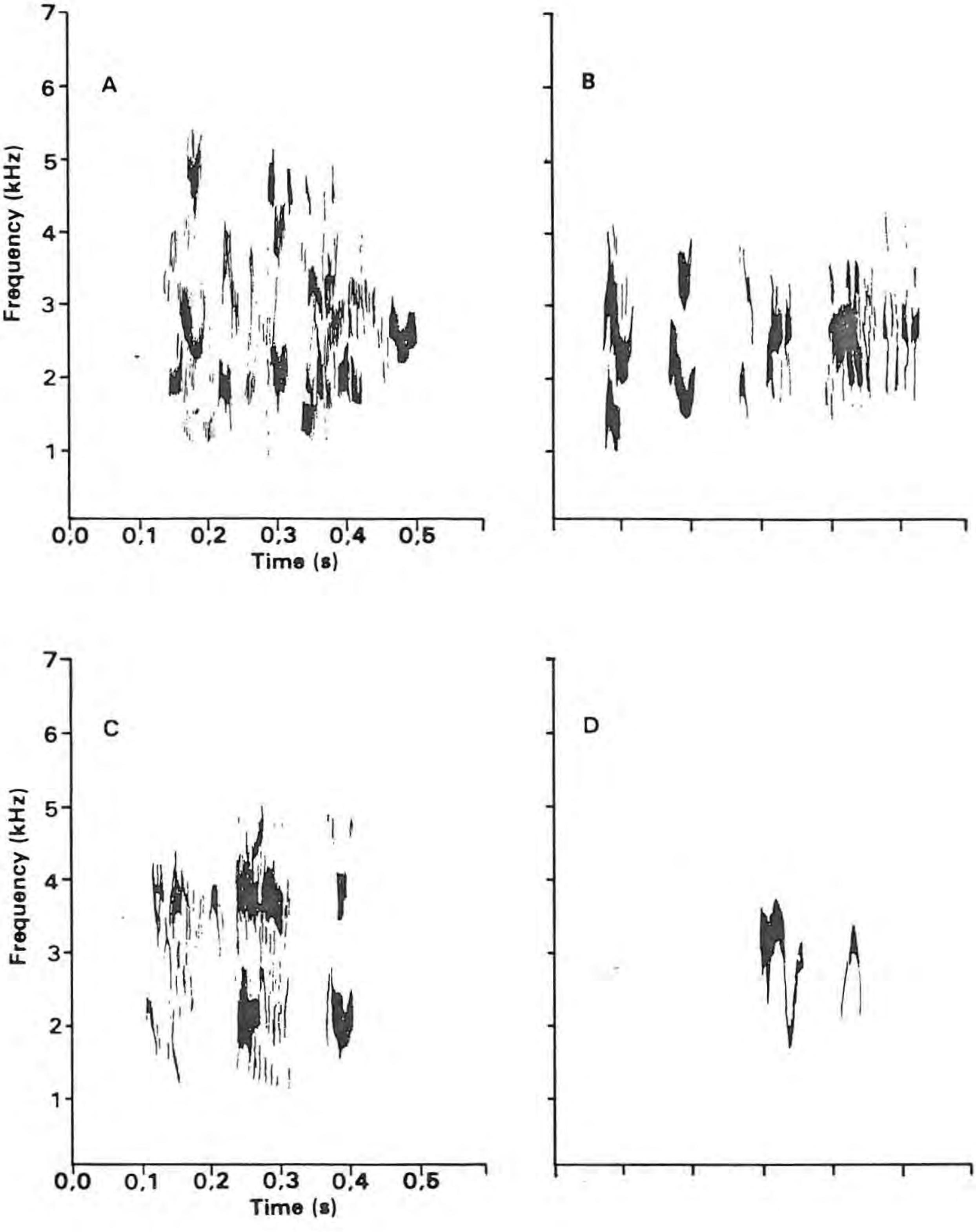


FIGURE 4-4

Vocalizations of *Hirundo spilodera* adults and chicks. (a) Chatter call, (b) Threat call, (c) Nest relief call, (d) Low intensity alarm call, (e) High intensity alarm call, (f) Distress call, (g) Adult contact call, (h) Chick food soliciting call. Pen drawings were made from sonograms.

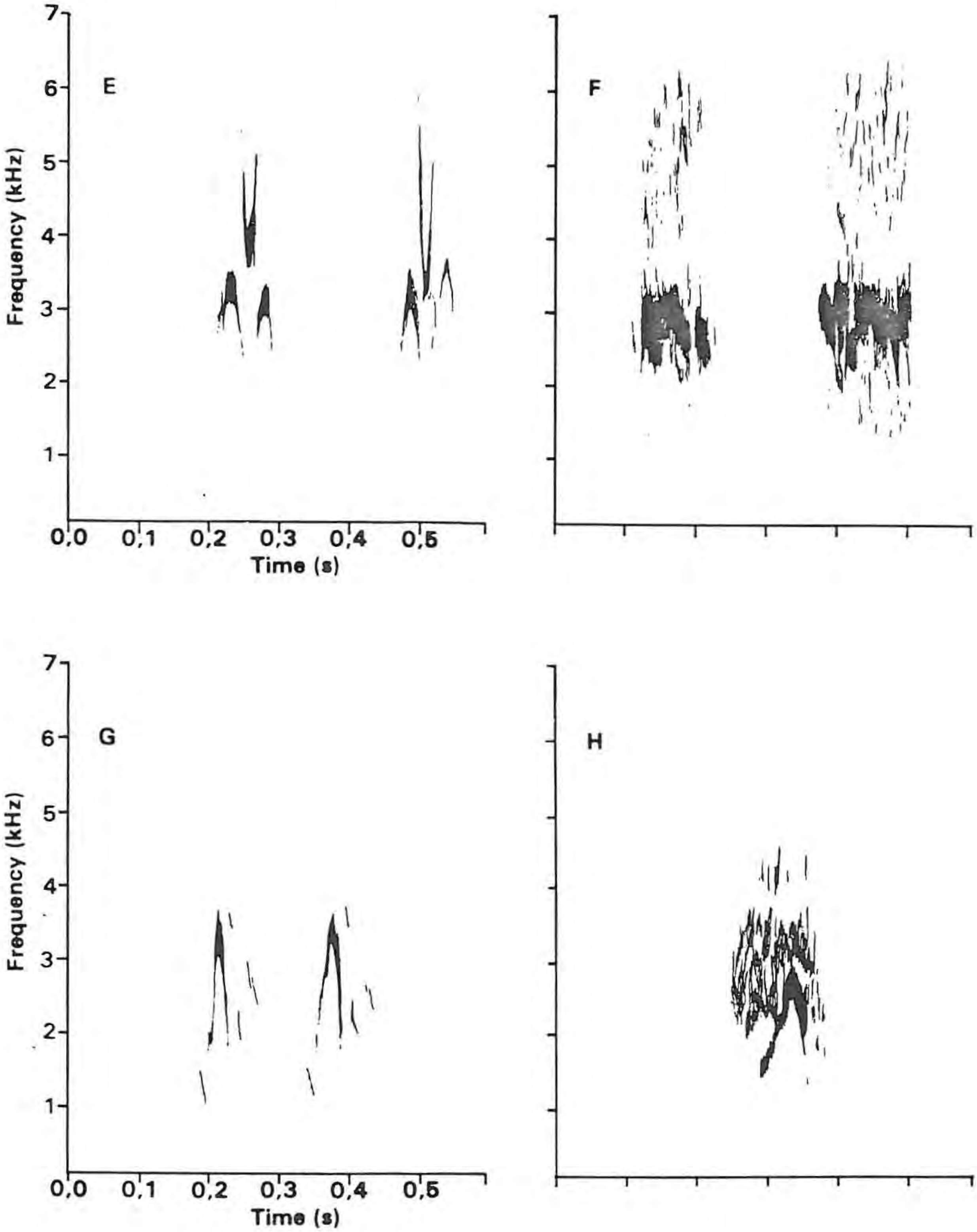


FIGURE 4-4 (Cont.)

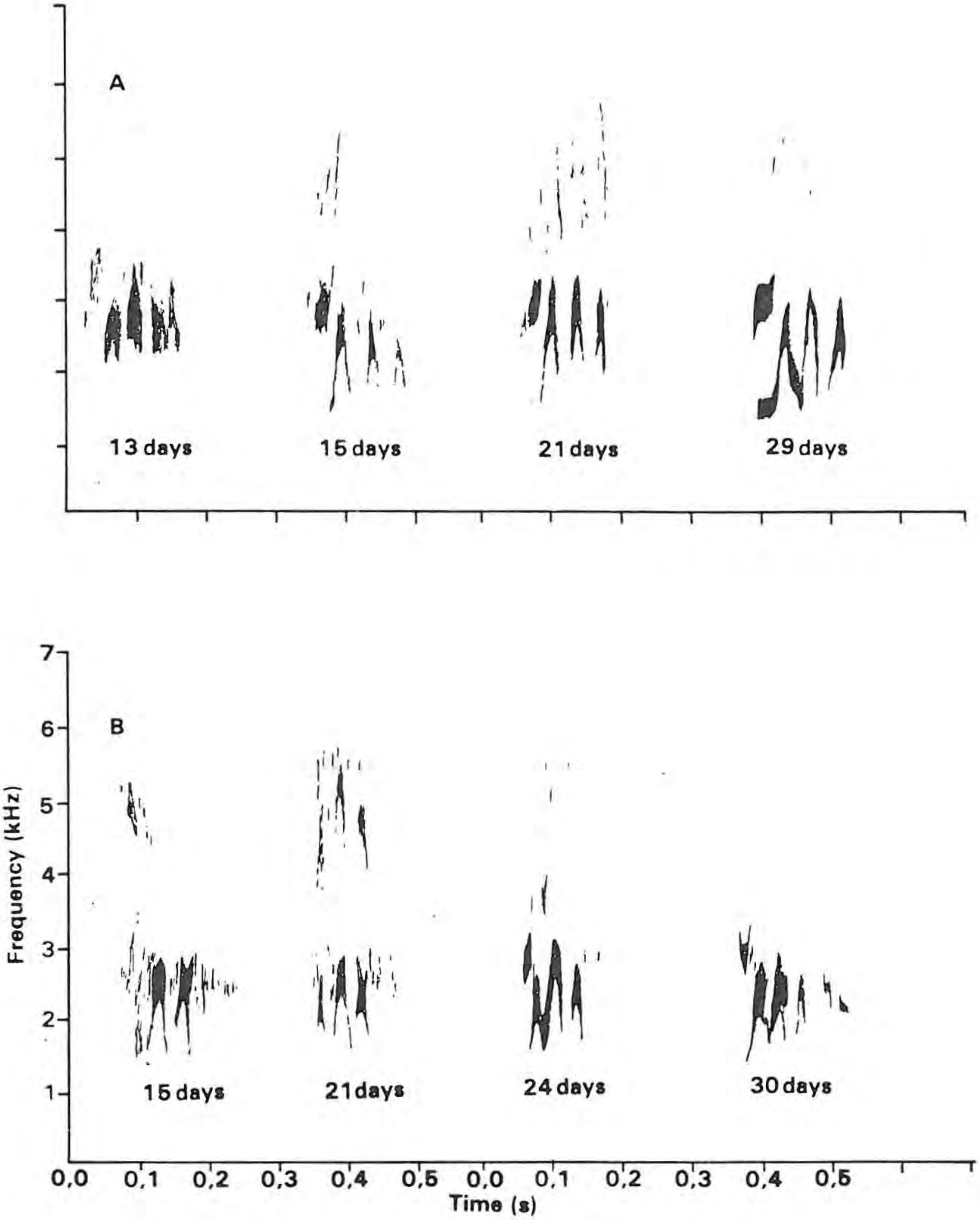


FIGURE 4-5

Development of the song of four unrelated *Hirundo spilodera* chicks. Ages of the chicks are given in days.

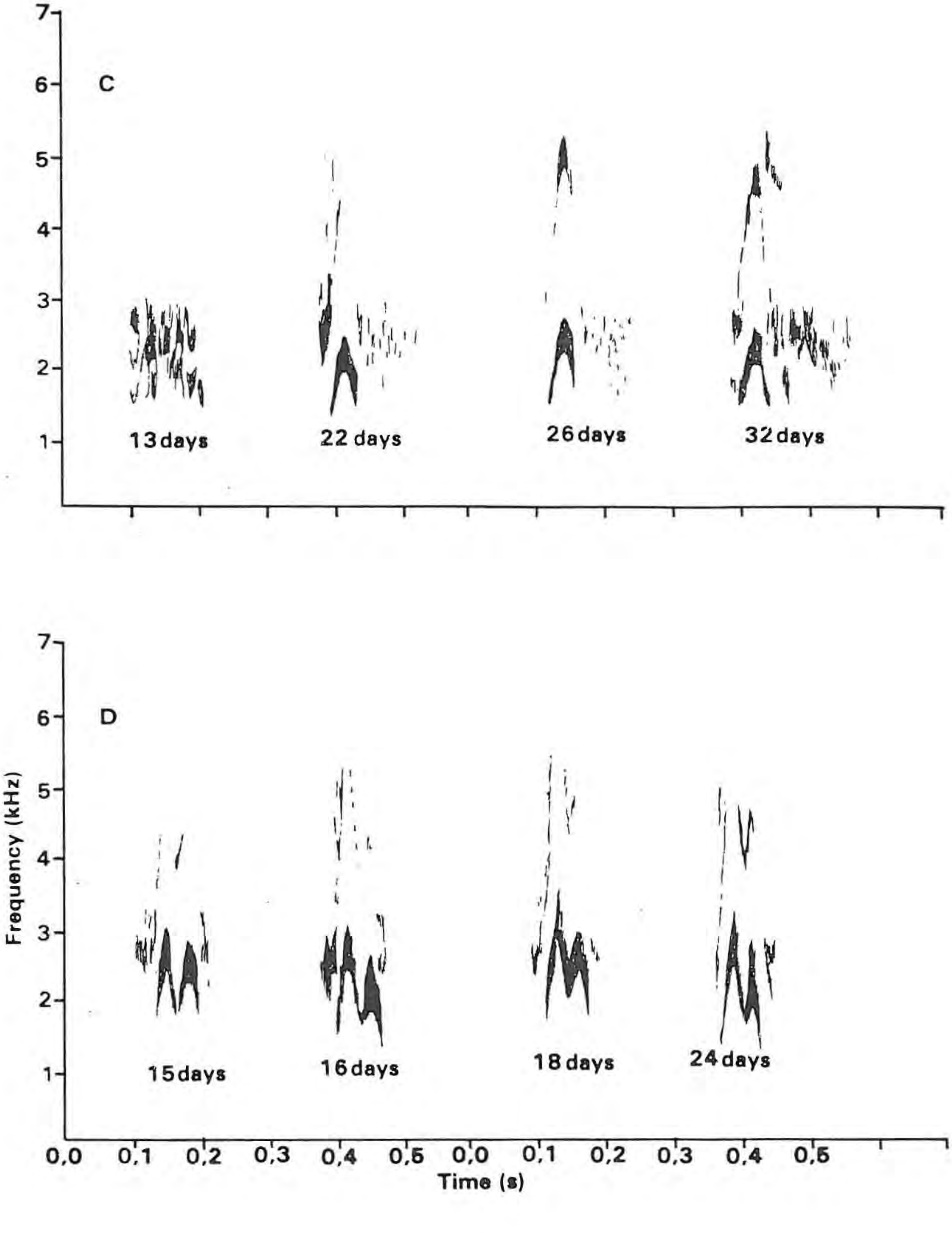


FIGURE 4-5 (Cont.)

DISCUSSION

Colonial nesting places spatial restrictions on the behavioural patterns of the Cliff Swallow. The behavioural and social patterns associated with colonial nesting probably have the same basic elements as the other non-colonial types of behaviour. These colonial types of behavioural patterns have probably evolved with the coloniality itself from the non-colonial patterns (Emlen 1952).

There is nothing in the general behaviour of this species which is unexpected for a passerine bird. The sociality has, however, probably reduced the scale of courtship in particular to a mere tolerance of another bird at the chosen nesting site. Matings also have to take place in the confined space of the nest so as to avoid the interference of other individuals. Although individual birds are sometimes very aggresive, aggression is seldom seen away from the nests indicating that aggression is directed towards maintaining the territory. The occurrence of "rapes" on individuals violating established territories is an interesting one. This seems to be the most intensive aggression ever shown.

I believe the most striking feature of the behaviour of the Cliff Swallow is the absence of territorial song and the unexpected large vocal repertoire for a colonial bird. Marler (1957), Wiley (1976) and Smith (1977) all mentioned that vocal communication may be inefficient in colonies of birds because too many signals from different individuals impinge on the receiver at any given time, creating confusion (the "cocktail party" effect). Brown (1983) suggests that directional visual displays, which can be orientated towards specific individuals, may be favoured in colonial birds. This is not the case in the Cliff Swallow with its relatively large vocal repertoire and very definite individual recognition of chick contact calls by parent birds and voice recognition by breeding partners. In the Cliff Swallow the absence of a territorial song of long duration is quite obvious as the territory is so small and must be "defended" so often that a song of long duration would serve little purpose. A threat call at the nest which was of much shorter duration has a dual function by being a territorial song as well as keeping intruders away from the nest by combining the call with threatening postures. The American Cliff Swallow *H. pyrrhonota,* which shows a number of behavioural patterns very similar to the Cliff Swallow, has a very much smaller vocal repertoire while the more solitary nesting European Swallow *H. rustica* has a larger repertoire (Samuel 1969, 1971a, Burtt 1977). It thus seems as if the American Cliff Swallow and even some solitary nesting American swallows such as the Violet-green Swallow *Tachycineta thalassina* do not rely heavily on vocal communication while the Cliff Swallow does.

With the vocal communication in the Cliff Swallow so well developed it is not surprising that voices are individually recognizable as this would aid the social organization in the colony and probably save a lot of energy by preventing misdirected aggression. The individuality of the chick contact calls assures that parental care is not misdirected. It also ensures that parents can find fledglings after they have left the nest but still need some parental care to enable the fledglings to learn and fend for themselves. This type of individual chick recognition is also a feature of the communication in both American Cliff Swallows (Stoddard & Beecher 1983) and Bank Swallows *Riparia riparia* (Beecher et al. 1981).

Although it was suggested by Stoddard & Beecher (1983) that the white facial markings of the American Cliff Swallow might also aid with the identification of chicks in addition to the voice it seems unlikely that this is very common. These authors gave the impression that all chicks had these facial markings but never actually stated the number that really had these markings. In the Cliff Swallow fewer than 25% of all chicks examined had any white markings, probably too few for facial recognition of chicks to be universal in a Cliff Swallow colony. The purpose of these markings becomes even more difficult to understand if one considers that some of the chicks return from their winter grounds for their first breeding season still with the markings around the face. Buckley & Buckley (1970, 1972) has demonstrated that the variation in the down coloration of Royal Tern *Sterna maxima* chicks is used for chick recognition and suggested that voice may also be used. Although dual modes of bird chick recognition by parents have still to be demonstrated there are some indications that this may occur even in unrelated bird species as terns and swallows. Facial patterns might not be important in the majority of Cliff Swallows in the colony but the presence of these markings does suggest some function.

CHAPTER 5

FORAGING BEHAVIOUR AND DIET

The swallows are the light cavalry of the army of birds, ever on the wing, always on the skirmish line, their wings tireless. From early dawn until night they forage the fields of air, constantly on the alert to cut off stagglers from insect camps and missing no opportunity to destroy these enemies of the farmer. (Beal 1918).

INTRODUCTION

No published data exist on the food taken by the South African Cliff Swallow *Hirundo spilodera*. Maclean (1985) states that the food consists of "aerial arthropods" but no other information is given. Only three instances of special foraging behaviour by the Cliff Swallow were recorded in the literature. Winterbottom (1971) recorded the Cliff Swallow as a bird following ploughs while Bilby (1957) lists it as one of the swallow species attracted to fires. Skead (1979) observed this species hovering above Helmeted Guineafowl *Numida meleagris* and feeding on the arthropods disturbed by these birds.

METHODS

Foraging height

The height at which the Cliff Swallow foraged was determined on four consecutive days. An aluminium pole, 6 m high was marked and set up in a favourite foraging area. The height at which the first 50 foraging birds flew past the marker was noted on each of the days. This was used to calculate the preferred foraging height of the Cliff Swallow.

The Cliff Swallow diet

The food of the Cliff Swallow was determined from stomach samples of collected birds in the 1983/84 season and from analyzing faecal samples in 1984/85. The stomach samples collected on the same day were pooled so that three or four samples were available per month. Although some stomach pump samples (Brensing 1977) were also taken in 1983/84 this was found to be more time consuming than collecting faeces and I thus opted for the latter in view of the success of this method with other hirundines (Bryant 1971, Turner 1980). However, the faecal samples taken in the 1984/85 season could not be identified in time and only the data from the 1983/84 stomach samples are considered here.

Both stomach and faecal samples were carefully checked with a dissecting microscope and all identifiable fragments of invertebrates selected and sorted into the different classes and orders for later identification by experts. Insects were identified to the most specific taxon possible which was usually family, sub-family or genus. Because the prey remains were usually very fragmentary, it was not possible to quantify the number of specimens in the different taxa of prey items, but subjective indications of the importance of the different taxa were found. The percentage occurrence of the different taxa was calculated as the number of times a specific taxon occurred in the total number of samples (25).

To measure the availability of flying insects potentially available to the Cliff Swallow a series of three suction traps (Prinsloo 1980) was used in the 1984/85 season to sample the insects. These traps were used near The Willows colony in areas where the swallows were often observed feeding. The traps were placed about 10 m apart 1,3 m above ground level and the suction fans were driven by a petrol generator. Suction traps were left in operation for four hours between 10h00 and 14h00 on the sample days. In addition to these suction trap samples which were taken three times per month, sweepnet samples were also taken on these days with a net 30 cm in diameter. Two-hundred sweeps were taken per sample, 0,5 - 1,5 m above ground level in the air above the vegetation. The suction trap samples were sorted into the different insect orders while the sweepnet samples were weighed.

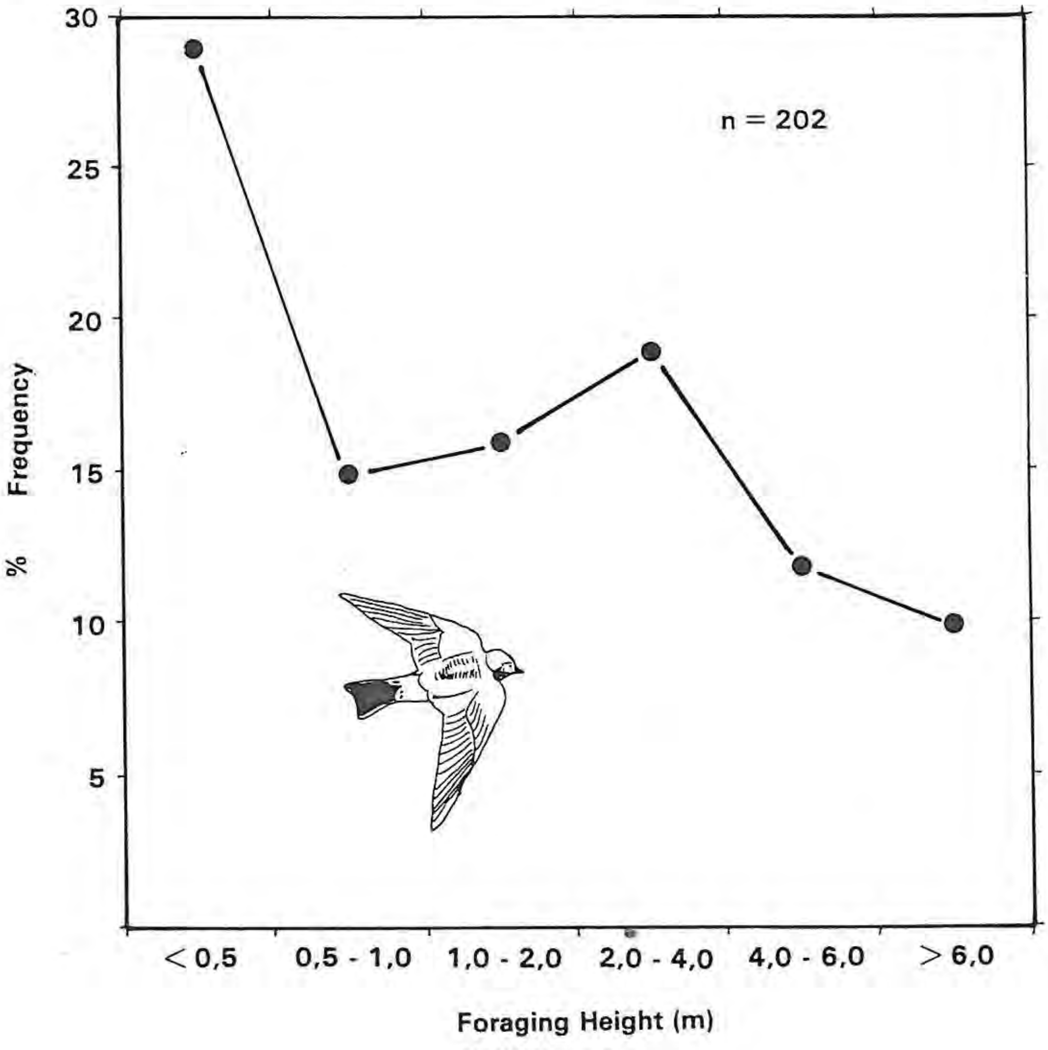


FIGURE 5-1

The foraging height of *Hirundo spilodera* individuals observed in preferred feeding habitat at "The Willows" colony.

RESULTS

FORAGING BEHAVIOUR

The Cliff Swallow is a typical aerial feeding bird which forages almost exclusively on the wing. Although the mean foraging height was 2,2 m, 44 % of foraging was done within 1 m of the ground (Figure 5-1). Foraging flight was slower and seldom in a straight line like purposeful flight e.g. when nest building. A number of special and unusual foraging methods were also observed. The most interesting is the flushing of prey from vegetation. This flushing method was used especially when moths (Lepidoptera) were numerous at certain times of the year when the karoo bushes were flowering. The swallow would hover only two or three centimetres above the selected bush and in that way disturb the moths on the bush. It would then forage above the bush for a short while probably still disturbing the insects with each fly past before selecting another bush to hover above. The wing strokes during this disturbing hover were slow with a full down swing, but shallow upswing. Large numbers of Cliff Swallows could be seen performing these disturbing flights in groups on some days.

The second unusual foraging method was picking up insects from the ground. The Cliff Swallow picked up insects from the ground in two observed situations. In November 1983 after two days of overcast weather about 300 individuals were seen foraging on the ground near The Willows colony. Large numbers of Haverster termites *Hodotermes mozambicus* were present in the area at the time. These termites were also found in the stomachs of the Cliff Swallow (Table 13). The Cliff Swallow also foraged on the ground when following ploughs to feed on the disturbed insects. Individual birds would often settle on the ploughed earth behind the plough and pick up insects from the ground. Ground-living arthropods were often found in the Cliff Swallow diet (Table 13) and ground foraging might be more common than observations would indicate. Lepidoptera larvae and spiders (Thomicidae) were also found in the diet, indicating that food was probably also taken from plants although wind-drifted spiders and air-borne Lepidopteran larvae can be common (Turner 1981).

DIET OF THE CLIFF SWALLOW

The availability of prey

The biomass of insects caught with the sweepnet was only high during November and December 1984 (Figure 5-2). Although some rain fell in the latter half of January (Figure 2-2) the biomass stayed low throughout February. The samples from the suction trap clearly show that the different insect orders had peak numbers at different times of the season (Figure 5-3). Coleoptera were probably the most reliable food source as they were available in reasonable numbers for the larger part of the seven months in which samples were taken (see also Appendix 1).

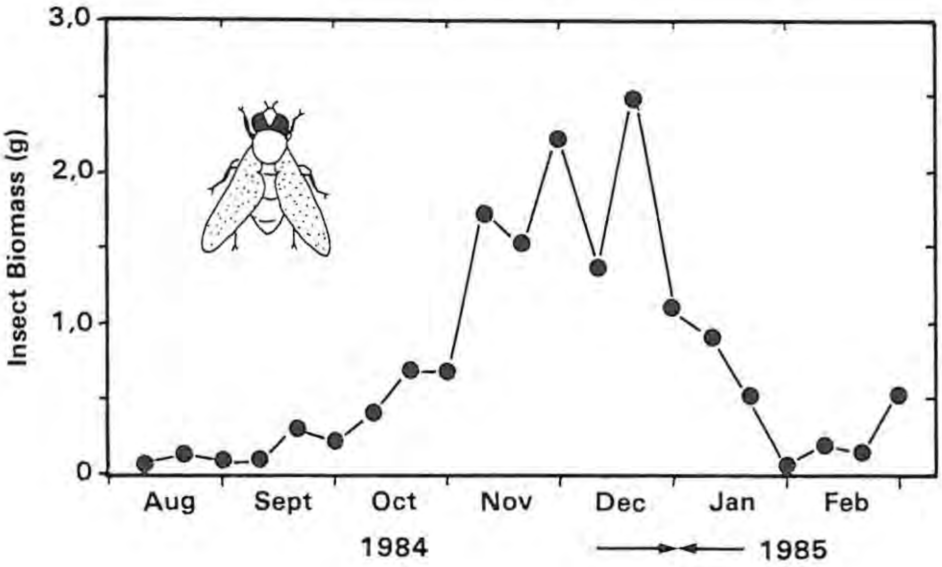


FIGURE 5-2

The biomass of insects available to *Hirundo spilodera* during the 1984/85 breeding season. Samples were taken with a sweepnet at 10-day intervals.

Diet

The presence of the different arthropod taxonomic groups found in the stomachs of collected Cliff Swallows in the 1983/84 season is given in Appendix 2 with a summary in Table 13. The Cliff Swallow preyed on a wide variety of insects with the Coleoptera, Diptera, Hymenoptera and Hemiptera the most important orders. These orders were also most commonly trapped in the suction trap (Figure 5-3). The only other insect taxon often trapped in the suction trap, the Thysanoptera, are very small (± 1 mm in length) and were seldom found in a stomach sample (Table 13). Dung beetles of the family Scarabaeidae and weevils of the family Curculionidae were the most important Coleoptera in the diet. In the Diptera the families Drosophilidae and Muscidae were by far the most important. Beetles of the family Carabidae are flightless and must have been taken on the ground or off vegetation as were the Coleoptera and Lepidoptera larvae and workers of the *Hodotermes sp.* termites. The spiders could either have been taken from vegetation or possibly while the spiders were drifting in the wind.

In 11 % of all the stomachs examined were small stones present ranging in size from 1-5 mm in diameter. Stones were found in both males and females and even in the stomachs of chicks. The captive chicks which were reared to study certain behavioural aspects were often fed impurities such as sand and pieces of grass together with insects, and this debris was cast out in the form of pellets.

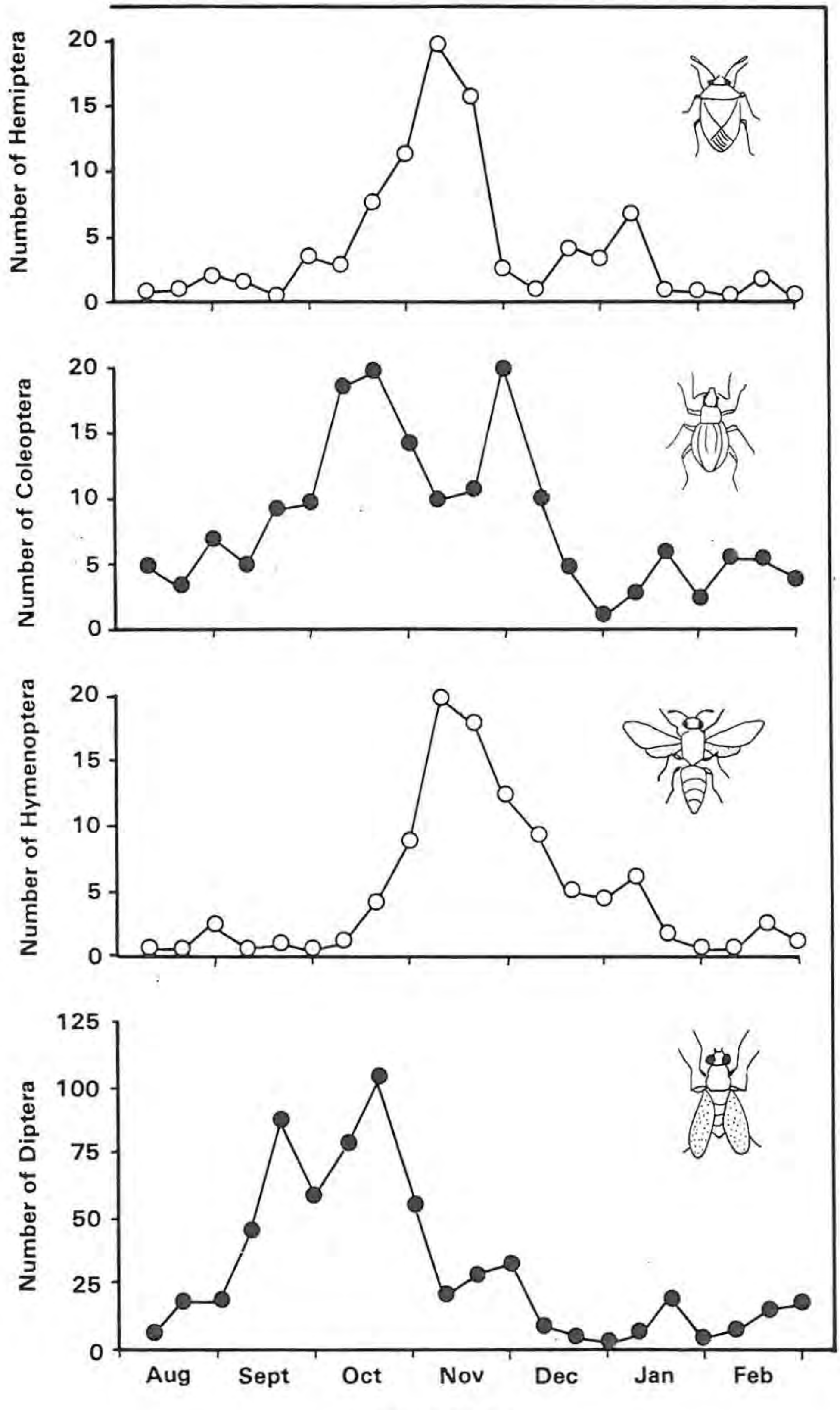


FIGURE 5-3

The number of insects of different orders available to *Hirundo spilodera* during the 1984/85 breeding season. Samples were taken from suction traps set up at "The Willows" colony at 10-day intervals. Sampling effort was identical during each sampling period. See also Appendix 1.

TABLE 13

IMPORTANCE INDEX* OF PREY TAXA IN THE *HIRUNDO SPILODERA* DIET. THE 21 MOST COMMONLY OCCURRING ITEMS ARE GIVEN.

Taxon	Index*	Taxon	Index*
Muscidae	2626	*Camponotus maculatus*	659
Onthophagus spp	2428	Chalcidoidea	622
Ichneumonoidea	1296	Cicadidae	557
Halicitidae	1152	Drosophilidae	540
Lygaeidae	1000	Erirhininae	450
Barinae	998	Pentatomidae	408
Hodotemes mozambicus	720	Aphodinidae	400
Scarabaeus sp	680	Staphylinidae	350
Adonia variagata	660	*Phalops* spp	338
Microlarinus sp	630	Anthilidae	336
		Dermestes maculatus	306

*Index taken as % occurrence multiplied by body length and number of months occurring.

DISCUSSION

Four methods are commonly used to determine the diet of swallows. Moody (1970) flushed the digestive tract of European Swallows *Hirundo rustica* and American Cliff Swallows *H. pyrrhonota* with a saline solution, thus taking samples from birds without having to destroy them. Beal (1918), Johnston (1967) and Hespenheide (1975) all examined the stomach contents of collected swallow specimens for the identification of prey items. Beal (1918) examined seven North American swallow species in this manner, Johnston (1967) the Purple Martin *Progne subis* and Hespenheide (1975) the Rough-winged Swallow *Stelgidopteryx ruficollis.* Most of the recent diet studies on swallows were done either by analyzing faecal samples (Bryant 1973, Waugh 1979, Turner 1983) or by the neckring method (Schulze-Hagen 1970, Kozená 1979) whereby a ring is placed around the neck of swallow chicks in the nest, which prevents them from swallowing the food bolus which the adults feed them. These boluses can then be taken and examined (von Gunten 1961, Schulze-Hagen 1970, Kozená 1979, Turner 1981, 1983).

In determining the prey taken by swallows there are certain shortcomings in each of the methods. Results based on analysis of stomach contents have inherent errors. The rate at which different food items digest cannot be compensated for, so that numbers of hard items in the stomach are likely to be higher than numbers of soft items. In the case of swallows, insect orders such as the Coleoptera, having a hard exoskeleton, would still be identifiable for quite some time after ingestion while the Diptera would not. Furthermore, the identification of the food items in the stomach tends to be superficial as the food is often highly fragmented and identification can rarely be done in a quantitative way below the subfamily level. However, most authors have only used the family level (e.g. Johnston 1967, Waugh 1979, Turner 1983). This superficial identification tends to make the different swallow species appear closer in their diet to one another than they really are, or tends to make it difficult to detect seasonal differences in diet of individual species.

Determining the diet from prey remains found in faeces has very much the same shortcomings as stomach contents samples. However, this has the advantage that samples can be taken without sacrificing or even disturbing the study animals, which is especially important when one works with a small population, or where other biological data such as breeding data are also gathered.

Although Hartley (1948) discussed possible sources of error when faecal analysis is used as a qualitative and quantitative method of diet analysis, it seems to be the most commonly used method for swallows and surely the least disturbing. It was also shown by Waugh & Hails (1983) that the analysis of faecal material provides a good method of dietary analysis for aerial-feeding birds.

The third sample method of swallow prey is by taking food boluses from neckringed chicks in the nest. This method probably has fewer shortcomings than any of the other methods, provided the chicks which are neckringed are not so small that the feeding adults might select smaller than usual prey. However, there are numerous difficulties. This method can only be used when the birds are breeding and can thus not give a continuous sample in most cases. It is also very difficult to use this method on species which do not breed in open, cup-shaped nests. When nests of swallow species breeding in closed nests are damaged to get at the chicks and apply the neckring, the adults usually spend most of the time repairing the nest and not feeding the chicks, which was the case with the Cliff Swallow.

To date there has been no detailed information on the diets of southern African Hirundinidae or any swallow species breeding regularly in the Afrotropical region. The diets and foraging ecologies of several species of the Hirundinidae breeding in the Holarctic region have been reasonably well studied. Beal (1918) and Stoner (1936) studied the diet of the Sand Martin (Bank Swallow) *Riparia riparia* in North America and Waugh (1979) provided a comparative dietary analysis for a population within Britain. Waugh (1979) also had data on the availability of prey and could thus get some idea of prey selection by this species. The diet of the House Martin *Delichon urbica* was the subject of some investigations in Germany (Von Gunten 1961, Von Gunten & Schwarzenbach 1962) and in Britain (Bryant 1973). The insect prey types taken by the European Swallow have been the subject of several investigations. Thomas (1933-39) supplied piecemeal information on this species' diet, while Schulze-Hagen (1970) and Kozená (1979) both studied the qualitative composition of the diet of *H. rustica* chicks.

The only American swallow species for which the diet was studied in some detail recently were the Purple Martin *Progne subis* (Johnston 1967) and the Blue-and-White Swallow *Notiochelidon cyanoleuca* in Venezuela (Turner 1983). Beal (1918) identified the insect remains from seven species of North American swallows but did not give any indication of seasonal differences, although the percentage occurrence of each food type is given.

To study the feeding ecology of a bird species, one needs to consider foraging behaviour, energetics, prey taken, and the availability of prey. The difficulties encountered in sampling flying insects and other arthropods in the air made it almost impossible in most of the earlier studies on the diet of swallows to compare the available prey to the diet of a particular species. This was overcome to a large extent when Bryant (1973) started using an aerofoil insect suction trap (Johnson 1950, Taylor 1962) for this purpose. This type of insect suction trap has been used in several studies since (Waugh 1979, Turner 1982). For swallow species foraging regularly within about 2 m from the ground, insect sweepnet samples can also be used (Johnston 1967, Turner 1982, 1983). An insect net held out of an open window or mounted on top of a vehicle roof was also used with great success for determining available prey for swallows (Johnston 1967, Hespenheide 1975).

Although the suction trap samples collected during this study probably gave a good indication of what flying insects were generally available to the Cliff Swallows, it underestimated the availability of poor or reluctant fliers such as the Hemiptera. These insects most commonly only flew for short distances between plants and close to the ground, as the vegetation is short karoo bushes. The bugs were surely available to the Cliff Swallows as nearly 30 % of foraging is done less than 0,5 m from the ground (Figure 5-1). However, the suction traps sampled only at 1,3 m, which is higher than the bugs tend to fly. The beetles and especially dung beetles, Scarabaeidae, are probably also underrepresented in the suction trap samples as they tend to fly at dawn and dusk when no sampling was done. The ideal would thus be to sample continuously and at different heights. This was not possible in this study because of the portable generator used which only ran for five hours before it needed refilling. It is clear that the samples from the stomachs and the suction traps are not directly comparable in indicating prey selection, for instance. However, the suction traps trapped large numbers of very small insects such as Thysanoptera and aphids, which were rarely found in Cliff Swallow stomachs (Table 13). Hespenheide (1971, 1975) described the food preferences of a number of insectivorous birds, including several of the family Hirundinidae. He concluded that the average prey size of prey taken is usually larger than that available. This seems to be the case with the Cliff Swallow as well. However, Turner (1982) found that it is profitable in terms of net energy gain for the European Swallow to take a mixture of large and small items, whereas optimal foraging theory would predict exclusive specialization on large items.

To get some measure of the energy provided by a certain food item the ideal would be to measure the ash-free weight of the arthropod specimen. As most of the prey items of swallows are winged, winglength can be used to facilitate rapid grouping of insects into different size classes both in sampled insects from traps and from faecal, stomach or neckringed chick samples. As dry weight is a better indication of the calories that an insect can provide than just its size, which can be determined by winglength (Lewis & Taylor 1967), Turner (1982) obtained formulae relating winglength to the dry weight of insect specimens of different taxa. Most of the Cliff Swallow stomach samples were highly fragmented and it was not possible to measure winglengths of all prey items and no attempt was thus made to calculate the dry weight of the Cliff Swallow prey.

Unusual prey items or foraging methods were reported often, such as European Swallows taking lepidopteran larvae (Brooke 1956, Turner 1981) or swallow species foraging on the ground (Bent 1942; p. 450, *H. rustica*, Weber 1980; *H. rustica, H. pyrrhonata,* and *R. riparia*) or following ploughs (Winterbottom 1971). Some insect taxa which are not permanent components of the aeroplankton are frequently found as prey items of certain swallow species. Kozená (1979) thus hypothesized that European Swallows often preys on insects which it flushes itself. Cliff Swallows often flush insects from vegetation so that one would expect poor flying insects such as bugs in the diet, which is the case (Table 13). The Cliff Swallow probably feeds on the ground often, and the variety of terrestrial insects and spiders taken is a sure indication of this.

The casting of pellets by swallows has not been reported previously although a number of species probably do so. Ingestion of stones or grit by several species of swallow is common. Beal (1918) found the American Cliff Swallow and the Bank Swallow *Riparia riparia* ingested stones while Brown (1976) recorded Purple Martins *Progne subis* picking up grit material and Barrentine (1980) documented and discussed grit selection among nesting European Swallows. Grit material probably facilitates the mechanical digestion of the hard exoskeletons of insects and that may be why stones were found in the stomachs of both adult and young and not just adults for which it might be a source of essential soluble minerals (Hill 1971).

CHAPTER 6

PREDATORS, PARASITES AND SYMBIONTS

INTRODUCTION

Because of the paucity of information on the general biology of the Cliff Swallow *Hirundo spilodera*, published records of predators, parasites and symbionts are few. No records of predators could be found but Maclean (1985) mentions several bird species using Cliff Swallow nests as roosts or for breeding purposes. The host-specific tick *Ornithodoros peringueyi* was described by Bedford & Hewitt (1925) from the nests of Cliff Swallows, while Zumpt (1966) and Milstein (1975) both found the blood-sucking fly *Ornithomya inocellata* on Cliff Swallows. Other ectoparasites recorded for the Cliff Swallow were the species-specific flea *Xenopsylla trispinis* (Zumpt 1966), a louse, *Myrsidea rustica* (Ledger 1980) found on several other passerine bird species and a mite, *Ornithomyssus bursa* (Burgerjon 1964). Dense, reliable populations of hosts such as at Cliff Swallow colonies offer excellent conditions for large numbers of parasites, as the difficult task of finding a host is virtually eliminated (Rothschild & Clay 1952). One would thus expect a high degree of host-specificity, and that the parasites would be adapted to remain in the swallow nests in winter.

METHODS

An attempt was made to collect ectoparasites from Cliff Swallows quantitively but as very few parasites were collected with the method of Fowler & Cohen (1983), it was abandoned after a few trials. Observations of symbionts and predators were made when incidents were noted.

RESULTS

PREDATORS

Cliff Swallows are apparently preyed on by relatively few species of animals, although the rate of predation especially at the nest can be high. For convenience the predators can be divided into:

(a) predators away from the nest; and
(b) nest predators.

Predators away from the nest

There is probably no predator able to take a healthy Cliff Swallow as prey. However, wing remains of adult swallows were seen from time to time. These were all found near the colonies and they were probably handicapped in some or other way. Live, injured birds, unable to fly, were found at two different colonies in September 1983. These birds probably hit telephone wires which ran very close to the bridge under which they were nesting. Two had broken wings while the third had a swollen and bloody left pectoralis major muscle. These helpless birds on the ground were probably easy prey for the Yellow mongoose *Cynictis penicillata* which was always in attendance below the colonies. The large numbers of eggs and chicks which fall from the nests (See Chapter 7) are preyed on by Yellow Mongooses which patrol the area below the nests at frequent intervals when there is little or no water below the nests. Clearing areas under the colony so that fresh tracks of mongooses could be noticed showed that as many as five visits per day were made to the colony by a mongoose. At some of the colonies such as The Willows and Driekloof where large populations of red ants *Techmomyremex albipes* and *Acantholepis capensis* were present, the fallen chicks were immediately attacked and killed by the ants (Figure 6-1). In September 1984 a Blackheaded Heron *Ardea melanocephala* was seen eating fallen chicks from the area below the Driekloof colony. This was probably a chance "finding" by the heron and this species was seen only once in the 1984/85 season at the Schoongezicht colony. At most of the larger colonies one or two Steppe Buzzards *Buteo buteo* were often perched near the colony, probably on the lookout for such helpless, injured swallows. Only once was one of the buzzards seen eating a bird while perched near the Schoongezicht colony but the identity of the bird was not known.

The regularity with which the buzzards were found would probably indicate that they were feeding actively from the colony.

In the 1984/85 season a fresh owl pellet found at the Driekloof colony consisted entirely of Cliff Swallow remains. The identity of the owl could of course not be determined, but it was almost certainly a Spotted Eagle Owl *Bubo africanus* which is common in the area.

The only other avian predator ever seen eating an adult Cliff Swallow was the Fiscal Shrike *Lanius collaris*. A half-eaten adult swallow was noticed hanging from a thorn of the Soetdoring *Acacia karroo* near the colony at The Willows on 12 September 1983. It was taken down, examined and placed on the ground next to the tree. Moments later a male Fiscal Shrike flew down from a nearby tree, picked the corpse up, and pinned it to the same thorn as before. When the corpse was again taken down, the shrike picked it up for a second time and flew to another tree where it proceeded to eat it. On 9 September 1983 a half-eaten swallow was also found below the same tree. It is highly unlikely that the shrike had caught the swallow but is was probably an injured bird which was killed by the shrike.

Nest predators

Due to the location of the nests in colonies, usually over water or very high up, there are few

FIGURE 6-1

Red ants attacking *Hirundo spilodera* chicks which have fallen on the ground from nests.

predators on the nest contents. A monitor lizard *Varanus niloticus* robbed several Cliff Swallow nests of its contents by climbing up a rough concrete wall of a bridge to the colony which was only 1,5 m above the small stream at a small colony about 80 km east of Bloemfontein (N.J. Grobler pers. comm.). The main threat at the nest is the two red ant species which attacks the chicks in the nest as was the case at The Willows in the 1983/84 season. No young reached the fledgling stage and breeding at this colony was abandoned in December when a new colony was established under a newer bridge just 50 m way. The only other serious threat is man. At the more accessible colonies the nests were often knocked down for no apparent reason, but sometimes the chicks were taken. However, the Leeukop colony was very accessible to man and the "B" part of the colony was totally destroyed by people in November 1983 after which the colony was abandoned. In late October 1984 all 148 nests monitored in the "A" part of this colony were again knocked down and the chicks taken for food.

Both the House Sparrow *Passer domesticus* and the Cape Sparrow *P. melanurus* were seen removing eggs from the nests of the Cliff Swallow before taking over the nest for breeding. These incidences of egg removal were observed only at the Meriba colony where there was a shortage of nests.

PARASITES

The different parasites of the Cliff Swallow did not occur in equal proportions at the different study colonies (Table 14). The very old colonies such as Driekloof and Schoongezicht were heavily infested with ticks, with smaller numbers of louse fly and fleas. Leeukop on the other hand was a new colony started only in late October 1983 and was virtually free of ticks, but large numbers of fleas and louse flies occurred here. A parasitic mite was also found at the Leeukop colony in 1983/84 and at Driekloof in 1984/85. Some biological information on the parasites was gathered in a bid to study the effect that these parasites might have on the breeding of the Cliff Swallow.

The Cliff Swallow Louse Fly *Ornithomya inocellata*

The only ectoparasites found regularly on the body of the adult Cliff Swallow is the Cliff Swallow Louse Fly *Ornithomya inocellata*. This is a host-specific parasite which has to live close to the body warmth of its host to be active. Each individual swallow usually only had one of these parasites and seldom more than two. However, at the Ou Hoogte colony as many as four louse flies were found on most of the swallows trapped and handled on 26 September 1984. These louse flies flew and moved sluggishly when away from the body of their host. During night mass-trapping operations of swallows, large numbers of the flies would leave the birds and would usually then die within a few hours of leaving the host. These parasites were also frequently seen inside nests, especially at the Leeukop colony.

When inspecting nests containing eggs these flies were usually seen on the eggs probably because the incubated eggs had a higher temperature which was certainly closer to the optimum temperature required by this louse fly to be active. In a sample of three nests taken down at the Leeukop colony the nests contained ten, seven and four adult flies respectively. Pupae of this louse fly were also found in these three nests, always near the upper interior where they are probably out of reach of the swallows.

At The Willows colony where the red ants preyed on these flies in the swallow nests especially in the 1983/84 season, the birds were almost completely free of the louse fly. These flies were never found at the colonies during winter when the Cliff Swallows were not present. However, overwintering pupae were found in the nests during the winter. *O. inocellata* were only found on adult Cliff Swallows and although no indication was found that chicks in the nest were parasitized, it is very likely that they were. The swollen and bloody feet of some swallows were probably the result of bites from these flies.

TABLE 14

NUMBER OF PARASITES IN SINGLE NESTS OF *HIRUNDO SPILODERA* FROM DIFFERENT COLONIES. ALL NESTS WERE COLLECTED ON 1 NOVEMBER 1984.

	Ornithodoros peringueyi (Tick)			*Xenopsylla trispinis* (Flea)	*Ornithomya inocellata* (Louse fly)	
Colony & Nest	**Eggs**	**Nymphs**	**Adults**	**Adults**	**Pupae**	**Adults**
Ouhoogte 1	0	57	151	5	2	7
Ouhoogte 2	33	64	110	2	1	2
The Willows 3	6	128	190	0	0	0
The Willows 4	168	453	481	0	0	2
Schoongezicht 5	76	264	177	0	1	1
Schoongezicht 6	1	263	107	1	0	0
Leeukop 7	0	0	2	46	4	7

The Cliff Swallow Flea *Xenopsylla trispinis*

This flea is also a host-specific parasite occurring in the nest of the Cliff Swallow parasitizing probably both adult swallows and chicks in the nest. These fleas were never found on the body of adult swallows handled during ringing operations. Because of their small size (about 1 mm in length) they might have been overlooked, but they were definitely not numerous on free-flying birds. These fleas were most commonly found amongst the nestpad material in the nest. In October 1984 three nests from the Leeukop colony were taken down and examined for these fleas. The nests all had eggs and harboured 45, 36 and 29 fleas respectively. *X. trispinis* were also found, in nests during the winter months when the Cliff Swallows were not present. Three nests examined during the 1983 winter contained 21, 11 and two live fleas on 10 May 1983, about one month after the Cliff Swallows had departed for their nonbreeding grounds.

The Cliff Swallow Tick *Ornithodoros (Proknekalia) peringueyi* (Figure 6-2)

The third host-specific parasite of the Cliff Swallow is the argasid tick *Ornithodoros (Proknekalia) peringueyi*. This tick is a nest parasite and was never found on any free-flying adult swallow. Although adult birds are attacked at night, the chicks in the nest were probably the main victims. Adults were bitten mainly on the abdomen and to a lesser extent on the breast. Spots where the ticks had recently fed could clearly be seen as bloody areas up to 5 mm in diameter. Chicks taken from nests for examination very often also showed these bloody feeding spots on the abdomen. Cliff Swallow chicks were however most commonly attacked by larvae nymphs of this tick. In all nests taken down at the end of the 1983/84 breeding season at the Schoongezicht and Driekloof colonies, tick eggs were found below the nest pad, attached to the mud of the nest. These eggs were probably dormant during the winter months and only hatched when the nest was once again occupied the following season.

On 1 November 1983 ten nests were selected at the Driekloof colony. Five of these were new nests started and completed in that season and five were nests which had been used at least once before in the previous season. A total of 11 chicks were taken from the new nests and nine from the old nests and examined for ticks. The chicks were all 7-15 days old. The chicks from the old nests had a mean number of 94 (range 46-144) tick larvae nymphs on them. These larvae and nymphs were mostly attached to the skin between the gape and the eye, but also in front of the eye and on the forehead. Very few nymphs were found elsewhere on the bodyand only one adult tick was found on the lower abdomen of one of the chicks. All 11 chicks from the new nests were completely free of *Ornithodoros* larvae and nymphs and only two adult ticks were found, one each on the abdomen of two nest mates. At the Leeukop A & B colonies no ticks were found during the 1983/84 season. The colonies were started in October 1983 and because the ticks are nest parasites, it would probably take at least a few seasons for enough ticks to reach such a new colony, as there is very little intercolony movement by the swallows which can be the "chance" carriers of the ticks to new colonies. Only two adult ticks were found at these Leeukop colonies after a thorough search in October 1984. All chicks at this colony were completely free of *Ornithodoros* larvae and

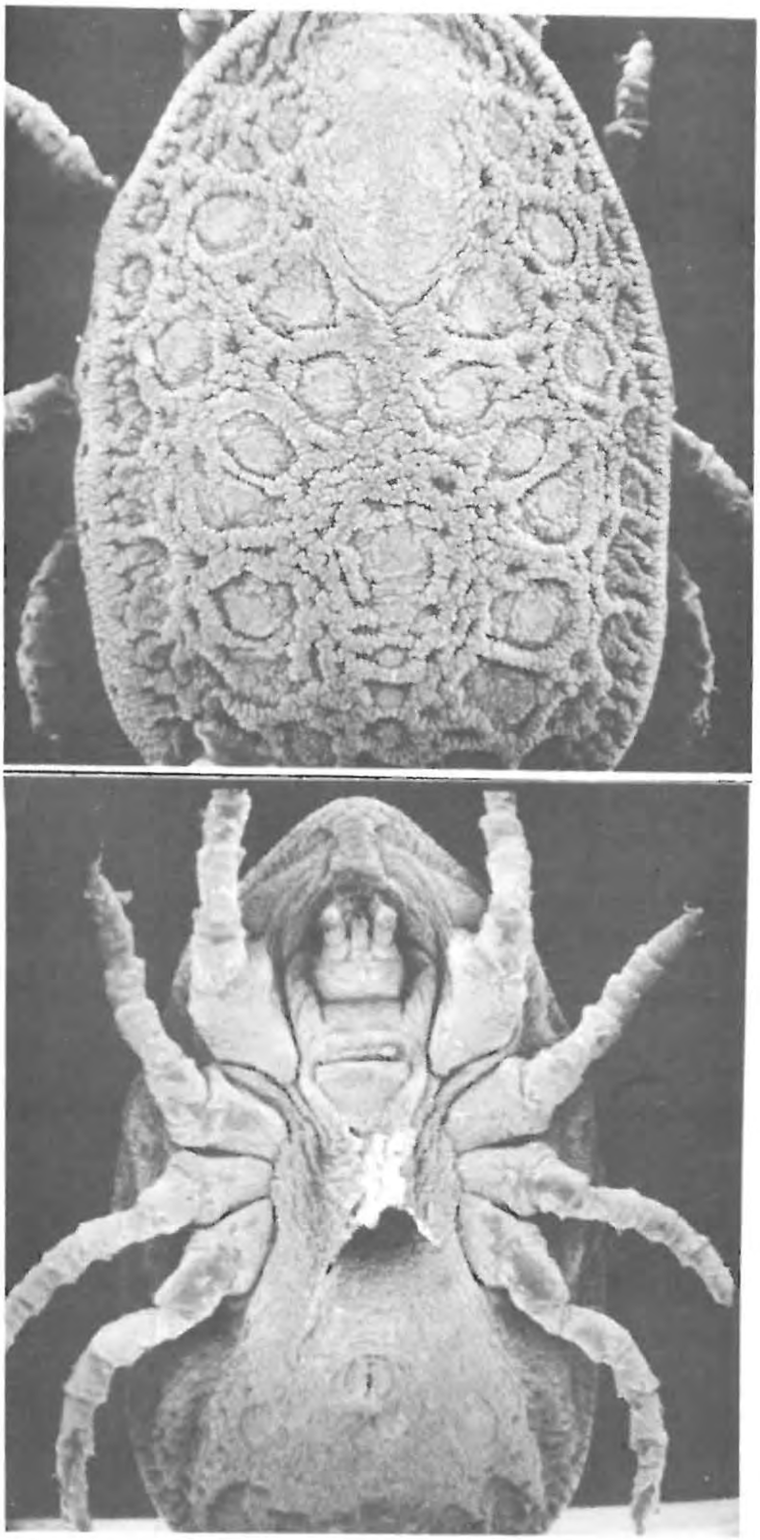


FIGURE 6-2

Scanning Electron Microscope photo of a female *Ornithodoros peringueyi* in a dorsal and ventral view.

nymphs indicating that no tick eggs were present in the nests. Although this tick is a nest parasite, nymphs are sometimes still found on newly fledged young. In a sample of 31 newly fledged young, judged to be out of the nest for less than two weeks, only two had seven and five *Ornithodoros* nymphs respectively still attached at the gape. When not feeding the ticks could be seen usually in large numbers near the top of the nests in the small crevices which result from building the nest with pellets. At the Driekloof colony masses of ticks were found below the nests under rocks.

Other body and nest parasites

Twice nymphs of *Hyalomma sp.* ticks were found on the heads of adult swallows. The adults of these ticks are usually parasites on large mammals but the nymphs are sometimes found on terrestrial birds. These *Hyalomma* ticks occurred so infrequently on the Cliff Swallow that their importance was negligible.

At the Leeukop colonies a mite *Ornithonyssus bursa* (Fam: Macronyssidae) was first noticed in the latter half of November 1983, and by the middle of January 1984 they were so numerous that it became virtually impossible to work at these colonies. When these nests were again checked in March 1984 the colony was deserted and many nests still contained eggs and dried-out corpses of young. It is not known for certain whether the heavy infestation of mites caused the desertion but it seemed likely. In the 1984/85 season this colony was completely destroyed by people in late October and the mites were not noticed at the colonies during the first part of the season. Very few of the mites were found on the bodies of the swallows when these were handled during the night ringing operations. In 1984/85 this mite was found at the Driekloof colony from November 1984 to the end of the season.

Free flying Cliff Swallows have very few body parasites apart from the louse fly *Ornithomya inocellata.* One species of sucking louse (Anoplura), *Myrsidea rustica,* was found on a few Cliff Swallows during ringing operations. Only one of these lice was found during the delousing attempts (Fowler & Cohen 1983). A second genus of sucking louse, *Menacanthus,* which occurs on Passeriformes and cannot be identified to species at present (J.A. Ledger in litt.), was collected from the Cliff Swallow at several colonies.

No endoparasites were found in a sample of 10 birds examined. Cestodes of the families Dilepididae and Hymenolepididae were found parasitizing the American Cliff Swallow (Stamper & Schmidt 1984) and the European Swallow *H. rustica* (Illescas-Gomez & Lopez-Roman 1980).

SYMBIONTS

In this section I shall deal with animals of other species that live and/or breed at the nest colonies. Because the swallow colonies were usually under bridges in constant shade and often over water, the temperatures were often substantially lower than elsewhere (See Chapter 7), and it is thus expected that a large number of animals at the colonies were just opportunistic occupants seeking a cool microhabitat.

Invertebrate symbionts

There were only two taxa of insects other than parasites which were regularly observed at the Cliff Swallow nests. The sap-sucking bugs of the family Pyrrhocoridae were plentiful at all the colonies, but the reason for this was not at all clear. The only other insects regularly seen at the nests were the mudnest-building Hymenoptera of the families Sphecidae and Vespidae. Several of these wasp nests were present at each of the colonies and sometimes the wasp nests got so big that the entrance to one of the swallow nests was at least partly blocked, causing the swallow pair to seek a new nest.

At the Driekloof colony, where there was no water under the bridge for the larger part of the study, and where the swallow faeces below the nests were up to 5 cm thick, an interesting array of Coleoptera was found. Dung beetles of the family Scarabeidae included *Scarabaeus* spp. (2), *Onthophagus* sp., *Epirhinus* sp., *Coptorhina klugi, Phalops* sp. and *Copris* sp. Of the Tenebrionidae both *Eurychora* sp. and *Gonocephalum* were very plentiful. *Dermestes maculatus* (Dermestidae) were also preying on corpses, mainly of chicks, below the nests.

Vertebrate symbionts

Apart from the single Common Cape Gecko *Pachydactylus capensis* found in the same nest at the Schoongezicht colony a few times (this nest contained a clutch of two swallow eggs), all the other symbionts were avian.

(a) House Sparrow *Passer domesticus*

All the colonies examined near Bloemfontein, except the Leeukop A colony, had at least one pair of House Sparrows breeding in one of the nests. Nests on the edge of the larger colonies were usually selected for breeding, but in the small colonies any nest was used. The sparrows were very aggressive, and usually no swallow was allowed to breed in nests next to those that the sparrows had selected. At the Meriba colony, where small numbers of nests were clustered together, the sparrows took over one or more nests and succeeded in keeping the swallows from entering their nests to incubate. At this colony the constant chasing of the swallows by both the male and female House Sparrow led to the desertion of virtually the entire colony about 10 days after the first eggs were laid. At the Driekloof colony where there were about 700 breeding swallow pairs, eight House Sparrow pairs had simultaneously active nests in this colony in 1983/84. The sparrows usually used nests with wide entrance holes, such as half completed or broken nests. The nests were stuffed with grass and House Sparrow nests are easily spotted in a Cliff Swallow colony.

(b) Cape Sparrow *Passer melanurus*

In the virtually treeless veld where most of the colonies were studied the Cape Sparrow also made good use of the Cliff Swallow nests for breeding. The Cape Sparrows were not as aggressive as the House Sparrows and although they were observed throwing out swallow eggs from a nest at the Meriba colony before breeding there themselves, other swallow pairs were left in peace and allowed to continue their breeding activities. During the winter months when the swallows were in their wintering grounds, large numbers of Cape Sparrows occasionally used the nests for roosting.

(c) Redheaded Finch *Amadina erythrocephala*

In April 1983, after the swallows had departed, a pair of Redheaded Finches started building a nest in one of the Cliff Swallow nests at The Willows colony. Eggs were never laid in the nest which was stuffed with feathers, and the finches were not seen again after June 1983. During a visit to the Tweespruit area in March 1984 several Redheaded Finches were found breeding in the nests of Cliff Swallows.

(d) Little Swift *Apus affinis* and White-rumped Swift *A. caffer*

At some of the high bridges such as over the Modder river at Glen and Krugersdrif, large colonies of Little Swifts were mingled with those of the Cliff Swallow. The swifts usually took over nests of the swallow and these were then lined with feathers and saliva in the usual manner. At Krugersdrift where the swallow nests were extensively damaged and only the rims of the nests remained, the swifts started building their own feather nests using the remaining mud only as a base. Although many hours of observations were done at a large mixed Little Swift/Cliff Swallow colony, no aggression between the two species was ever observed.

Most of the Cliff Swallow colonies studied were probably too low for the White-rumped Swift to breed, (although they were breeding in a 1,7-m-high culvert in a Greater Striped Swallow *Hirundo cucullata* nest and were found to use culverts as low as 0,6 m (Brooke 1974)) but these swifts were regularly seen at all the colonies. Only at the Welgevonden colony did the swifts breed in the 1983/84 season. A nest was completed at the Schoongezicht colony under the large bridge but breeding only took place in the 1984/85 season.

(e) Pied Barbet *Lybius leucomelas*

A single Pied Barbet roosted for about three months in one of the Cliff Swallow nests at The Willows colony during the winter of 1983 when no swallows were present.

(f) Other bird species

A number of other bird species roosted, especially during very hot days, on the half completed cups of nests usually at the edge of the colony. The following birds were observed: Familiar Chat *Cercomela familiaris*, Mountain Chat *Oenanthe monticola*, Greyheaded Sparrow *Passer griseus* and Pied Starling *Spreo bicolor*. On 16 January 1985 a single juvenile European Swallow *Hirundo rustica* was trapped at one of the Cliff Swallow colonies during a mass-trapping operation at night.

(g) Bird species not directly associated with the nest masses

Several swallow and swift species which mixed freely with the flocks of Cliff Swallows flying around the nesting colonies were also noted.

The most interesting observations were those of the House Martins *Delichon urbica* which were observed at all the colonies during October 1983. At the Meriba colony, where 12-hour watches were done on several occasions during October 1983, one or two House Martins were often seen flying around with the Cliff Swallows. On 15 and 17 October one individual landed on a small ledge on the wall of the quarry and later moved to a half-built nest cup where it remained for about 25 min before a Cliff Swallow drove it from the nest. House Martins were also seen at The Willows colony hanging against the wall of the bridge below the colony while another sat on a mud ledge on the edge of the colony. At both The Willows and Schoongezicht colonies, House Martins were also observed on telephone wires with Cliff Swallows, preening. During a heavy rainstorm at Schoongezicht about 200 Cliff Swallows together with 12 House Martins were perched on a barbed wire fence near the nests. All the Cliff Swallows continuously ruffled their feathers and preened as if they were bathing but the House Martins sat still. House Martins also associated with a breeding colony of Redthroated Cliff Swallows *H. rufigula* in Zambia (Taylor 1982) and with Greater Striped Swallows *H. cucullata* (Fellowes 1971) in very much the same manner as described above.

A Whitethroated Swallow *H. albigularis* associated with the small colony at Meriba for several days during October 1983, often sitting on the sand below the nests or joining the Cliff Swallows at mud gathering sites.

Greater Striped Swallows, Black swifts *A. barbatus*, European Swallows *H. rustica* and European Swifts *A. apus* were all often seen flying in flocks of the Cliff Swallow near the nesting colonies.

DISCUSSION

Probably because of the relatively safe nesting place of the Cliff Swallow, usually on high bridges and often over water, I could not find any sign of large scale predation on eggs and nestlings by avian, mammalian or any other predator, as was the case with other colonially breeding birds such as the Sociable Weaver *Philetairus socius* (Maclean 1973). Although Cape and House Sparrows were seen to remove eggs from nests when taking over nests for their own breeding, the incidence of this was very low and probably negligible. There was definitely no large scale killing of swallow chicks by House Sparrows as was the case with the American Cliff Swallow *H. pyrrhonota* (Buss 1942). It would seem as if only the very small colonies would suffer from displacement by these sparrows and that the presence of the sparrows have very little effect, if any, on the swallows in the larger colonies provided that there were surplus nests available, which was the case in all the larger colonies studied. S.F. Townsend observed the breeding of Cape Sparrows in the nests of the Cliff Swallow near Beaufort West as early as 1879 (Winterbottom 1962) but did not record attacks by the sparrow on the swallow.

The only total destruction of eggs, chicks and nests were by people at the two Leeukop colonies; one in November 1983 and the other in October 1984. The chicks were taken for food and although the adults deserted the colonies the destruction had very little effect on the population as a whole. The heavy predation by red ants on chicks at The Willows in 1983/84 must be regarded as exceptional. The populations of these ants were much larger than in previous years and although these ants have always been at the nests scavenging on fallen insects, faeces and young which have fallen from the nest, they attacked young in the nest only this one year when the stream below the bridge contained no water.

In this study the results would indicate that there is no predation on eggs or nestlings of Cliff Swallows in the nest other than by the ant species and humous, provided that the nests are high enough or over water so that man cannot reach them. This is in sharp contrast to the predation at other colony nesting hirundines such as the Sand Martin *Riparia riparia* (Mead & Pepler 1975, Blem 1979), where reptiles and mammals were recorded as predators on nest contents.

It seems as if most of the predation on the Cliff Swallow is by animals taking helpless chicks which have fallen from the nest to the ground below, injured adults and possibly young inexperienced fledglings. Mead & Pepler (1975) also recorded the Steppe Buzzard as a predator of Sand Martins and as in the case of the Cliff Swallows it was seen eating a bird but not actually killing it.

The tick *Ornithodoros (Proknekalia) peringueyi* together with the two other swallow-nest ticks *O. (P.) peusi* parasitizing chiefly the Redrumped Swallow *Hirundo daurica* in Greece and *O. (P.) vansomereni* parasitizing the Lesser Striped Swallow *H. abyssinica* and the Redrumped Swallow in Kenya comprise a highly distinctive subgenus of argasid ticks (Keirans et. al. 1977). These three species are described as having strict to total specificity for their hosts (Hoogstraal & Aeschlimann 1982), indicating the strong evolutionary relationship between the Cliff Swallow and *O. (P.) peringueyi*. Laboratory studies by H. Hoogstraal (in. litt.) on the Cliff Swallow tick have proved to be quite difficult as the larvae hatching from eggs refused to feed on the substitute hosts. Small larvae and nymphs of this tick not only fed solely on the Cliff Swallow chicks but also preferred specific areas to feed on, namely the area around the gape and below the eyes, confirming the statement by Hoogstraal (1978) that "numerous ethological characteristics ... point to the intimate and complex relationships that have evolved between individual tick species and kinds of hosts. Each species aims toward a preferred feeding area of the host ..." The fact that the tick larvae, with few exceptions, all drop off the swallow chicks before the chicks leave the nest, means that the ticks stay in the nest where the succeeding stage will have an opportunity for finding a new host (Hoogstraal 1978). This once again indicates a close relationship between the Cliff Swallow and its tick. As no ticks were ever found on any of the Cliff Swallows trapped during night mass-trapping operations, the ticks are probably well adapted to drop off the host at the slightest disturbance (e.g. when the birds prepare to leave the nest) so that they stay in the nest where they are sure to find a new host. Although the "clustering" areas of this tick are usually near the top of swallow nests, the preferred feeding area of adult ticks on the swallow is the abdomen. "Clustering" near the top of the nest has the advantage that the possibility of being disloged from the nest by the birds' activities is very low whereas feeding on the abdomen while the bird is in the nest had the advantage that the tick can "drop-off" quickly without having to climb. The abdomen is also devoid of feathers making feeding easier to some extent.

Although some work has been done on isolating the Chenuda virus *Orbivirus* (fam: Reoviridae) from *O. (P.) peringueyi* in South Africa (Hoogstraal 1973) very little else is known about the biology of this tick species (Keirans et. al. 1977) and no life cycle data for species of the subgenus *Proknekalia* are available at present (Hoogstraal in. litt.). The information presented here is thus the first describing some aspects of the biology of *O. (P.) peringueyi*.

Judging by the large numbers of *O. (P.) peringueyi* especially at the older Cliff Swallow colonies, one would expect that these ticks would have some effect on the swallows in such a colony. At both the Schoongezicht and The Willows colonies there were always some parts of the colony, containing complete but old nests, which were not used at any specific time.

This might be due to heavy tick infestation. J.B. Walker (in litt.) writes: "I suspect that the (Cliff) Swallows would desert heavily infested nests or colonies. If I were a swallow I am sure I should not be very enthusiastic about staying in a nest in which I got well and truly bitten! The bites of some argasids are said by humans who have been bitten to be very painful."

A number of studies have reported on the species of ticks attacking other swallow species notably the American Cliff Swallow. *H. pyrrhonota* (Baerg 1944, Kohls 1947, Howell & Chapman 1976, Hopla & Loye 1983, Loye & Hopla 1983) but only Baerg (1944) concluded that the ticks had no effect on the swallows without substantiating his statement. Among colonial seabirds the evidence is strong that ticks cause desertion by nesting adults with resultant mortality of eggs and young (Feare 1976, King et al. 1977a, 1977b, Duffy 1981). This was not observed during this study, at least not on a large scale, although there are indications that parts of the colony and even individual nests could have been deserted because of the tick populations building up to very high levels. However, there is also strong evidence from this study that there is often very heavy predation on the tick itself by ants which might keep the tick population in check. Ant predation on ticks was also recorded in Zaïre (Nuttall & Warburton 1908).

Although there is no evidence that the ticks had a direct influence on the mortality of Cliff Swallow chicks there were always some, seemingly healthy, chicks falling from the nests at especially Driekloof and Schoongezicht, the two colonies with the largest populations of ticks. I would suspect that chicks in heavily infested nests were very restless when bitten often and fell from nests when trying to get rid of some of the ticks. Restless behaviour in adult Peruvian Booby *Sula variegata* accompanied by a dramatic increase in preening always preceded nest desertions as a result of heavy tick parasitism (Duffy 1983). Preening starts relatively early in the Cliff Swallow (see Chapter 4) and this "uncoordinated" preening of chicks at an early age might result in them falling from nests. If this is the case, the Cliff Swallow tick *O. (P.) peringueyi* does have an effect on nesting success and mortality of Cliff Swallow chicks in heavily infested colonies even though this influence may be indirect.

The Afrotropical region has very few avian fleas (Siphonaptera). Only two fleas have been recorded from the Brownthroated Martin *Riparia paludicola* while the only host known for *Xenopsylla trispinis* is the Cliff Swallow. Nothing is known about the biology of the Cliff Swallow flea and its effects on its host. As this flea was found in the nests of the Cliff Swallow during winter when the swallows were not present, at least some fleas must overwinter in the swallow nests as the flea *Ceratophyllus styx* does in the burrows of the Sand Martin *R. riparia* (Rothschild & Clay 1952, Mead & Pepler 1975). The biology of the flea usually found on American Cliff Swallows, *Ceratophyllus petrochelidoni* has evolved to compensate for the swallows' long absence from the nest during the non-breeding season

(Traub 1972, Nelson et al. 1979). This might also be the case with *X. trispinis*. Fowler et. al. (1983) found that both the number of fleas per bird as well as the number of birds infected by fleas were highest during the period of dispersal from communal winter roosts and nestbuilding in the Blackbird *Turdus merula*. It is during this period that the fleas would have a greater opportunity of finding new hosts. In the Cliff Swallow colony the flea finds new hosts easily, which is probably why fleas parasitizing colonial breeding hirundines have opted for overwintering in the nest rather than accompanying the birds on their migration.

The mite *Ornithonyssus bursa* is a continuous parasite of several bird species (Powlesland 1978) a lizard (Cameron 1938) and man (Murray 1950). As it requires a blood meal at least every 4-6 weeks (Powlesland 1977) it cannot survive at the Cliff Swallow colonies through the winter when the birds are absent. However, as several other bird species, notably the House and Cape Sparrows, occupy nests in several Cliff Swallow colonies during winter, at least some of the mites can survive to reinfest the colony when the swallows return. Only the relatively small Leeukop colonies were heavily infested by this mite during this study and it was probably the cause of total desertion of the colony late in the 1983/84 season. Even well grown chicks were deserted, indicating the impact of the mite on the colony. Burgerjon (1964) suggested that the low breeding success of the Cliff Swallow during one of the breeding seasons when the bird was under study was the result of the heavy infestation by this mite. The Leeukop colony was the only which did not contain House or Cape Sparrows to "carry" the mites through the winter, and mites were not noticed again at this colony before it was destroyed. However, it is possible that some mites overwintered ectoparasitically on the swallows as it may do on the European Starling *Sturnus vulgaris* (Petersen 1979). This nuclear population can then build up rapidly in the swallow colony during the breeding season. Powlesland (1977) found that *O. bursa* had no demonstrable major effects on the growth rate, weight, mortality, blood characteristics and lipid stores of starling nestlings. However, Moss & Carmin (1970) found clear evidence of a significant decrease in productivity of Purple Martins *Progne subis* as a result of parasitism by blood-feeding mites *Dermanyssus prognephilus*. They also showed that Purple Martins, in the absence of these parasites produced young heavier than parasitized young of the same brood size. As unparasitized Purple Martins tended to have larger clutches than parasitized nests, these authors suggested that nest parasitism is potentially important in the determination of clutch size in birds. Although this was not investigated in the Cliff Swallow colonies, no obvious effects of *O. bursa* on either growth of the young or clutch size were noticed except for possible desertions late in the 1983/84 season. This aspect would need a lot more carefull study in the future.

The only host known for the louse fly *Ornithomya inocellata* is the Cliff Swallow. Another species *O. fur* is widespread among the swallows and other passerines. Although no life-cycle data are available for *O. inocellata*, it probably follows the typical hippoboscid pattern as described by Rothschild & Clay (1952), Ledger (1968) and Wood (1983) whereby the egg and larval stages develop while still in the female and the larvae very soon pupate and hatch into adult flies. I could find very little evidence that the mechanical damage to the tissue by the bites of these flies leads to bacterial infections and possible death of young nestlings (Ledger 1968), but large numbers of individuals at certain colonies had swollen and often bleeding feet as a result of bites from these parasites.

The major point to emerge from the foregoing is that the Cliff Swallow has two body parasites and one nest parasite not known from any other hosts. These host-specific relationships are probably only possible as a result of the colonial nesting behaviour of this swallow. For all of the parasites, hosts are easy to get at and the mud nests are a relative stable environment to overwinter in when the swallows are not present.

CHAPTER 7

BREEDING BIOLOGY

INTRODUCTION

Being a colonial breeding bird has certain advantages as well as a number of disadvantages. The adaptive significance of coloniality in some of the Hirundinidae, notably the cliff swallow group and members of the sand martin group, has often been debated (Snapp 1976). In the Cliff Swallow the first step in trying to explain why it is a colonial breeding bird was to collect basic breeding data which was sadly lacking for this species. By monitoring breeding in a bird species one can get some measure of recruitment, which is vitally important to the population structure. The factors determining breeding success in a colonial bird may also be the factors determining the size of colonies or the population structure as a whole. Social breeding habits are probably the result of adaptation to a number of environmental pressures which will surely be reflected in the breeding behaviour, clutch size and type of nest built by the birds.

METHODS

General methods

Breeding activities were monitored at five colonies, namely Schoongezicht, Leeukop A & B, Meriba, The Willows and Driekloof (Fig. 2-1). At Schoongezicht the part of the colony below the high tarred road bridge was monitored. Nests were numbered with a stencil and spray paint against the concrete of the bridge. All nests below this bridge were monitored in the 1983/84 season. This part of the Schoongezicht colony was not used in the 1984/85 season. The Leeukop colonies were started in the 1983/84 season and all nests in these colonies were monitored during this season. In the 1984/85 season only 13 nests in the Leeukop B colony were used and data were mainly from the A part of the colony.

At Meriba all the nests were monitored in 1983/84 but the colony was not used in 1984/85, while at Driekloof 25 nests were selected in the 1983/84 season and another sample of 36 in the 1984/85 season. A sample of 99 nests were monitored at The Willows in 1984/85 in the new part of the colony under the bridge over the tarred road.

Nest record cards were completed for all the nests. The nests were inspected with a "hirundoscope". This is a modified pen flash-light with a small mirror of 25 mm at the end in front of the light bulb (Figure 7-1). By manoeuvring the mirror inside the nests with the light switched on the nest contents could be checked. Eggs were much easier to count than pulli, and when the pulli were more than 15 days old it was sometimes easier to count them by inserting a finger into the nest and counting the heads which were usually close to the entrance.

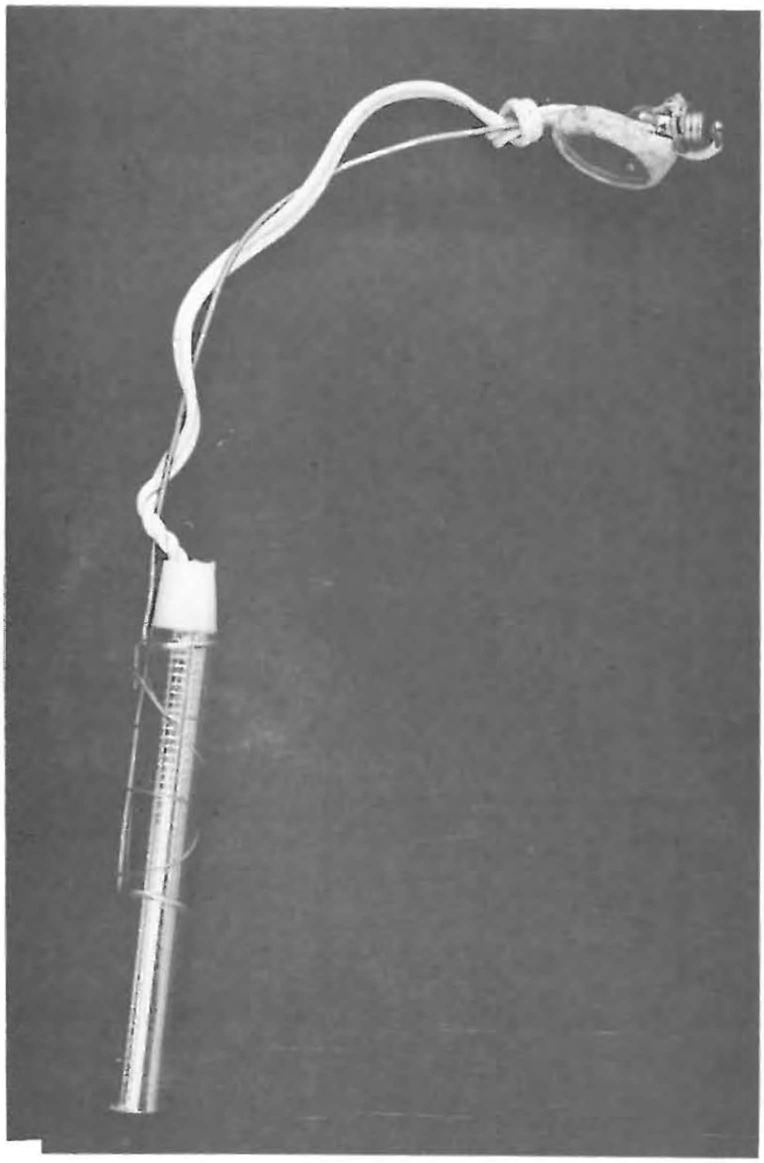


FIGURE 7-1

The "hirundoscope". A modified "penlite" with a mirror and 1,5 V bulb used to inspect the nests of *Hirundo spilodera.*

All nests were checked at least twice a week at the Meriba and Driekloof colonies and at least three times per week at Schoongezicht, The Willows and Leeukop A & B.

Measurements of eggs were taken whenever the opportunity arose, either when eggs had fallen from nests and were picked up below the colonies, or where the construction of specific nests made it possible to take eggs from nests and return them to the nest. In 1984/85 a scoop, made of a loop of wire with a 1 mm mesh net for the spoon body, was used to take eggs from the nest and return them without damage.

To collect data on the growth rate of chicks certain nests were selected from which it was possible to take the pulli at regular intervals, usually daily, and measure them. This was done whenever and wherever the opportunity arose and these nests were not always used to monitor general breeding activities.

Observations on the incubation and feeding rate of pulli in the nest were made from a hide of hessian set up about 8 m from the nests at Schoongezicht, Meriba and The Willows. Readings of nest, brood patch and egg temperatures were made on a Bailey model BAT 12 digital thermometer. To measure egg temperatures test eggs were taken from fallen eggs collected below the nest and in two cases the fresh eggs of owners were used. The thermocouple wire was pushed through the bottom of the nest and nest pad and taken out through the nest opening. A small hole was then punched in the egg, the temperature probe inserted, and the wire glued to the egg with a dab of cyanocryllic cement. The egg was then pulled back into the nest and positioned between the other eggs. The data were recorded on standard forms printed by the National Museum. Because of the position of the probe the egg could not be moved by the incubating bird and thus remained in contact with the other eggs. To measure the brood patch temperature the bird was held in the hand and a probe was then placed against the pectorial muscle.

Collecting of specimens

For one whole season from September 1983 to March 1984 Cliff Swallow adults were collected every 10 days. Collections were made on, or as close as possible to, the 5th, 15th and 25th of each month. An attempt was made to collect at least three males and three females on each of these days, but often more were collected. The swallows were taken from mistnets erected at Driekloof, Schoongezicht or The Willows. These three colonies were relatively close to each other (Fig 2-1) and in similar surroundings. The data gathered from these collected birds are thus comparable, although climatic factors such as rainfall might have had an undetermined different effect on members of each of these colonies. In all 163 swallows were collected, 77 males and 86 females. The birds were killed with anaesthetic ether soon after capture, weighed, tagged and then stored in a deepfreeze until dissection.

Upon dissection the carcasses were thawed for about one hour, then a slit was made through the abdominal skin and muscle, and the gizzard lifted out, detached and stored in 70 % alcohol for later examination. The gonads were then also taken out, measured and stored in Bouins fluid.

Time and energy budgets

For time and energy studies the times spent on each of the three activities considered were calculated from 24 h watches at three different nests on different occasions. The actual time spent at the nests was from 04h30 to 19h30 and it was assumed that the specific individuals watched spent the other nine hours during the night in the nest, which was found to be the case, as the individuals only left the nests after observations started and unless disturbed, Cliff Swallows sleep in their nests at night. Nest building was observed on 12 October 1983 at the Meriba colony where mud was collected from a temporary pool 20 m from the nest. Incubating birds were watched at the Schoongezicht colony on 29 November 1983, while birds feeding 20 day old nestlings were observed on 16 October 1984 at The Willows colony.

A sample of 36 adult Cliff Swallows was captured by mist net at The Willows colony in October 1984 and body weight, wing span and wing length measured. To calculate the time spent flying it was assumed that the swallows only perched at the nest. Flight velocity was determined on a calm day over a 100 m course by timing 30 birds with a stopwatch. Times required to collect a mud pellet, carry it to the nest and pack it into the nest were also measured.

The equation of Lasiewski & Dawson (1967) was used to predict standard metabolic rate (SMR) of the Cliff Swallow and the cost of flight was estimated from aerodynamic theory of flapping flight as given by Pennycuick (1969) and Tucker (1973)(See Appendix).

RESULTS

NEST AND NEST BUILDING

The nest site

With the exception of the small colony at Meriba all the breeding colonies of the Cliff Swallow in the study area were situated under man-made concrete road bridges of various heights and dimensions (Figure 7-2). No clear pattern in the selection of bridges for nesting colonies was apparent. Large and small bridges and even large culverts, in the case of the Leeukop colony, were used. Larger bridges usually had larger colonies if suitable foraging areas were nearby. Some of the new larger bridges were, however, constructed with beams running lengthwise close to each other and over the whole breadth of the construction and seldom attracted the Cliff Swallow. Some of the newer bridges also had very smooth vertical surfaces which prevented the swallows from nestbuilding as they could not get a foothold.

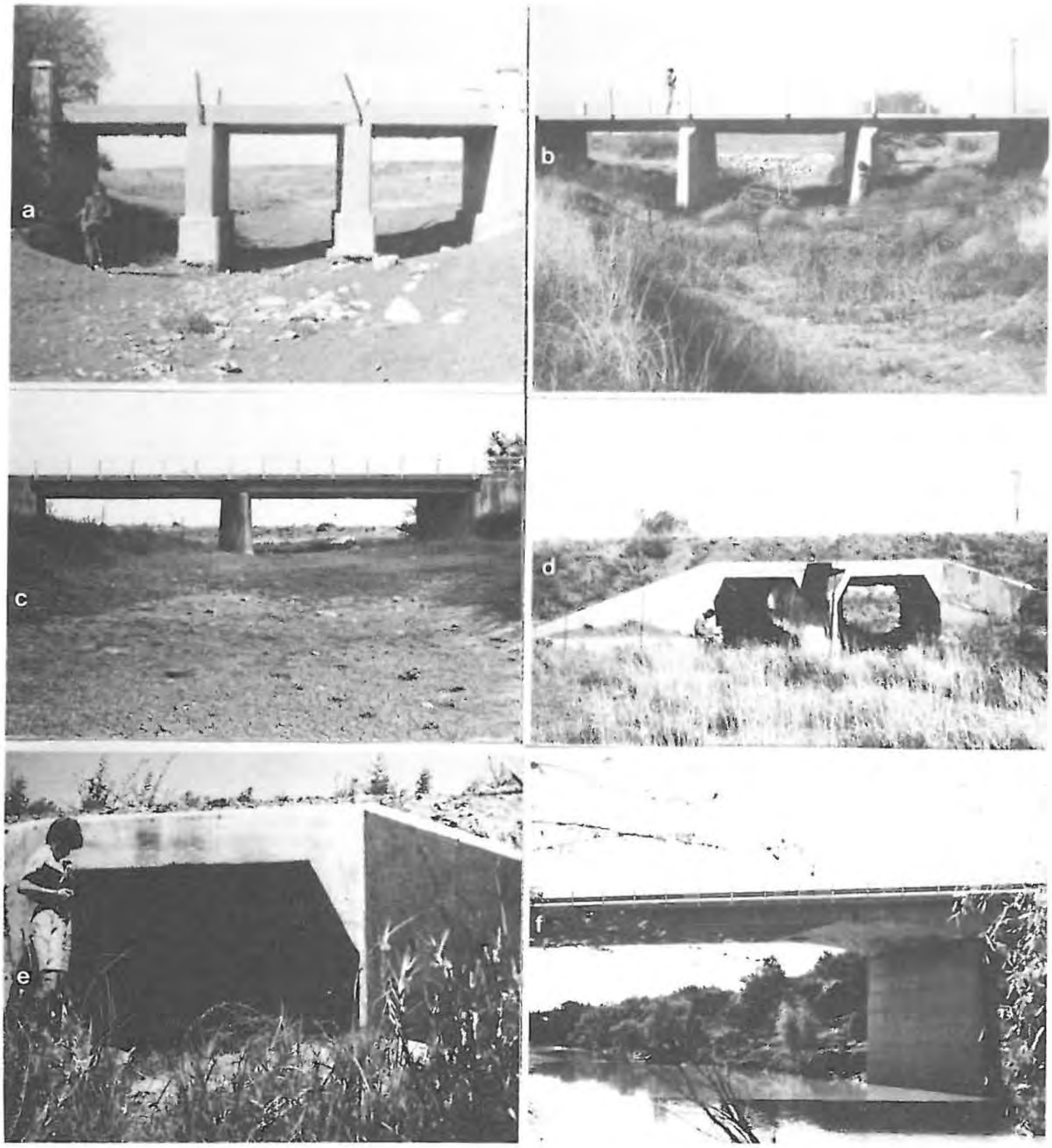


FIGURE 7-2

Various bridges used as nesting sites by *Hirundo spilodera*. (a) The Willows, (b) Driekloof, (c) Schoongezicht, (d) Welgevonden, (e) Leeukop and (f) Glen.

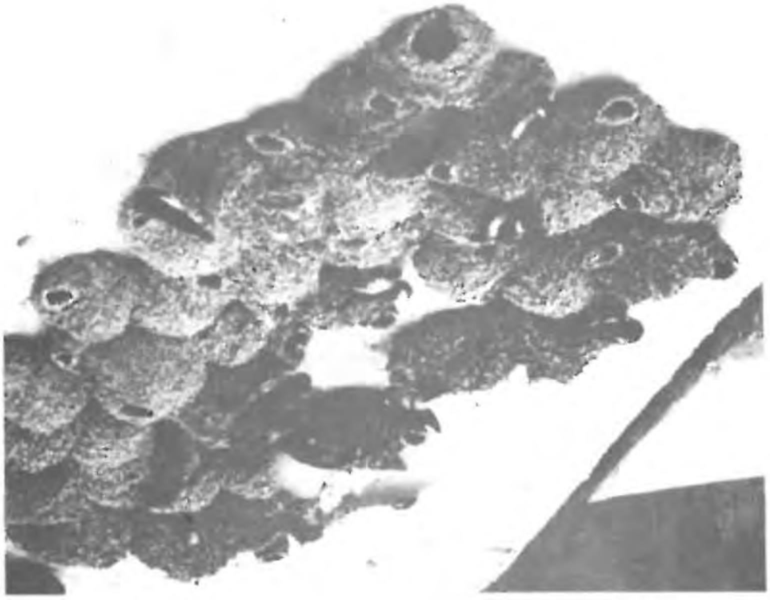


FIGURE 7-3

At the colony at Glen the first place where nests were started was around a drainage pipe leading through the bridge.

FIGURE 7-4

At the "Meriba" colony the nests were built against the wall of an old quarry.

On one such a bridge at Glen, building of the first nests started around the edge of a 2 cm diameter pipe cast into the bridge to drain water from the road surface (directly through the bridge). This was the only place where the birds could get a foothold and a clump of nests were built around this pipe (Figure 7-3). The first nests built at a site were located at the junction of the vertical wall of the bridge and the roof of the bridge. Later builders would then usually utilize completed or partially built nests for attachment of their own nests. The colony would thus expand as new nests are built both horizontally outward against the bridge roof and vertically downward from the first row of nests. Only in the older colonies was there a downward extension of the colony and most of the new nests built were against the roof of the bridge. The mean distance between adjacent nest openings were 51,8 mm (n= 53; range 20-100) in a randomly selected part of the dense Driekloof colony.

Only the Meriba colony was not situated under a concrete bridge and the nests were built on the overhanging wall of a man-made quarry (Figure 7-4). Skead (1974) also mentions the Cliff Swallow building nests against the wall of a quarry in the S.A. Lombard nature reserve. A few other "natural" breeding places were found in the Orange Free State, all being in man-made quarries. No colonies were found on cliffs which do not occur in the central Orange Free State.

There were always parts of the larger colonies which were not in use and where the nests fell into decay. At The Willows colony, only two of the three sections of the small bridge were in use. The middle section had many irregular and broken walls of old nests which were not used at all. These were taken down before the 1983/84 breeding season, but no new nests were started in this section during this or the 1984/85 season.

There was no obvious height requirement for the colony. Most of the colonies, however, were out of reach when standing on ground level and could only be reached with a stepladder for inspection. The colony at Leeukop was an exception in that it was only 1,35 m high and thus within easy reach from the ground. Although most of the streams running below the nesting bridges held water at some stage, at least, it was by no means clear that the swallows preferred sites over water. It is more likely that these were the only suitable places available. In the Orange Free State at least, all the colonies were distant from any human habitation and no colonies were located in a barn or on any other structures occupied by humans.

Nesting material

Mud for nest construction was gathered from 6 m to about 300 m from the nesting colony. After rains just about all temporary pools were used as a source of mud, but when no rain fell for some period they usually utilized mud from the edge of the streams near the nesting colonies. The availability of mud affected the rate of construction of nests and rain which formed temporary pools greatly stimulated nest building. During the dry 1983/84 season it was striking that when temporary pools were available as a mud source, other sources such as the stream banks were ignored even though it meant travelling an additional few hundred meters.

The quality of mud varied considerably amongst colonies depending on the local conditions. The nests at Meriba had a high percentage of coarse sand in the mud used for building. The nests at The Willows built with mud from the small stream were again high in clay. In many of the nests several types of mud were found indicating that various sources had been utilized in their construction.

The principal elements found in the mud samples from nests are given in Table 15. The "grey" mud from the nest body is high in calcium and silicate and relatively lower in all the other elements. Mud from the mud gathering site and the mud ledge had very much the same composition as the ledge was built from this site which was a temporary pool formed after rain had fallen. McNiel & Clark (1983) analized the mud from a House Martin *Delichon urbica* nest, and also found that mud from different sources had different chemical compositions and thus there seemed to be no real selection of mud for nestbuilding. The grain size distribution is discussed in Earlé (1985) (see Appendix 4).

TABLE 15

PRINCIPAL ELEMENTS IN MUD SAMPLES TAKEN FROM *HIRUNDO SPILODERA* NESTS AND FROM A MUD COLLECTING SITE AT THE WILLOWS COLONY FIGURES GIVEN AS A PERCENTAGE OF THE TOTAL SAMPLE ANALYSED

Source of the mud	**Amount of mud analysed (g)**	**Elements**											**Organic mate-rial**	**Total**
		Si	**Ti**	**Al**	**Fe**	**Mn**	**Mg**	**Ca**	**Na**	**K**	**P**	**L.O.I.[4]**		
Mud gather site	121,9	55,4	0,7	13,0	5,6	0,1	1,0	0,8	0,6	1,7	0,2	13,1	7,4	99,6
Mud ledge[1]	119,4	57,8	0,7	13,6	5,6	0,1	1,2	0,8	0,4	2,0	0,2	11,7	5,8	99,9
Nest body[2]	113,7	70,8	0,6	7,9	3,5	0,1	1,2	2,6	0,5	1,6	0,1	8,6	2,1	99,6
Nest roof[3]	118,5	60,5	0,6	11,9	5,1	0,1	1,3	1,0	0,4	2,0	0,1	9,3	7,3	99,6

[1]. The mud ledge is attached to the concrete bridge.

[2]. "Grey" mud from calcareous stream.

[3]. "Red" mud from temporary pool after rain.

[4]. L.O.I. = lost on ignition.

Nests in which breeding occurred were lined with a pad consisting of sheep's wool and plantdown with some feathers (Table 16). In most of the pads three distinct layers of the different materials could be recognized. At the bottom was the plantdown with a layer of sheep's wool on top. If feathers were present they were always found on top of the sheep's wool, but were usually too few to form a complete layer. No grass was ever found in any of the nests. The pad only covered the depression in the bottom of the nest and was not visible through the nest opening.

TABLE 16

NESTPAD ANALYSIS OF *HIRUNDO SPILODERA* NESTS.

Nest Number	Plantdown Mass (g) (% of total)	Sheep's wool Mass (g) (% of total)	Feather Mass (g) (% of total)	Total Mass of Nestpad (g)
1	3,3 ((4,7)	1,7 (33,3)	0,1 (1,9)	5,1
2	2,3 (51,1)	1,6 (35,5)	0,6 (13,3)	4,5
3	11,4 (73,3)	3,9 (25,0)	0,25 (1,6)	15,6
4	4,8 (44,4)	6,0 (55,5)	0,1 (1,0)	10,8
Mean	5,5 (61,1)	3,3 (36,7)	0,2 (2,2)	9,0

Nesting material, both mud and nest pad material, were stolen from nests of other building birds by certain individuals. At The Willows colony one pair built a complete nest by stealing mud from a nest about 1 m away from their own. The victim was not paired and could thus not guard its nest and build. Each time when the bird was away from its nest to collect mud, the pellet built into the nest earlier were taken by the other building birds. Birds carrying nest pad material were also often harrassed by other birds, especially if it included large items such as feathers, and if these were dropped they were quickly picked up and carried off to a nest.

Form and construction of the nest

Typical nests of the Cliff Swallow are shown in Figure 7-5. There is a globular nesting chamber with a short tubular entrance tunnel directed downwards. The dimensions of a sample of nests measured are given in Table 17. The measurements taken from a typical nest are given in Figure 7-6. The walls of the nest were always thinner near the roof and towards the entrance hole.

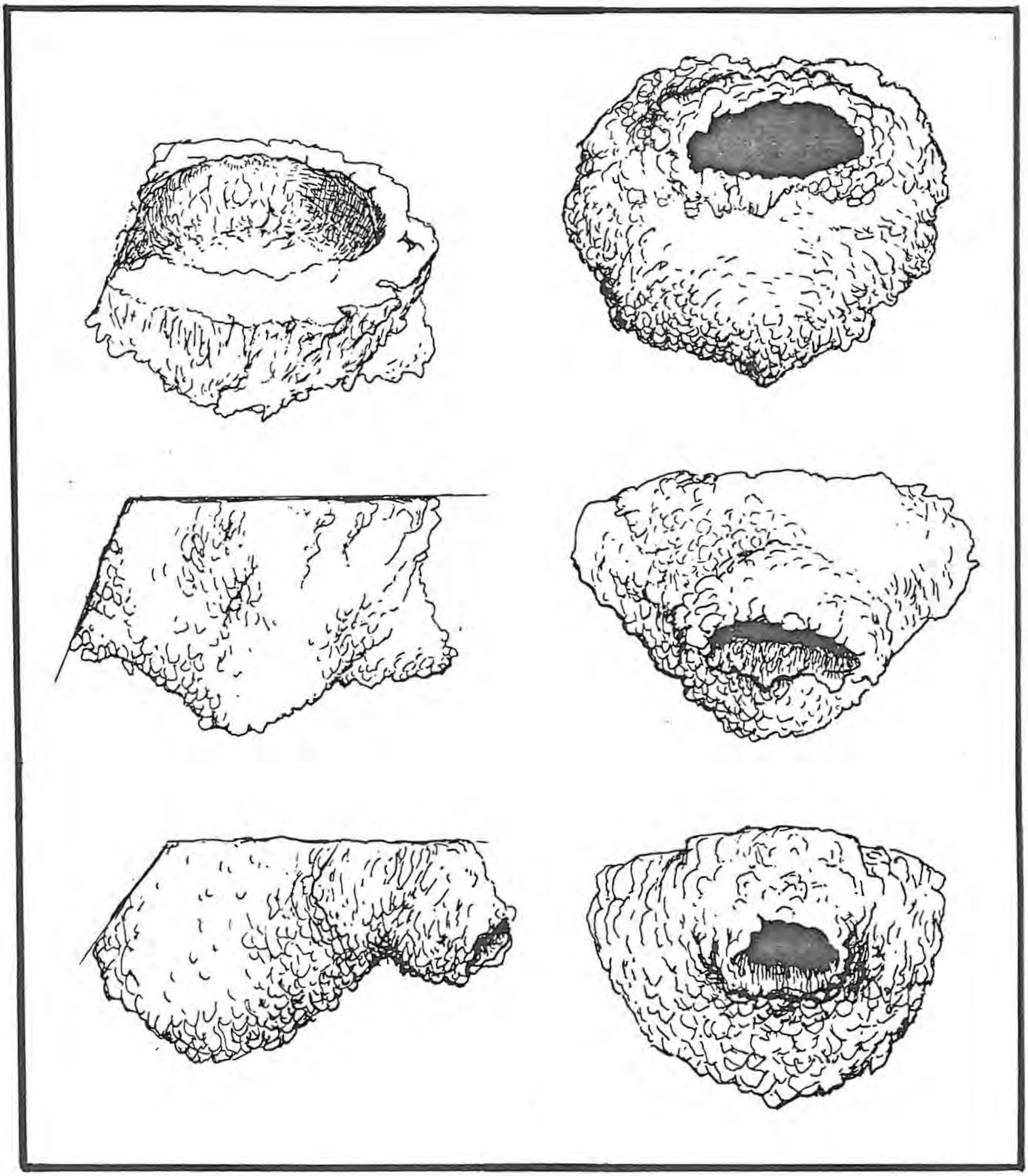


FIGURE 7-5

Drawings of nests of *Hirundo spilodera* showing side and front views.

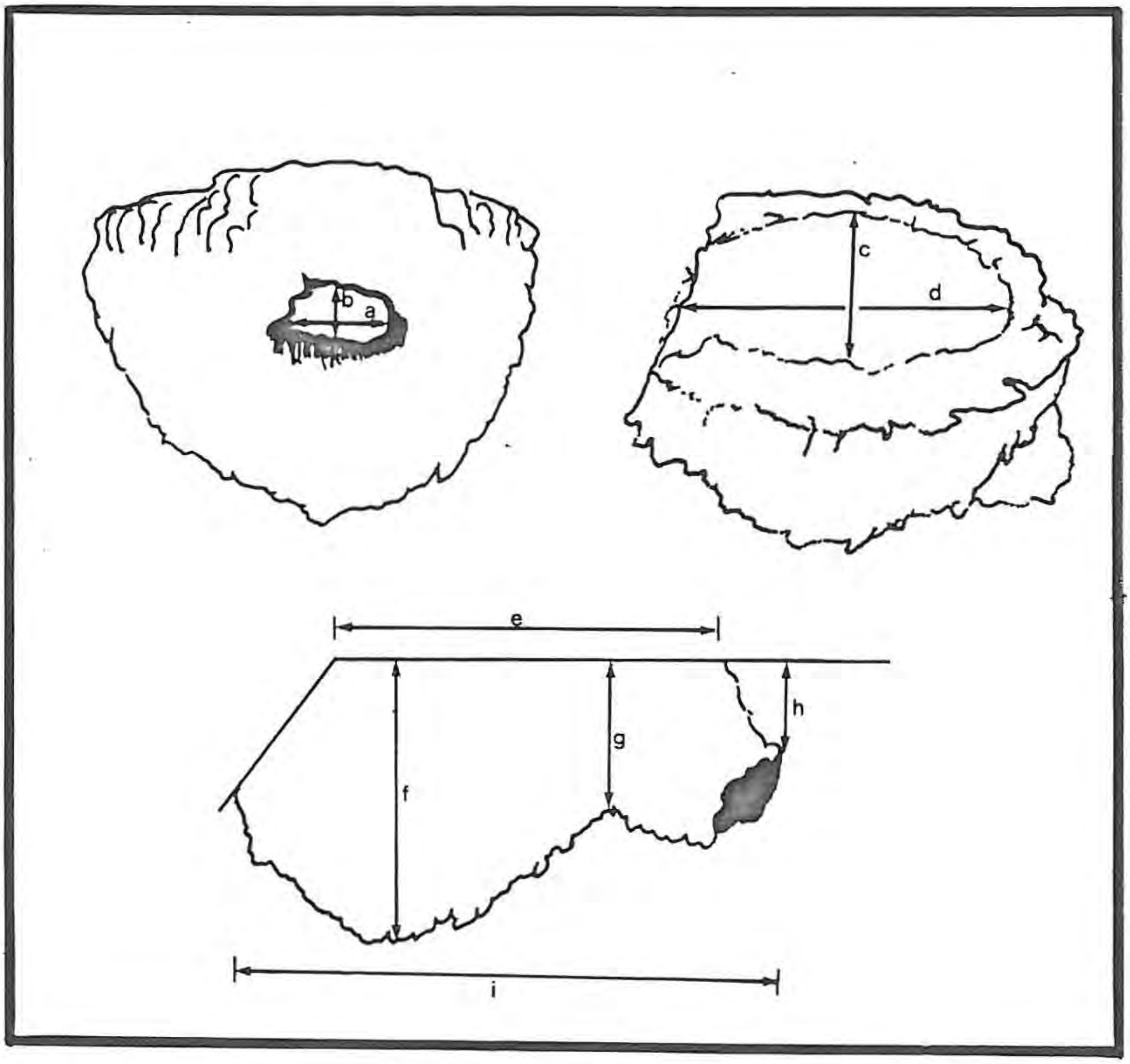


FIGURE 7-6

Outline drawing of *Hirundo spilodera* nests showing the measurements taken as given in Table 17.

Variations in the size and shape of different nests were mostly the result of the nature of the site. Nests built on the horizontal roof of the bridge were more rounded as they were attached at the top of the nest to the surface of the bridge. As the nests were clustered, a large number of nests were irregularly shaped by using the walls of existing nests as a side or back wall for the new nest. At the Meriba colony where the nests were built against an irregular wall, a number of the nests were built partly in crevices and mud was only used to close up the natural opening of the crevice and to form an entrance tunnel (Figure 7-7).

FIGURE 7-7

At the "Meriba" colony some nests were built in crevices by merely closing the crevice with a wall of mud.

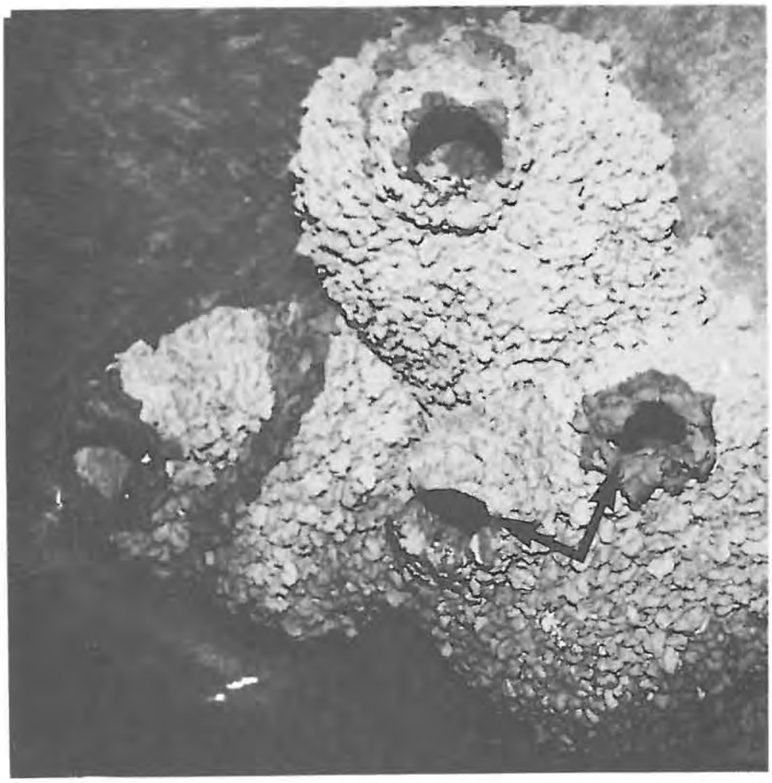


FIGURE 7-8

A nest with two entrance tunnels was used throughout the 1984/85 breeding season at The Willows colony by a *Hirundo spilodera* pair. Different mud sources were used in constructing the nests resulting in the nest showing layers.

All nests had a depression in the centre which was filled up with the lining to form the nest pad.

At each of the colonies a large number of the nests were undamaged from year to year and were used repeatedly. Partly broken nests were rebuilt and holes in the walls of damaged nests repaired. Holes drilled into the sidewalls of several nests at Meriba for inspection purposes and about 2 cm in diameter were all repaired within one hour after discovery by the birds. Holes in the floor of the nest below the nest pad were not repaired with mud. When old nests with large breaks were repaired, new entrance holes were usually built. If an old entrance hole was still present, this was then usually filled in but at The Willows colony a nest with two entrance holes was used throughout the 1984/85 season (Figure 7-8). Often swallows got stuck in entrance holes and when such nests were rebuilt after breaks, the skeletons of such stuck birds were merely partly covered with mud pellets and a new entrance hole constructed.

TABLE 17

DIMENSIONS OF *HIRUNDO SPILODERA* MUD NESTS. MEASUREMENTS CORRESPOND TO ALPHABETIC LETTERS IN FIGURE 7-6.

Measurements (mm)	n	Mean	S.D.	Range
Nest entrance width (a)	11	43,0	7,72	34 - 57
Nest entrance height (b)	11	29,7	3,20	25 - 37
Inside width (c)	7	133,0	12,85	111 - 155
Inside length (d)	7	130,7	16,10	109 - 154
Roof attachment length (e)	7	153,5	20,91	125 - 180
Outside depth (f)	8	90,5	7,70	77 - 126
Entrance neck (g)	9	71,2	8,43	64 - 91
Nest opening - roof (h)	9	6,0	1,51	3,7 - 9,0
Total length (i)	6	184,4	30,55	140 - 210
Internal depth	7	81,9	14,21	65 - 110
Mud mass (in grams)	9	840	77,29	731 - 979

Where nest openings were very close, they were facing in different directions e.g. the top ends met (Figure 7-9) so that when birds were hanging in front of each nest they were out of pecking range of each other.

Two nests which were watched from start to finish took five and seven days respectively to complete the mud section. It was difficult to determine the time taken to complete the nest

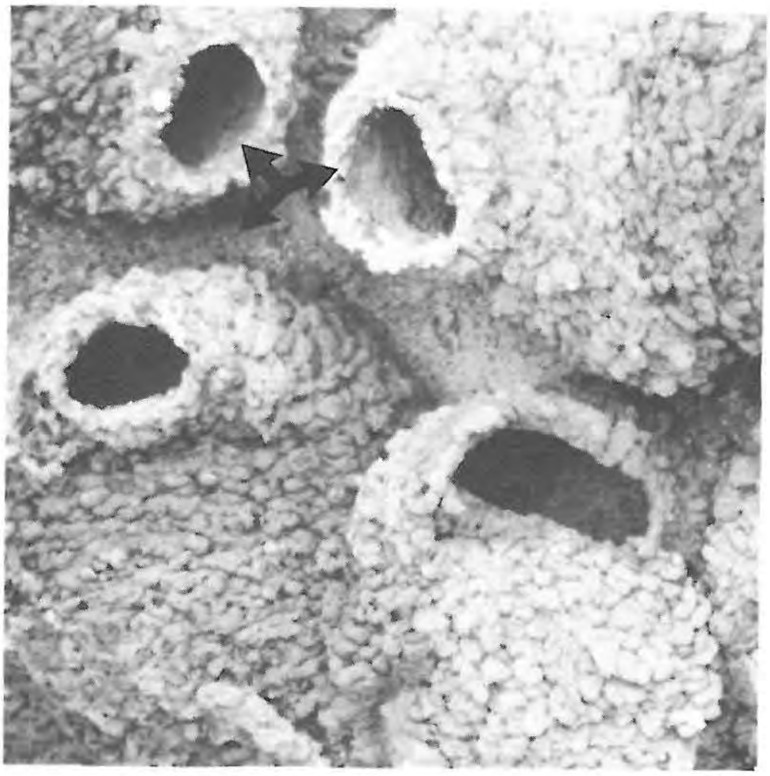


FIGURE 7-9

When the openings of two *Hirundo spilodera* nests are very close they face in different directions so that when birds cling to the entrances they are out of pecking range from each other.

pad as material was still added to the pad even after the clutch was completed. No nest was ever found with a completed clutch and no nesting material, although the first eggs in new nests were frequently laid before any nesting material was added to the nest. Newly completed nests had smaller pads than nests already in use for a number of years, as nesting material is added to the pad each year.

The number of pellets incorporated in a nest is difficult to determine, but between one and three distinct pellets are usually visible per square cm of the outer surface. There is probably at least one additional pellet per square cm which is not visible. There are thus about two or three pellets per square cm and with a surface area of 650-800 cm^2 per nest there was a total of 1300-1800 pellets per average sized nest depending on its actual size.

During active nestbuilding, pellets were added to the nest at a rate of about one per minute at the Meriba colony where mud was collected only 20 m from the nests (Table 18). The mean time taken by different individual birds to build a pellet into the nest was remarkably similar, although the actual time for single pellets may differ widely (Table 18). Individual birds spend a mean time of 11,4 s (n= 64; S.D. 4,8; range 4-23) on the mudgathering site and pecked into the mud a mean of 12,4 times (n = 28; S.D. 3,7; range 9-20) before flying away.

TABLE 18

NEST BUILDING STATISTICS AT MERIBA COLONY

Nest Number	**Number Pellets Collected**	**Total Time Spent Building (min)**	**Pellets/Hour**	**Mean time to Collect Pellet * (s)**	**Mean time to Build Pellet (s)**
				Range	Range
II - 4 (1)	28	30	56	23(17-62)	40(22-72)
II - 4 (2)	31	12	155	20(15-48)	40(23-56)
I - 7 (1)	19	19	60	21(16-59)	43(25-60)
I - 5 (1)	35	37	58	22(16-63)	42(22-60)
I - 2 (1)	58	60	58	20(14-40)	44(19-86)

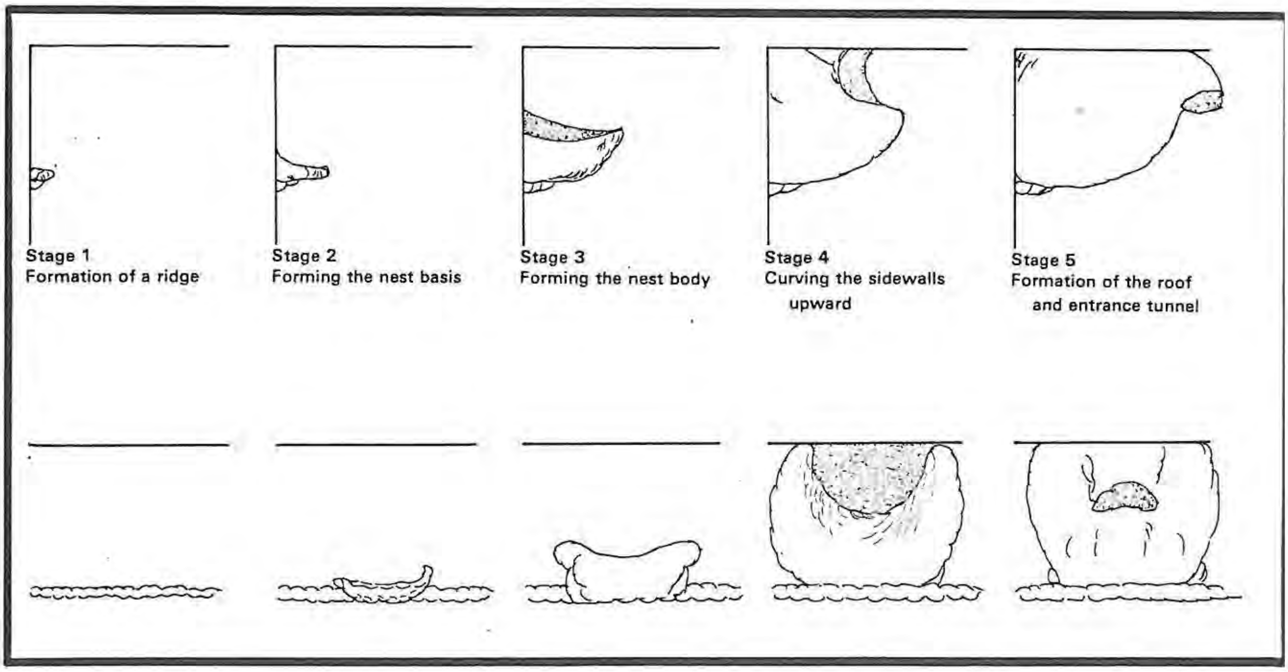
(1) = 1 Individual building
(2) = 2 Individuals building

*Pellets were collected about 20 m from the nests.

The first mud pellets at a new nest site were always deposited in a horizontal ridge (Figure 4-2) when building on a vertical surface. This ridge was at the position of the foothold of the birds when clinging to the vertical surface. This ridge is built by all the individuals squatting at the new site and pellets are deposited on a wider area than is necessary for the base of the nest so that the pellets deposited by individuals next to each other form a continuous ridge. The ridge is then used as a base for the first new nests at this new site.

There were several easily recognizable stages in the construction of the nest. Although there was not always a clearcut separation between the stages, different behaviour patterns were present at each stage. The description that follows is for birds starting nests at a new site on a vertical surface just below the roof of the bridge. Nests built with another existing nest as starting point have basically the same stages, but were usually slightly modified depending on the site.

Stage 1 – Formation of a ridge (Figure 7-10)
After a nesting site has been selected, the birds cling to the surface of the site. This "squatting" at a specific site may last for several days before building starts. The birds selecting the nest sites were all males in the five cases where the sex of the birds was known. Although females were observed to "squat" as well, not one was ever seen to start the nestbuilding. The first mud pellets are placed at the level of the feet of the clinging bird. This is done by the bird bending laterally to the left or right and depositing the pellet against the substrate. After depositing about 50-100 pellets the ridge is formed and it is now quite easy for the building bird to get a foothold on this ridge and effectively guard his site against other squatters.



Stage 1
Formation of a ridge

Stage 2
Forming the nest basis

Stage 3
Forming the nest body

Stage 4
Curving the sidewalls upward

Stage 5
Formation of the roof and entrance tunnel

FIGURE 7-10

A schematic presentation of the different stages of nestbuilding by *Hirundo spilodera*. See the text for details of each stage.

Stage 2 - Forming the nest base

When the ridge was formed, the packing of the mud pellets was concentrated on a specific area of about 10 cm. Here pellets were deposited mostly on top of the ridge to form a thicker ridge about 2-3 cm high and protruding up to 4 cm away from the concrete surface. The outer rim often slopes a bit downward, probably as a start to the depression in the nest. The building bird alighted sideways on this base with the collected mud and then placed the pellet on the outer edge of the base and worked the pellet into the rim with a rapid vibrating movement toward its own body.

Stage 3 - Forming the nest body

By adding mud pellets to the ventral and lateral walls of the nest base, a broad cup was formed. The birds either perched laterally or facing forward when placing the pellets on the edge of the cup.

Stage 4 - Curving the sidewalls upward

The lateral walls of the nest were now extended upward towards the roof of the bridge and the opening still present was being filled in as the roof was reached to form a narrower retort leading to the entrance tunnel. All building was done from inside the nest.

Stage 5 - Formation of the roof and entrance tunnel

When the sidewalls reached the roof of the bridge they were connected and a nest roof was formed by extending the wall downward to form the roof of the entrance tunnel. At the same time the ventral lip of the nest was turned down and narrowed to form a short entrance tunnel facing downward. During this stage material for the nesting pad was collected and placed in the nest.

EGGS, INCUBATION AND FLEDGING

The Egg

The measurements of a sample of eggs of the Cliff Swallow are given in Table 19. Occasionally very small eggs were found. One such egg found in a half completed nest at Leeukop, measured only 16,1 X 11,8 mm and weighed 1,2 g. These small eggs were all very thin shelled and all were laid in nests where no breeding took place such as half completed nests. Normal eggs were white but botched and spotted with various amounts of red-brown and grey, often concentrated at the thick end, but also evenly dispersed over the whole egg (Figure 7-11). In the 1984/85 season a pure white clutch of three eggs were laid by the female of nest WB 20 at The Willows colony. The dimensions of eggs from the same clutch were usually very similar (Figure 7-12) as were the markings on the eggs.

TABLE 19

MEASUREMENTS OF FRESH EGGS OF *HIRUNDO SPILODERA*.

Measurements	n	Mean	S.D.	Range
Length (mm)	81	20,8	1,07	18,5 - 24,7
Width (mm)	81	14,1	0,52	12,9 - 15,0
Mass (g)	26	2,2	0,25	1,5 - 2,6

FIGURE 7-11

A selection of eggs laid by *Hirundo spilodera* showing variation in the amount of speckling, size and shape. Eggs grouped together are from the same clutches.

Clutch size

The clutch size of the Cliff Swallow varied from one to four eggs, with most clutches being two or three eggs. A clutch of six eggs was laid in one nest at the Leeukop B colony in 1983/84 but this was regarded a clear case of "egg dumping" by a second female. Most of the four-egg clutches and probably quite a number of the three-egg clutches were the result of conspecific parasitism which occurred regularly in the Cliff Swallow and which will be discussed later. The mean clutch size was higher in the 1984/85 season than in 1983/84 (Table 20) and no one-egg clutches were laid in the 1984/85 season. However, there were no

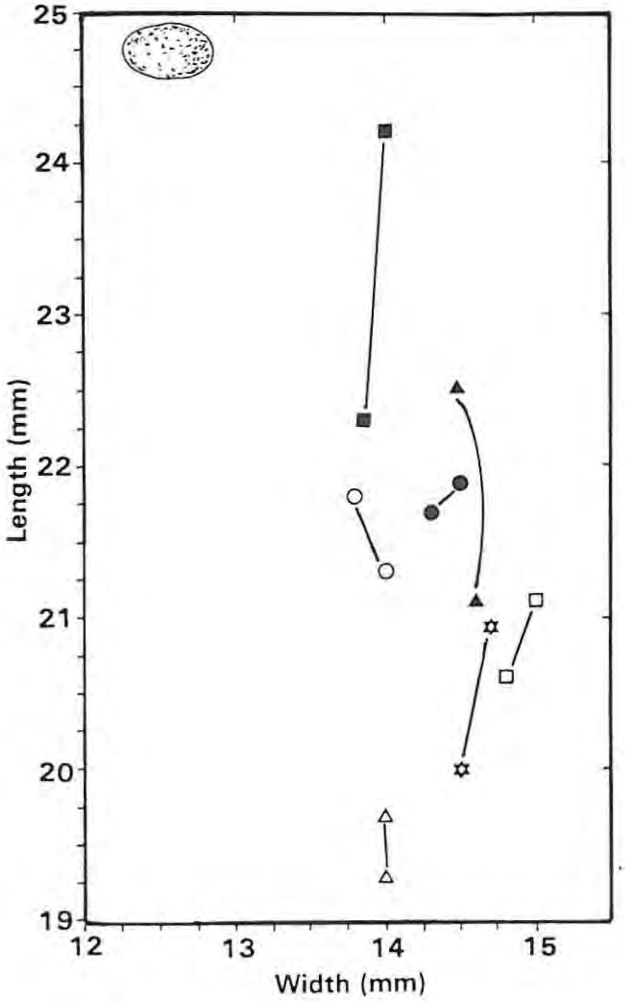


FIGURE 7-12

The sizes of individual eggs of seven two-egg clutches of *Hirundo spilodera* laid at the Leeukop colony in the 1983/84 season.

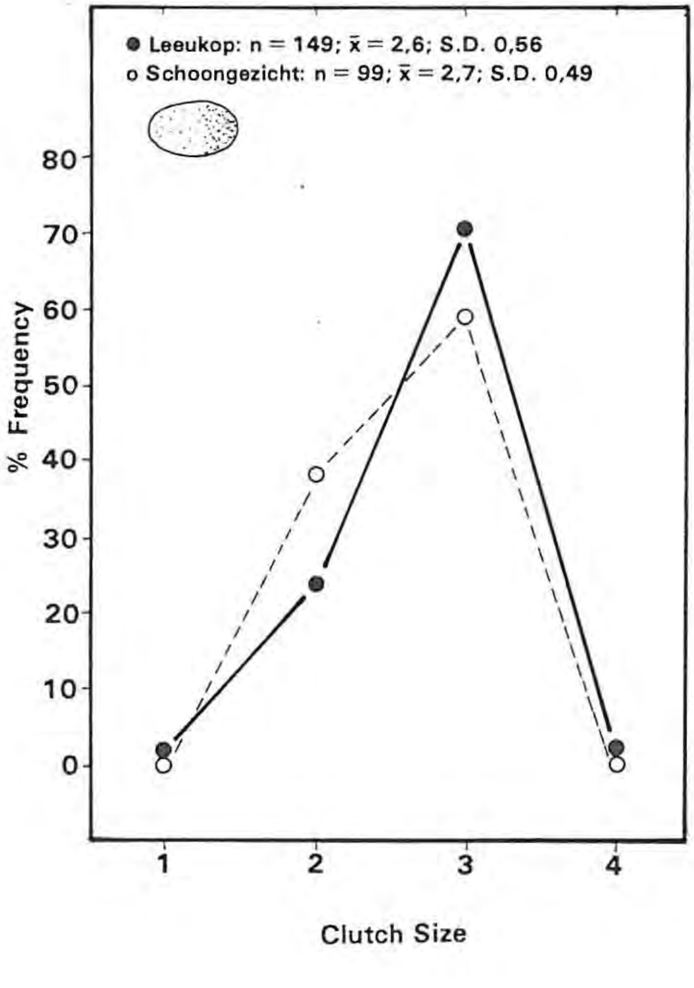


FIGURE 7-13

The frequency of occurrence of different clutch sizes of first clutches laid at the Schoongezicht colony in 1983 and at the Leeukop A colony in 1984 by *Hirundo spilodera.*

TABLE 20

MEAN CLUTCH SIZES OF *HIRUNDO SPILODERA* AT DIFFERENT COLONIES.

Colony and season	Number of clutches	Mean clutch size	S.D.	Range	Median size (% Occurence of median)
Schoongezicht 83/84	455	2,3	0,58	1-4	2 (57,8%)
Leeukop A 83/84	154	2,3	0,58	1-3	2 (55,8%)
Leeukop B 83/84	70	2,3	0,56	1-4	2 (55,1%)
Meriba 83/84	36	2,3	0,52	1-3	2 (58,3%)
Driekloof 83/84	29	2,6	0,51	2-3	3 (55,2%)
Leeukop A 84/85	230	2,7	0,56	1-4	3 (62,1%)
Leeukop B 84/85	15	2,3	0,50	2-3	2 (66,7%)
Driekloof 84/85	89	2,6	0,55	2-4	3 (52,8%)
The Willows 84/85	148	2,5	0,61	1-4	2 (50,0%)
ALL TOTALS	1 226	2,4	0,55	1-4	2 or 3

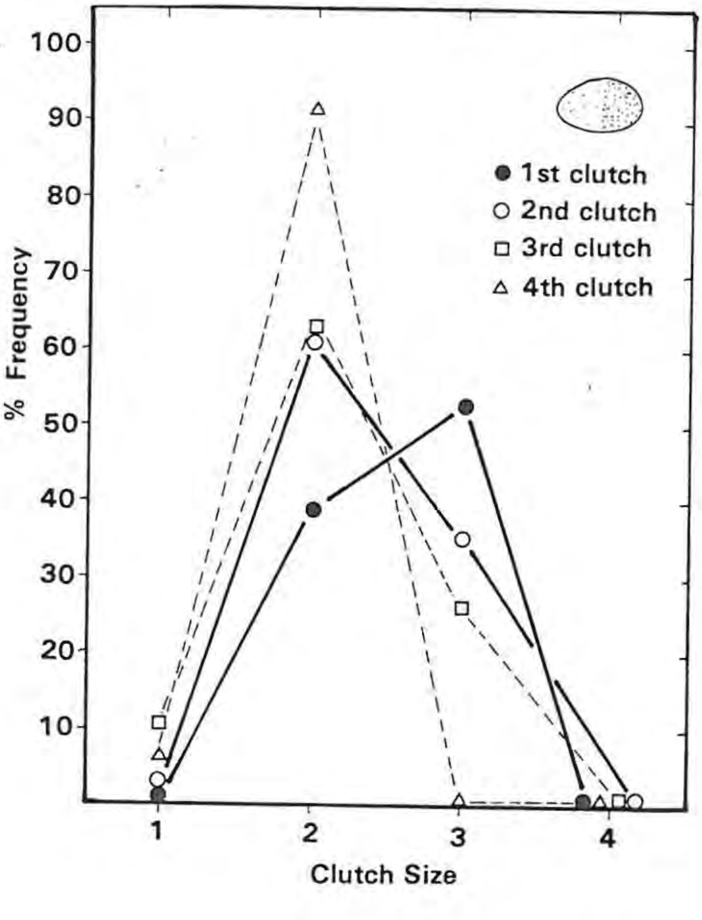


FIGURE 7-14

The frequency of occurrence of clutch sizes of first, second, third and fourth breeding attempts of *Hirundo spilodera* at the Schoongezicht colony in the 1983/84 season.

● $\bar{x} = 2,56$, S.D. 0,49
o $\bar{x} = 2,37$, S.D. 0,51
□ $\bar{x} = 2,17$, S.D. 0,60
△ $\bar{x} = 1,92$, S.D. 0.27

Mean clutch sizes are not significantly different for first, second, third and fourth clutches of the season.

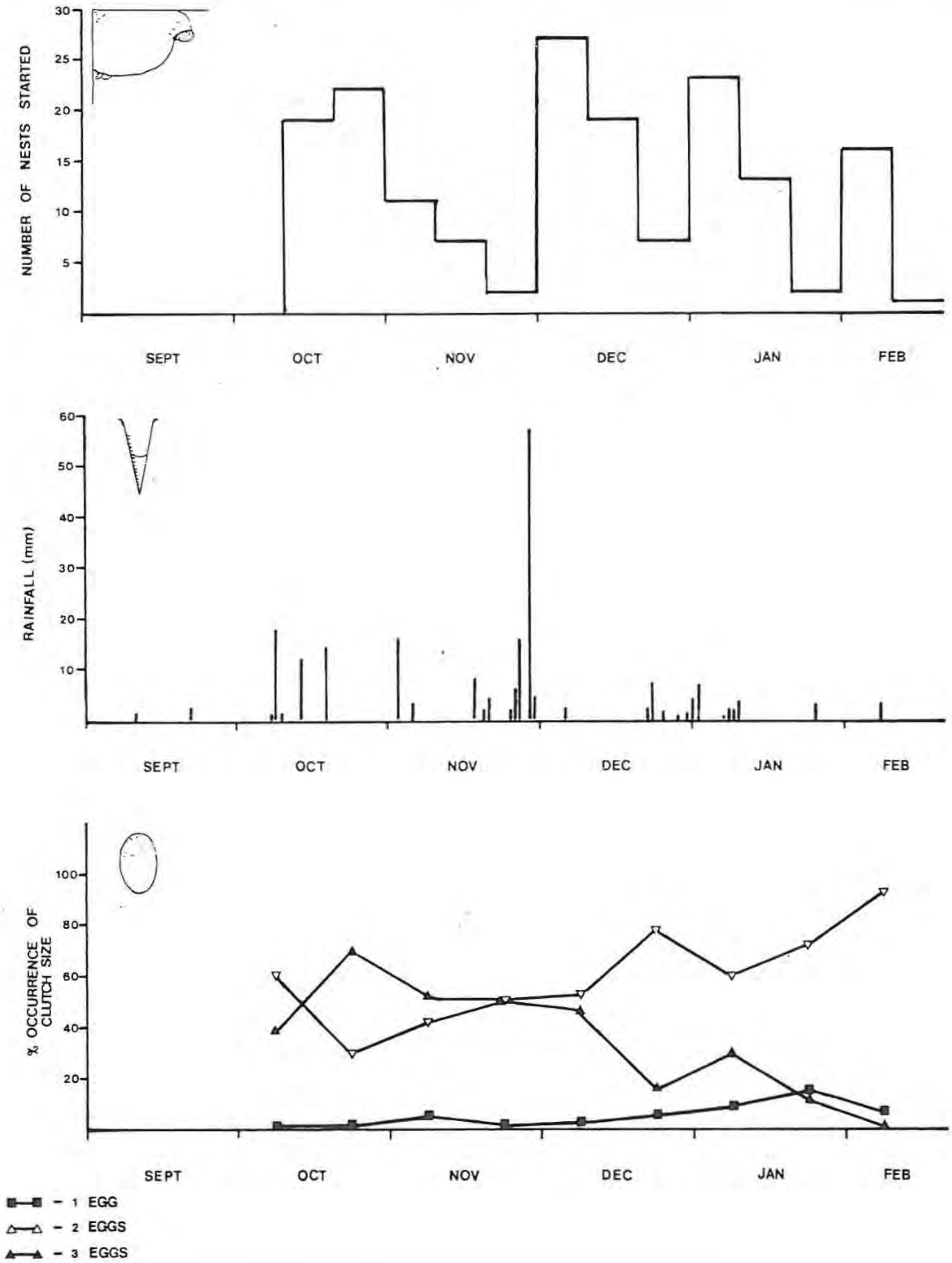


FIGURE 7-15

The number of clutches started per 10-day period by *Hirundo spilodera* at the Schoongezicht colony in the 1983/84 breeding season. This is compared with the daily rainfall and the percentage occurrence of different clutch sizes during the first and second halves of each month.

significant differences between the mean clutch sizes at the same colony in different years. (Table 20). Three-egg clutches were more frequent in first clutches (Figure 7-13) while two-egg clutches again were more frequent in second, third and fourth clutches (Figure 7-14). At the Schoongezicht colony there was a steady decline in the number of three-egg clutches laid throughout the season, while two-egg clutches were more often laid later in the season than early (Figure 7-15).

Egg-laying and incubation

Eggs were laid at 24-hour intervals till the clutch was complete. This occurred during the night or early morning hours in the seven nests checked at 19h00 one day and at 05h30 the next morning.

It was not possible to establish when incubation started as birds would often spend considerable periods inside the nest and slept there at night whether there were eggs in the nest or not. However, as chicks often hatched at intervals it is probably safe to assume that at least some incubation took place as soon as the first egg was laid, even though this may not be deliberate incubation as such.

The incubation period of the Cliff Swallow is given as 14 days by Maclean (1985) and 14,2 days by Burgerjon (1964). The 16 cases where exact laying and hatching dates of marked eggs were known, the mean incubation period was 14,6 days (Table 21). Two incubation periods of 16 days were recorded at single-egg clutches. The exact hatching times of three marked eggs were known, all hatching between 11h00 and 13h00 giving weight to the calculated period of 14,6 days. Eggs were probably laid in the early hours of the morning.

TABLE 21

INCUBATION TIME AND NESTLING PERIOD OF *HIRUNDO SPILODERA*.

Period measured	Number of observations	Mean length of period (Days)	Range of observations	S.D. (Days)	S.E. (Days)
Incubation time	16	14,6	14-16	0,72	0,18
Nestling period	21	24,1	23-26	0,86	0,19

Incubation rate

Although the male Cliff Swallow does not possess a featherless brood patch like the female it was well established that both sexes incubate as will be shown later. The mean time of incubation bouts for all birds of both sexes observed, was 9,2 min with the shortest period being just over 1 minute and the longest 27 minutes. At nest I-1 at Meriba, the female incubated for a mean of 12,0 minutes (4-27) while the males' periods had a mean of 10,14 (3-22). The attentive periods of the female and male at nest W 20 at The Willows colony were 7,3 (4-12) minutes and 7,6 (5-11) minutes respectively over a 6 hour period.

FIGURE 7-16

(a) **The broodpatch of a female *Hirundo spilodera* at the height of the breeding season.**
(b) **The broodpatch of a female *Hirundo spilodera* at the end of the breeding season when the feathering of the patch is about half complete.**

The incubating bird does not normally leave the nest before its mate comes to relieve it except in "alarm" situations when all incubating and brooding birds would leave the nests. The reasons for this close attentiveness when incubating will be discussed later.

Nest relief was quite simple. The relieving bird flew to the nest and clung to the entrance while the sitting bird left. The sitting bird would only leave if the clinging bird was its mate, other "strange" birds were chased away by the sitting bird indicating that mates could recognize each other as is discussed further in the section on vocalizations. The relieving bird sometimes called before alighting at the nest, prompting the sitting bird to leave. The bird leaving, whether the male or female, nearly always gave the "nest relief warble" when leaving the nest.

Nest and egg temperatures during incubation

Although only the female Cliff Swallow posessed a brood patch devoid of feathers (Figure 7-16) both sexes incubated for about equal periods. The temperatures measured at the skin surface of the female and male brood patches were also nearly identical (Males: x̄ = 40,6° C; S.D. 1,14; range 37,8-42,6; n = 23. Females: x̄ = 41,2° C; S.D. 0,98; range 39,4-42,9; n = 23).

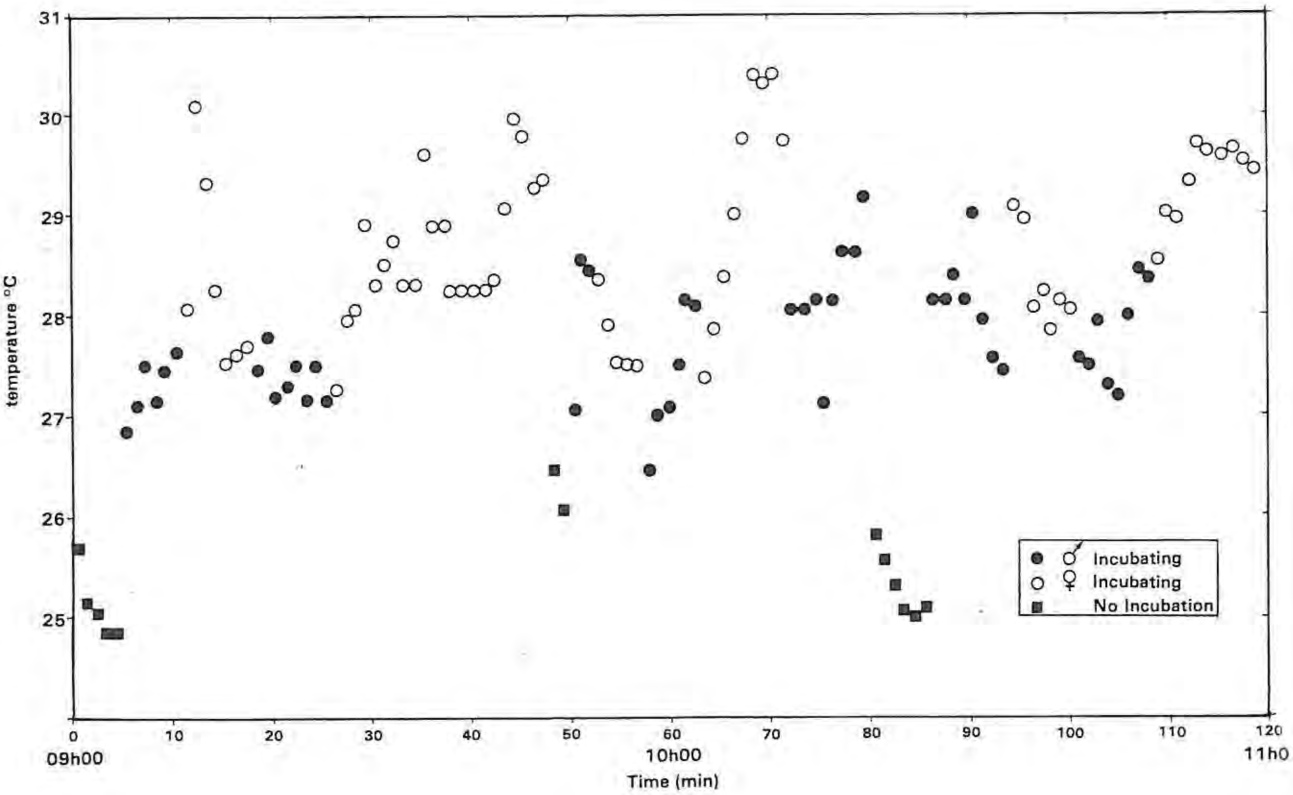


FIGURE 7-17

Egg temperatures of *Hirundo spilodera* during male (●) and female (○) incubation bouts in nest W1 containing a clutch of three eggs. Air temperatures outside the nest were between 18° C and 24° C.

This would indicate that males and females might have been equally effective as incubators. Figure 7-17 gives the egg temperatures when the male and female of nest W 1 were incubating over a 2 h period. Although the female maintained a higher mean temperature ($\bar{x}$ = 28,7° C; S.D. 0,84) than the male ($\bar{x}$ = 27,8° C; S.D. 0,61) both maintained a higher temperature when incubating than the air temperature when the eggs were not covered (Figure 7-17). It was of course not possible to determine, due to the closed nest, how tightly the male sat but it seems as if the male was truly incubating. The air temperature between eggs differed widely between different nests but in all the nests the eggs hatched (Figure 7-18).

The nest temperatures of occupied nests were higher than the ambient temperatures up to about 24° C after which the temperatures were generally lower than that of the environment (Figure 7-19). The temperatures in unoccupied nests kept rising with the ambient temperatures and were with few exceptions higher than the ambient temperatures (Figure 7-19).

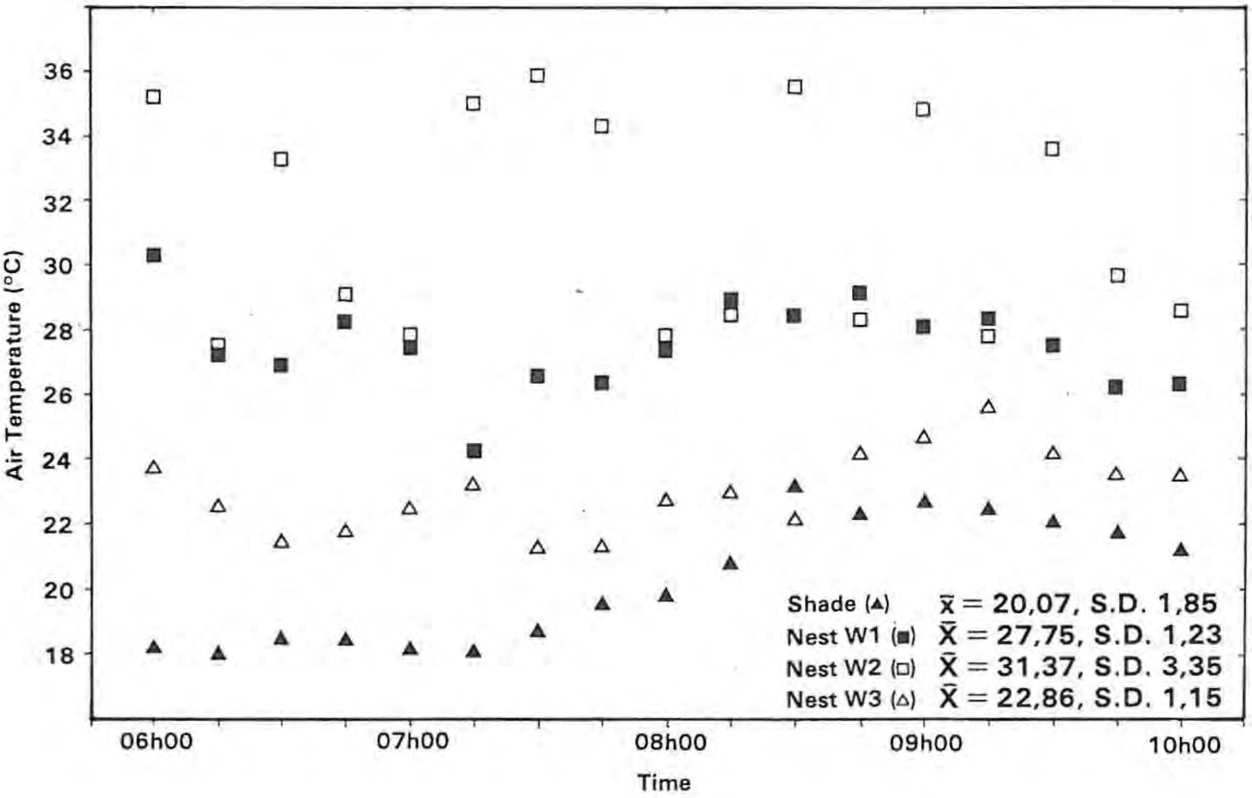


FIGURE 7-18

Air temperature inside three nests of *Hirundo spilodera* at "The Willows". Nest W1 (■) contained three eggs and a nestpad. Nest W3 (△) contained three eggs with virtually no nestpad. Nest W2 (□) contained three one-day old chicks. The ambient temperature (▲) is also given.

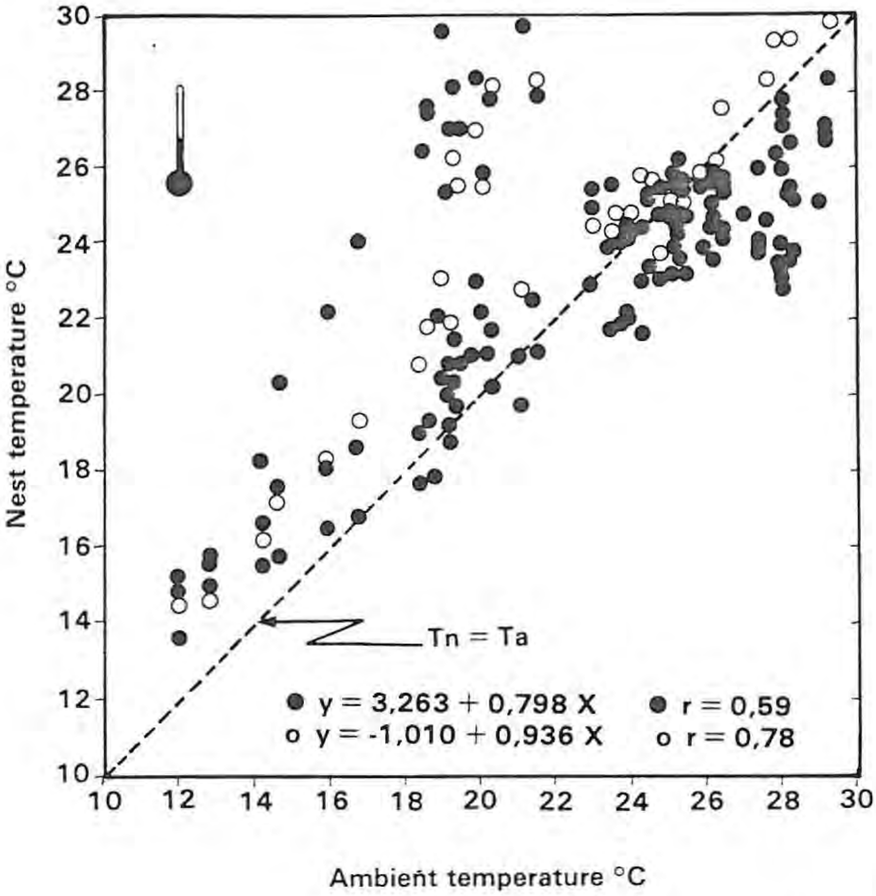


FIGURE 7-19

Air temperature (Tn) in *Hirundo spilodera* nests as a function of ambient temperature (Ta). Closed circles (●) were occupied nests and open circles (o) unoccupied nests.

The nestling period

Maclean (1985) gives the nestling period of the Cliff Swallow as 24,5 days while Burgerjon (1964) gives it as 24,55 - 25,42 days depending on the frequency of observation at nests. A mean nestling period of 24,1 days was recorded during this study (Table 21). Two nestling periods of 23 days were recorded for single chicks. The period of 24,1 days might be slightly biased as the regular inspections of the nests might have caused the chicks to fly earlier. As can be seen from the section on nestling growth, the chicks were capable of flight on about day 23 when the wings were more than 93 mm in length. Chicks which left the nests when these were inspected were all quite capable of flying, and it seems as if they would not leave the nests more than a day early when disturbed.

Chicks did return to the nest after their initial departure for at least four days. Two instances were recorded where fledglings which have left the nest earlier (one and three days

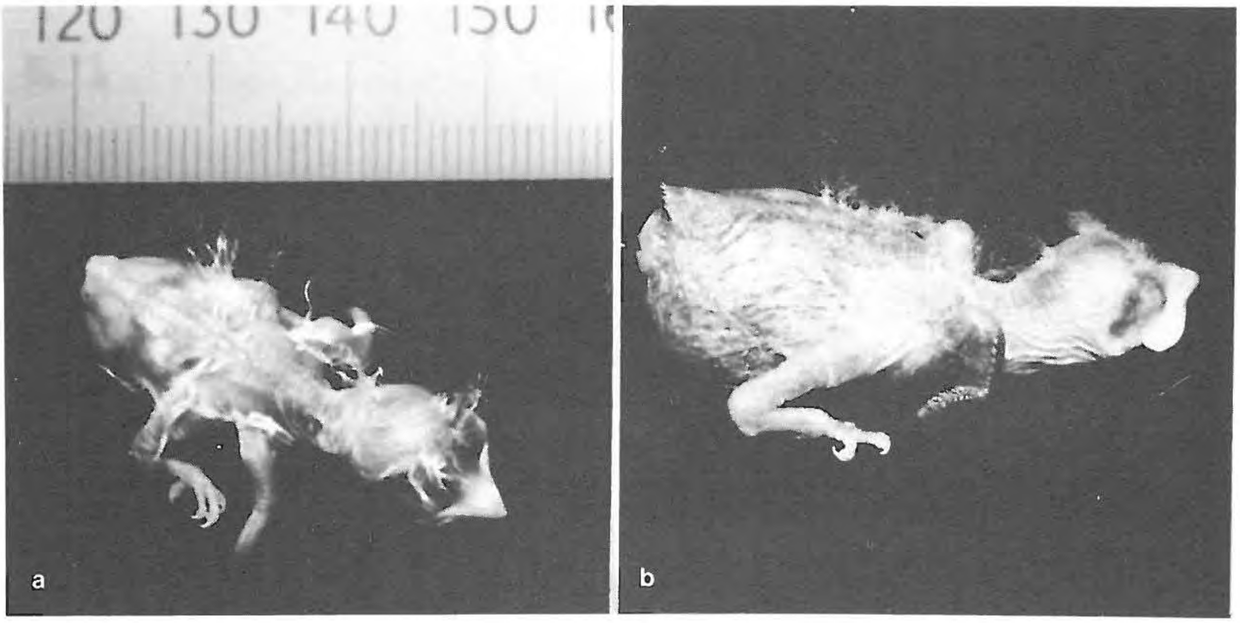


FIGURE 7-20

One day (a) and five day (b) old *Hirundo spilodera* chicks. See text for details of development.

respectively) were lured into the nest by one of the parent birds in the nest. The sequence of events was the same in both cases. The chick alighted on a nearby (0,3 m away) half completed but unoccupied nest and started giving the chick contact call, to which the adult bird replied with the nest relief warble. After about 20 seconds the chick flew to the nest and alighted at the opening. The adult bird inside the nest then tried to pull the chick inside by grabbing it by its bill. After 30 seconds of this tug of war the adult released the chick which entered the nest on its own accord.

Development of the chicks

At hatching the chicks are blind with a pink skin colour (Figure 7-20). The gape is yellow and

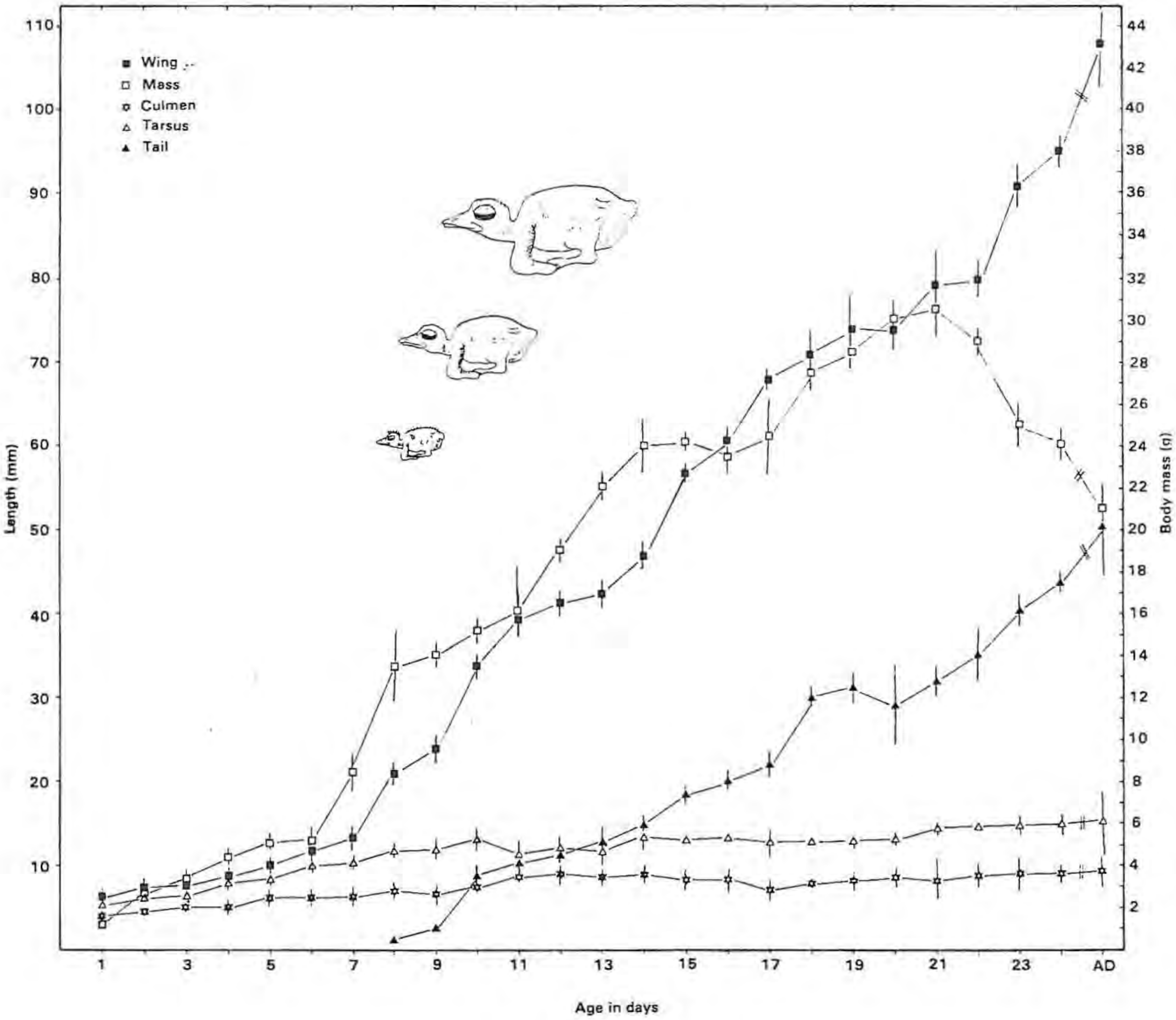


FIGURE 7-21

The growth of *Hirundo spilodera* nestlings. The measurements of adults (AD) are the mean measurements for a sample of 50 birds netted at Driekloof. At least four chicks were measured at each age and the means are given. Day 1 is within 24h of hatching. Verticle lines are 1 S.D. from the mean.

the inside of the mouth is a pale orange. On about the third or fourth day both the blue-black feathers as well as the rufous white areas on the body show papillae where the feathers were going to appear (Figure 7-20). The eyes started to open at about day four and were fully open by day nine. The feathers of the primaries break the sheath on about day nine or ten and the tail feathers on day 11 or 12. The culmen and tarsus reaches adult size about halfway through the nestling period on about day 12 (Figure 7-21) while maximum weight of the nestlings is reached between days 19 and 22, when the chicks can weigh as much as 31 g which is 11 g more than the average adult weight (Table 1).

The downy plumes on the head, above the eye, were only lost when the chicks left the nest and some free flying young were even caught with the plumes still present. The yellow gape only disappeared completely about 4-6 weeks after leaving the nest. When leaving the nest, the buff edgings of the feathers on the back are just about gone, but the buff edges to the tertiaries remain for most of the season till the chicks depart for their winter grounds.

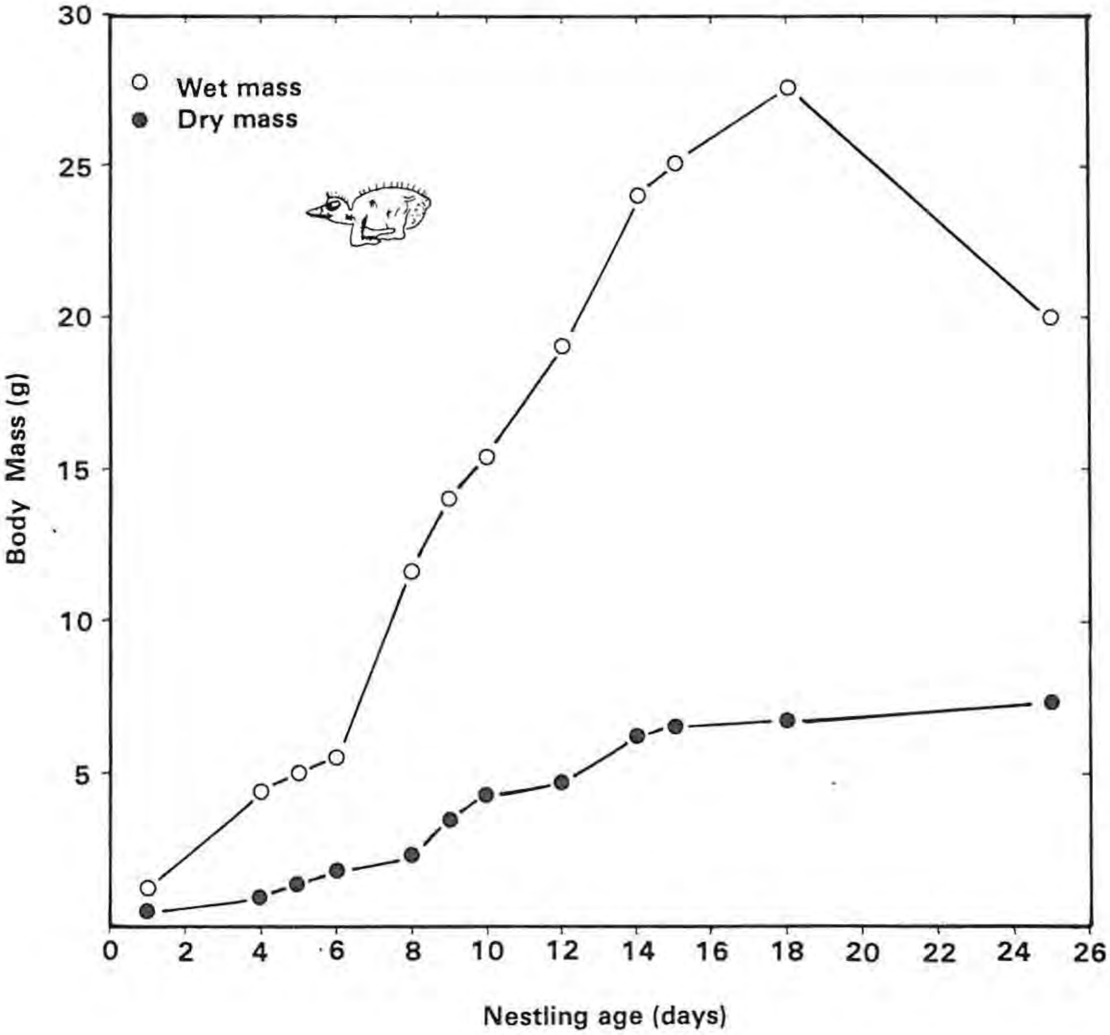


FIGURE 7-22

Mean wet and dry mass of *Hirundo spilodera* chicks of different ages. The 27 carcasses were weighed wet and then dried for seven days at 100° C. By drying carcasses at this temperature some of the more volatile lipids might be lost. The dry mass might thus be slightly underestimated.

The live weight of nestlings reached an asymptote during the nestling period around day 20 or 21 and then declined until fledging (Figure 7-21). The increase in dry mass of nestling gave a sigmoidal graph (Figure 7-22) without declining, indicating that the decline in wet mass is the result of the loss of water during the final days in the nest. The growth of the wing and primary feathers approached linearity (Figure 7-21) but it is in fact slightly sigmoidal. The mean wing length of the chicks when leaving the nest was 95 mm. This is about as soon as the chicks were capable of sustained flight. It was noticed that the handreared chicks could gain

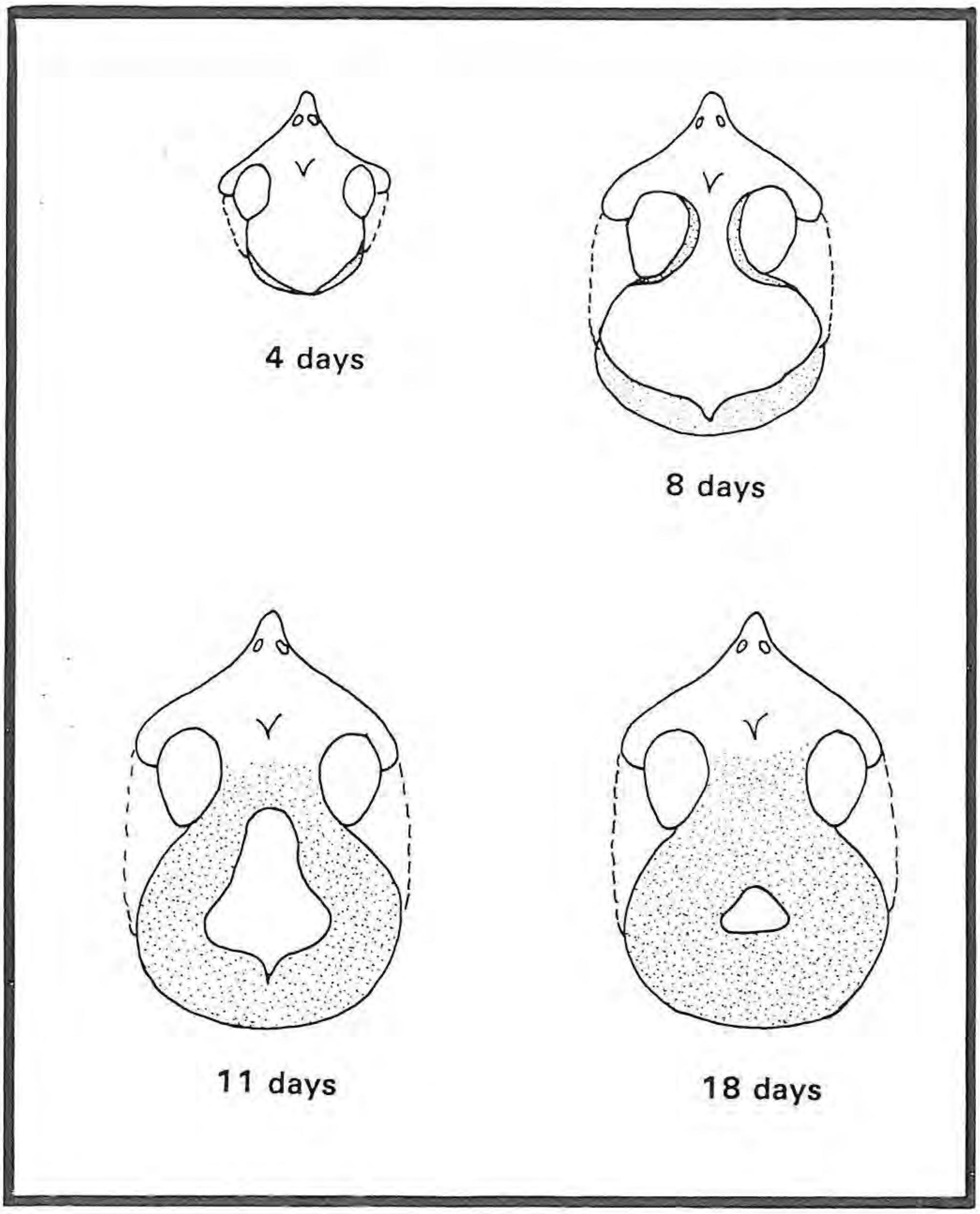


FIGURE 7-23

A schematic representation of the skull ossification stages of *Hirundo spilodera* chicks. Stippled areas are ossified.

height only when the wing was more than 93 mm, but they were probably not capable yet of sustained flight at this stage. The quills of the rectricies only broke the skin on day 8 and the growth of the tail was also nearly linear (Figure 7-21) but about 3 mm short of the adult tail length when the chicks left the nest. Both the tarsus and culmen appeared to reach adult length about half way through the nestling period.

Skull ossification started at the back of the skull and ossified areas were detected as early as day three. The skull around the occipital area started ossification at about one week and when the chicks reached 11 days only the area on top of the skull was still not ossified (Figure 7-23). Full ossification was probably attained at or shortly after fledging.

Feeding of the chicks

Feeding of Cliff Swallow chicks was done by both parents in about equal proportions in the few cases where the sex of the feeding adults was known (Table 22). The food was carried in the bill and not formed into in food bolus as far as could be established. Adults caught by mist net when feeding young always had the food in the bill, even very small items. Large items such as grasshoppers or large moths were often seen carried in the bill to the nest. Up to about the 10th day the chicks were fed in the nest or the parent bird went into the nest at least partly to feed the chicks. It was thus not possible to determine feeding rates during the first few days of brooding, as all visits to the nest were not feeding visits. From about day 12 the chicks position themselves so that food is received at the nest opening.

TABLE 22

FEEDING RATES OF *HIRUNDO SPILODERA* AT SEVERAL NESTS.

Nest	Date	Number of young	Age of young (days)	Total observation time (min)	Number of feeds Parent 1	Number of feeds Parent 2	Total feeds	Minutes/ feed	Feeds/ young/h
D38	24.11.83	3	20	676	29	40	69	9,9	2,04
D42	24.11.83	1	20	632	?	?	68	9,3	6,46
D41	24.11.83	2	16	630	23 (♀)	25 (♂)	48	13,1	2,29
D99	29.11.83	2	20	120	18 (♀)	16 (♂)	34	3,5	8,50
D101	29.11.83	2	20	120	?	?	18	6,6	4,50
D102	29.11.83	2	17	120	11	26	37	3,2	9,00
E	25.10.84	3	21	320	?	?	75	4,3	4,69
A	25.10.84	3	21	320	?	?	73	4,4	4,50
B	16.10.84	3	12	360	59 (♀)	53 (♂)	112	3,2	6,17

The number of feeds that chicks received in the nest per hour varied widely at the different nests and on different days (Table 22). There was no indication that feeding visits were more frequent where the broods were large or less frequent when small broods were being fed. The rate of feeding chicks probably depended on the weather and the availability of food as well as the time of day when the observations were done and the individuality of the feeding birds. More extensive sampling throughout the nestling period and at more nests in future would probably give some clues to the variability found in the feeding rates. Feeding rate was not the same throughout the day (Figure 7-24 & Figure 7-25). In the three nests observed for two hours each in the morning, at midday and in the afternoon all showed the highest

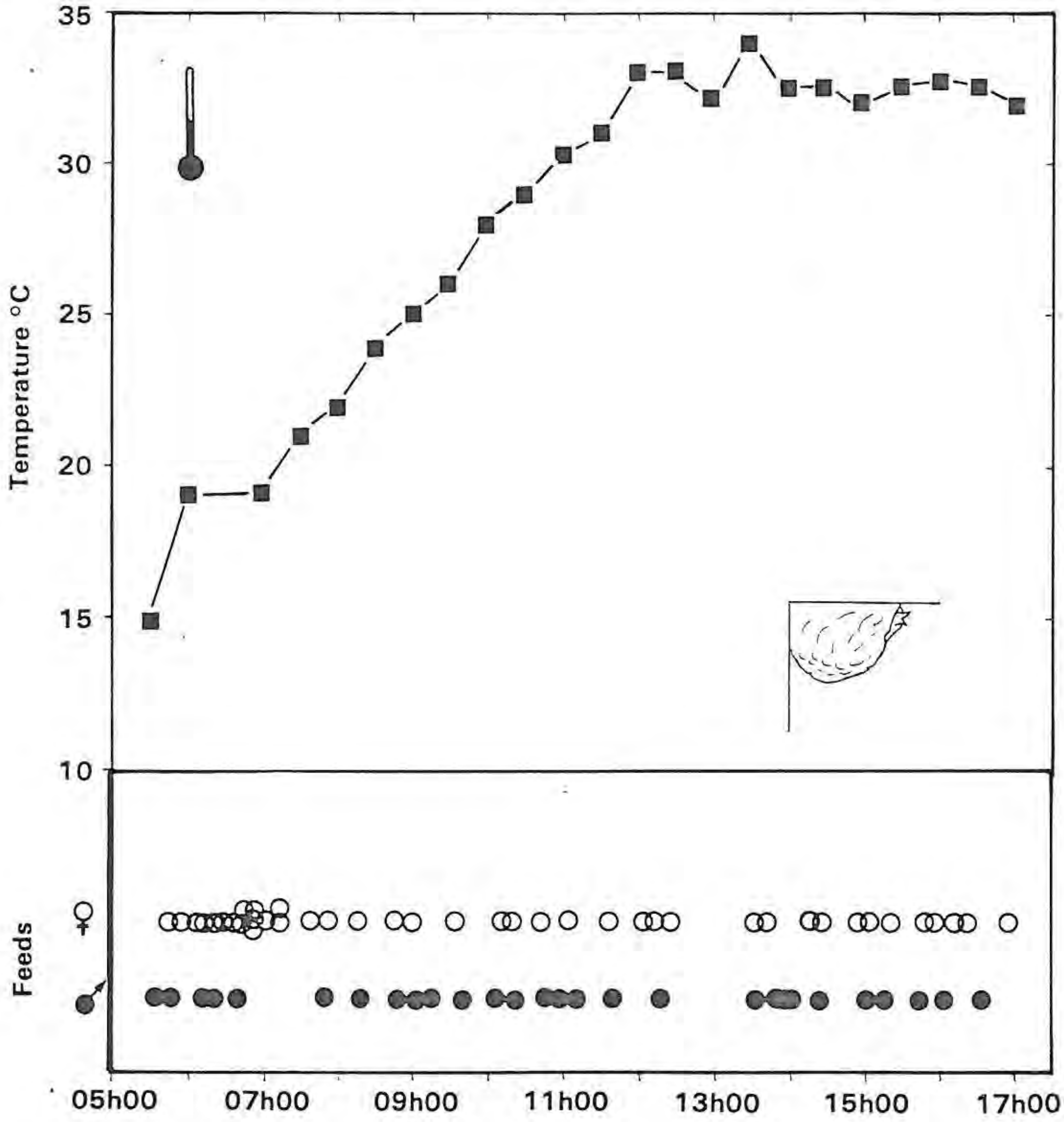


FIGURE 7-24

Feeding rate of *Hirundo spilodera* chicks at nest D38 of the Schoongezicht colony in relation to air temperature over a 12h period.

rate of feeding during the midday hours (Table 23) when the prey was relatively abundant but not as abundant as in the late afternoon (Table 23). During the morning feeding period when foraging was probably more difficult because of the lower availability of prey, the feeding rate was not only less but visits to the nest were more or less evenly spaced (Figure 7-25). During the midday and afternoon periods the visits to the nest were in quick succession for periods of 30 - 45 minutes (Figure 7-25). On a very hot day in the 1983/84 season the chicks in nest D 38 which was under observation were not fed for one hour when the temperature reached 34° C.

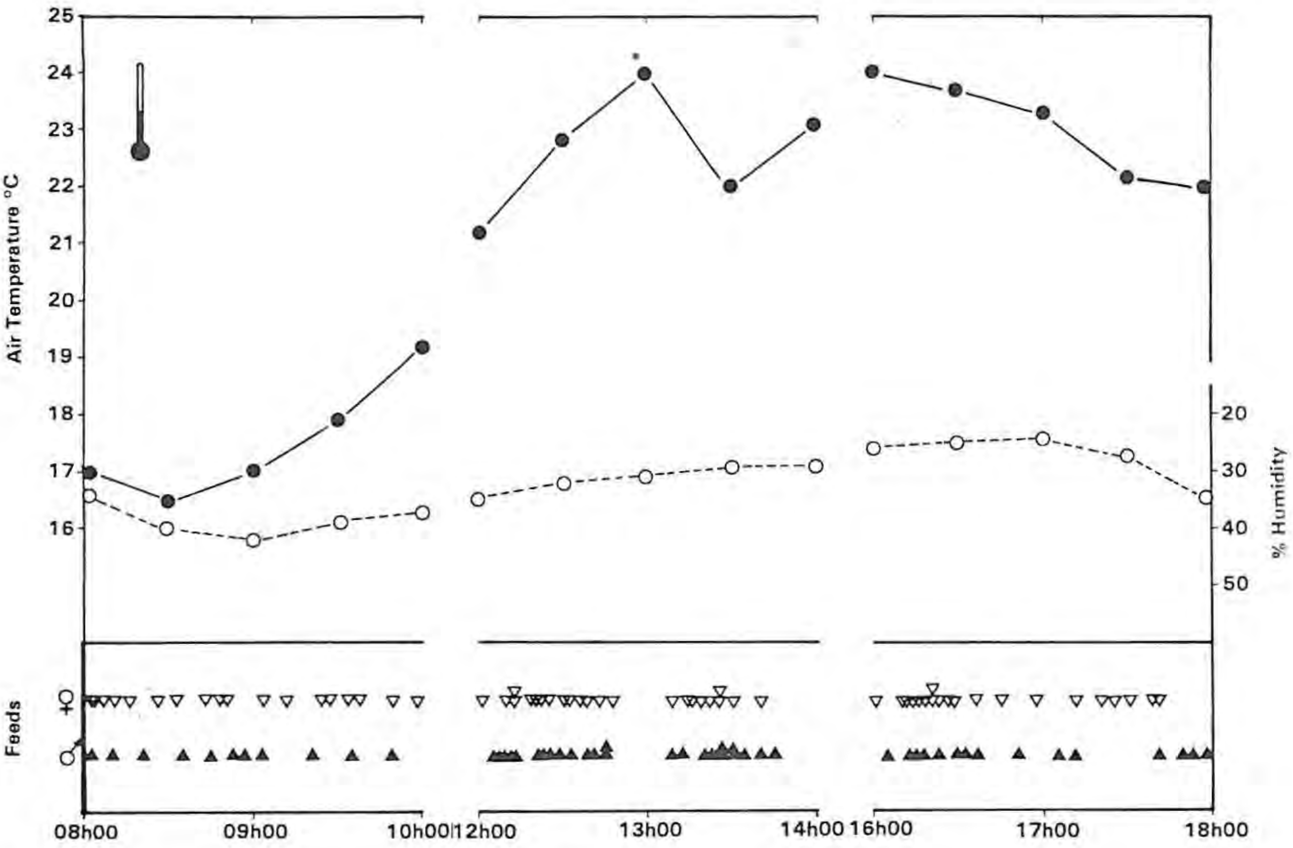


FIGURE 7-25

Feeding rate of *Hirundo spilodera* chicks for two-hour periods in the morning, at midday and in the afternoon in relation to air temperature and humidity as measured at nest W15 in "The Willows" colony.

TIMING OF BREEDING

The breeding season

The first Cliff Swallows reached their breeding colonies around Bloemfontein during the second and first weeks of August respectively in the 1983/84 and 1984/85 seasons. Old nests were immediately occupied but building on new nests only started later when mud became

TABLE 23

FEEDING RATES OF *HIRUNDO SPILODERA* DURING DIFFERENT TIMES OF THE DAY IN RELATION TO THE AVAILABILITY OF PREY AND TEMPERATURE.

Observation	**TIME**		
	08h00-10h00	**12h00-14h00**	**16h00-18h00**
Nest B:			
Number of feeds	29	48	35
Prey available*	41	183	316
Temperature (° C)	17 (09h00)	21 (13h00)	25 (17h00)
Nest A:			
Number of feeds	15	43	20
Prey available	26	120	258
Temperature (° C)	15 (09h00)	22 (13h00)	28 (17h00)
Nest E:			
Number of feeds	19	38	22
Prey available	26	120	258
Temperature (° C)	15 (09h00)	22 (13h00)	28 (17h00)

*Expressed as the number of Diptera in suction trap samples during the period.

available. The start of breeding probably depended on several factors, one of which was the size of the colony. Breeding in both years started earlier in the larger, well established colonies than in the smaller and newer colonies (Figure 7-26) and ended earlier in the 1984/85 season than in 1983/84. In 1984/85 the first eggs were laid on 20 August in the Driekloof colony, while at the Leeukop colony the first eggs were only laid on 13 September. At the Schoongezicht colony the first eggs were laid on 23 September in 1983 while in the newer part of the colony breeding only started on 14 October 1983 (Figure 7-15). The early breeding in the 1984/85 season was probably caused by the late winter rains on 30 & 31 August and the relatively warm weather after this rain. Rain, or its effects, had a definite influence on the timing of breeding and the starting of new clutches, especially in the newer colonies where nestbuilding preceded egg laying. Figure 7-15 shows that a number of breeding peaks occurred during the 1983/84 season at the Schoongezicht colony. Breeding only started after good rains on 8 October and after some more rain on 13 and 18 October a peak occurred during the last 10 days of October. A second breeding peak occurred after

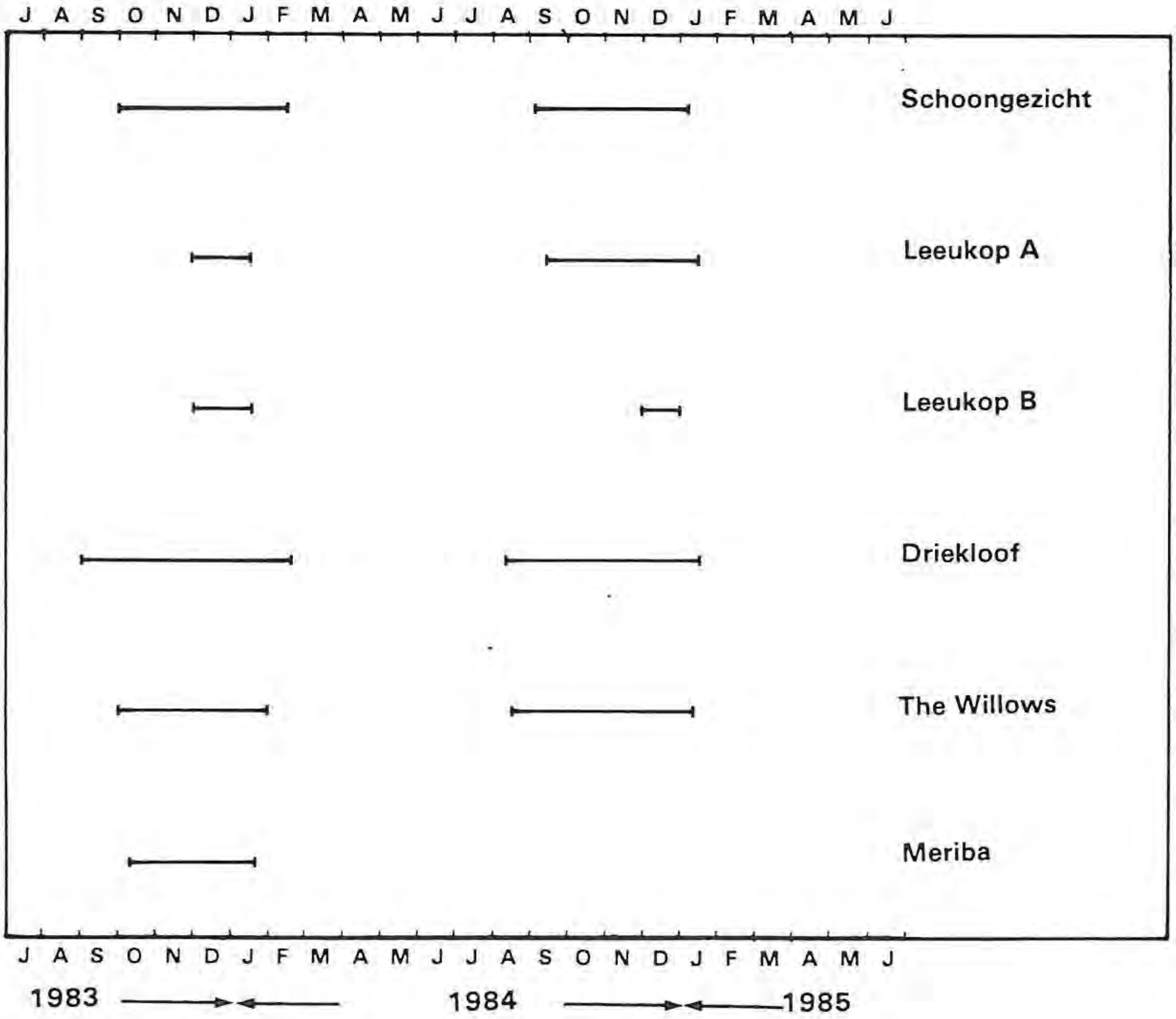


FIGURE 7-26

The timing of the breeding season of *Hirundo spilodera* at different colonies during two breeding seasons.

exceptionally good rains late in November while a third peak occurred early in January 1984 after a relatively cool period of 10 days during which 25 mm of rain fell late in December The peak early in February was the result of replacement clutches in a part of the colony not used earlier by pairs which lost nest through human destruction on 25 January (Figure 7-15). Rainfall therefore was probably both the main direct proximate factor, as well as indirectly causing a better food supply for some period (eg. see Earlé 1981c). It also seemed as if a certain minimal amount of rain was needed before there was an upsurge in the number of new clutches started. The 19 mm of rain early in November 1983 did not trigger off breeding (Figure 7-15) but on the other hand a period of cool weather late in January 1984, without much rain resulted in 16 new clutches started during the first 10 day period in February.

Physiologically the Cliff Swallow males seemed to be in breeding condition for at least six months, September to February (Figure 7-27), but some birds started breeding as early as August in the 1984/85 season indicating that some individuals at least could breed probably for even seven months. Retrogression of the testes started in March when only a single testis out of 18 in the sample was more than 5 mm in length (Figure 7-27). Active testes were between 6 and 10,5 mm in length.

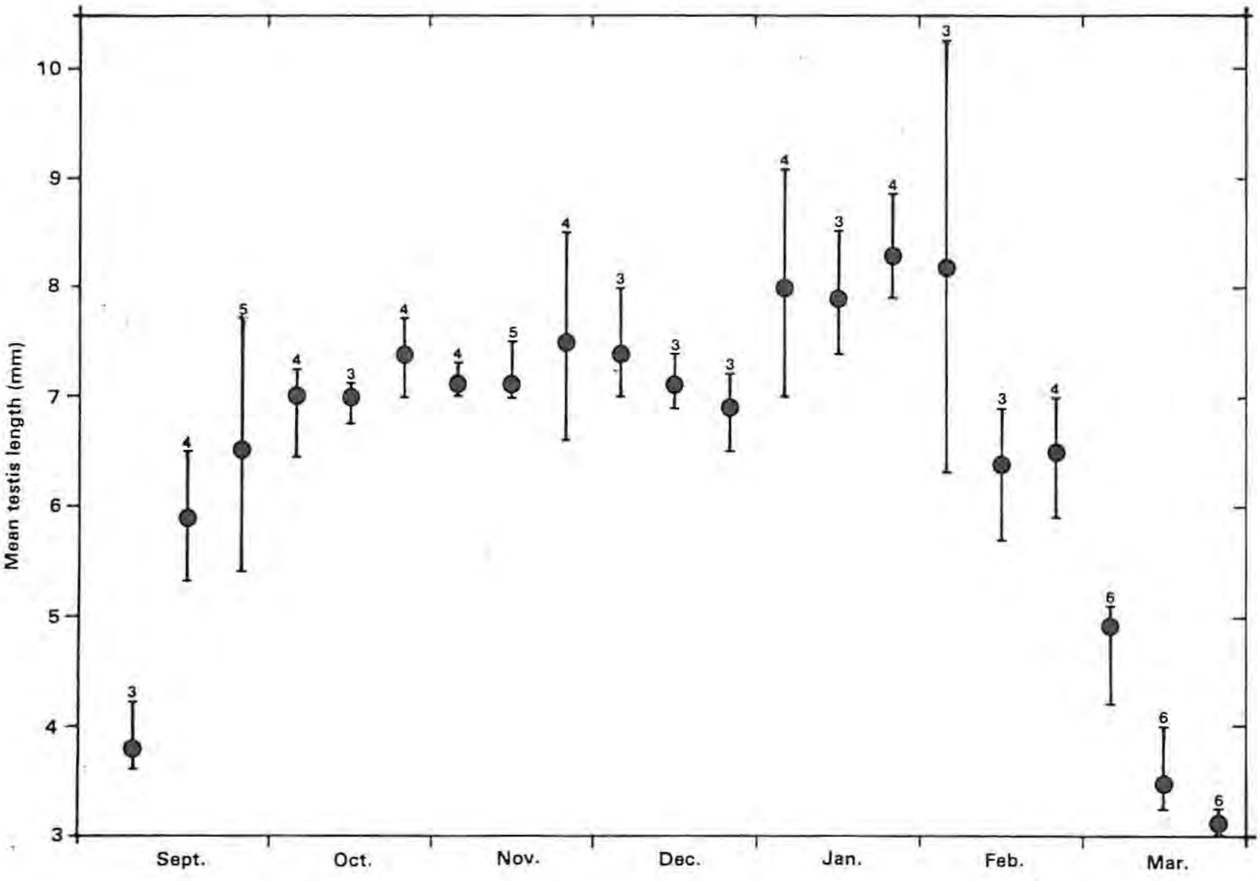


FIGURE 7-27

Testis length of *Hirundo spilodera* specimens collected during the 1983/84 season. Vertical bars indicate the range of the measurements and numbers the sample size.

Breeding success

Because of the frequent checking of nests during this study there was no need to calculate breeding success with the method suggested by Mayfield (1961) whereby the time that the nest was exposed is taken into consideration. Breeding success was expressed as the percentage of eggs laid which gave rise to chicks that leave the nest successfully. This percentage varied between years as well as between the different colonies (Table 24). There were very few pairs which made more than one breeding attempt and were totally unsuccessful in producing fledglings (Table 25). At the Schoongezicht colony 14,3% of the

TABLE 24

BREEDING SUCCESS OF *HIRUNDO SPILODERA* AT SEVERAL COLONIES OVER TWO BREEDING SEASONS.

	Colony	Number of pairs	Number of breeding birds	Number breeding attempts	Number of eggs laid	Number of young fledging	Young: egg success (%)	Recruitment Young: adult
83/84 Season	Schoongezicht	91	182	161	360	167	46,4	0,9 : 1,0
	Leeukop A	158	316	164	350*	285	81,4	0,9 : 1,0
	Leeukop B	74	148	81	176**	98	55,7	0,7 : 1,0
	Driekloof	25	50	30	81	55	67,9	1,1 : 1,0
	Meriba	33	66	44	98	42	42,9	0,6 : 1,0
Totals 83/84		381	762	480	1 065	647	60,8	0,8 : 1,0
84/85 Season	Leeukop A	195	390	234	611	403	66,0	1,0 : 1,0
	Leeukop B	13	26	15	35	20	57,1	0,8 : 1,0
	Driekloof	36	72	64	153	55	35,9	0,8 : 1,0
	The Willows	99	198	158	381	143	37,5	0,7 : 1,0
Totals 84/85		343	686	471	1 180	621	52,6	0,9 : 1,0
Totals 83/84 & 84/85		724	1 448	951	2 245	1 268	56,5	0,87 : 1,0

*excluding 41 eggs of which the outcome was not known.
**excluding 8 eggs of which the outcome was not known.

pairs had both or all three of their nesting attempts successful. In 33% of all pairs only making one attempt the nest fell down and because of the shortage of mud due to the drought there was no chance of making a second attempt, at least not at the same nest site (Table 26).

The overall breeding success of the Cliff Swallow was no higher than that of most other members of the Hirundinidae (Table 27) while the recruitment rate of 0,9 young per adult bird means that the population is nearly doubled by the end of the breeding season (Table 24).

TABLE 25

BREEDING SUCCESS OF A SELECTION OF INDIVIDUAL *HIRUNDO SPILODERA* PAIRS BREEDING AT THE SCHOONGEZICHT COLONY DURING THE 1983/84 SEASON.

Nest Number	Number of breeding attempts	Number of eggs laid	Number of Young hatched	Number of Young fledged	%Success Young/ eggs
D35	4	8	3	3	37,5
D41	2	5	5	5	100
D43	3	7	4	4	57,1
D47	3	7	6	5	71,4
D48	3	7	5	5	71,4
D50	4	11	9	5	45,5
D51	4	8	6	4	50,0
D53	2	4	4	4	100
D57	3	5	3	0	0,0
D63	2	5	2	2	40,0
D65	3	9	8	6	66,7
D89	3	7	4	2	28,6
D93	2	5	4	4	80,0
D99	3	6	6	4	66,7
D101	3	7	7	6	85,7

Conspecific parasitism

Conspecific brood parasitism occurred to a greater or lesser extent in all the colonies where breeding records were kept. Behavioural observations were not made at all the colonies, and it was thus impossible to tell if the observed clutch size was the real size or whether the clutch was parasitized. At the Meriba colony where close behavioural observations were done in 1983/84, certain females were watched while repeatedly trying to enter other nests than their own. The significance of this was not realized until it was discovered that extra eggs appeared in these nests. In the 1984/85 season a large number of parasitized clutches were found at the Leeukop A colony. Nests were thought to be parasitized when more than one egg appeared in a clutch during a 24 h period or when one egg of a clutch was obviously different, especially in four-egg clutches, or when an extra egg appeared in a nest more than two days after the completion of the clutch. Of the 177 clutches laid at the Leeukop A colony in 1984/85, 17 were parasitized and a further two had one chick which was at least eight days younger than the rest of the chicks and these nests were also considered to be parasitized. Thus about 16% of the nests were parasitized. Some egg and clutch size discrimination tests were done both at The Willows colony and at Leeukop A but in no instance were the owners of the nest able to distinguish between their own and other eggs or recognize an enlargement of the clutch.

TABLE 26

***HIRUNDO SPILODERA* PAIRS MAKING ONE OR MORE BREEDING ATTEMPTS WITH THE OUTCOME OF THESE ATTEMPTS AT THE SCHOONGEZICHT COLONY IN THE 1983/84 SEASON.**

S = successful; R = nest contents disappeared; F = nest fell; D = nest was deserted.

	Outcome of breeding attempt (%)															
	First attempt				Second attempt				Third attempt				Fourth attempt			
Number of pairs making....	S	R	F	D	S	R	F	D	S	R	F	D	S	R	F	D
One Attempt=45	22,2	40,0	33,0	4,4												
Two Attempts=25	56,0	32,0	8,0	4,0	68,0	28,0	0,0	4,0								
Three Attempts=18	83,0	16,7	0,0	0,0	66,7	27,8	0,0	5,6	27,8	72,2	0,0	0,0				
Four Attempts=4	25,0	75,0	0,0	0,0	75,0	25,0	0,0	0,0	50,0	50,0	0,0	0,0	0,0	100	0,0	0,0

The use of time and energy during the breeding season and nestbuilding.

The Cliff Swallows spent most of the 24 hour day in the nest (Table 28). This included about 9 hours spent sleeping in the nest at night. Nestbuilding was a minor activity during the incubation and nestling period, while most time was spent foraging during the nestling period (Table 28).

TABLE 27

BREEDING SUCCESS OF *HIRUNDO SPILODERA* AND SOME OTHER MEMBERS OF THE HIRUNDINIDAE

Species	Clutches analized	Eggs laid	Young fledged	%Breeding success	Reference
Delichon urbica	132	440	352	80,0	Bryant 1975
Progne subis	29	143	55	38,5	Allen & Nice 1952
Iridoprogne bicolor	219	1 123	679	60,5	Chapman 1939
Iridoprogne bicolor	352	1 759	857	48,7	Low 1934
Iridoprogne bicolor	60	363	340	93,7	Weydemeyer 1935
Hirundo rustica	376	1 750	1 382	79,0	Snapp 1976
Hirundo rustica	177	472	360	76,3	McGinn & Clark 1978
Hirundo neoxena	305	1 173	608	52,7	Marchant & Fullagar 1983
Hirundo tahitica	83	250	94	37,6	Hails 1984
Hirundo atrocaerulea	8	21	16	76,2	Snell 1969
Hirundo spilodera	310	621	303	48,8	Burgerjon 1964
Hirundo spilodera	951	2 245	1 268	56,5	This study

Flight velocity was determined to be 9,2 ms^{-1} (33,2 kmh^{-1}). At this velocity the metabolic cost of flight for a 21,7 g bird is predicted to be 2,59 W (or 6,8 SMR) (Tucker 1973). Measurements of flight velocity were made on a calm day so that there was no need for correction because of ambient wind velocity. Existence metabolism in the nest was taken to be 1,5 SMR (0,57 W) and metabolic cost of nest building (i.e. packing mud and collecting mud) was assumed to be 2 SMR (0,76 W). These SMR figures were similar to those used for the American Cliff Swallow by Withers (1977), who also pointed out that an error as much as 50% in these two assumptions would only result in a 7% error in the daily energy expenditure because of the large contribution of flight relative to nonflight activities.

The highest daily energy expenditure was during the feeding of nestlings when 0,062 W $(g)^{-1}$ was expended in comparison to nest construction and during incubation when 0,059 and 0,053 W $(g)^{-1}$ was expended respectively. The highest food harvest rates were obtained during incubation when only 7 h per day was spent foraging (Table 28). The harvest rate given in Table 28 is probably an underestimation, as some time on the wing is surely spent in social activities and not foraging.

To calculate the cost of building a nest, the time spent on the three actions which constitute a nestbuilding trip was measured for a number of individual birds. The mean time spent on the mud gathering site, on the nest site and travelling between the nest and mud source were used to calculate energy expenditure while building a nest. A single mud pellet was assumed to have a mass of 0,54 g (mean nest mass 840 g, mean number of pellets 1 550 per nest. (See *Form and Construction of the nest*). By carrying this mud pellet about 1% is added to the metabolic cost of flying which was considered a small enough extra cost to be ignored in further calculations. The number of trips required to build a nest was about 1 550 if it is assumed that each pellet in the nest required a trip.

TABLE 28

DAILY TIME AND ENERGY BUDGETS OF *HIRUNDO SPILODERA* DURING NEST CONSTRUCTION, INCUBATION AND NESTLING PERIODS.

	Nest construction		**Incubation**		**Nestlings**	
	Hours	**kJ**	**Hours**	**kJ**	**Hours**	**kJ**
Foraging	8,21	76,5	7,00	65,2	9,22	85,9
Nest building	3,69	10,1	0,11	0,3	0,03	0,1
In nest	12,10	24,8	16,89	34,6	14,75	30,3
TOTAL	24,00	111,4	24,00	100,1	24,00	116,3
Harvest rate (Total/h foraging; W)	3,77		3,97		3,51	
Daily energy expenditure $W(g)^{-1}$	0,059		0,053		0,062	
X SMR	3,37		3,03		3,54	

Conversion of time to energy assumes flight cost (foraging) = 2,59 W, cost of nest construction = 0,76 W, and existence metabolism = 0,57 W.

During each 60 s period of nest building 11,4 s was spent on the mud gathering site (see *Form and construction of the nest*), 28,6 s was spent on the nest site packing mud and 20 s flying between the two sites. The metabolic rate during such a 60 s cycle was found to be 3,6 SMR 6= (^{11,4}/60 x 2) + (^{28,6}/60 x 2) + (^{20}/60 x 6,8)) and the total cost of nest construction was thus:

Mean cost of whole cycle (x SMR)	X	SMR (W)	X	*number of trips*	X	*length of whole cycle*	= kJ (Withers 1977)
3,6	X	0,38	X	1 550	X	60	= 127 kJ

DISCUSSION

The Cliff Swallow uses a variety of man made concrete road bridges in the central Orange Free State for nesting. The use of a specific site is probably a direct result of the environment surrounding the site and to a lesser extent the site itself. Emlen (1954) stated that the American Cliff Swallow requires:

(a) an open area for foraging;

(b) a vertical object, preferably with an overhang, for nest attachment, and

(c) a supply of mud of the proper consistency for nest building.

In addition to these, Grinnell & Miller (1944) list another requisite, some smooth-surfaced fresh water for drinking. The requirements for the Cliff Swallow seem to be very much the same. The obvious lack of definite requirements for the height of nests above ground or water is surely an indication that the nest site used was the only available or alternatively the lack of specific requirements in this respect. Open surface water was not always available at any of the sites mainly as a result of the low rainfall experienced during the two seasons. Although the birds did not abandon the colonies because of this lack of drinking water there were periods such as in March 1984 and late October 1984 when they were in bad condition and mortality in both adults and young was high (see Chapter 3 - *Mortality*).

The nests, if high enough above ground level or over water, do afford valuable protection against predators as is also the case with the American Cliff Swallow (Bent 1942). The building of a gourd-shaped nest with narrow entrance tunnel scales down the territory of the Cliff Swallow to defending the nest opening, thus allowing individuals to nest very close to each other with only a wall of mud separating broods.

The mud nest of the Cliff Swallow contributes little towards maintaining a constant nest temperature. In unoccupied nests the temperature often rose to above that of the environment (Figure 7-19). It is probably only the behaviour of the birds in the nest which ensures that the nest temperatures do not rise too high (Ricklefs 1974). On the other hand the nest does offer protection against radiative heat loss to the night sky and wind chill (Calder 1974). The nests of many bird species do provide very adequate insulation e.g. Cactus Wrens *Campylorhynchus brunneicapillus* (Ricklefs & Hainsworth 1969) and Sociable Weavers *Philetairus socius* (White et al. 1975). Because of the social breeding habits of Cliff Swallow there is probably no need for a nest which would keep a constant temperature throughout the day. To guard a territory, which is only a nest in a colony, an adult bird should be in the nest almost all of the time, and being in the nest means that the temperature in the nest can be controlled.

As the nest of the Cliff Swallow is usable for a number of years and up to four broods can be raised in a single nest per year, the amount of energy spend in building a nest namely 127 kJ is very small. The nearly identical energy output for nestbuilding in the American Cliff Swallow (122 kJ) (Withers 1977) indicates a very similar strategy in nestbuilding and probably breeding. The estimated daily energy expenditure in raising nestlings of 3,54 SMR is higher than both that of the American Cliff Swallow (Withers 1977) and the Purple Martin (Utter & Le Febvre 1973) where the costs are 3,05 and 3,02 SMR respectively. This high expenditure might be a result of the mostly unfavourable conditions prevailing during the observations. The Cliff Swallow had to spend more time finding food in these conditions. Only more extensive sampling under different conditions can positively explain the observed differences.

When individual Cliff Swallows return from their winter range areas, the undamaged nests of the previous season are the first ones to be occupied. Breeding in these old nests often started even before the building of new nests commenced. There are certain advantages in moving into an old nest. Breeding can start almost immediately, increasing the chances of raising more young by making up to four attempts during the seven month breeding season. However, there are also distinct disadvantages in using an old nest for breeding. At the older colonies such as Driekloof where the parasite load was very high, using an old nest means being well and truly bitten by parasites especially the Cliff Swallow tick *Ornithodoros peringueyi*. The larvae and nymphs of these ticks feed on the chicks in the nest and as many as 144 larvae were counted on one chick at Driekloof (see Chapter 6). When a new nest is built at the start of the season it is sure to be free of at least tick larvae and nymphs which probably have, an impact on the survival of young. However, by building a new nest each year valuable time is lost which might just be the time needed to raise the extra brood. If mud is not readily available at all times as was the case in both years during this study, opting for building a new nest might mean that a certain pair may not finish the nest and in extreme cases may not breed at all. The fact that there was always, at all of the colonies, a number of old nests which were not used during the season while some pairs opted for building their own nests, indicated that there was probably a threshold of parasites in a nest above which it became impossible to breed successfully in a certain nest and the alternative is to build a new nest.

The increased probability of being parasitized by ectoparasites is seemingly the greatest disadvantage of breeding colonially in the Cliff Swallow. Another big disadvantage is the increased probability of misdirected parental care both towards eggs and young (Hoogland 1979). The feeding of young other than the own young is, at least in the later stages, when the young are more than about 15 days old, very unlikely as the recognition and communication system as described in Chapter 4 probably totally prevents this in the Cliff Swallow. However, there is no mechanism in the Cliff Swallow which prevents misdirected parental care towards eggs. In none of the few experiments carried out during this study was any of the birds able to distinguish between their own and other eggs, nor were they able to recognize the size of their clutches. Cliff Swallows are thus very prone to parasitism by conspecifics and by other species such as the House Sparrow *Passer domesticus* which was found parasitizing the American Cliff Swallow (Stoner 1939). Intraspecific brood parasitism also frequently occurs in non-colonial species such as the European Starling *Sturnus vulgaris* (Yom-Tov et al. 1974). Brown (1984) reported that intraspecific brood parasitism is common in the American Cliff Swallow and that the incidence of parasitism increases with colony size, although there is no correlation between colony size and the percentage of nests parasitized for colonies of more than 10 nests. If a parallel can be drawn between the South African and American Cliff Swallows then it seems as if the South African Cliff Swallow would only have very little chance of being parasitised if they breed in colonies smaller than 10 nests. No such small colonies were found anywhere in the Orange Free State indicating that the benefits derived from breeding colonially outweighed the costs of being parasitized. Brown (1984) also found that "parasitic" eggs required less time to hatch as is the case with other interspecific parasites (Jensen & Jensen 1969, Payne 1973). No evidence of this was found in the Cliff Swallow but if it is the case, conspecific brood parasitism in this species might be greatly underestimated. However, it does seem as if being parasitized is not very costly in the Cliff Swallow otherwise one might have expected adaptations that would minimize brood parasitism occurring. The most obvious defence in this regard would be intraspecific egg recognition (Brown 1984) something which is totally lacking in this species. On the other hand, one of the breeding pair is nearly constantly on guard at the nest thus to a large extend preventing brood parasitism occurring. No evidence was found that the Cliff Swallow was a cooperative breeder although Grimes (1976) listed this species as a possible case.

Many bird species develop a brood patch during the breeding season to facilitate the transfer of heat from the body to the egg during incubation (Jones 1971). The development of such a patch is normally correlated with the sex incubating (Drent 1975). It was shown in this study that the Cliff Swallow male, although it does not possess a featherless brood patch like the female, is an effective incubator. Males without brood patches in two other swallow species the European Swallow *Hirundo rustica* (Ball 1983) and the Sand Martin *Riparia riparia* (Petersen 1955) were also found to be effective incubators suggesting that functional incubation in male swallows might be more common than has been reported up to now. The question arises, why do so many birds possess a brood patch if it is not vital for functional incubation? Bailey (1952) suggests that the advantage of such a patch is only apparent during times of thermal stress, e.g. at night. As both the male and the female of the Cliff Swallow pair sleep in the nest at night, unlike the European Swallow in which the female always incubated at night (Samuel 1971b), there is no indication at present that only the female incubated at night.

Birds in tropical and subtropical regions generally lay smaller clutches than their closely related allies in temperate regions (Ricklefs 1969, Snow 1976). This is also the case if the clutch size of the Cliff Swallow is compared to that of the American Cliff Swallow, a closely related species. Bent (1942) gives the clutch size of the American Cliff Swallow as 2-6 eggs with 4 or 5 eggs the size occurring most often, while Samuel (1969) gives the range as 1-5 eggs with 3 and 4 egg clutches occurring with about the same frequency in both first and second clutches. The Cliff Swallow lays 2 or 3-egg clutches most often (Table 20), with 4-egg clutches only occurring regularly in the 1984/85 season and most of these were probably the result of intraspecific parasitism. Snow (1976) suggested that the smaller clutch size in tropical passerines can be considered an antipredator adaptation, as the broods of tropical passerines suffer a stronger impact of predation than those in the temperate zone. Earlé (1981a) also found the breeding success of sub-tropical species to be very low mainly because of predation. However, Dyrcz (1984) found that the Mangrove Swallow *Tachycineta albilinea* and the Grey-breasted Martin *Progne chalybea* laid clutches equal sized to those of their congeneric temperate zone allies namely the Violet-green Swallow *Tachycineta bicolor*, the Tree Swallow *T. thalassina* and the Purple Martin *Progne subis* (Allen & Nice 1952, Combellack 1954, Paynter 1954). He attributed this to the safe nesting sites of these two tropical species. The Cliff Swallow has a relatively safe nesting site as can be seen from the near absence of predators on nest contents (see Chapter 6), but still lays smaller clutches than its allies e.g. the American Cliff Swallow. It thus seems as if Lack's (1954) suggestion that clutch size of a species is probably related to the highest number of nestlings that can be reared successfully by the parents is the more likely explanation for the clutch size of the Cliff Swallow. By laying smaller clutches but breeding more often during the breeding season, which is usually much longer in tropical and subtropical than in temperate zone species, the same number of young is probably raised in a season. None of the four-egg clutches of the Cliff Swallow, which were all probably the result of intraspecific parasitism, produced four fledgelings, indicating that a Cliff Swallow pair can probably only successfully raise a maximum of three young in a brood.

Maclean (1985) gives the clutch size of the Cliff Swallow as "2-4 eggs (usually 3)" and Burgerjon (1964) found the clutch size to be one, two or three eggs. This study revealed a clutch size of one to four eggs with two and three eggs occurring most often (Table 20). Winterbottom (1962) also gave some indication of the clutch size from the notes of S.F. Townsend who recorded the following: "Have never found more than two young in a nest. In three instances only were there three eggs."

It has been shown for several passerine birds such as the European Starling *Sturnus vulgaris* (Dunnet 1955), the Bar-throated Apalis *Apalis thoracica* (Earlé 1981a), the American Cliff Swallow and the European Swallow (Samuel 1969), that second clutches are smaller on average than first clutches. This was also the case in the Cliff Swallow in the present study. The reason for this decreasing clutch size was not clear but there are some indications that Cliff Swallows cannot raise large brood later in the season and that smaller clutches may thus be more successful later in the season. It has been demonstrated in several passerine bird species that the amount of protein reserve in the body decreases as the breeding season progresses (Earlé 1981b), which might also be the reason for smaller second and later clutches in the Cliff Swallow. Jones & Ward (1976) even found a direct connection between the amount of reserve protein and the number of eggs laid in a clutch by the Redbilled Quelea *Quelea quelea.*

Weight recession towards the end of the nestling period in Hirundinidae chicks has been attributed to many factors, most recently to the loss of water from the integument and digestive organs (Ricklefs 1968, O'Connor 1977). Bryant (1971) also attributed the weight regression in House Martins to water loss, as the ash-free lean dry weight of nestlings showed a near linear increase throughout the nestling period. The increase in the dry weight of Cliff Swallows is slightly sigmoidal (Figure 7-22), which was also the case in the House Martin studied by O'Connor (1977) and by Bryant & Gardiner (1979). The growth and weight regression pattern of the Cliff Swallow chicks thus resembles other hirundines (Edson 1930, Ricklefs 1968) although it might be different from many other passerines. The reason why Hirundinidae chicks reach the maximum mass (and thus peak energy content) about halfway through the nestling period is open to speculation. By concentrating the main demand of energy for growth into the first half of the nestling period, a lipid reserve is established early, giving the nestlings a better chance of surviving when conditions force the adults to reduce their feeding rate of the young.

The breeding season of most birds coincides with the time of year when their food is abundant (Moreau 1950, Lack 1954), but the peak of breeding often precedes the peak of food abundance (Dunnett 1955, Earlé 1981c). Among aerial feeding birds, the Purple Martin breeds when aerial insects are most plentiful (Johnson 1967) as is the case with the House Martin (Bryant 1975). In the Cliff Swallow, where as many as four broods can be raised per season by a single pair, breeding starts early, even in August, suggesting that the Cliff Swallow does not time its breeding to coincide with maximum food availability (Figure 5-2). Chicks are being fed in the nests as early as the first week of September and as late as the last week of March, with indications that second attempts in October and November are more successful (Table 26), probably as a result of the better food supply at this stage (Figure 5-3), coupled with the fact that no nests fell down during this period (Table 26).

CHAPTER 8

THE SOUTH AFRICAN CLIFF SWALLOW: ITS POSITION, ORIGIN AND EVOLUTION OF COLONIALITY

Biological studies of swallows add to the evidence from morphological and zoogeographical studies that the Hirundininae (not the Pseudochelidoninae) are a close-knit and highly specialized, yet plastic group (Lunk 1962). In this family the cliff swallows is a natural group with both morphological and biological characters unique to them. To gain understanding of the position of the cliff swallows as a group and in particular *Hirundo spilodera* in the family, the data obtained during this study will be tested, in this chapter, against life-history data of other swallow species in Africa. The possible origin and radiation of the cliff swallow group as well as the evolution and the advantages and disadvantages of coloniality in the Hirundininae will also be discussed.

Amongst the burrow-nesting swallow species, the *Riparia* species, which excavate there own burrows, are usually colonial. However, some species such as *R. cincta* which occur in habitats with few large sandbanks do nest solitarily. The saw-wing swallows *Psalidoprocne*, which nest in sandbanks but do not excavate their own burrows, always nest solitarily, probably because of distribution of such holes in well-wooded or forested areas.

Four types of mud nests are built by members of the Hirundininae in Africa. Open, cupshaped nests are built by species such as *Hirundo dimidiata* and *H. albigularis*, and closed gourd-shaped nests with no entrance tunnel are built by *Delichon urbica*. The cliff swallow group all build closed gourd-shaped nests with short entrance tunnels, while *H. cucullata* and *H. semirufa* build thick walled nests with long tubular entrance tunnels. The open cup nesters as well as the long tubular builders are solitary breeders, although Snapp (1967) found European Swallows *H. rustica* sometimes breed in loose colonies where nesting sites are scarce. The House Martin *D. urbica* habitually breeds in loose colonies but the nests in such a colony usually do not touch each other and colonies are never of the magnitude of the cliff swallow colonies where hundreds or even thousands of pairs nest very close, the nests often being built on top of each other. The species which build long tubular entrance tunnels are all solitary nesters.

Mayr & Bond (1943) suggested that the availability of nesting sites may have played an important role in the evolution of both social patterns and nest-building behaviour in swallows, thus suggesting a link between coloniality and nest site availability. The scarcity of nest sites is probably the critical factor influencing colony formation in seabirds (Lack

1967), some weaverbird species (Crook 1962, 1964) and some swift species (Brooke 1973). Some colonial swallow species such as Sand Martins clearly nest close to each other even when nest sites are freely available (Emlen 1971). Although nest sites of the Cliff Swallow are much more freely available since man started building permanent structures, the availability of sites might have been a factor when Cliff Swallows were breeding in "natural" situations only. No colonies of Cliff Swallows are known from natural sites such as cliffs but the other cliff swallows of Africa *H. preussi, H. rufigula* and *H. fuliginosa* still used cliffs as nesting sites in the recent past (Bannerman 1939) but also use man-made structures such as houses (Searle 1965). Other mud-nest builders in Africa also use man-made structures such as houses and concrete road bridges, but natural sites such as overhangs are used by both open cup nesters and long entrance tunnel nest builders (pers. obs.).

If the colour pattern of the eggs of the Cliff Swallow is considered, it seems as if colonial nesting is a derived habit. Solitary open-cup nesting swallows all lay speckled eggs, probably because of the need to camouflage the eggs while the species which build nests with long tubular entrances (as well as *Delichon* which builds a closed nest but with no tubular entrance), lay pure white eggs as most hole-nesting bird species do. The Cliff Swallow lays speckled eggs, probably indicating that there was a need to camouflage the eggs. This points to the possibility that coloniality only developed later in the evolution of the Cliff Swallow and that the ability to build closed nests developed relatively quickly but as there was no need for white eggs in a hole (colour is irrevelant there) Cliff Swallows do not lay pure white eggs. Cliff Swallows cannot recognize their own eggs (see Chapter 7) surely indicating that the eggs are speckled for a reason other than egg recognition. The Cliff Swallow's nest is probably a product of colonial breeding, as it only has a short tubular entrance and a thin mud wall. It would not be possible to construct a long entrance tunnel in a dense colony. Secondly, and probably more important, it would be very difficult to defend a nest-opening at the end of a long tunnel and incubate or brood at the same time. A short entrance tunnel also takes less time to construct thus the Cliff Swallow can spend more time defending the opening and perhaps more time foraging to build up energy reserves in preparation for breeding. Cliff Swallow nests are thin walled structures if compared with for instance solitary Greater Striped Swallows. This may be another result of colonial breeding as the Cliff Swallows have to close up the nest as quickly as possible, so that only a small tubular opening has to be defended. Cliff Swallow nests can take as little as five days to complete whereas long tubular nestbuilders use a minimum of 14 days (Schmidt 1962). Thin walled Cliff Swallow nests deteriorate quicker than the thick-walled, long tubular, nests but in a colony, with sometimes up to a thousand or more nests, there is always the possibility of occupying an old nest from a previous breeding season, which saves time spent nestbuilding. By using old nests, a pair can mate very early in the season (matings in the Cliff Swallow only take place inside a nest) and thus raise up to four broods per season.

From the above it would seem as if coloniality in the Cliff Swallow developed from a solitary open-cup nesting situation, and that the speckled eggs are the clearest indication of this. The solitary swallows which build long tubular entranced tunnels and lay pure white eggs have presumably lost the ability to lay speckled eggs. This leaves only the *Delichon* spp. which lay pure white eggs but build a closed nest with no tubular entrance tunnel. It would seem as if *Delichon* has secondarily lost the ability to build a long tubular entrance tunnel to the nest, as coloniality is still in the process of developing in this genus. The cliff swallow species and the *Delichon* spp. are both colonial, although not to the same degree, but have developed coloniality from different starting points under the same environmental pressures, such as a scarcity of nesting sites.

The European Swallows sometimes breed in loose colonies (Snapp 1976) but never as close as the Cliff Swallow. The strife that would result from nesting too close in open-cup nesters could spend so much energy that the birds would not be able to breed successfully. Cup-nesters nest in loose colonies probably in response to a shortage of suitable nesting places. This might explain why Cliff Swallows are colonial, but not social and cooperative breeders in the sense of many other colonial aerial feeding birds such as bee-eaters, *Merops* spp. (Fry 1984) which often have askew sex ratios (Fry 1972) and wood-swallows, *Artamus* spp. (Estbergs 1975). These birds may be social for very different reasons. Bee-eaters hunt from perches and this makes the maintenance of a feeding territory feasible, something which is not possible in the swallow species. The high annual mortality in the Cliff Swallow (see Chapter 3) indicates that cooperative breeding is not viable, as most individuals are too short lived to postpone breeding and help at another nest.

The breeding habits of some species vary with environmental conditions, and are a result of adaptations to a variety of environmental pressures (Crook 1965). The great variety in nesting strategies and degrees of coloniality even within a single species of swallow has been the subject of a number of studies in this close-knit family of birds. The adaptive significance of colonial breeding as well as the advantages and disadvantages of coloniality have often been debated (e.g. Hoogland & Sherman 1976, Snapp 1976, Shepard 1977, Wilkinson & English-Loeb 1982, Brown 1984).

The Cliff Swallow has a breeding range in the highveld regions of South Africa, an area where naturally occurring breeding sites are few, and this might have been a major factor in the development of coloniality. The fact that the Cliff Swallow nest adds little to a stable thermal environment around the egg or young is probably the result of coloniality in as much as there is no great need for the nest to be well insulated. The nest opening has to defended constantly and thus incubation is nearly continuous. The Cliff Swallow thus spends little energy in building a nest, as do open cup-nest breeders, but large amounts of energy defending the nest and incubating. The long tubular, thickwalled mudnest-builders spend large amounts of energy in building a nest and much less in incubating, as the thick wall of the nest keeps the temperature in the nest within narrow limits if the individual is not incubating (pers. obs.).

There are many costs associated with coloniality. A high degree of aggressiveness towards conspecifics and towards other species competing for nest sites is displayed by several swallow species, especially natural cavity nesters such as the Blue Swallow *Hirundo atrocaerulea* (Snell 1969), Purple Martin *Progne subis* (Johnston & Hardy 1962) and Rough-winged Swallow (Lunk 1962). Colonial Cliff Swallows would only defend the nest opening, in contrast to the European Swallow which defends both the nest site and the approach to the nest (Snapp 1976). Aggression towards individuals not directly threatening the nest would waste much energy, and it seems likely in the Cliff Swallow that individuals are aggressive towards conspecifics which threaten the nest contents. Intraspecific brood parasitism was found to be quite common (see Chapter 7), as was the case with the American Cliff Swallow (Brown 1984). Although the removal of eggs by brood parasites was never observed in the Cliff Swallow, the number of apparently perfect eggs found below nests probably indicated that egg removal is as common in this species as in the American Cliff Swallow (Brown 1984). Conspecific brood parasitism is not as common as might be expected among colonial species. Hoogland & Sherman (1976) did not find any parasitism in Sand Martins but some noncolonial species, particularly waterfowl, often use this reproductive strategy (e.g. Cooke & Mirsky 1972, Yom-Tov 1980).

A further cost of coloniality related to breeding is the possibility of misdirected parental care towards offspring. The parent-offspring recognition system which is highly developed in at least two colonial swallow species, the Sand Martin and American Cliff Swallow (Beecher et. al 1981, Stoddard & Beecher 1983) represents an evolutionary response to this cost, and at the same time it is evidence for its existence (Hoogland 1979). If brood parasitism does not occur and "wrong" eggs are not incubated, the possibility of feeding unrelated young is very small in the Cliff Swallow. The development of chick recognition systems suggests that the Cliff Swallow has been colonial for a long time.

There seems to be no automatic or universal advantage of coloniality (Hoogland 1979), but different species of swallows benefit in different ways. The degree of coloniality in the swallows may be influenced by the distribution and availability of food. Turner (1980) compared aerial feeding insectivores in Britain and found that colonial species feed higher on small, more sparsely distributed prey. The European Swallow, which breeds solitarily in Europe, feeds on larger prey close to the ground or on vegetation, while the House Martin *Delichon urbica* and the European Swift *Apus apus,* both of which are to some extent colonial, feed higher. Thus one advantage of coloniality to individuals may be finding food, or at least increasing the possibility of finding suitable foraging sites and in that way increasing the efficiency of feeding. However, the Cliff Swallow which is highly colonial, much more so than either the House Martin or the European Swift, feeds close to the ground (Figure 5-1). Large populations of Cliff Swallows could not be maintained on very small and widely distributed insects. Insect density diminishes with increasing height above the ground (Johnson 1950). The Little Swift *A. affinis* which usually breeds colonially (Naik & Razack 1967), feeds higher than the Cliff Swallow, but so do all the swift species occurring in the area, the Whiterumped Swift *A. caffer* (solitary breeder), the Horus Swift *A. horus* (usually solitary) and Alpine Swift *A. melba* (usually colonial) (pers. obs., see also Donelly 1974).

Ward & Zahavi (1973) suggested that groups of animals might act as centres where information on a temporally or spatially varying food supply could be passed between individuals. This would imply that socially breeding aerial insectivores also forage socially, which is the case for several swallow species e.g. the American Cliff Swallow *Hirundo pyrrhonota* (Emlen 1952) and Sand Martins *Riparia riparia* (Emlen 1971). Emlen & Demong (1975) also argued that social facilitation of foraging in Sand Martins is important, and that asynchronous breeding decreases the effectiveness of social foraging in this species. However, synchronized breeding in colonial birds may lead to increased intraspecific competition for food, and even though information on where to find food might be maximal, the foraging efficiency might be low. There is evidence for this in the House Martin, where nestlings produced at the peak of breeding were relatively light (Bryant 1978).

In the Little Swift only the most efficient feeders were able to build up their body weight to a stage where they were able to breed during the short first breeding season of the year in India (Naik & Razack 1967). There is little evidence of social foraging in this species, but breeding activities are somewhat synchronized. In the Cliff Swallow there was no clear evidence that individuals benefitted from coloniality by foraging socially. Breeding in the colonies under study was not synchronized, and it seems likely that social foraging observed in this species was opportunistic, by chance, as a result of locally abundant food supplies at specific times. However, this does not exclude the possibility that individuals may have benefitted from social foraging early in the season or after breeding has ceased, when they could stay away from the colonies for many hours. Especially early in the season, the members of a colony returned to the nests in large groups before settling to roost, presumably after social foraging trips. In the Cliff Swallow it is likely that flocks building up in good feeding sites attract more birds to such areas, benefitting especially the inexperienced birds such as juveniles.

Another explanation for the adaptive value of coloniality is protection against predation. The most obvious way in which protection can be afforded is by mobbing the predator and thus forcing it away from the nest site. Mobbing activities are however only highly developed in the solitary-nesting species such as the Tree Swallow *Iridoprocne bicolor,* which is reported to be very aggressive in defending its nest against nestsite competitors of other species (Kuerzi 1941, Chapman 1955). Group mobbing of predators has also been observed for the Roughwinged Swallows *Stelgidopteryx ruficollis* (Lunk 1962), House Martins (Lind 1960) and European Swallows (Smith & Graves 1973, Waugh 1978). Highly colonial species such as the American Cliff Swallow and Sand Martin (Emlen 1952, 1954, Windsor & Emlen 1975) are quite ineffective in defence against predators. Hoogland & Sherman (1976) found large colonies of Sand Martins to be more effective in mobbing predators than small ones, but they have yet to demonstrate that predation actually decreases with increasing colony size, although one expects that to be the case. Snapp (1976) concluded that mobbing behaviour in European Swallow aggregations did not decrease mortality due to predation, and coloniality thus had very little adaptive value as protection against predators. Mobbing behaviour in Cliff Swallows has never been observed and no potential predators at colonies were ever mobbed during this study, indicating that active defence against predators is not the major reason for coloniality in this species. However, "passive" defence against predators probably does occur. The multitude of individuals in a dense colony might be so confusing that the predator seldom presses its attack. If this is so, colonial breeding is a very successful protective strategy and behaviour such as mobbing is not required.

The biggest cost of coloniality is the increased probability of being the victim of ectoparasites. Although it seems logical, no studies on birds as yet have clearly demonstrated that parasitism decreases fitness. Suggestions of a decrease in fitness were found in the Eastern Phoebe *Sayornis phoebe,* a non-colonial bird occasionally breeding in American Cliff Swallow colonies (Hopla & Loye 1984). It does, however, seem as if the Cliff Swallow, which has evolved with its species-specific parasites (Hoogstraal & Aeschlimann 1982), is relatively unaffected by the heavy parasite load in most colonies.

The present world distribution of cliff swallows suggests a tropical African origin. The fact that cliff swallow species occur in tropical Africa, Australia, India and America fits well into the pattern of a Gondwanaland origin of these species. Africa is the richest in cliff swallows species and thus probably the centre of origin. In both Africa and America the species all occur or spend the non-breeding season at or near the tropics but two species, *Hirundo spilodera* in Africa and *H. pyrrhonota* in America undertake migrations to breeding areas. These two species are the most numerous probably indicating that the phylogenetic spread (*sensu* Wiley 1981) of these two species from the ancestral stock at the origin makes them the most recent developed species of the cliff swallows. *H. spilodera* is the only African cliff swallow to migrate to breeding grounds during the southern hemisphere summer months. The three other cliff swallow species in Africa are allopatric, except for a small area of overlap between *H. preussi* and *H. fuliginosa* (Hall & Moreau 1970). These two species together with *H. rufigula* breed during April to August (Chapin 1953, Serle 1940, 1965, Bannerman 1939). However, *H. rufigula* like *H. spilodera* sometimes breeds during the southern summer months September to March (Benson *et al.* 1973). *H. spilodera* thus spends the non-breeding season in tropical Africa during the dry period, when the other species are breeding. At this time *H. spilodera* occurs primarily in areas where no suitable nesting sites for the resident cliff swallows occur.

To conclude, the Cliff Swallow probably had its origin in tropical Africa and it undertakes a breeding migration to southern Africa. The speckled eggs of this species suggest that coloniality developed fairly recently. The nest form and structure is probably a result of coloniality.

The cost of being colonial in the Cliff Swallow is high considering the high populations of ectoparasites, the occurrence of conspecific brood parasitism, and the large amount of energy spent in continuously defending a small nest site. Although the advantages of being colonial are not at all clear, they must be substantial to outweight the disadvantages in the highly colonial Cliff Swallow.

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SUMMARY

The general biology of the South African Cliff Swallow was studied at several breeding colonies around Bloemfontein in the Orange Free State over two breeding seasons.

1. There was no difference in the sizes of male and female Cliff Swallows but birds were very easily sexed on brood patch criteria. Only females develop a featherless brood patch. The sex ratio was found to be 1:1.

2. Adult birds were usually faithful to their breeding colony and only 1,2 % of all birds ringed were ever recaptured at a site other than their original colony. There was no indication that one of the sexes was more inclined to change colonies.

3. The general behavioural patterns of the Cliff Swallow are described. The Cliff Swallow has a surprising large vocal repertoire for a swallow and seven adult and two chick vocalizations are presented. Chick contact calls were found to be individually recognizable.

4. The Cliff Swallow typically foraged close to the ground and very often flushed insects from vegetation. Non-flying arthropods were found in stomach samples as were stones of various sizes. Coleoptera, Diptera, Hymenoptera and Hemiptera were the most important insect orders in the diet.

5. Two nest- and one body ectoparasite are species-specific parasites of the Cliff Swallow. Up to 900 *Ornithodoros peringueyi* ticks were found in single nests of the Cliff Swallow. The tick larvae and nymphs usually attacked the nestling swallows and a maximum of 144 larvae was found on a single chick. The parasites had no noticeable negative effect on the swallows. Various other bird species used the nests of the Cliff Swallow for breeding or roosting.

6. Breeding started earlier in larger than in smaller colonies, but there was no synchronization of breeding in any colony.

7. The clutch size varied between one and four eggs with larger clutches laid during first breeding attempts. Up to four attempts were made by some pairs during the breeding season.

8. Males, which do not possess a featherless brood patch, were found to incubate as effectively as females. Both sexes feed the young.

9. Intraspecific brood parasitism occurred frequently in the Cliff Swallow. Cliff Swallows could not recognize their own eggs or an increase in the clutch size.

10. In all 56 % of all eggs laid produced flying young. The recruitment rate was 0,9 young : 1 adult bird.

11. The advantages and costs of Cliff Swallow coloniality are discussed. It is concluded that although the costs are high they are probably still low enough for the Cliff Swallow to be highly colonial and very successful.

OPSOMMING

Die algemene biologie van die Familieswael *Hirundo spilodera* was die onderwerp van 'n studie wat oor twee broeiseisoene in die omgewing van Bloemfontein in die Oranje-Vrystaat gedoen is.

1. Daar was geen grootte verskil tussen mannetjie en wyfie swaels nie, maar volwasse voëls se geslag kon maklik bepaal word aangesien slegs wyfies 'n veerlose broeikol besit het.

2. Volwasse voëls keer gewoonlik jaar na jaar terug na hulle oorspronklike kolonies en slegs 1,2 % van alle voëls wat bering is het na 'n ander kolonie beweeg. Daar was geen aanduiding dat een van die geslagte meer van kolonie verwissel het nie.

3. Die algemene gedrag van die Familieswael word beskryf. Die Familieswael het 'n verbasende groot repertoir gesien in die lig dat swaels oor die algemeen nie baie sing nie. Sewe volwasse en twee kuiken roepe is onderskei en die roepe van kuikens was individueel herkenbaar.

4. Die Familieswael jag gewoonlik naby die grond en jaag selfs insekte op uit plante. Verskeie soorte nie-vliëende geleedpotiges sowel as klein klippies is dikwels in die mae van dié swael gevind. Die Coleoptera, Hymenoptera, Diptera en Hemiptera was die belangrikste insekordes in die Familieswael dieet.

5. Drie spesie-spesifieke ektoparasiete (twee nes- en een liggaamsparasiet) is volop in die Familieswael kolonies. Tot 900 *Ornithodoros peringueyi* bosluise is in 'n enkele nes van dié swael gevind. Die bosluis larwes en nimfe val neskuikens aan en tot 144 larwes is op een kuiken getel. Die parasiete het geen sigbare negatiewe effek op die swaels gehad nie. Verskeie ander voëlspesies gebruik Familieswael neste as rus of broeiplek.

6. Broei aktiwiteite begin vroeër in die groter as die kleiner kolonies maar daar was geen sinchronisasie in broei aktiwiteite in enige kolonie nie.

7. Die broeiselgrootte het gewissel tussen een en vier eiers met meer, groter broeisels vroeg in die seisoen. Tot vier broeisels kan per seisoen deur 'n enkele wyfie gelê word.

8. Mannetjies, alhoewel hulle nie 'n veerlose broeikol het nie, kan die eiers net so effektief soos die wyfie bebroei. Albei ouers voer die kleintjies.

9. Intraspesie broei parasitisme kom algemeen by die Familieswael voor. Die voëls was nie in staat om hulle eie eiers te herken nie en kon ook nie 'n vergroting in die broeiselgrootte bemerk nie.

10. Van al die eiers wat gelê is het 56 % kleintjies opgelewer wat die nes verlaat het. Vir elke 1 volwasse voël is daar per jaar 0,9 kuikens wat die nes verlaat het, geproduseer.

11. Die voordele en nadele verbonde aan die Familieswael se kolonialiteit word bespreek. Die gevolgtrekking word gemaak dat alhoewel die nadele aan kolonialiteit hoog is, is dit blykbaar nog laag genoeg dat die Familieswael 'n baie suksesvolle koloniale voël is.

ZUSAMMENFASSUNG

Die allgemeine Biologie der südafrikanischen Klippenschwalbe *Hirundo spilodera* Sundevall wurde anhand verschiedener Brutkolonien dieser Spezies in der Gegend von Bloemfontein, Oranje Freistaat, über zwei aufeinanderfolgende Brutzeiten hin untersucht:

1. Obwohl kein Unterschied in der Körpergrösse zwischen den Geschlechtern nachzuweisen ist, sind die Weibchen doch durch ihre Brutflecke leicht auszukennen. Geschlechtsrate war 1:1.

2. Geschlechtsreife Vögel sind ziemlich kolonientreu; von allen beringten Vögeln wurde nur 1,2 % je in einer anderen Kolonie wiedergefangen. Auch in dieser Hinsicht, d.h. Kolonientreue, scheint es keinen Unterschied zwischen den Geschlechtern zu geben.

3. Allgemeine Verhaltensweisen sind samt mit dem, für eine Schwalbe überraschend umfangreichen Vokalinventar beschrieben und Lautäusserungen von sieben Altvögeln und zweier Nestjungen sind auch mit präsentiert. Kontaktrufe von Nestjungen scheinen unterschiedliche individuelle Kennmerke aufzuweisen.

4. Typisch für diese Schwalbe ist die Nahrungsuche in der Bodennähe; beim niedrigen Fluge von der Vegetation aufgescheuchte Insekte werden oft erbeutet. In den Ingluvien wurden aber nicht-fliegende Arthropoden und selbst Steinchen von verschiedener Grösse auch mit festgestellt. Coleoptera, Hymenoptera, Diptera und Hemiptera sind die wichtigsten Insekten-Ordnungen in der Nahrung.

5. Zwei Nest- und eine Körper-Ektoparasiten sind spezifisch für die Klippenschwalbe. Von der Zecke *Ornithodoros peringueyi* wurden bis auf 900 Stück in einzelnen Nestern gefunden; die Nymphen befallen gewöhnlich die Nestjungen und an einem Nestjungen wurden 144 (max.) gefunden. Doch scheint der Parasitenbefall keinen negativen Effekt auf die Schwalben auszuüben. Verschiedene andere Vogelarten machen aus den Nestern der Klippenschwalbe als Schlaf- und Brutgelegenheit gebrauch.

6. Brutgeschäft beginnt früher in den grösseren als in den kleinen Kolonien; es gab keine Synchronisation zwischen den einzelnen Brutgeschäften in derselben Kolonie.

7. Gelegevariation war 1 bis 4 Eier; die grösseren Gelegen wurden gewöhnlich bei dem ersten Brutversuch gemacht. Einzelne Brutpaare hatten es bis auf vier Brutversuche in einem Saison gebracht.

8. Die brutflecklosen Männchen sind doch am Bebrüten ebenso effektiv wie ihre Weibchen. Beide Geschlechter füttern die Nestjungen.

9. Intraspezifischer Brutparasitismus kommt oft in dieser Spezies vor. Brütende Eltern konnten weder ihre eigene von fremden Eiern unterscheiden, noch eine gelegenthliche Zunahme in der Anzahl von Eiern merken.

10. Insgesamt 56 % von allen Eiern erreichten das Stadium vom Flüggewerden; auf jeden adulten Vogel entfiel 0.9 % Jungvogel.

11. Die Vorteile und Risikos vom Kolonialbrüten bei dieser Schwalbenart werden erörtert und die Schlussfolgerung gezogen, dass trotz der anscheinend hohen Risken Kolonialbrüten gewährleistet doch die besten Bruterfolge für diese Schwalbe.

APPENDIX 1

COMPOSITION OF SWEEPNET AND SUCTION TRAP SAMPLES OF ARTHROPODS COLLECTED AT THE WILLOWS TO TEST PREY AVAILABILITY

l = Large items; s = small items. Large items were > 5 mm in length.

SUCTION TRAP (NUMBERS)

Sample Date	Sweepnet Mass (g)	Diptera		Hymenoptera		Coleoptera		Hemiptera		Other	
		l	s	l	s	l	s	l	s	l	s
07.08.84	0,036	4	3	0	0	0	5	0	0	0	5
15.08.84	0,121	8	11	0	0	2	2	0	1	0	18
28.08.84	0,084	9	10	0	3	2	5	0	3	0	11
06.09.84	0,089	13	35	0	0	1	4	0	2	0	12
17.09.84	0,346	31	51	0	1	1	8	0	0	1	16
25.09.84	0,250	18	37	0	0	2	8	0	4	1	35
05.10.84	0,401	24	52	0	1	2	17	0	3	2	12
16.10.84	0,681	16	88	0	5	1	19	0	8	5	18
25.10.84	0,654	17	37	1	8	3	12	1	10	1	18
07.11.84	1,732	4	16	1	19	1	9	2	18	1	32
15.11.84	1,500	7	20	0	19	0	11	1	15	8	16
26.11.84	2,22	11	24	0	12	2	18	0	3	7	45
05.12.84	1,399	3	5	1	7	1	9	0	1	1	19
17.12.84	2,498	2	2	0	5	0	5	0	5	6	31
26.12.84	1,096	1	0	0	4	0	1	1	3	1	15
07.01.85	0,982	3	2	0	6	0	3	0	8	0	4
15.01.85	0,490	8	10	0	1	1	5	0	1	0	18
25.01.85	0,026	2	3	0	0	1	2	0	1	1	11
05.02.85	0,193	2	3	0	0	1	5	0	0	0	1
14.02.85	0,137	6	10	0	3	3	3	0	2	0	4
25.02.85	0,511	8	12	0	1	0	5	0	0	0	1

APPENDIX 2

PREY OF *HIRUNDO SPILODERA* AS REVEALED BY ANALYSIS OF STOMACH CONTENTS. THE PERCENTAGE OCCURRENCE OF EACH TAXON IS ALSO GIVEN

(* = 2 species; ** = 3 species).

Taxonomic group	**1983/84 Months present**							
	SEPT	OCT	NOV	DEC	JAN	FEB	MAR	% Occurrence
COLEOPTERA								
SCARABAEIDAE								
Aphodiinae*	X	X	X				X	20
Cantoninae			X					4
Rutelinae		X						8
Scarabaeinae								
Scarabaeus sp.	X	X			X	X		20
*Onthophagus*** spp.	X	X	X	X	X	X	X	68
Phalops sp.				X	X	X		12
larvae	X		X		X	X		16
CURCULIONIDAE	X							4
Erirhininae	X	X	X		X		X	20
Barinae**		X	X	X	X	X	X	52
Cleoninae			X	X				8
Microlarinus sp.		X		X	X	X	X	28
Brachyderinae								
Protostrophus sp.				X				4
Gymnetrinae			X					4
HYDROPHILIDAE*	X		X		X			8
COCCINELLIDAE						X		
Adonia variagata		X	X	X	X	X		24
CHRYSOMELIDAE		X			X			8
Cassidinae*	X		X	X				8
Eumolpinae				X	X			8
Alticinae	X	X						4
APIONIDAE		X						4
ANTHICIDAE				X	X	X	X	24
ALLECULIDAE			X		X			8
PHALACRIDAE*			X					4
HISTERIDAE**			X	X				8
DERMESTIDAE								
Dermestes maculatus			X	X		X		12
CARABIDAE*			X		X			8
STAPHYLINIDAE*			X	X	X			16
Bledius sp.								4
Philonthus spp*					X		X	8
BOSTRYCHIDAE					X			4

APPENDIX 2 (Cont.)

LEPIDOPTERA						X		
HETEROCERA			X			X		12
RHOPALOCERA			X			X		8
larvae			X					4
ORTHOPTERA								
ACRIDIDAE			X					4
DIPTERA								
BOMBYLIIDAE		X	X			X		12
DROSOPHILIDAE	X	X	X	X		X	X	36
CALLIPHORIDAE					X			4
SEPSIDAE			X	X		X		12
TEPHRITIDAE		X	X					8
SPHAEROCERIDAE			X					4
SCIARIDAE			X	X				12
MUSCIDAE	X	X	X	X	X	X	X	56
HYMENOPTERA								
FORMICIDAE								
Cerapachyinae								
Simopone sp.		X	X					8
Myrmicinae				X	X	X		12
Messor capensis			X	X			X	12
Messor sp.		X	X					8
Pheidole sp.			X	X				8
Solenopsis punctaticeps			X					4
Tetramoruim spp.*			X		X	X		16
Triglyphothrix microps	X			X				12
Formicinae								
Amoplopelis custodiens			X	X		X		12
Anoplolepis sp.		X					X	8
Camponotus maculatus		X	X	X				36
Camponotus sp.			X			X		8
ICHNEUMONOIDEA*	X	X	X	X		X	X	24
POMPILIDAE	X		X	X				12
HALICTIDAE**	X	X	X		X	X	X	32
SPHECIDAE			X				X	8
Ampulicinae*		X	X			X	X	16
BRACONIDAE			X	X		X		16
Chelonus sp.			X					8
BETHYLIDAE*		X		X	X	X	X	24
CHRYSIDIDAE							X	4
CHALCIDOIDEA	X		X	X	X	X	X	28
CHALCIDIDAE								
Peltochalcidia sp.			X			X		12
PTEROMALIDAE			X			X		12
Pachyneuron sp.		X	X					8
EURYTOMIDAE								
Eurytoma sp.						X		4
EULOPHIDAE			X					4
Diclyphus sp.			X	X			X	12
ORMYRIDAE								
Ormyrus sp.			X	X				8

APPENDIX 2 (Cont.)

TORYMIDAE							
Megastigmus sp.			X	X			
HEMIPTERA							
CICADELLIDAE*		X			X		16
RHOPALIDAE		X			X		8
FULGOROIDEA*					X		4
CYDNIDAE		X		X	X	X	16
PENTATOMIDAE*		X		X		X	16
LYGAEIDAE		X	X	X	X	X	40
REDUVIIDAE				X	X		12
CICADIDAE		X	X				24
COREIDAE						X	4
DELPHACIDAE		X		X			8
CIXIIDAE		X	X				8
PSYLLIDAE		X	X	X			12
APHIDIDAE		X			X		8
TINGIDAE		X	X			X	12
ISOPTERA							
TERMITIDAE							
Hodotermes mozambicus		X	X		X		16
PLECOPTERA	X	X					8
THYSANOPTERA	X						4
ARACHNIDA							
THOMISIDAE	X						4

APPENDIX 3

MEASUREMENTS AND FORMULAE USED IN CALCULATING THE USE OF TIME AND ENERGY DURING THE BREEDING SEASON AND FOR BUILDING A NEST.

Measurements of *Hirundo spilodera* for energy estimates:

Body weight 21,7 ± 1,4 g (n = 36)

Wing length 111 ± 2,6 mm (n = 36)

Wing span 311 ± 5,2 mm (n = 36)

wing disc load 0,0286 g $(cm)^{-2}$

Mean flight velocity 9,2 m $(s)^{-1}$ (n = 30)

All units are S.I. and the conversion factors are:

1 Watt (W) = 0,86 kcal/h and
1 kilojoule (kJ) = 0,239 kcal.

Weight (W) is measured in newtons and mass (m) in kilograms.

$W = mg$ where $g = 9{,}81$ m $(s)^{-2}$.

Formulae used for:

Basal metabolic rate (Standard metabolic rate = SMR)

$P_{ib} = 6{,}15\ m^{0{,}724}$ (Lasiewski & Dawson 1967).

(The units have been changed to make results directly comparable with those of Withers (1977) and Utter & Le Febvre (1973)).

where
P = power
i = input
b = basal
m = mass (kg)

Metabolic cost of flight:

$P_i/(WV) = 0{,}896\ W^{0{,}227}$ (Tucker 1973)

where
W = weight (N)
V = flight velocity

Estimating daily energy expenditure (DEE):

Total kJ *(converted to watt)* ÷ *24*(h) ÷ *weight of bird* (g) = $W(g)^{-1}$

Estimating food harvest rate

Total kJ *(converted to watt)* ÷ *total hours foraging* = W

APPENDIX 4

PUBLICATIONS ARISING FROM THIS THESIS

EARLÉ, R.A. 1985. Predators, parasites and symbionts of the South African Cliff Swallow *Hirundo spilodera* (Aves: Hirundinidae). *Navors. nas. Mus., Bloemfontein* 5(1): 1-18.

EARLÉ, R.A. 1985. The nest of the South African Cliff Swallow *Hirundo spilodera* (Aves: Hirundinidae). *Navors. nas. Mus., Bloemfontein* 5(2): 21-36.

EARLÉ, R.A. 1985. A description of the social, aggressive and maintenance behaviour of the South African Cliff Swallow *Hirundo spilodera* (Aves: Hirundinidae). *Navors. nas. Mus., Bloemfontein* 5(3): 37-50.

EARLÉ, R.A. 1985. Foraging behaviour and diet of the South African Cliff Swallow *Hirundo spilodera* (Aves: Hirundinidae). *Navors. nas. Mus., Bloemfontein* 5(4): 53-66.

EARLÉ, R.A. 1986. Time budget of South African cliff swallows during breeding. *S. Afr. J. Zool.* 1986, 21: 57-59.

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EARLÉ, R.A. 1986. The breeding biology of the South African Cliff Swallow. *Ostrich* 57: 000-000.

EARLÉ R.A. 1986. Vocalizations of the South African Cliff Swallow *Hirundo spilodera. S. Afr. J. Zool.* 21: 000-000.

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PREDATORS, PARASITES AND SYMBIONTS OF THE SOUTH AFRICAN CLIFF SWALLOW *HIRUNDO SPILODERA* (AVES: HIRUNDINIDAE)

by

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(With 2 figures)

ABSTRACT

Earlé, R.A. 1985. Predators, parasites and symbionts of the South African Cliff Swallow *Hirundo spilodera* (Aves: Hirundinidae). *Navors. nas. Mus., Bloemfontein* 5(1): 1-18. Because of the relatively safe nesting colonies of the South African Cliff Swallow *Hirundo spilodera* and the agility of free-flying birds, there are probably no predators which regularly take healthy Cliff Swallows and only injured birds are taken often. The Cliff Swallow has two body parasites and one nest parasite not known from other hosts. None of these species-specific parasites, the tick *Ornithodoros peringueyi*, the flea *Xenopsylla trispinis* and the louse fly *Ornithomya inocellata* seems to have a noticeable negative effect on the swallows although high populations of ticks may indirectly affect chick mortality. The high degree of parasite-host specificity between the three named parasites and the Cliff Swallow is probably possible only as a result of the colonial nesting behaviour of the swallow. Mud nests are a relative stable overwintering environment for the parasites to overwinter in when the swallows are not present. A variety of invertebrate and vertebrate animals makes use of the nests of the Cliff Swallow. Most of these symbionts use the nest for roosting but certain bird species such as the House Sparrow *Passer domesticus* and the Cape Sparrow *P. melanurus* use Cliff Swallow nests extensively for breeding **(South African Cliff Swallow, *Hirundo spilodera*, *Ornithodoros*, *Xenopsylla*, *Ornithomya*, *Ornithonyssus*, tick, parasites).**

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INTRODUCTION

Because of the paucity of information on the biology of the South African Cliff Swallow *Hirundo spilodera,* published records of predators, parasites and symbionts are few. No records of predators could be found but Maclean (1985) mentions several bird species using South African Cliff Swallow nests as roosts or for breeding purposes. The host-specific tick *Ornithodoros peringueyi* was described by Bedford & Hewitt (1925) from the nests of South African Cliff Swallows, while Zumpt (1966) and Milstein (1975) both found the blood-sucking fly *Ornithomya inocellata* on South African Cliff Swallows. Other ectoparasites recorded for the South African Cliff Swallow were the host-specific flea *Xenopsylla trispinis* (Zumpt 1966), a louse, *Myrsidea rustica* (Ledger 1980) found on several other passerine bird species and a mite, *Ornithonyssus bursa* (Burgerjon 1964). Dense, reliable populations of hosts such as at South African Cliff Swallow colonies offer excellent conditions for large numbers of parasites, as the difficult task of finding a host is virtually eliminated (Rothschild & Clay 1952). There might thus be a number of advantages to a parasite in becoming highly adapted to a colonial birds' seasonal regime.

For the sake of brevity the South African Cliff Swallow will be referred to as the Cliff Swallow throughout.

STUDY AREA AND METHODS

Most observations were made at 20 colonies in a radius of 40 km around Bloemfontein, Orange Free State, South Africa (Figure 1). An attempt was made to collect ectoparasites from Cliff Swallows quantitively but as very few parasites were collected by the method of Fowler & Cohen (1983), it was abandoned after a few trials. Observations of symbionts and predators were made opportunistically.

RESULTS

PREDATORS

The Cliff Swallow is apparently preyed on by relatively few species of animals, although the rate of predation especially at the nest can be high. For convenience the predators can be divided into:
(a) predators away from the nest; and
(b) nest predators.

Predators away from the nest

There is probably no predator able to take a healthy Cliff Swallow as prey. However, wing remains of adult swallows were seen from time to time near the colonies. Live, injured birds, unable to fly were found at two different colonies in September 1983. These birds probably hit telephone wires which ran very close to the bridge under which they were nesting. Two had broken wings while the third had a swollen and bloody left pectoralis major muscle. These helpless birds on the ground were probably easy prey for the Yellow Mongoose *Cynictis penicillata* which was always in attendance below the colonies. The large numbers of eggs and chicks which fall from the nests are preyed on by Yellow Mongooses which patrol the area below the nests at frequent intervals when there is little or no water below the nests. Clearing areas under the colony so that fresh tracks of mongooses could be noticed

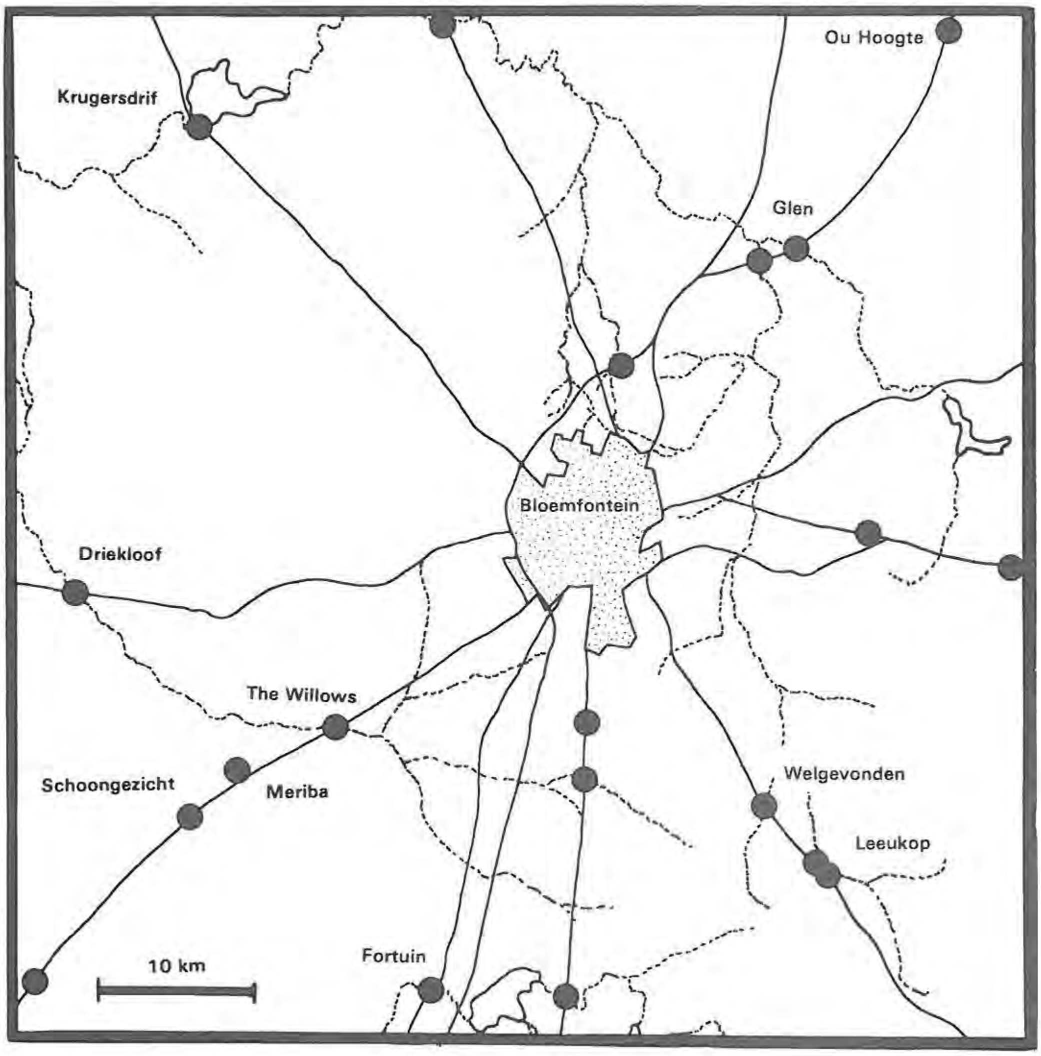

Figure 1: Map of the Bloemfontein area showing the location of the various *Hirundo spilodera* colonies.

showed that as many as five visits per day were made to the colony by a mongoose. At some of the colonies such as The Willows and Driekloof where large populations of red ants *Techmomyrmex albipes* and *Acantholepis capensis* were present, the fallen chicks were immediately attacked and killed by ants. In September 1984 a Blackheaded Heron *Ardea melanocephala* was seen eating fallen chicks below the Driekloof colony. This was probably a chance "finding" by the heron and this species was seen only once in the 1984/85 season at the Schoongezicht colony. At most of the larger colonies one or two Steppe Buzzards *Buteo buteo* were often perched near the colony, probably on the lookout for such helpless injured swallows. Only once was one of the buzzards seen eating a bird while perched near the Schoongezicht colony but the identity of the bird was not known. The regularity with which the buzzards were seen at the colony would probably indicate that they were exploiting it as a food source.

In the 1984/85 season a fresh owl pellet found at the Driekloof colony consisted entirely of Cliff Swallow remains. The identity of the owl was not known but is was almost certainly a Spotted Eagle Owl *Bubo africanus* which is common in the area.

The only other avian predator ever seen eating an adult Cliff Swallow was the Fiscal Shrike *Lanius collaris*. A half-eaten adult swallow was noticed hanging from a thorn of the Soetdoring *Acacia karroo* near the colony at The Willows on 12 September 1983. It was taken down, examined and placed on the ground next to the tree. Moments later a male Fiscal Shrike flew down from a nearby tree, picked the corpse up, and pinned it to the same thorn as before. When the corpse was again taken down, the shrike picked it up for a second time and flew to another tree where it proceeded to eat it. On 9 September 1983 a half-eaten swallow was also found below the same tree. It was probably an injured bird which was killed by the shrike.

Nest predators

Because nests in colonies are usually over water or very high up, few predators can reach the nest contents. A monitor lizard robbed several Cliff Swallow nests of their contents by climbing up a rough concrete wall of a bridge to the colony which was only 1,5 m above the small stream at a small colony about 80 km east of Bloemfontein (Grobler & Jacobs 1985). The main threat at the nest is the two red ant species which attacks the chicks in the nest as was the case at The Willows in the 1983/84 season. No young were reared and breeding at this colony was abandoned in December when a new colony was established under a newer bridge just 50 m away. The only other serious threat is man. At the more accessible colonies the nests are often knocked down for no apparent reason, but sometimes the chicks were taken. However, the Leeukop colony (Figure 1) was very accessible to man and the "B" part of colony was totally destroyed by people in November 1983 after which the colony was abandoned. In late October 1984 all 148 nests monitored in the "A" part of this colony were again knocked down and the chicks taken for food.

Both the House Sparrow *Passer domesticus* and the Cape Sparrow *P. melanurus* were seen removing eggs from the nests of the Cliff Swallow before taking over the nest for breeding. These incidences of egg removal were observed only at the Meriba colony where there was a shortage of nests.

PARASITES

The different parasites of the Cliff Swallow did not occur in equal proportions at the different study colonies (Table 1). The very old colonies such as Driekloof and Schoongezicht were heavily infested with ticks, with smaller numbers of louse flies and fleas. Leeukop on the other hand was a new colony started only in late October 1983 and was virtualy free of ticks, but large numbers of fleas and louse flies occurred here. A parasitic mite was also found at the Leeukop colony in 1983/84 and at Driekloof in 1984/85. Some biological information on the parasites was gathered in a bid to study the effect that these parasites might have on the breeding of the Cliff Swallow.

TABLE 1

NUMBER OF PARASITES IN SINGLE NESTS OF *HIRUNDO SPILODERA* FROM DIFFERENT COLONIES. ALL NESTS WERE COLLECTED ON 1 NOVEMBER 1984.

	Ornithodoros peringueyi **(Tick)**			***Xenopsylla trispinis*** **(Flea)**	***Ornithomya inocellata*** **(Louse fly)**	
Colony & Nest	**Eggs**	**Nymphs**	**Adults**	**Adults**	**Pupae**	**Adults**
Ouhoogte 1	0	57	151	5	2	7
Ouhoogte 2	33	64	110	2	1	2
The Willows 3	6	128	190	0	0	0
The Willows 4	168	453	481	0	0	2
Schoongezicht 5	76	264	177	0	1	1
Schoongezicht 6	1	263	107	1	0	0
Leeukop 7	0	0	2	46	4	7

The Cliff Swallow Louse Fly *Ornithomya inocellata*
The only ectoparasite found regularly on the body of the adult Cliff Swallow is the Cliff Swallow Louse Fly *Ornithomya inocellata*. This is a host-specific parasite which has to live close to the body warmth of its host to be active. Each individual swallow usually had only one of these parasites and seldom more than two. However, at the Ou Hoogte colony as many as four louse flies were found on most of the swallows trapped and handled on 26 September 1984. These louse flies flew and moved sluggishly when away from the body of their host. When mass-trapping swallows at night, large numbers of the flies would leave the birds and would then usually die within a few hours. These parasites were also frequently seen inside nests, especially at the Leeukop colony. When inspecting nests containing eggs these flies were usually seen on the eggs, probably because the incubated eggs had a higher temperature than the nest material. The temperature of the eggs was certainly closer to the optimum temperature required by this louse fly to be active. Three nests were taken down at the Leeukop colony and contained ten, seven and four adult flies respectively. Pupae of this louse fly were also found in these nests, always near the upper interior where they are probably out of reach of the swallows and could thus not be knocked down by the swallow during activities in the nest.

At The Willows colony where the red ants preyed on these flies in the swallow nests, especially in the 1983/84 season, the birds were almost completely free of the louse fly. These flies were never found at the colonies during winter (April—August) when the Cliff Swallows were not present. However, overwintering pupae were found in the nests in winter. *O. inocellata* were found only on adult Cliff Swallows. Although no indication was found that chicks in the nest were parasitized, it is very likely that they were. The swollen and bloody feet of some nestlings and adults were probably the result of bites from these flies.

The Cliff Swallow Flea *Xenopsylla trispinis*

This flea is also a host-specific parasite occurring in the nest of the Cliff Swallow, parasitizing probably both adults and chicks. These fleas were never found on the body of adult swallows handled during ringing operations. Because of their small size (about 1 mm in length), they might sometimes have been overlooked, but they were definitely not numerous on free-flying birds. These fleas were most commonly found in the pad of nest material. In October 1984 three nests from the Leeukop colony were taken down and examined for these fleas. The nests all had eggs and harboured 45, 36 and 29 fleas respectively. *X. trispinis* were also found in nests during the winter months when the Cliff Swallows were not present. Three nests examined during the 1983 winter contained 21, 11 and two live fleas on 10 May 1983, about one month after the Cliff Swallows had departed for their nonbreeding grounds.

The Cliff Swallow Tick *Ornithodoros (Proknekalia) peringueyi* (Figure 2)

The third host-specific parasite of the Cliff Swallow is the argasid tick *Ornithodoros (Proknekalia) peringueyi.* This tick is a nest parasite and was never found on any free-flying adult swallow. Although adult birds are attacked at night, the chicks in the nest were probably the main victims. Adults were bitten mainly on the abdomen and to a lesser extent on the breast. Spots where the ticks had recently fed could clearly be seen as bloody areas up to 5 mm in diameter. Chicks taken from nests for examination very often also showed these bloody feeding spots on the abdomen. Cliff Swallow chicks were, however, most commonly attacked by nymphs of this tick. In all nests taken down at the end of the 1983/84 breeding season at the Schoongezicht and Driekloof colonies, tick eggs were found under the nest lining, attached to the mud of the nest. These eggs were probably dormant during the winter months and hatched only when the nest was once again occupied the following season.

On 1 November 1983 ten nests were selected at the Driekloof colony. Five of these were new nests started and completed in that season and five were nests which had been used at least once before in the previous season. A total of 11 chicks were taken from the new nests and nine from the old nests and examined for ticks. The chicks were all 7-15 days old. The chicks from the old nests had a mean number of 94 (range 46-144) tick larvae and nymphs on them. These larvae and nymphs were mostly attached to the skin between the gape and the eye, but also in front of the eye and on the forehead. Very few larvae and nymphs were found elsewhere on the chicks and only one adult tick was found on the lower abdomen of one of the chicks. All 11 chicks from the new nests were completely free of *Ornithodoros* larvae and nymphs and only two adult ticks were found, one each on the abdomen of two siblings. Only two adult ticks were found at these Leeukop colonies after a thorough search in October 1984. All chicks at this colony were completely free of *Ornithodoros* larvae and nymphs, indicating that no tick eggs were present in the nests. Although this tick is a nest parasite nymphs are sometimes still found on newly fledged young. In a sample of 31 newly fledged young, judged to have been out of the nest for less than two weeks, only two had seven and five *Ornithodoros* nymphs respectively still attached at the gape. When not feeding the ticks

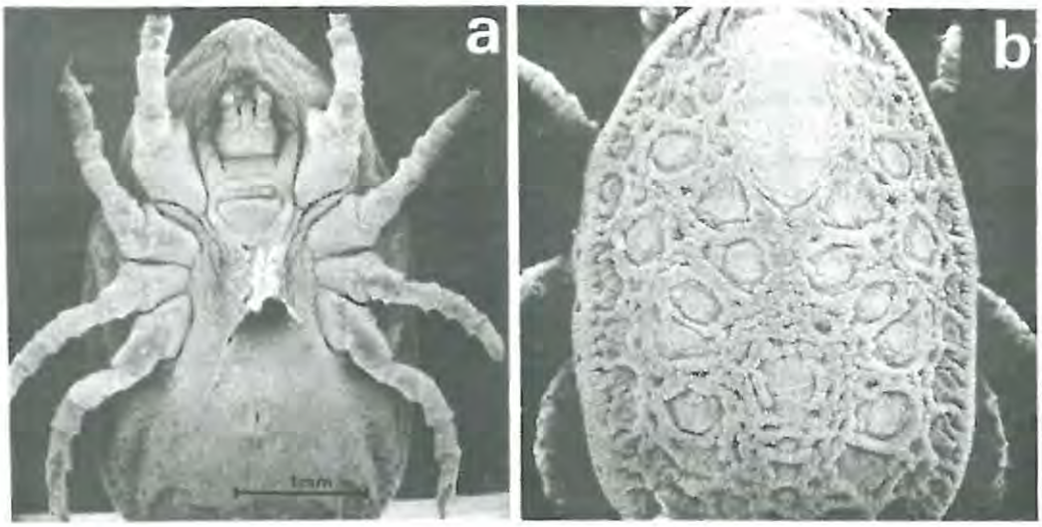

Figure 2: Ventral (a) and dorsal (b) view of a female Cliff Swallow tick *Ornithodoros peringueyi* showing discs and integumental ridges on the dorsal side. Photos supplied by J.E. Keirans. Dorsal view reproduced from Keirans *et al.* 1977.

could be seen, usually in large numbers, near the top of the nests in the small crevices between the mud pelets. At the Driekloof colony masses of ticks were also found below the nests under rocks.

Other body and nest parasites

Twice nymphs of *Hyalomma* sp. ticks were found on the heads of adult swallows. The adults of these ticks are usually parasites on large mammals but the nymphs are sometimes found on terrestrial birds. These *Hyalomma* ticks occurred so infrequently on the Cliff Swallow that their importance was negligible.

At the Leeukop colonies a mite *Ornithonyssus bursa* (Fam: Macronyssidae) was first noticed in the latter half of November 1983, and by the middle of January 1984 they were so numerous that it became virtually impossible to work at these colonies. When these nests were again checked in March 1984 the colony was deserted and many nests still contained eggs and dried-out corpses of young. It is not known for certain whether the heavy infestation of mites caused the desertion but it seems very likely. In the 1984/85 season this colony was completely destroyed by people in late October and the mites were not noticed at the colonies during the first part of the season. Very few of the mites were found on the bodies of the swallows when these were handled during nocturnal ringing operations. In 1984/85 this mite was found at the Driekloof colony from November 1984 to the end of the season.

Free-flying Cliff Swallows have very few body parasites apart from the louse fly *Ornithomya inocellata.* One species of sucking louse (Anoplura), *Myrsidea rustica,* was found on a few Cliff Swallows during ringing operations. Only one of these lice was found during the delousing attempts (Fowler & Cohen 1983). A second genus of sucking louse, *Menacanthus,* which occurs on Passeriformes and cannot be identified to species at present (J.A. Ledger *in litt.*), was collected from the Cliff Swallow at several colonies.

No endoparasites were found in a sample of 10 birds examined. Cestodes of the families Dilepididae and Hymenolepididae were found parasitizing the American Cliff Swallow (Stamper & Schmidt 1984) and the European Swallow *H. rustica* (Illescas-Gomez & Lopez-Roman 1980).

SYMBIONTS

This section deals with animals of other species that live and/or breed at the nest colonies. Because the swallow colonies were usually under bridges in constant shade and often over water, the temperatures were often substantially lower than elsewhere, and it is thus expected that a large number of animals at the colonies were opportunistic occupants seeking a cool micro-habitat.

Invertebrate symbionts

Only two orders of insects, other than parasites, were regularly observed at the Cliff Swallow nests. The sap-sucking bugs of the family Pyrrhocoridae were plentiful at all the colonies but the reason for this is not clear. The only other insects regularly seen at the nests were the mudnest-building Hymenoptera of the families Sphecidae and Vespidae. Several of these wasp nests were present at each of the colonies and sometimes those nests got so big that the entrance to one of the swallow nests was at least partly blocked, causing the swallow pair to seek a new nest.

At the Driekloof colony, where there was no water under the bridge for the larger part of the study, and where the swallow faeces below the nests were up to 5 cm thick, an interesting array of Coleoptera was found. Dung beetles of the family Scarabaeidae included *Scarabaeus* spp. (two), *Onthophagus* sp., *Epirhinus* sp., *Coptorhina klugi, Phalops* sp. and *Copris* sp. Of the Tenebrionidae both *Eurychora* sp. and *Gonocephalum* sp. were plentiful. *Dermestes maculatus* (Dermestidae) were also preying on corpses, mainly of chicks, below the nests.

Vertebrate symbionts

Apart from the single Common Cape Gecko *Pachydactylus capensis* found in the same nest at the Schoongezicht colony a few times (this nest contained a clutch of two swallow eggs), all the other symbionts were avian.

(a) House Sparrow *Passer domesticus*

All the colonies examined near Bloemfontein, except the Leeukop A colony, had at least one pair of House Sparrows breeding in one of the nests. Nests on the edge of the larger colonies were usually selected for breeding but in the small colonies any nest was used. The sparrows were very aggressive, and usually no swallow was allowed to breed in nests next to those that the sparrows had selected. At the Meriba colony, where small numbers of nests were clustered together, the sparrows took over one or more nests and succeeded in keeping the swallows from entering their nests to incubate. At this colony the constant chasing of the swallows by both the male and female House Sparrow led to the desertion of virtually the entire colony about 10 days after the first eggs were laid. At the Driekloof colony where there were about 700 breeding swallow pairs, eight House Sparrow pairs had simultaneously active nests in this colony in 1983/84. The sparrows usually used nests with wide entrance holes, such as half completed or broken nests. The nests were stuffed with grass and House Sparrow nests were easily spotted in a Cliff Swallow colony.

(b) Cape Sparrow *Passer melanurus*

In the almost treeless veld where most of the colonies were studied the Cape Sparrow also made good use of the Cliff Swallow nests for breeding. Cape Sparrows were not as aggressive as House Sparrows and although they were observed throwing out swallow eggs from a nest at the Meriba colony before breeding there themselves, other swallow pairs were left in peace and allowed to continue their breeding activities. during the winter months when the swallows were absent, large numbers of Cape Sparrows occasionally used the nests for roosting.

(c) Red-headed Finch *Amadina erythrocephala*

In April 1983 just after the swallows had departed, a pair of Redheaded Finches started building a nest in one of the Cliff Swallow nests at The Willows colony. Eggs were never laid in the nest which was stuffed with feathers, and the finches were not seen again after June 1983. During a visit to the Tweespruit area in March 1984 several Red-headed Finches were found breeding in Cliff Swallow nests.

(d) Little Swift *Apus affinis* and White-rumped Swift *A. caffer*

At some of the high bridges (10 m+) over the Modder River at Glen and Krugersdrif (Figure 1), large colonies of Little Swifts were mingled with those of the Cliff Swallow. The swifts usually took over nests of the swallow and these were then lined with feathers and saliva in the usual manner. At Krugersdrif dam, where the swallow nests were extensively damaged and only the rims of the nests remained, the swifts started building their own feather nests, using the remaining mud only as a base. Brooke (1959) also found Little Swifts making use of broken Cliff Swallow nests. Although many hours of observations were made at a large mixed Little Swift/Cliff Swallow colony, no aggression between the two species was ever observed.

Most of the Cliff Swallow colonies studies were probably too low for the White-rumped Swift to breed, (although they were breeding in a 1,7-m-high culvert in a Greater Striped Swallow *Hirundo cucullata* nest and were found to use culverts as low as 0,6 m (Brooke 1974)) but these swifts were regularly seen at all the colonies. Only at the Leeukop colony did the White-rumped Swifts breed in the 1983/84 season. A nest was completed at the Schoongezicht colony under the large bridge but breeding only took place in the 1984/85 season. Brooke (1959) found that about half of the Cliff Swallow nests at a colony near Britstown was taken over by White-rumped Swifts. It thus seem as if these swifts are not short of other breeding sites in the Bloemfontein area and do not take over Cliff Swallow colonies on a large scale.

(e) Pied Barbet *Lybius leucomelas*

A single Pied Barbet roosted for about three months in one of the Cliff Swallow nests at The Willows colony during the winter of 1983 when no swallows were present.

(f) Other bird species

A number of other bird species (Familiar Chat *Cercomela familiaris*, Mountain Chat *Oenanthe monticola*, Greyheaded Sparrow *Passer griseus* and Pied Starling *Spreo bicolor*) roosted, especially on very hot days, on the half completed cups of nests usually at the edge of the colony. On 16 January 1985 a single juvenile European Swallow *Hirundo rustica* was trapped at one of the Cliff Swallow colonies during a nocturnal mass-trapping operation (Earlé 1984).

(g) Bird species not directly associated with the nest masses

Several swallow and swift species which mixed freely with the flocks of Cliff Swallows flying around the nesting colonies were also noted.

The most interesting observations were those of the House Martin *Delichon urbica* which was observed at all the colonies during October 1983. At the Meriba colony, where 12-hour watches were done on several occasions during October 1983, one or two House Martins were often seen flying around with the Cliff Swallows. On 15 and 17 October one individual landed on a small ledge on the wall of the quarry and later move to a half-built nest cup where it remained for about 25 min before a Cliff Swallow drove it from the nest. House Martins were also seen at The Willows colony hanging against the wall of the bridge below the colony while another sat on a mud ledge on the edge of the colony. House Martin nests are structurally nearly indistinguishable from those of Cliff Swallows and this might attract them to Cliff Swallow colonies. At both The Willows and Schoongezicht colonies, House Martins were also observed on telephone wires with Cliff Swallows, preening. During a heavy rainstorm at Schoongezicht ± 200 Cliff Swallows together with 12 House Martins were perched on a barbed wire fence near the nests. All the Cliff Swallows continuously ruffled their feathers and preened as if they were bathing but the House Martins sat still. House Martins also associated with a breeding colony of Redthroated Cliff Swallows *H. rufigula* in Zambia (Taylor 1982) and with Greater Striped Swallows (Fellowes 1971) in very much the same manner as described above.

A Whitethroated Swallow *H. albigularis* associated with the small colony at Meriba for several days during October 1983, often sitting on the sand below the nests or joining the Cliff Swallows at mud-gathering sites.

Greater Striped Swallows, European Swallows *H. rustica*, Black Swifts *Apus barbatus* and European Swifts *A. apus* were all often seen flying amongst flocks of the Cliff Swallow near the nesting colonies.

DISCUSSION

Probably because of the relatively safe nesting place of the Cliff Swallow, usually under high bridges and often over water, I could not find any sign of large-scale predation on eggs and nestlings by any predator, as was the case with other colonially breeding birds such as the Sociable Weaver *Philetairus socius* (Maclean 1973). Although Cape and House Sparrows were seen to remove eggs from nests when taking over nests for their own breeding, the incidence of this was very low and probably negligible. There was definitely no large scale killing of swallow chicks by House Sparrows as was the case with the American Cliff Swallow *H. pyrrhonota* (Buss 1942). It would seem as if only the very small colonies would suffer from displacement by these sparrows and that the presence of the sparrows have very little effect, if any, on the swallows in the larger colonies, provided that there were surplus nests available, as was the case in all the larger colonies studied. S.F. Townsend observed the breeding of sparrows in the nests of the Cliff Swallow near Beaufort West as early as 1879 (Winterbottom 1962) but did not record attacks by the sparrow on the swallow. Townsend probably referred to Cape Sparrows or possibly Greyheaded Sparrows *P. griseus* as House Sparrows did not occur in the Karoo until the 1950's (Brooke *in litt.*).

The only total destruction of eggs, chicks and nests were by people at the two Leeukop colonies; one in November 1983 and the other in October 1984. The chicks were taken for food and although the adults deserted the colonies, the destruction had very little effect on the population as a whole. The heavy predation by red ants on chicks at The Willows in 1983/84 must be regarded as exceptional. The populations of these ants were much larger than in previous years and, although these ants have always been at the nests scavenging on fallen insects, faeces and young which have fallen from the nest, they attacked young in the nest only this one year when the stream below the bridge contained no water.

The results would thus indicate that there is very little predation on eggs or nestlings of Cliff Swallows in the nest, provided that the nests are high enough or over water so that man cannot reach them. This is in sharp contrast to the predation at other colony nesting hirundines such as the Sand Martin *Riparia riparia* (Mead & Pepler 1975, Blem 1979), where reptiles and mammals were recorded as predators on nest contents.

It seems as if most of the predation on the Cliff Swallow is by animals taking helpless chicks which have fallen from the nest to the ground below, injured adults and possibly young inexperienced fledglings. Mead & Pepler (1975) also recorded the Steppe Buzzard as a predator of Sand Martins and, as in the case of the Cliff Swallows, it was seen eating a bird but not actually killing it.

The major point emerging from this study of the parasites of the Cliff Swallow is that it has two body parasites and one nest parasite not known from any other hosts. The tick *Ornithodoros (Proknekalia) peringueyi* together with the two other swallow-nest ticks *O. (P.) peusi* parasitizing chiefly the Redrumped Swallow *H. daurica* in Greece and *O. (P.) vansomereni* parasitizing the Lesser Striped Swallow *H. abyssinica* and the Redrumped Swallow in Kenya comprise a highly distinctive subgenus of argasid ticks (Keirans *et al.* 1977). These three species are described as having strict to total specificity for their hosts (Hoogstraal & Aeschlimann 1982), indicating the strong evolutionary relationship between the Cliff Swallow and *O. (P.) peringueyi.* Laboratory studies by H. Hoogstraal (*in. litt.*) on the Cliff Swallow tick have proved to be quite difficult as the larvae hatching from eggs would not readily feed on the substitute hosts. Larvae of this tick not only fed solely on Cliff Swallow chicks but also preferred specific areas to feed on, namely around the gape and below the eyes, confirming the statement by Hoogstraal (1978) that "numerous ethological characteristics ... point to the intimate and complex relationships that have evolved between individual tick species and kinds of hosts. Each species aims toward a preferred feeding area of the host ..." For nymphs to feed around the eyes and mouths of nestlings is sensible since the nestlings cannot preen such areas and, presumably, their parents do not do it for them. The fact that the tick nymphs, with few exceptions, all drop off the swallow chicks before the chicks leave the nest, means that the ticks stay in the nest where the succeeding stage will have an opportunity for finding a new host (Hoogstraal 1978). This once again indicates a close relationship between the Cliff Swallow and its tick. As no ticks were ever found on any of the Cliff Swallows trapped during nocturnal mass-trapping operations, the ticks are probably well adapted to drop off the host at the slightest disturbance, e.g. when the birds prepare to leave the nest, so that they stay in the nest where they are sure to find a new host. Although the "clustering" areas of this tick are usually near the top of swallow nests, the preferred feeding area of adult ticks on the swallow is the abdomen. "Clustering" near the top of the nest reduces the possibility of being disloged from the nest by the birds' activities, whereas feeding on the abdomen while the bird is in the nest allows the tick to "drop-off" quickly when the need arises. The abdomen is also devoid of feathers making feeding easier to some extent.

Although some work has been done on isolating the Chenuda virus *Orbivirus* (fam: Reoviridae) from *O. (P.) peringueyi* in South Africa (Hoogstraal 1973) very little else is known about the biology of this tick species (Keirans *et al.* 1977) and no life cycle data for species of the subgenus *Proknekalia* are available at present (Hoogstraal *in litt.*). The information presented here is thus the first describing some aspects of the biology of *O. (P.) peringueyi.*

At the Leeukop colonies no ticks were found during the 1983/84 season. The colonies were started in October 1983 and because the ticks are nest parasites, it would probably take at least a few seasons for enough ticks to reach such a new colony, as there is very little intercolony movement by the swallows which can be the "chance" carriers of the ticks to new colonies. Judging by the large numbers of *O. (P.) peringueyi* especially at the older Cliff Swallow colonies, one would expect that these ticks would have some effect on the swallows in such colonies. At both the Schoongezicht and The Willows colonies there were always some parts of the colony, containing complete but old nests, which were not used at any specific time. This might be due to heavy tick infestation. J.B. Walker (*in. litt.*) writes, "I suspect that the (Cliff) Swallows would desert heavily infested nests or colonies. If I were a swallow I am sure I should not be very enthusiastic about staying in a nest in which I got well and truly bitten! The bites of some argasids are said by humans who have been bitten to be very painful".

A number of studies have reported on the species of ticks attacking other swallow species, notably the American Cliff Swallow *H. pyrrhonota* (Baerg 1944, Kohls 1947, Howell & Chapman 1976, Hopla & Loye 1983, Loye & Hopla 1983) but only Baerg (1944) concluded that the ticks had no effect on the swallows though without substantiating his statement. Among colonial seabirds the evidence is strong that ticks cause desertion by nesting adults with resultant mortality of eggs and young (Feare 1976, King *et al.* 1977a, 1977b, Duffy 1981, 1983). This was not observed during my study, at least not on a large scale, although there are indications that parts of the colony and even individual nests could have been deserted because of the tick populations building up to very high levels. However, there is also strong evidence from this study that there is often very heavy predation on the tick itself by ants which might keep the tick population in check. Ant predation on ticks was also recorded in Zaïre (Nuttall & Warburton 1908).

Although there is no evidence that the ticks had a direct influence on the mortality of Cliff Swallow chicks there were always some, seemingly healthy, chicks falling from the nests at especially Driekloof and Schoongezicht, the two colonies with the largest populations of ticks. I suspect that chicks in heavily infested nests were very restless when bitten often and fell from nests when trying to get rid of some of the ticks. Restless behaviour in adult Peruvian Boobies *Sula variegata* accompanied by a dramatic increase in preening always preceded nest desertions as a result of heavy tick parasitism (Duffy 1983). Preening starts relatively early in the Cliff Swallow and this "uncoordinated" preening of chicks at an early age might result in them falling from nests. If this is the case, the Cliff Swallow tick *O. (P.) peringueyi* does have an indirect effect on nesting success and mortality of Cliff Swallow chicks in heavily infested colonies.

The Afrotropical Region has very few avian fleas (Siphonaptera). Only two fleas have been recorded from African swallows. The widespread *Echidnophaga gallinacea* has been recorded from the Brownthroated Martin *Riparia paludicola* while the only host known for *Xenopsylla trispinis* is the Cliff Swallow. Nothing is known about the biology of the Cliff Swallow flea and its effects on its host. As this flea was found in the nests of the Cliff Swallow during winter when the swallows were not present, at least some fleas must overwinter in the swallow nests as the flea *Ceratophyllus styx* does in the burrows of the Sand Martin (Rothschild & Clay 1952, Mead & Pepler 1975). The biology of the flea usually found on American Cliff Swallows, *Ceratophyllus petrochelidoni,* has evolved to compensate for the swallows' long absence from the nest during the non-breeding season (Traub 1972, Nelson *et al.* 1979). This might also be the case with *X. trispinis.* Fowler et al. (1983) found that the number of fleas per birds as well as the number of birds infected by fleas was highest during the period of dispersal from communal winter roosts and nestbuilding in the Blackbird *Turdus merula.* It is during this period that the fleas would have a greater opportunity of finding new hosts. In the Cliff Swallow colony the fleas find new hosts easily which is probably why fleas parasitizing colonial breeding hirundines have opted for overwintering in the nest rather than accompanying the birds on their migration.

The mite *Ornithonyssus bursa* is a continuous parasite of several bird species (Powlesland 1978), a lizard (Cameron 1938) and man (Murray 1950). As it requires a blood meal at least every 4-6 weeks (Powlesland 1977) it cannot survive at the Cliff Swallow colonies through the winter when the birds are absent. However, as several other bird species, notably the House and Cape Sparrows, occupy nests in several Cliff Swallow colonies during winter, at least some of the mites can survive to reinfest the colony when the swallows return. Only the relatively small Leeukop colonies were heavily infested by this mite during this study and it was probably the cause of total desertion of the colony late in the 1983/84 season. Even well grown chicks were deserted, indicating the impact of the mite on the colony. Burgerjon (1964) suggested that the low breeding success of the Cliff Swallow during one of the studied breeding seasons was the result of the heavy infestation by this mite. The Leeukop colony was the only which did not contain House or Cape Sparrows to "carry" the mites through the winter, and mites were not noticed again at this colony before it was destroyed. However, it is possible that some mites overwintered ectoparasitically on the swallows as it may do on the European Starling *Sturnus vulgaris* (Petersen 1979). This nuclear population can then build up rapidly in the swallow colony during the breeding season. Powlesland (1977) found that *O. bursa* had no demonstrable major effects on the growth rate, weight, mortality, blood characteristics and lipid stores of starling nestlings. Although this was not investigated in the Cliff Swallow colonies, no obvious effects were noticed except for possible desertions late in the 1983/84 season.

The only host known for the louse fly *Ornithomya inocellata* is the Cliff Swallow. Another species *O. fur* is widespread among the swallows and other passerines. Although no life-cycle data are available for *O. inocellata,* it probably follows the typical hippoboscid pattern as described by Rothschild & Clay (1952), Ledger (1968) and Wood (1983), whereby the egg and larval stages develop while still in the female and the larvae very soon pupate and hatch into adult flies. I could find very little evidence that mechanical damage to the skin by the bites of these flies leads to bacterial infections and possible death of young nestlings (Ledger 1968), but large numbers of individuals at certain colonies had swollen and often bleeding feet as a result of bites from these parasites.

OPSOMMING

As gevolg van die relatief veilige nesmaakplek van die Familieswael *Hirundo spilodera* en sy ratsheid is daar blykbaar geen predator wat gereeld Familieswaels vang nie. Beseerde voëls val roofdiere egter dikwels ten prooi. Twee liggaams en een nes ektoparasiet is spesiespesifiek tot die Familieswael. Geeneen van dié drie parasiete, die bosluis *Ornithodoros peringueyi*, die flooi *Xenopsylla trispinis* of the luisvlieg *Ornithomya inocellata* het 'n ooglopende negatiewe effek op die Familieswael nie, maar daar is tog aanduidings van indirekte kuikenmortaliteit waar hoë populasies bosluise voorkom. 'n Groot verskeidenheid vertebrata en invertebrata maak ook gebruik van die neste van Familieswaels en sekere voëlspesies soos die Gewone Mossie *Passer melanurus* en die Huis Mossie *Passer domesticus* broei baie gereeld in Familieswael neste.

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Two of the major study colonies, namely The Willows and Schoongezicht were on farms where the farmers, Mr Dirk Bredenkamp and Mr Louis van Aswegen allowed me free access to the farms whenever I wished for which I am very grateful. I would also like to thank my technicians, Ben Bester and Hester du Toit for invaluable help throughout the study. Drs Jane Walker and John Ledger identified some of the ectoparasites while Schalk Louw identified the invertebrate symbionts. Prof Gordon Maclean of the Department of Zoology, University of Natal (Pietermaritzburg) and Mr Richard Brooke of the Percy Fitzpatrick Institute of African Ornithology, University of Cape Town critically reviewed this paper and made comments which led to a much improved paper.

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THE NEST OF THE SOUTH AFRICAN CLIFF SWALLOW *HIRUNDO SPILODERA* (AVES: HIRUNDINIDAE)

by

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National Museum, Bloemfontein

(With 9 figures)

ABSTRACT

Earlé, R.A. 1985. The nest of the South African Cliff Swallow *Hirundo spilodera* (Aves: Hirundinidae). *Navors. nas. Mus., Bloemfontein* 5(2): 21-36. The South African Cliff Swallow *Hirundo spilodera* builds a closed mud nest with a short entrance tunnel and nests colonially. In the Orange Free State most of the colonies were under concrete road bridges. Mud from both temporary pools and permanent streams was used and there seems to be no selection of certain types of mud for nestbuilding. The nestpad consisted of sheep's wool, plantdown and sometimes feathers. There are five recognizable stages in nestbuilding. Two nests took five and seven days respectively to complete. **(South African Cliff Swallow, *Hirundo spilodera*, nest building).**

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CONTENTS

INTRODUCTION

The avian nest has a central role in the reproductive success of the species. Nests are thus often very complex and built with special materials in specific places. Among the members of the family Hirundinidae a wide variety of nests are built ranging from a simple nest pad in a sandbank tunnel to a very thick walled closed mud nest under an overhanging rock. Mayr & Bond (1943) regarded the swallow species using natural holes or holes excavated by other animals for breeding as more primitive and the species building closed mud nests as more advanced. The South African Cliff Swallow *Hirundo spilodera* builds a thin-walled closed mud nest with only a short entrance tunnel and thus probably forms a link between the hole nesters and thickwalled mud nest builders. Aspects of the nest and nestbuilding of the South African Cliff Swallow were studied to gain insight into the importance of the nest as a breeding environment, especially as the South African Cliff Swallow is a highly social bird which breeds colonially (Maclean 1985).

STUDY AREA AND METHODS

Observations were made at various South African Cliff Swallow colonies in the central Orange Free State. The nest was studied in the 1983/84 breeding season which was an exceptionally dry year with only occasional thunderstorms. Most observations were done at two colonies, namely at Meriba, a small colony with about 100 South African Cliff Swallow pairs, situated on the wall of a quarry and The Willows, containing about 400 paris and situated under an old disused concrete road bridge. The location of the colonies around Bloemfontein was given by Earlé (1985). Building on one nest each at Meriba and The Willows were watched on three consecutive days throughout the daylight hours. At Meriba most of the birds were individually recognizable as they were either colourringed or some parts of the body, mostly primaries and rectrices, were died with acetone based paint. The birds, which were paint-marked, were thus recognizable both at the nest and away from it.

X-ray florescence was used to determine principal elements in mud samples while grain size of mud was determined by using a series of sieves.

RESULTS

The nest site

With the exception of the small colony at Meriba, all the breeding colonies of the South African Cliff Swallow in the study area were situated under man-made concrete road bridges of various heights and dimensions (Figure 1). No clear pattern in the selection of bridges for nesting colonies was apparent. Large and small bridges and even large culverts, in the case of the Leeukop colony, were used. Larger bridges usually had larger colonies if there were suitable foraging areas nearby. Some of the new larger bridges were, however, constructed with beams running lengthwise close to each other and over the whole breadth of the construction and seldom attracted the South African Cliff Swallow. Some of the newer bridges also had very smooth vertical surfaces which prevented the swallows from nestbuilding as they could not get a foothold. On one such a bridge at Glen, building of the first nests started around the edge of a 2 cm diameter vertical pipe cast into the bridge to drain water from the road surface (directly through the bridge). This was the only place where the birds could get a foothold and a clump of nests were built around this pipe. The first nests built at a site were located at the junction of the vertical support wall of the bridge and the roof of the bridge. Later builders then usually attached their own nests to the completed or partially built nests. The colony would thus expand as new nests were built both horizontally outward against the bridge roof and vertically downward from the first row of nests. Only in the older colonies was there a downward extension of the colony and most new nests built were against the roof of the bridge. The mean distance between adjacent nest openings was 51,8 mm ($n = 53$; range 20-100) in a randomly selected part of the dense Driekloof colony.

The Meriba colony was the only one observed which was not situated under a concrete bridge and the nests here were built on the overhanging wall of a man-made quarry (Figure 2). Skead (1974) mentions South African Cliff Swallows building nests against the wall of a quarry in the S.A. Lombard Nature Reserve. A few other "natural" breeding sites were found in the Orange Free State, all being in man-made quarries. No colonies were found on cliffs as these do not occur in the central Free State.

There were always parts of the larger colonies which were not in use and where the nests fell into decay. At The Willows colony, only two of the three sections of the small bridge were in use. The middle section had many irregular and broken walls of old nests which I took down before the 1983/84 breeding season, but no new nests were started in this section during this or the 1984/85 season.

There was no obvious height requirement for the colony. Most of the colonies, however, were out of reach of a man standing on ground level and could only be reached with a stepladder for inspection. The colony at Leeukop was an exception in that it was only 1,35 m high and thus within easy reach from the ground. Although most of the streams running below the nesting bridges held water for at least part of the summer, it was by no means clear

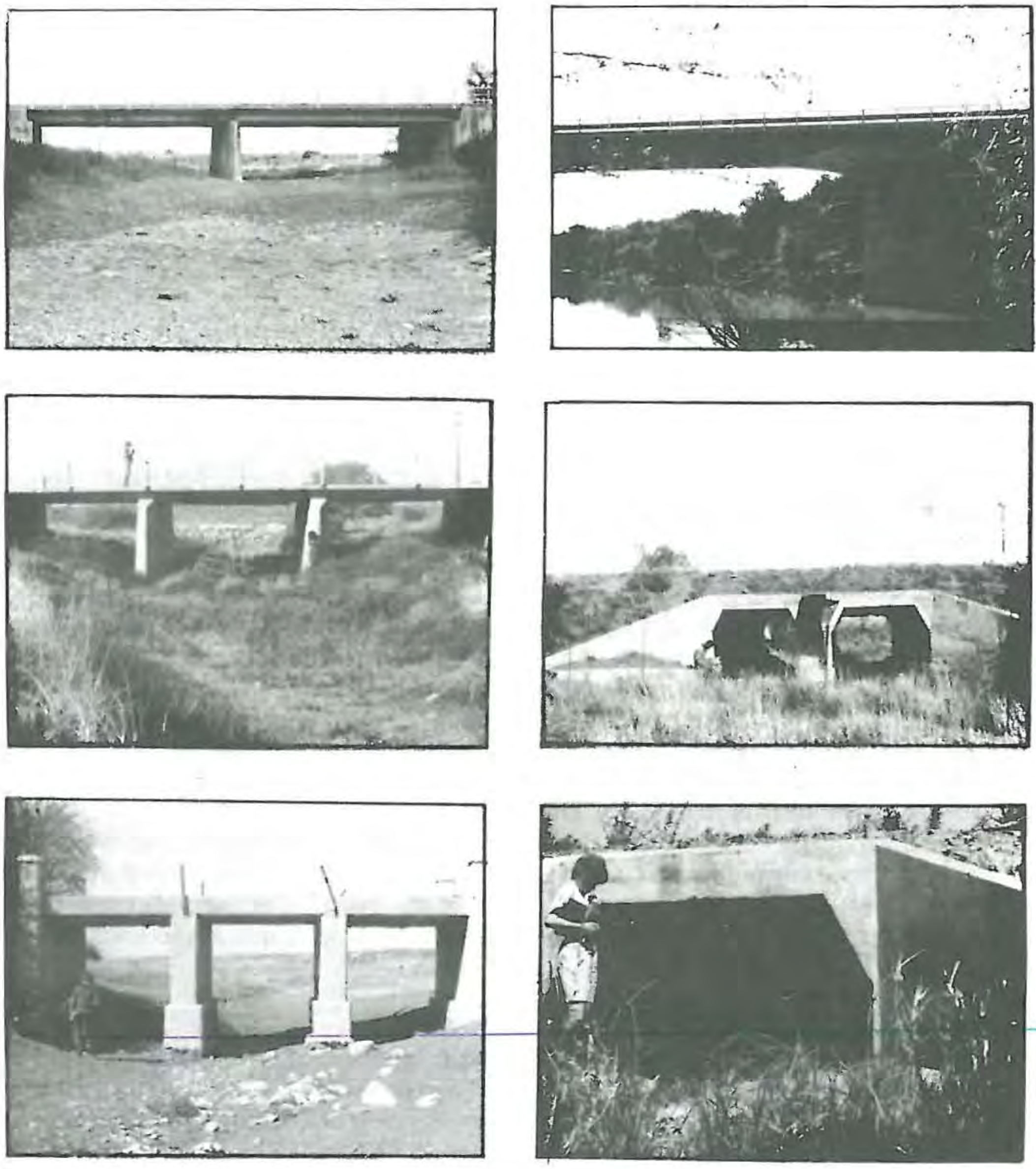

Figure 1: Concrete road bridges used for nesting by *Hirundo spilodera.*

that the swallows preferred sites over water. It is more likely that these were the only suitable places available. All the colonies observed in the Orange Free State were away from human habitation; none were located in a barn or on any structure occupied by humans.

Nesting Material

Mud for nest construction was gathered from 6 m to about 300 m from the nesting colony. After rains temporary pools are mainly used as a source of mud, but during rainless periods the swallows usually used mud from the edge of the streams near the nesting colonies. The

Figure 2: The small colony at Meriba against the wall of a quarry.

availability of mud affected the rate of construction of nests and rain which formed temporary pools greatly stimulated nest building. During the dry 1983/84 season it was striking that when temporary pools were available as a mud source, other "usual" sources such as the stream banks were ignored even though the birds had to fly an additional few hundred meters.

The quality of mud varied considerably amongst colonies and probably depended on the local source. The nests at Meriba had a high percentage of coarse sand in the mud used for building whereas nests at The Willows built with mud from the small stream were high in clay. In many of the nests several types of mud were found indicating that various sources had been utilized in their construction.

The principal elements found in the mud samples from nests are given in table 1. The "grey" mud from the nest body is high in calcium and silicate but relatively lower in all the other elements. The mud from the mud-gathering site and from the mud ledge had very much the same composition as the ledge was built from this site which was a temporary pool formed after rain had fallen. The grain size of samples from mud-gathering sites and of nests are given in figure 3. Mud with a grain size of 260 *u*m and smaller was considered as clay. The accumulative clay fraction of mud from the mud-gathering site and the nest is very similar (60 % clay in nest; 65 % clay at mud site). No indication was found of saliva in mud samples. Water from temporary pools contained the same amount of enzymes and organic material as wet mud in the nests. Neither was any indication found that nests built with any type of mud, was more durable.

TABLE 1

PRINCIPAL ELEMENTS IN MUD SAMPLES TAKEN FROM *HIRUNDO SPILODERA* NESTS AND FROM A MUD COLLECTING SITE AT THE WILLOWS COLONY. FIGURES GIVEN AS A PERCENTAGE OF THE TOTAL SAMPLE ANALIZED.

Source of the mud	Amount of mud analized (g)	Elements												
		Si	Ti	Al	Fe	Mn	Mg	Ca	Na	K	P	LOI[4]	Organic material	Total
Mud gather site	121,9	55,4	0,7	13,0	5,6	0,1	1,0	0,8	0,6	1,7	0,2	13,1	7,4	99,6
Mud ledge[1]	119,4	57,8	0,7	13,6	5,6	0,1	1,2	0,8	0,4	2,0	0,2	11,7	5,8	99,9
Nest body[2]	113,7	70,8	6,6	7,9	3,5	0,1	1,2	2,6	0,5	1,6	0,1	8,6	2,1	99,6
Nest Roof[3]	118,5	60,5	0,6	11,9	5,1	0,1	1,3	1,0	0,4	2,0	0,1	9,3	7,3	99,6

[1] The mud ledge is attached to the concrete bridge.
[2] "Grey" mud from calcereous stream.
[3] "Red" mud from temporary pool after rain.
[4] LOI Elements lost on ignition, mostly H_2O and CO_2.

TABLE 2

NESTPAD ANALYSIS OF *HIRUNDO SPILODERA* NESTS

Nest Number	Plantdown Mass (g) (% of total)	Sheepswool Mass (g) (% of total)	Feather Mass (g) (% of total)	Total Mass of Nestpad (g)
1	3,3 (64,7)	1,7 (33,3)	1,0 (1,9)	5,1
2	2,3 (51,1)	1,6 (35,5)	0,6 (13,3)	4,5
3	11,4 (73,3)	3,9 (25,0)	0,25 (1,6)	15,6
4	4,8 (44,4)	6,0 (55,5)	0,1 (1,0)	10,8
Mean	5,5 (61,1)	3,3 (36,7)	0,2 (2,2)	9,0

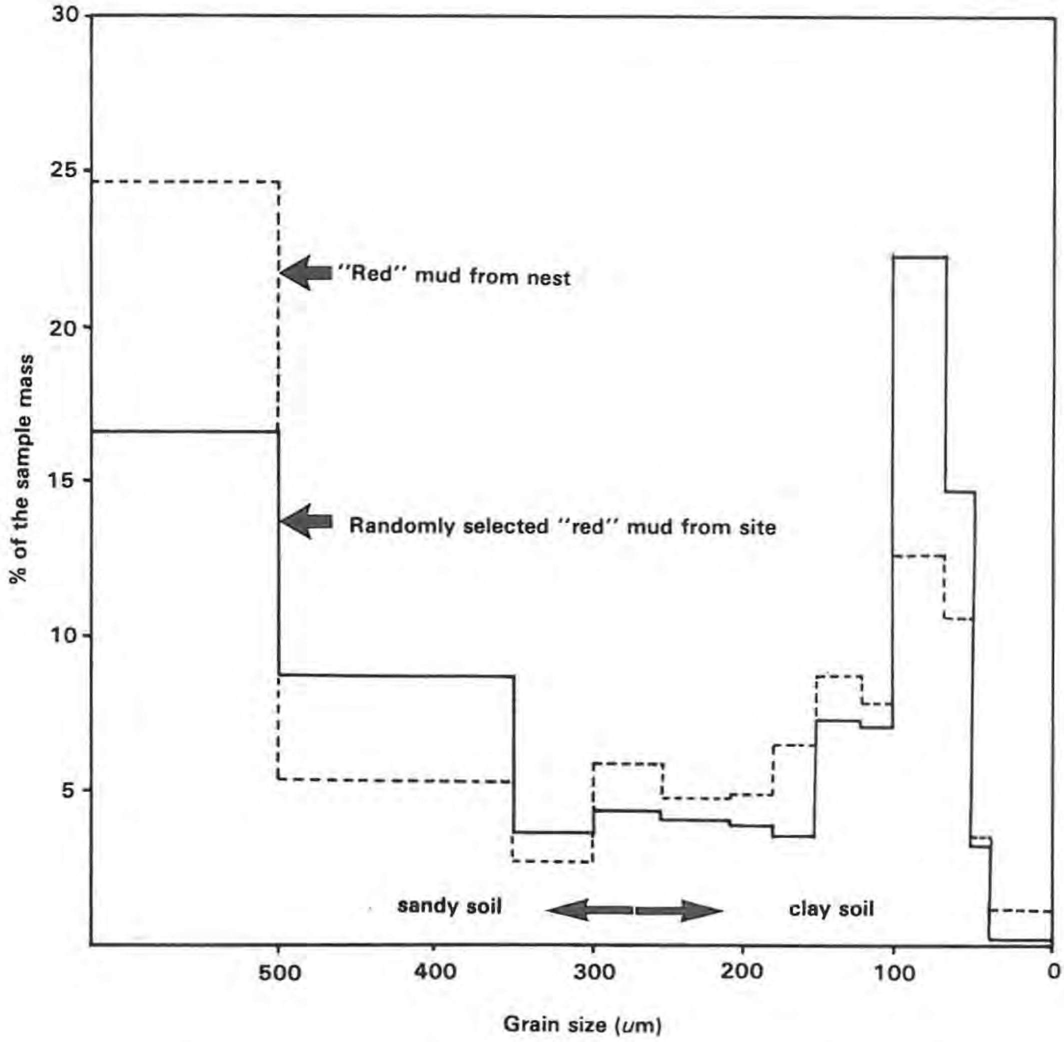

Figure 3: The occurrence of different grain sizes of the mud used in the nests of *Hirundo spilodera.*

Nests in which breeding occurred were lined with a pad consisting of sheep's wool and plantdown with some feathers (Table 2). In most of the pads three distinct layers of the different materials could be recognized. At the bottom was the plantdown with a layer of sheep's wool on top. If feathers were present they were always found on top of the sheep's wool, but were usually too few to form a complete layer. No grass was ever found in any of the nests. The pad only covered the depression in the bottom of the nest and was not visible through the nest opening.

Nesting material, both mud and nest pad material, was stolen from nests of other building birds by certain individuals. At The Willows colony one pair built a complete nest by

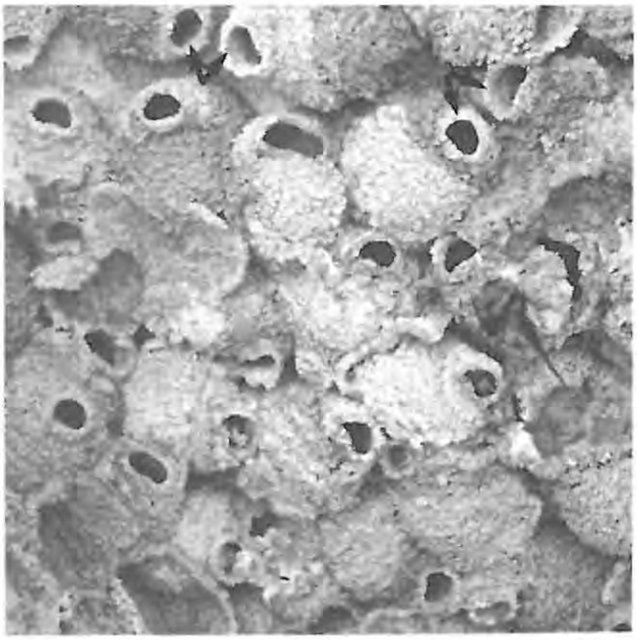

Figure 4: Typical *Hirundo spilodera* nests in a colony. When the top ends of adjacent *Hirundo spilodera* nests met, they faced away from each other so that the occupants of the nests were out of pecking range from each other.

TABLE 3

DIMENSIONS OF *HIRUNDO SPILODERA* MUD NESTS.
MEASUREMENTS CORRESPOND TO ALPHABETIC LETTERS IN FIGURE 5.

Measurement (mm)	n	Mean	S.D.	Range
Nest entrance width (a)	11	29,7	3,20	25 — 37
Nest entrance height (b)	11	43,0	7,72	34 — 57
Inside width (c)	7	133,0	12,85	111 — 155
Inside length (d)	7	130,7	16,10	109 — 154
Roof attachment length (e)	7	153,5	20,91	125 — 180
Outside depth (f)	8	90,5	7,70	77 — 126
Entrance neck (g)	9	71,2	8,43	64 — 91
Nest opening — roof (h)	9	6,0	1,51	3,7 — 9,0
Total length (i)	6	184,4	30,55	140 — 210
Internal depth	7	81,9	14,21	65 — 110
Mud mass	9	840	77,29	731 — 979

stealing mud from a nest about 1 m away. The victim was not paired and could thus not guard its nest while collecting mud. Each time when the bird left its nest to collect mud, the pellets built into the nest earlier were taken by the other building birds. Birds carrying nest pad material were also often harrassed by other birds, especially if it included large items such as feathers, and if these were dropped they were quickly picked up and carried off to a nest.

Form and construction of the nest

Typical nests of the South African Cliff Swallow are shown in Figure 4. There is a globular nesting chamber with a short tubular entrance tunnel directed downwards. The dimensions of a sample of nests measured are given in Table 3, the position of these measurements in a typical nest is shown in Figure 5. Nest walls were always thinner near the roof and towards the entrance hole.

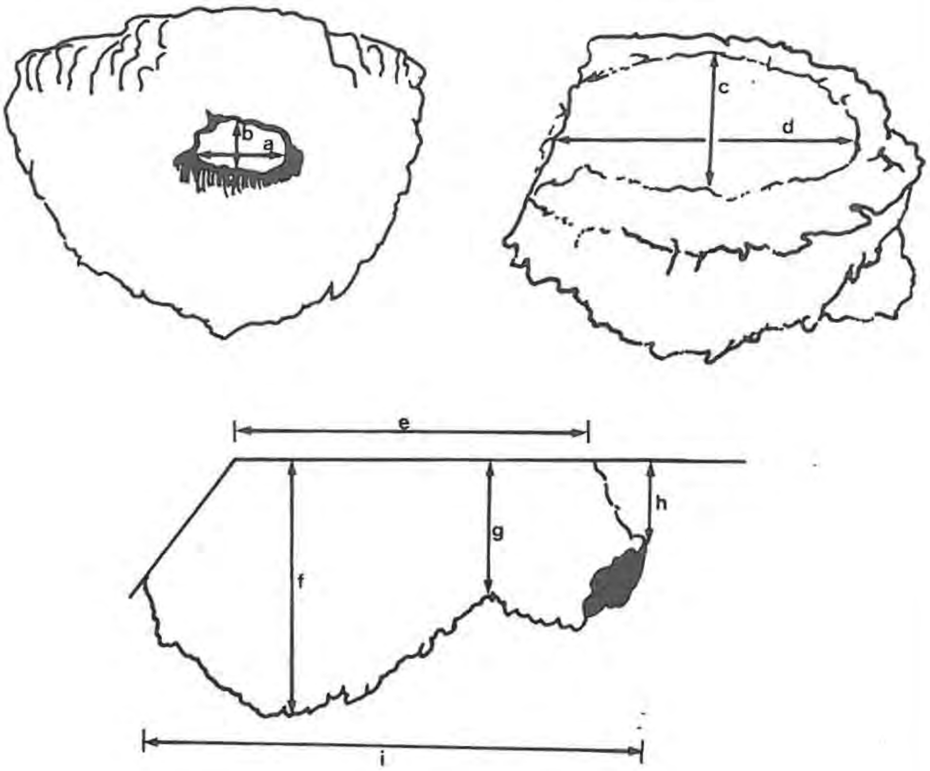

Figure 5: Line drawings of a typical *Hirundo spilodera* nest showing the measurement taken from each nest.

Figure 6: At the Meriba colony some *Hirundo spilodera* nests were built in crevices by merely closing the front with a wall of mud.

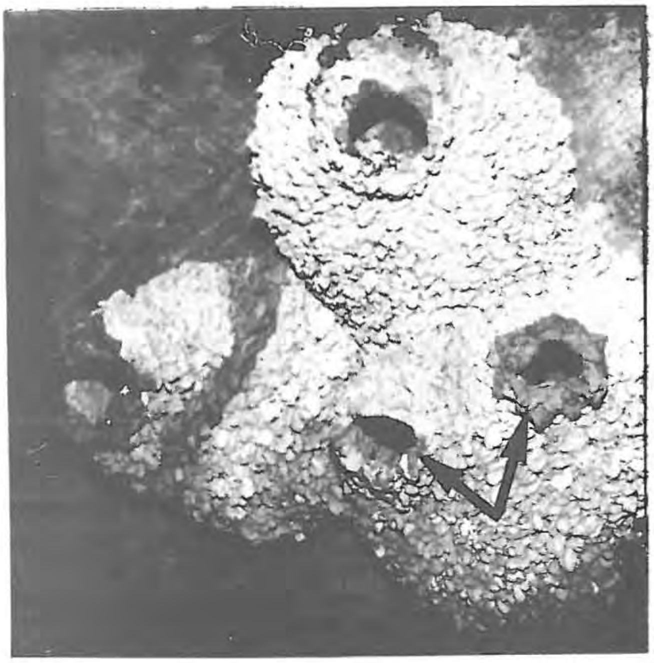

Figure 7: At The Willows colony a nest with two entrance tunnels was used throughout the 1984/84 season.

Variations in the size and shape of nests were mostly the result of the nature of the site. Nests built on the horizontal roof of the bridge were more rounded as they were attached at the top of the nest to the surface of the bridge. As the nests were clustered, a large number of nests were irregularly shaped through using the walls of existing nests as a side or back wall for the new nest. At the Meriba colony, where the nests were built against an irregular wall, a number of the nests were built partly in crevices and mud was only used to close up the natural opening of the crevice and to form an entrance tunnel (Figure 6).

All nests had a depression in the centre which was filled with lining to form the nest pad.

At each of the colonies, many of the nests were undamaged from year to year and were used repeatedly. Partly broken nests were rebuilt and holes in the walls of damaged nests repaired. Holes, which I drilled into the sidewalls of nests at Meriba for inspection purposes (about 2 cm in diameter), were all repaired within one hour after discovery by the birds. Holes in the floor of the nest below the nest pad were not repaired with mud. When old nests with large breaks were repaired, new entrance holes were usually built. If an old entrance hole was still present, this was then usually closed but at The Willows colony a nest with two entrance holes was used throughout the 1984/85 season (Figure 7). Often swallows got stuck in entrance holes and when such nests were rebuilt after breaks, the skeletons of such stuck birds were merely partly covered with mud pellets and a new entrance hole constructed.

Where nests openings were very close (e.g. where the top ends met (Figure 4)), they faced in different directions so that when birds were hanging in front of each nest they were out of pecking range of each other.

Two nests, the construction of which were watched from start to finish, took five and seven days respectively to build. It was difficult to determine the time taken to complete the nest pad as material was still added to the pad after the clutch was completed. No nest was ever found with a completed clutch and no nesting material, although the first eggs in new nests were frequently laid before any nesting material had yet been added. Newly completed nests had smaller pads than nests in use for a number of years as nesting material is added to the pad each year.

The number of pellets incorporated in a nest is difficult to determine, but between one and three distinct pellets are usually visible per square cm of the outer surface. There is probably at least one additional pellet per square cm which is not visible. There are thus about two or three pellets per square cm. An average size nest having a surface area of 650-800 cm^2 would thus comprise a total of 1300-1800 pellets.

During nestbuilding at the Meriba colony where mud was collected only 20 m from the nestsite (Table 4), pellets were added to the nest at a rate of about one per minute. The mean time taken by different birds to build a pellet into the nest was remarkably similar although the actual time for single pellets may differ widely (Table 4). Individual birds spend a mean time of 11,4 s ($n = 64$; S.D. 4,8; range 4-12) on the mudgathering site and pecked into the mud a mean of 12,4 times ($n = 28$; S.D. 3,7; range 9-20) before flying away.

TABLE 4

NEST BUILDING STATISTICS AT MERIBA COLONY

(1) = Individual building (2) = Individuals building

Nest Number	**Number Pellets** Collected	**Total Time Spent** Building (min)	**Pellets/Hour**	**Mean time to Collect Pellet*** (s)	**Mean time to** Build Pellet (s)
				Range	Range
II — 4 (1)	28	30	56	23 (17 — 62)	40 (22 — 72)
II — 4 (2)	31	12	155	20 (15 — 48)	40 (23 — 56)
I — 7 (1)	19	19	60	21 (16 — 59)	43 (25 — 60)
I — 5 (1)	35	37	58	22 (16 — 63)	42 (22 — 60)
I — 2 (1)	58	60	58	20 (14 — 40)	44 (19 — 86)

*Pellets were collected about 20 m from the nests.

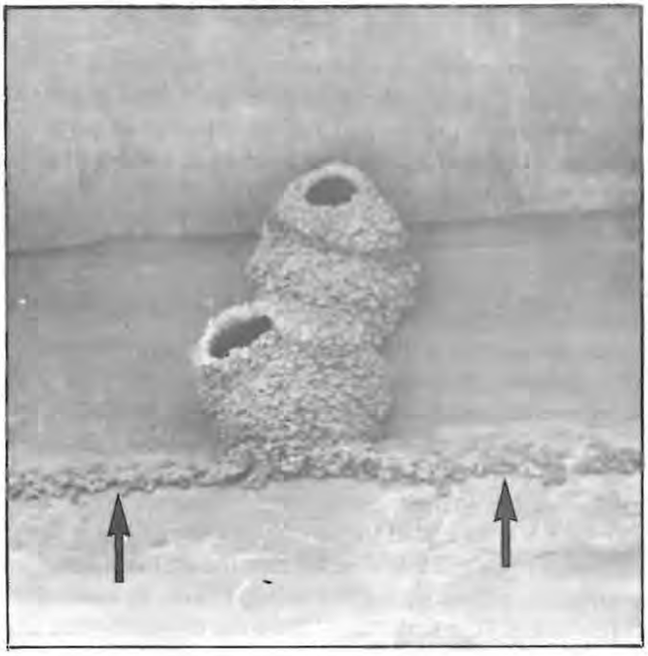

Figure 8: A continuous mud ledge built by *Hirundo spilodera* individuals "squatting" at a site. This ledge later forms the base of the nest.

The first mud pellets at a new nest site were always deposited in a horizontal ridge (Figure 8) when building on a vertical surface. This ridge was at the position of the foothold of the birds when clinging to the vertical surface. This ridge was built by all the individuals squatting at the new site and pellets were deposited on a wider area than was necessary for the base of the nest so that the pellets deposited by individuals next to each other formed a continuous ledge. The ledge was then used as a base for the first new nests at this new site.

There were several easily recognizable stages in the construction of the nest (Figure 9). Although there was not always a clearcut separation between the stages, different behaviour patterns were present at each stage. The description that follows is for birds starting nests at a new site on a vertical surface just below the roof of the bridge. Nests built with another existing nest as a starting point, have basically the same stages, but were usually slightly modified depending on the site.

Stage 1 — Formation of a ridge
After a nesting site has been selected, the birds cling to the surface of the site. This "squatting" at a specific site may last for several days before building starts. The birds selecting the nest sites were all males in the five cases where the sex of the birds was known. Although females were observed to "squat" as well, not one was ever seen to start the nestbuilding. The first mud pellets were placed at the level of the feet of the clinging bird. This was done by the bird bending laterally to the left or right and depositing the pellet against the substrate. After depositing about 50-100 pellets the ridge was formed and it was now quite easy for the building bird to get a foothold on this ridge and effectively guard his site against other squatters.

Stage 2 — Forming the nest base
When the ridge was formed, the packing of the mud pellets was concentrated on a specific area of about 10 cm. Here pellets were deposited mostly on top of the ridge to form a thicker ridge about 2-3 cm high and protruding up to 4 cm away from the concrete surface. The outer rim often slopes a bit downward, probably as a start to the depression in the nest. The building bird alighted sideways on this base with the collected mud and then placed the pellet on the outer edge of the base and worked the pellet into the rim with a rapid vibrating movement toward its own body.

Stage 3 — Forming the nest body
By adding mud pellets to the ventral and lateral walls of the nest base, a broad cup was formed. The birds either perched laterally or facing forward when placing the pellets on the edge of the cup.

Stage 4 — Curving the sidewalls upward
The lateral walls of the nest were now extended upward towards the roof of the bridge and the opening still present was being filled in as the roof was reached to form a narrower retort leading to the entrance tunnel. All building was done from inside the nest.

Stage 5 — Formation of the roof and entrance tunnel
When the sidewalls reached the roof of the bridge they were connected and a nest roof was formed by extending the wall downward to form the roof of the entrance tunnel. At the same time the ventral lip of the nest was turned down and narrowed to form a short entrance tunnel facing downward. During this stage material for the nesting pad was collected and placed in the nest.

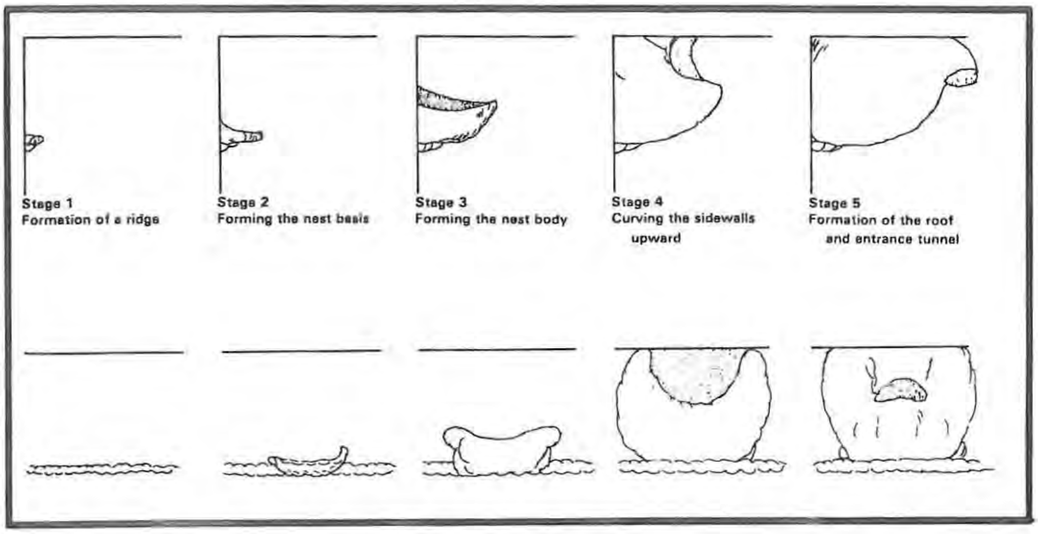

Figure 9: Stages in the building of nests by *Hirundo spilodera.* See text for details of the stages.

DISCUSSION

The South African Cliff Swallow uses a variety of man made concrete road bridges in the central Orange Free State for nesting. The use of a specific site is probably dependent on the environment surrounding the site and to a lesser extent the site itself. Emlen (1954) stated that the American Cliff Swallow *Hirundo pyrrhonota* requires:

(a) an open area for foraging;
(b) a vertical object, preferably with an overhang, for nest attachment, and
(c) a supply of mud of the proper consistency for nest building.

In addition to these, Grinnell & Miller (1944) list another requisite, some smooth-surfaced fresh water for drinking. The requirements for the South African Cliff Swallow seems to be very much the same. The variability found in the height of nests above the ground or water suggests either that the nest site used was the only one available or that the birds had no specific requirements in this respect. Open surface water was not always available at any of the sites mainly as a result of the low rainfall experienced during the study period. Although the birds did not abandon the colonies because of this lack of drinking water, there were periods such as during March 1984 when the birds were in poor condition. During these dry periods there was often no source of mud so that no nest building took place; this obviously affected the breeding. There seems to be no definite selection of specific types of mud as mud with a wide spectrum of grain sizes is used in the nest. It seems more likely that the water content of the mud is more critical than the grain size. McNiel & Clark (1983) analized the mud from a House Martin *Delichon urbica* nest and also found that mud from different sources had different chemical compositions and thus there seemed to be no real selection of mud for nestbuilding in this swallow species.

The nests, if high enough above ground level or over water, afford protection against predators as is the case with the American Cliff Swallow (Bent 1942). Apart from man, only one nest predator, a monitor lizard *Veranus niloticus* is known (Grobler & Jacobs 1985). The building of a gourd-shaped nest with narrow entrance tunnel scales down the territory of the Cliff Swallow to defending the nest opening, thus allowing individuals to nest very close to each other with only a wall of mud separating broods.

OPSOMMING

Die Familieswael *Hirundo spilodera* bou 'n toe moddernes met slegs 'n kort tuit by die ingang. Neste word dig teenmekaar gebou in kolonies. In die Oranje Vrystaat was meeste van die kolonies onder beton pad brûe. Beide tydelike poele en permanente strome word as 'n bron van modder gebruik vir die bou van neste. Dit wil voorkom asof daar geen seleksie van modder plaasvind tydens nesbou nie. Nesmateriaal het bestaan uit skaapwol, die pluime van sade en soms ook enkele vere. Gedurende nes konstruksie kon vyf stadia maklik onderskei word en twee neste wat goed dopgehou is het vyf en sewe dae onderskeidelik geneem om te voltooi.

ACKNOWLEDGEMENTS

I would like to thank the following people for help in various ways. Mr. Dirk Bredenkamp and Mr. Louis van Aswegen allowed me to work at the Cliff Swallow colonies on their farms. Audrey van Eeden did some of the illustrations while Prof Nic Grobler and Mr van der Westhuizen analized the mud from the nests. Ben Bester and Hester du Toit assisted me ably, both in the field and during the preparation of the paper. Prof Nic Grobler discussed the interpretation of the mud analysis with me for which I am grateful. Dr Adrian Craig commented on drafts of the manuscripts while Isabel van Rooyen and Hannelien de Villiers typed it swiftly and efficiently. Mr Terry Oatley of the South African Bird-Ringing Unit, University of Cape Town and Mr Warwick Tarboton of the Transvaal Nature Conservation Division reviewed the paper and their suggestions greatly improved it.

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A DESCRIPTION OF THE SOCIAL, AGGRESSIVE AND MAINTENANCE BEHAVIOUR OF THE SOUTH AFRICAN CLIFF SWALLOW *HIRUNDO SPILODERA* (AVES: HIRUNDINIDAE)

by

ROY A. EARLÉ

National Museum, Bloemfontein

(With 3 figures)

ABSTRACT

Earlé, R.A. 1985. A description of the social, aggressive and maintenance behaviour of the South African Cliff Swallow *Hirundo spilodera* (Aves: Hirundinidae). *Navors. nas. Mus., Bloemfontein* 5(3): 37-50. The South African Cliff Swallow *Hirundo spilodera* is a highly social animal and most of its activities are performed as part of a group. Colonial nesting places spatial restrictions on the behavioural patterns of this swallow and sociality has probably reduced the scale of courtship in particular to a mere tolerance of another bird at the chosen nesting site. Aggressive behaviour is seldom seen away from the nests indicating that aggression is directed towards maintaining the nest site. **(South African Cliff Swallow, *Hirundo spilodera*, social behaviour, aggressive behaviour, maintenance behaviour).**

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CONTENTS

INTRODUCTION

There is no published description of the behaviour of the South African Cliff Swallow *Hirundo spilodera.* Winterbottom (1971) mentioned this species as following ploughs to obtain insects disturbed by this activity. The Cliff Swallow was also recorded as one of the swallow species which regularly visit fires so as to feed on fleeing insects or probably "smoke-bathing" (Bilby 1957). There have been a number of studies into the behaviour of several members of the Hirundinidae. Johnston & Hardy (1962) gave a descriptive account of reproductive, aggressive and group behaviour of Purple Martins *Progne subis* while Allen & Nice (1952) also described especially the behaviour associated with pair-bonding in this species.

The most complete description of the behaviour of any member of the Hirundinidae is that of Lind (1960) for the House Martin *Delichon urbica* and the description of social behaviour in nesting American Cliff Swallows *Hirundo pyrrhonota* (Emlen 1952). In the latter study, done on a close relative of *H. spilodera,* special attention was given to manifestations of positive and negative social responses and the balance of these in foraging, loafing and nesting activities.

Wing fluttering is an interesting occurrence, mainly found in the swallow genus *Hirundo.* This behaviour was very commonly reported in the American race of *H. rustica,* only occasionally in the nominate European race and apparently never recorded in the Eastern race (Bilby 1957). Wing fluttering does not occur in *H. spilodera* but is quite common in *H. pyrrhonota* (Butler 1982) and was also recorded for *D. urbica* and *P. subis* (Bilby 1957).

STUDY AREA AND METHODS

Observations on the general and social behaviour of the South African Cliff Swallow were made opportunistically at several colonies around Bloemfontein in the central Orange Free State (Figure 1). The Meriba colony was a small colony consisting of about 80 nests and was the only colony not situated under a concrete road bridge. Ten full-day observations were also made from a hide mounted on a platform 1,2 m high set up about 8 m from the Meriba colony in the 1983/84 season. Most of the individuals at the Meriba colony were either paint-marked or colour-ringed and thus individually recognizable. Individual Cliff Swallows were caught with mist nets and paint-marked by applying an acetone based paint to the outer four primaries of the wing (Figure 2) or to the rectrices or any combination of these (Samuel 1970). Five colours were used, white, yellow, green, red and blue. Being acetone based, the paint dried very quickly and about 10 minutes after painting the swallow was ready to fly again. The individual primaries were kept apart during painting. A number of birds were also colour-ringed at the Meriba colony. Two colour rings on one leg in combination with a metal ring on the other leg were used. Nine colours were available: white, yellow, dark blue, light blue, green, mauve, black, red and pink.

Ten swallow chicks were hand reared from about eight days till about 40 days to observe the development of certain behavioural patterns. Observations made were either written down or recorded on a small casette tape recorder and later transcribed. Zeiss 10 X 40 dialyt binoculars were used for observations.

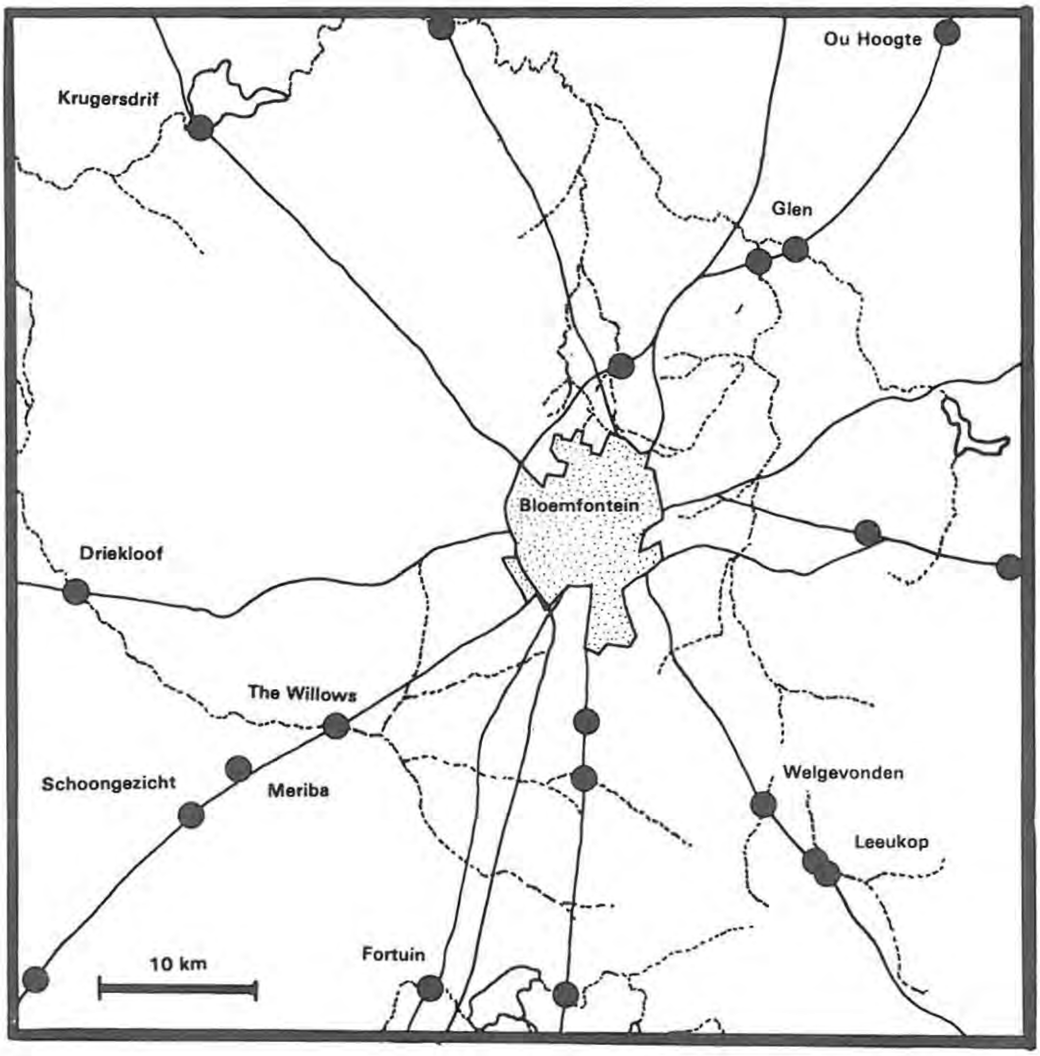

Figure 1: Map of the Bloemfontein area showing the various *Hirundo spilodera* colonies.

RESULTS

SOCIAL BEHAVIOUR

The South African Cliff Swallow was a highly social animal and most of its activities were performed as part of a group, except foraging, which was mostly done individually, except perhaps at locally abundant food sources.

Figure 2: Wing of *Hirundo spilodera* with the outer primaries painted white.

Sociality at nesting sites

During the greater part of the breeding season, when most pairs had chicks to feed or were incubating eggs, there was a constant flow of individuals to and from the nests. Although the actions of these birds flying to and fro, were probably quite independent of each other, certain events triggered more social activity patterns. Disturbance at the colonies, such as by humans, caused all individuals present to fly from the nest with many giving the alarm call. If the disturbance continued for some time e.g. when I checked the nests which took 30—45 minutes, the whole colony of birds would circle above the nests in a close group, usually rising very high until they were almost out of sight. The contact calls given by members of this flying group always attracted attention to such a group, even when they were mere specks in the sky. The alarm call mostly had the effect that the flying group moved closer together. The stimulus for this close flying was not always apparent, but it probably had some social function as it could be observed quite often, especially at the larger colonies. A small number of birds was often seen circling above the colony and when one initiated the contact call, all would join and within seconds other individuals from all sides were observed joining this group which circled higher and higher until almost out of sight.

Before breeding started early in the season the birds would, after the early morning quarrels over nesting sites, leave the colonies to forage. The colony would then be deserted for up to four hours, before the contact calls of individual swallows circling almost out of sight above the colony were heard again. Individuals could then be seen joining this group from all sides, as the group descended to the nests. The group, which would now be almost the entire colony, would eventually enter the nests and after about five minutes, only single birds would be seen flying around the colony searching for an empty nest to roost. At The Willows colony where this colonial roosting was observed on five consecutive days in September 1983, the birds arrived at the nests between 11h00 and 11h30 and left only between 15h00 and 16h00 on each of the days.

Rain was also a social stimulus and apart from bathing, it induced the birds to chase each other excitedly.

Sociality while nest building

During nest building the gathering of mud and soft materials for the nest pad was a major activity in the colony. Mud gathering was a highly social activity and at a peak period of nest building, e.g. after rain almost the whole colony would participate during such a nest building spell. All the birds collecting mud at a site, would do so from a very small area along the edge of the water. A maximum of about 40 birds would be sitting at such a site at any one time, but there was always a stream of swallows collecting mud that would move to and from this site. If the mud collectors were disturbed at the site, e.g. by humans, they would circle around and usually go back to the same site when the danger had moved away. If the danger did not move away it would take some time before one individual would alight at another site which would be the stimulus for the rest of the colony to follow and all individuals would then again start collecting mud from this newly selected site.

When a few mud gatherers were sitting on a spot, a new arrival would usually try to alight as close as possible to them, often in the middle of the group. When an individual landed on a mud gathering site too far from the middle of the group, or too far from suitable mud, the bird would walk by placing one foot in front of the other to get to a better position.

The sociality of the mud-gathering activity was most clearly seen during the breeding season when most pairs already had young or were incubating eggs. The mud gathering at that stage of the breeding cycle was centered mainly upon nest repairs, but as soon as one bird started collecting mud, most followed suit even only to collect one or two pellets which were added to the spouts of completed nests. After about 30 minutes only the few pairs which were really repairing nests persisted in collecting mud, but most of the colony had at least collected a few pellets of mud.

The collection of material for the lining of the nest was less social, but in some cases, e.g. at newly established colonies, the majority of the individuals could also at some stage be seen collecting lining material. The material was collected while hovering above the flowerheads of the Compositae species and by pecking the seed plumes. Large numbers of the birds, spread over a wide area, could be seen collecting plant down in such a manner at the same time. Feathers were collected when encountered in flight, while sheep's wool was taken from the barbed wire fence where pieces were stuck. Feathers were often brought to the nest long after incubation had started and even when chicks were already present. It thus seems as if feathers were added to the nest whenever the opportunity arises, which in turn would indicate that collecting certain nestpad material would be a social activity while others would not be.

Social foraging
Although most of the Cliff Swallows foraged individually, several instances of social foraging were observed. On several occasions at the Schoongezicht colony, groups of 10-50 birds could be seen foraging as a closely knit group close to the ground. This behaviour could have been the result of a super abundance of arthropods in a small area. However, no evidence for the greater abundance of food was found. This behaviour was interpreted as social foraging. Several such groups could be seen at any one stage in the area around the colony, with very few other swallows feeding individually. This might be a "learning" ground for newly fledged young, as the incidence of this social foraging was far more frequent after the first young had left the nest. Ground foraging by most members of a colony was also observed after three days of rain and drizzle, when large numbers of Harvester termites *Hodotermes mozambicus* were out near The Willows colony.

Social play
Several actions by groups of Cliff Swallows were interpreted as social play, but might have had some other function which was not apparent.

Early in the season, before nest building started, swallows encountering objects such as feathers and leaves in the air would grab them repeatedly. An excited bird would soon attract several other individuals which would all try to get hold of the object. When such objects were on the surface of the water, such as in the quarry at Meriba, several individuals would attempt to pick up the object from the water surface. As soon as one succeeded in picking the object from the surface, all would start playing as described above.

COURTSHIP, MATING AND AGGRESSIVE BEHAVIOUR

Judging by the number of pairs of the South African Cliff Swallows defending nests within a few days of arriving from their winter quarters, it seems as if the courtship and pairbonding period can be very short. The acquisition of a nest site by a male is evidently the first and most important step in forming a pairbond. As the old, existing nests were the first ones occupied in a new season, this was where the first pairs were formed. It was impossible to establish the exact sequence of events leading to the formation of a pairbond in these old nests, but a few definite actions could be seen in cases where males occupied half completed nests or sites where new nests were to be built.

At new sites where there were no existing nests, individual birds were repeatedly observed clinging to the same spot against the vertical wall of the bridge. This spot was then defended against all other birds within pecking range. A threatening, or probably luring posture was also directed towards any birds flying past the bird squatting against the wall. The squatting bird would fly off every now and again and then return to settle on the same spot. These squatting birds, all males in the few cases where the sex was known, were continuously harrassed by other birds which hovered close to them or even alighted on their backs. As soon as the squatting birds were sufficiently stimulated, e.g. after rain or when most birds in the colony were participating, they started building a mud ledge on their squatting sites (Figure 3). Pairbonds were probably formed soon after the squatters started building, as two birds started to build at the same site when about 20-50 pellets had been packed by one individual. There were no definite stages in the formation of the pair bond and it seemed as if the squatting bird merely tolerated the presence of the second bird, invariably a female, at the selected nest site. Most birds who attempted to alight on or close to the squatting bird

Figure 3: A mud ledge build by various individuals squatting on a new site. This ledge will later form the base of the nests.

were chased away, but occasionally the squatting bird started quivering its wings as a bird alighted. The selected mate could be recognized by the squatter, as it was allowed to settle while all other birds were still being chased away from the site. The squatter probably recognized its mate by vocalization, even at some distance. Squatters often started calling as soon as their mates, which were calling, approached the colony.

The only easily recognizable action by unmated birds in attracting a mate, was by individuals occupying half completed nests. These individuals would sit on the half cup and sing at each swallow flying past the cup. The singing bird crouched low, with the neck touching the rim of the half cup. Some birds flying past were obviously attracted to the singing bird; several birds, after passing the singing bird, would turn around and approach the nest of the singing bird, hovering in front of the nest. As soon as the singing bird had succeeded in attracting an individual flying past to alight on the rim of the halfcup, the singing individual would turn its tail end towards the possible mate and while still crouched, start quivering its wings. If the prospective mate did not make an attempt to get into the nest within 15-90 seconds, it was usually chased off by the nest owner and the process of attracting a mate was repeated. Once again it seems as if tolerance of the bird attracted with this luring towards the halfcup in the end leads to the formation of the pairbond. One bird would repeatedly alight on the nestcup rim of the luring bird and although it would be chased away several times it would come back, and eventually succeed in getting into the nest cup with the owner of the nest cup. When both birds sat on the nest cup they both crouched low while quivering their wings. At one nest at the Meriba colony, nestbuilding started immediately after both birds sat in their halfcup for about 15 minutes. One interesting observation the significance of which was not known, was that when a nest owner went into a nest, a second bird, which was not its mate, would try to follow closely and also attempt to enter the nest. This was observed often and is probably either related to the tolerance of a nest owner towards a strange bird or to conspecific parasitism.

No mating was ever observed in the open and the only two matings observed were in half completed nests at The Willows. As far as could be judged, matings took place in the completed nests, or at least on the nest site.

Although there is always some chasing among individuals when circling above the colony, the only really aggressive behaviour between individual Cliff Swallows was observed at the nests or as a result of earlier fights at the nests. On four occasions actual contact between birds chasing each other was observed. All of these pursuits started at the nests and when the pursuing bird caught up, the fleeing bird was grabbed on the rump. After a pairbond was established, the nest site was defended by both partners and it was no different from defence of the original site chosen by the squatter. The size of the territory defended was apparently determined by the reach of the bill from the nest rim. Threatening postures were adopted by one or both individuals of a pair when other swallows flew past too close, but such individuals were only attacked when they alighted within reach. As the nests were completed, neighbouring pairs were out of reach from each other as birds defended only the area which was within pecking distance of the nest opening. Defence of the nest opening could not be directed upward towards the upper rim of the nest opening and often a new nest was started on top of the spout of a completed nest.

There was no clearcut difference in the defence pattern or intensity of defence of the nest between males and females. Some males were more aggressive than others and at the Meriba colony, five of the seven physical attacks witnessed during an observation period, were made by the same bird.

The threatening posture could be clearly seen to have four phases which followed each other and when threatening to the full all the phases could be seen at once.

1. The first phase was the raising of the crown feathers when the possible intruder was sighted.
2. During the second phase, as the intruder approached, the bill was opened and the bird started giving a "threat" call.
3. If the intruder alighted the defending bird would start quivering its wings, and
4. If the intruder was close enough the defending bird would peck at it or if it was too far away, would fly towards it to chase it off.

This chain of events in defence of a nest rarely led to a physical battle between two individuals. The intruder nearly always retreated and flew away before the attacker could reach it. Of the total of 46 physical battles witnessed at the Meriba colony during the 1983/84 season, only 9 were as a result of the intruder not flying away quickly enough from the area which was defended by another bird. All the other attacks were by nest owners returning to their sites and finding an intruder there. The territory owner would then fly directly towards the intruder, striking it at the nape or head with its bill and clinging to its back with its feet. At the Meriba colony, where there was sand below the nests, both birds would then fall onto the sand. The attacker would then usually try to mate with the victim while on the ground. The intruder would continuously give an alarm call which then attracted several other swallows which would all attempt to mate. During one fight on the sand at the Meriba colony, a bird attracted to the fight was mated by an onlooker. As many as four birds would attack the fighting pair. The longest battle timed lasted nearly five minutes before the attacker flew away leaving the intruder exhausted on the sand. Although during most of these attacks there was only an attempt at mating with the attacked bird, on at least two occasions mating apparently took place, although there was no evidence of sperm transfer.

All attackers of known sex which made mating attempts were males. None of the victims were sexed. As far as could be established they were unmarked birds, probably from other colonies seeking mates.

When a nest owner is inside the nest and a strange individual land at the nest entrance, they are attacked from inside the nest by pecking at their feet or head. The intruder could often be seen hanging from the nest opening while the owner was still gripping a toe or other part of the body in its bill. When an intruder succeeded in entering a nest, when the owner was inside, a fight usually ensued. After a few seconds the intruder would be forced out of the nest, often with the nest owner following closely. The longest fight inside a nest continued for more than 30 minutes before one bird flew from the nest. Birds were often found stuck in nest openings and most of these were believed to be the result of fights in the nests. At one nest at the Meriba colony an unringed bird was found stuck in the nest opening while the owner of the nest, a female, was still alive inside.

Pairs with adjacent nests showed very little aggression toward each other, and often a whole group of territory holders would show aggression towards an intruder, even simultaneously attacking such an intruder.

The South African Cliff Swallow never showed any aggression towards other bird species and even the House Sparrow *Passer domesticus* which usurped most of the nests at the Meriba colony in the 1983/84 season, was never attacked or even threatened. The House Sparrow as well as the Cape Sparrow *P. melanurus* was aggressive towards the swallows. On several occasions, when the sparrows alighted at the colonies, they tried to attack the swallows, which were much too agile and I never saw a sparrow succeed in striking a Cliff Swallow. The hand-reared Cliff Swallows were often very aggressive towards each other, especially over space. When two individuals would sit next to each other on a perch and a third individual was placed between them both would attack this "intruder" by pecking at it. If the "intruder" was placed about 5 cm away the typical threatening posture, described earlier, whereby the feathers of the crown are raised and the bill opened, was shown.

MAINTENANCE BEHAVIOUR

Some behavioural aspects of the South African Cliff Swallow were not directly associated with social behaviour or breeding behaviour. However, these behaviour patterns might have had a social or other signalling function and thus have a bearing on the daily activities of the birds.

Locomotion

(a) Aerial

Cliff Swallows spent the major part of the daylight hours on the wing. Their flight is straight and fast with continuous wing beats when e.g. carrying mud to the nest site or the wing beats are interspersed with short periods of gliding when foraging. During the characteristic hovering of the Cliff Swallow at the nest site, the wing beats are fast but shallow, and considerable manoeuvrability was attained by using the tail.

(b) Terrestrial

When on the ground such as at mud gathering sites the Cliff Swallow advanced by walking. Walking was also the only way of terrestrial locomotion observed in the hand-reared individuals.

Comfort movements

McKinney (1965) described comfort activities for the Anatidae in great detail and the terminology used here follows that author except where the terminology was not suitable for describing the comfort activities of the South African Cliff Swallow. Sleeping postures and bathing are also included here.

Stretching movements

Most of the observations on stretching were made on the hand-reared individuals. Stretching was usually seen after these birds were taken from their nesting boxes and placed on the side of the box, as well as after they had been fed. At the colonies stretching was performed at the loafing sites on telephone wires and barbed wire fences.

(i) Wing-stretch: This was the first stretch movement performed by the captive individuals. Only one wing at a time is stretched while the head is usually held low. The wing is extended slightly backwards.

(ii) Wing-and-leg-stretch: The action is very similar to the wing-stretch except that the leg is also extended slightly backward and the rectrices are fanned.

(iii) Both-wings-stretch: The wings, with the carpal joints flexed, are extended above the back while the head is held very low. This both-wings-stretch commonly followed the wing- or wing-and-leg-stretch.

(iv) Jaw-stretch: Jaw-stretch was observed regularly in the captive Cliff Swallows and was usually accompanied by the partial closing of the eyes. This jaw-stretch movement only lasted for about one second and was probably often overlooked. Jaw-stretching was not observed to precede regurgitation as mentioned by Kemp (1976) for the hornbills *Tockus* spp.

Scratching
Scratching in the Cliff Swallow is direct. The leg is brought up between the body and the wing to scratch the head while the head is slightly tilted towards the scratching leg.

Preening
Preening occurred at two sites. The most obvious preening sites were the loafing perches on fences or telephone wires. At each of the colonies there were particular sections of these wires where the majority of the colony members would sit to loaf and preen. Why these sections of the wires were selected was not at all clear, but certain areas were so consistently used throughout the season that there must have been some reason for not using the rest of the fence for loafing as well. These loafing sites were always close to the nesting colony, except at The Willows colony where one loafing site was nearly 500 m from the bridge.

Individuals also preened while loafing and hanging at the nest openings. In the heat of the day most of the individuals returned to the nests and while one of a pair was incubating or brooding the chicks, the other would hang at the nest opening, preening.

Most of the observations on preening were done on the Cliff Swallows which were hand-reared and where behaviour patterns could be observed closely. Preening was first observed when the chicks were 14 days old. The actions at this stage were still very uncoordinated and only by day 20 were the preening actions well developed.

Nibbling preening was done on all regions of the body except the head, upper neck and the abdomen. The remiges were preened from the ventral side of the wing and only occasionally from the dorsal side. This preening of the primaries from the ventral side of the wing gave rise to the characteristic "arch winged" posture. When preening the tail the rectrices were held to one side and slightly fanned. Preening was usually accompanied by wing and tail shaking.

Shaking movements
Two types of shaking movements were recorded for the Cliff Swallow.

(i) Wing-and-tail shake: This shake accompanied preening and always followed after the bird had preened some part of the body but especially the wings or tail. It lasted up to three seconds.

(ii) Bumble bee shake: This shaking action of the whole body was often seen in individuals who had just emerged after a long period in the nest e.g. when they left the nest in the morning. This action was performed while on the wing. The bird appeared to "puff" its body feathers, thus resembling a bumble bee. The whole body was then shaken with a very characteristic "wirr" sound. When the whole colony left the nests together these shakes could be heard and seen in as many as 30 % of the individuals in the flock at any one time.

Bill cleaning
Because of the "clean" way of feeding in the South African Cliff Swallow, and for that matter aerial feeding birds in general, there is seldom a need for bill cleaning. It was only observed in some of the hand-reared individuals when fed messy food such as grated hard-boiled chicken egg. Only the tip of the bill was wiped. The food stuck in the gape was not

removed by bill wiping but often by scratching. Mud which collected on the bill during nestbuilding often stayed on the bill for several days. There was no direct effort to remove this mud.

Bathing

Two ways of bathing were observed. The most frequent method was by flying low over the water and then "falling" into the water breast-first before flying out of the water again to repeat the process. Several House Martins *Delichon urbica* were also seen to bath in this manner. After a few "falls" the birds would fly to a perch, usually a barbed wire fence or telephone line to preen. As soon as one individual started bathing in this way, a large number of other colony members would follow suit and soon most of the colony members would be participating.

The second method of bathing was during rain when large numbers of the birds would perch on wires and continuously shuffle and preen their feathers. On one occasion seven House Martins, which were perched amongst the South African Cliff Swallows, did not preen and shuffle and were obviously not bathing.

DISCUSSION

Colonial nesting places spatial restrictions on the behavioural patterns of the South African Cliff Swallow. The behavioural and social patterns associated with colonial nesting probably have the same basic elements as the other non colonial types of behaviour. These colonial types of behavioural patterns have probably evolved with the coloniality itself from the non-colonial patterns (Emlen 1952).

There is nothing in the general behaviour of this species which is unexpected for a passerine bird. The sociality has, however, probably reduced the scale of courtship in particular to a mere tolerance of another bird at the chosen nesting site. Matings also have to take place in the confined space of the nest so as to avoid the interference of other individuals. Although individual birds are sometimes very aggressive, such behaviour is seldom seen away from the nests indicating that aggression is directed towards maintaining the territory. The occurrence of "rapes" on individuals violating established territories is an interesting one. This seems to be the most intensive aggression ever shown.

OPSOMMING

Die Familieswael *Hirundo spilodera* is 'n baie sosiale voël en meeste van hul aktiwiteite word in groepe gedoen. As gevolg van die koloniale nesgewoontes van die spesie word sekere ruimtelike beperkings op die gedrag van die swael geplaas. Hofmakery is byvoorbeeld gereduseer tot die blote verdraagsaamheid van twee voëls teenoor mekaar by 'n sekere nes. Agressiewe gedrag word gewoonlik net waargeneem by en om die nes wat daarop dui dat agressiewe gedrag gerig is op die instandhouding van die area om die nes.

ACKNOWLEDGEMENTS

I would like to thank my technicians, Ben Bester and Hester du Toit for invaluable help throughout the study. I am also grateful to Dr. Adrian Craig for his interest in the study and encouragement during the three years. Dr. Barnie Penzhorn of the Department of Genesiology, University of Pretoria and Mr. Carl Vernon of the East London Museum, suggested valuable changes when reviewing the paper.

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FORAGING BEHAVIOUR AND DIET OF THE SOUTH AFRICAN CLIFF SWALLOW *HIRUNDO SPILODERA* (AVES: HIRUNDINIDAE)

by

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(With 3 figures)

ABSTRACT

R.A. Earlé, 1985. Foraging behaviour and diet of the South African Cliff Swallow *Hirundo spilodera* (Aves: Hirundinidae). *Navors. nas. Mus., Bloemfontein* 5(4): 53-66. The South African Cliff Swallow *Hirundo spilodera* is an aerial feeder which characteristically foraged close to the ground with 44 % of the foraging done within 1 m of the ground. Insects were often flushed from vegetation by the birds and non-flying arthropods such as Coleoptera and Lepidoptera larvae and spiders (Arachnida) also formed part of the diet. Although very small prey, such as Thysanoptera and aphids, was available to the swallows, they were seldom found in the diet. Beetles, especially from the families Scarabaeidae and Curculionidae, together with flies from the families Muscidae and Drosophilidae and wasps from the Chalcidoidea and Halictidae, were the most important insect prey. **(*Hirundo spilodera*, diet, foraging behaviour).**

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INTRODUCTION

No published data exist on the food taken by the South African Cliff Swallow *Hirundo spilodera*. Maclean (1985) states that the food consists of "aerial arthropods" but no other information is given. Only three instances of special foraging behaviour by the South African Cliff Swallow were recorded in the literature. Winterbottom (1971) recorded the South African Cliff Swallow as a bird following ploughs while Bilby (1957) lists it as one of the swallow species attracted to fires. Skead (1979) observed this species hovering above Helmeted Guineafowl *Numida meleagris* and feeding on the arthropods disturbed by these birds.

For the sake of brevity the South African Cliff Swallow will be referred to as the Cliff Swallow throughout.

STUDY AREA AND METHODS

Study area

A map indicating the location of different Cliff Swallow colonies in the area around Bloemfontein, was given by Earlé (1985). The area where observations or foraging and diet was done was surrounded by Karoo veld where karoo bushes such as *Chrysocoma, Pentzia* and *Senecio* dominated with some grass cover between bushes. Suction trap and sweepnet samples were all taken on the farm "The Willows" (29° 15'S, 26° 03'E,) west of Bloemfontein.

Foraging behaviour and foraging height

The height at which the Cliff Swallow foraged was determined on four consecutive days in October 1984 between 10h00 and 12h00. An aluminium pole, 6 m high was marked at 0,5 m intervals and set up in a favourite foraging area The height at which the first 50 foraging birds flew past the marker was noted on each of the days. These data were used to calculate the preferred foraging height of the Cliff Swallow.

Availability of insects

To measure the flying insects potentially available to the Cliff Swallow, a series of three suction traps (Prinsloo 1980) was used to sample the insects. These traps were used near The Willows colony in the 1984/85 season in an area where the swallows were often observed feeding. The traps were placed about 10 m apart, 1,3 m above the ground and the suction fans were driven by a petrol generator. Suction traps were left in operation for four hours between 10h00 and 14h00 on the sample days. In addition to these suction trap samples which were taken every 10 days, sweepnet samples were also taken on these days with a net 30 cm in diameter. Sweeping was done just above the vegetation 0,5 and 1,5 m above ground level. The vegetation consisted of low, woody karoo bushes.

The suction trap samples were sorted into the different arthropod orders while the arthropods in the sweepnet samples were weighed.

Determination of Cliff Swallow diet

The food of the Cliff Swallow was determined from stomach samples of birds collected in the 1983/84 season. The stomach samples collected on the same day were pooled so that three or four samples were available per month. In total 163 birds were collected.

Stomach samples were examined with a 10X dissecting microscope and all identifiable fragments of invertebrates sorted into classes and orders for later identification by experts. Insects were identified to he lowest taxon possible, usually family, sub-family or genus. Because the prey remains were usually very fragmented it was not possible to quantify the number of specimens in each taxon of prey items. The occurrence of the different taxa was calculated as the percentage a specific taxon occurred in the total number of 25 samples.

RESULTS

FORAGING BEHAVIOUR

The Cliff Swallow was a tyical aerial feeding bird which largely foraged on the wing. Although the mean foraging height was 2,2 m, 44 % of foraging was done within 1 m of the ground (Figure 1). Foraging flight was slower and seldom in a straight line like "purposeful" flight e.g. when nest building. Two special foraging methods were also observed.

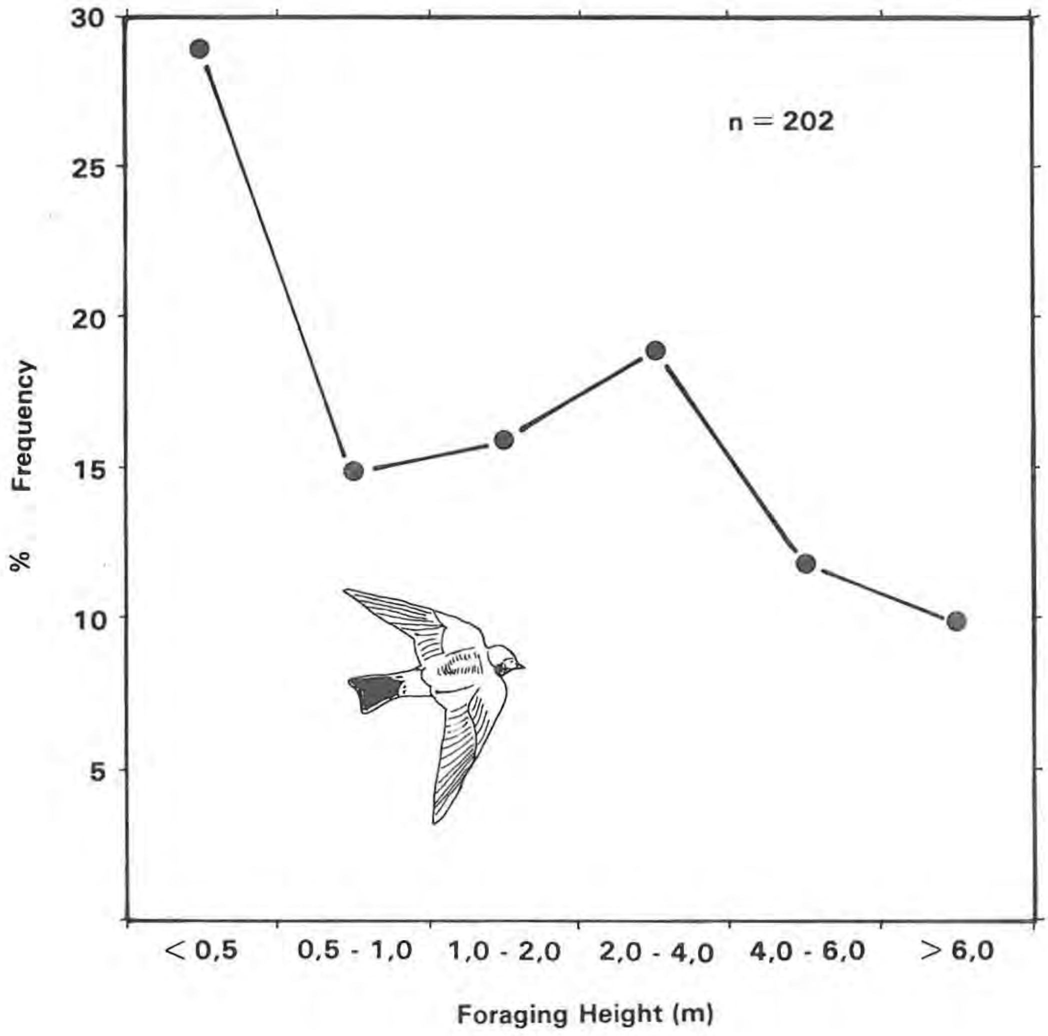

Figure 1: The frequency of occurrence of *Hirundo spilodera* individuals foraging at different heights above ground level.

Flushing prey from vegetation
This method was used especially when moths (Lepidoptera) were numerous, when the karoo spp. bushes were flowering. The swallow would hover two or three centimetres above the selected bush and in that way disturb the moths on the bush. It would then forage above the bush for a short while, probably disturbing more insects with each fly past, before moving to another bush to hover above. The wing strokes during these hovers were slow, with a full downswing but shallow upswing. Large numbers of Cliff Swallows, often in groups, could be seen performing these disturbance flights on some days.

Picking insects from the ground
The Cliff Swallow picked up insects from the ground in two observed situations. In November 1983, after two days of overcast weather, about 300 individuals were seen foraging on the ground near The Willows colony. Large numbers of harvester termites *Hodotermes mozambicus* were present in the area at the time. These termites were also found in the stomachs of the Cliff Swallow (Table 1). The Cliff Swallow also following ploughs to feed on the ground. Individual birds would often settle on the ploughed earth behind the plough and pick up disturbed insects from the ground.

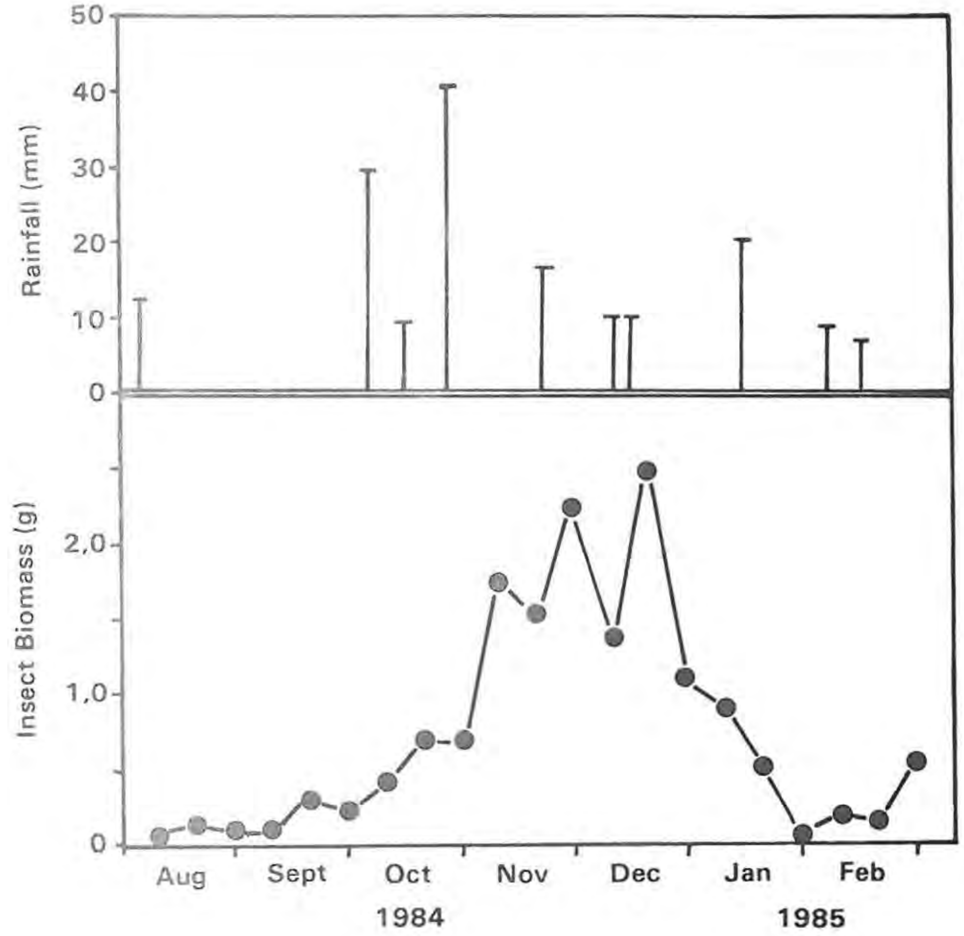

Figure 2: The biomass of insects collected with a sweepnet in preferred *Hirundo spilodera* feeding areas. The rainfall recorded near the feeding area is also given.

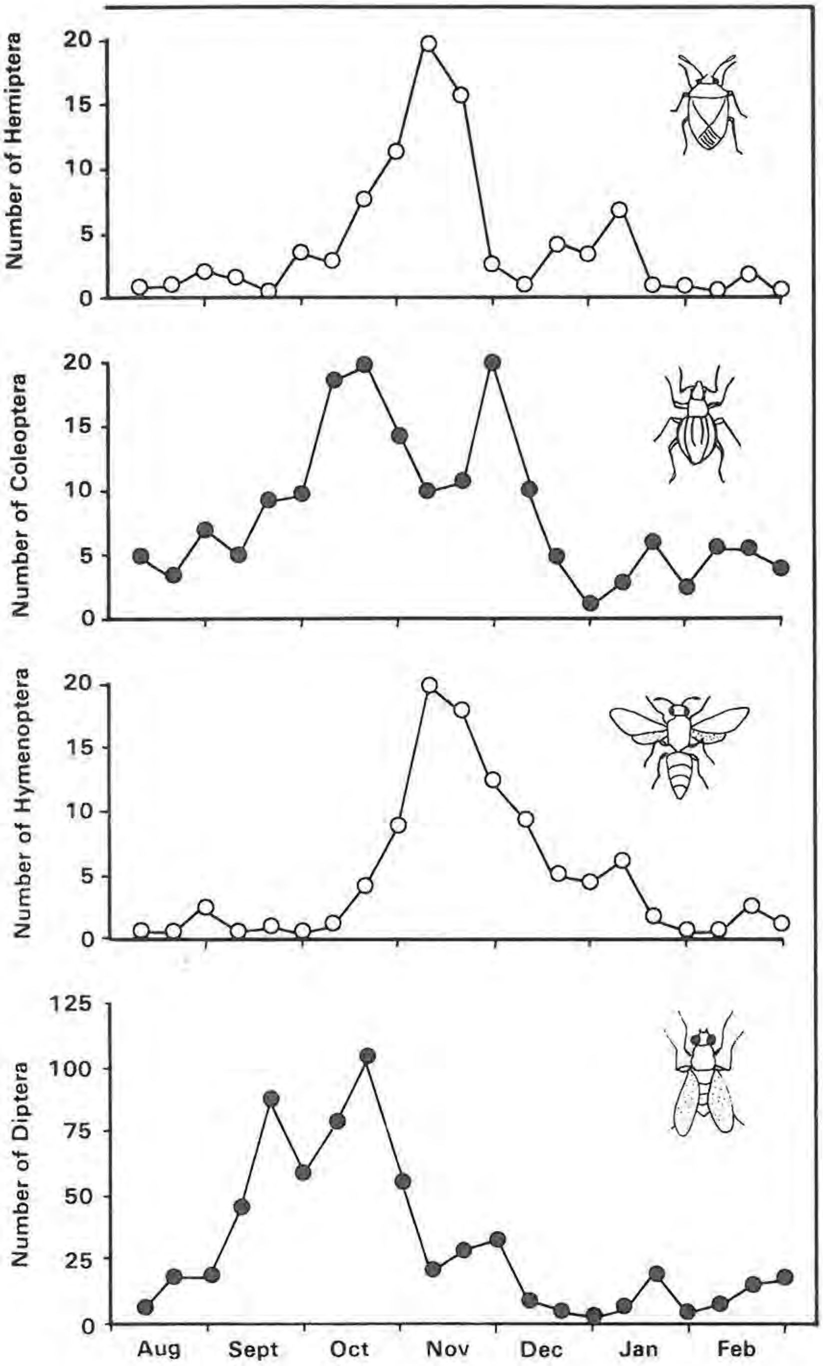

Figure 3: The number of insects of different orders collected with a suction trap in a preferred *Hirundo spilodera* feeding area.

DIET

Availability of prey
The biomass of insects caught with the sweepnet was only high during November and December 1984 (Figure 2). Although some rain fell in the latter half of January the biomass stayed low throughout February. The samples from the suction traps clearly show that different insect orders had peak numbers at different times of the season (Figure 3). Coleoptera were probably the most reliable food source as they were available in reasonable numbers for most of the seven months in which samples were taken.

TABLE 1

PREY OF *HIRUNDO SPILODERA* AS REVEALED BY ANALYSIS OF STOMACH CONTENTS. THE PERCENTAGE OCCURRENCE OF EACH TAXON IS ALSO GIVEN. n = NUMBER OF INDIVIDUAL CLIFF SWALLOWS COLLECTED THREE OR FOUR TIMES PER MONTH.

(* = 2 species; ** = 3 species).

Taxonomic group		1983/84 Months present							
		SEPT	OCT	NOV	DEC	JAN	FEB	MAR	% Occurrence
	n	19	26	28	21	27	23	18	
COLEOPTERA									
SCARABAEIDAE									
Aphodiinae*		X	X	X				X	20
Canthoninae				X					4
Rutelinae			X						8
Scarabaeinae									
Scarabaeus sp.		X	X			X	X		20
*Onthophagus*** spp.		X	X	X	X	X	X	X	68
Phalops sp.					X	X	X		12
larvae		X		X		X	X		16
CURCULIONIDAE		X							4
Erirhininae		X	X	X		X		X	20
Barinae**			X	X	X	X	X	X	52
Cleoninae				X	X				8
Microlarinus sp.			X		X	X	X	X	28
Brachyderinae									
Protostrophus sp.		X							4
Gymnetrinae				X					4
HYDROPHILIDAE*		X		X		X			8
COCCINELLIDAE									
Adonia variagata			X	X	X	X	X		24

Table 1 (continued)

Taxonomic group	1983/84 Months present								
		SEPT	OCT	NOV	DEC	JAN	FEB	MAR	% Occurrence
	n	19	26	28	21	27	23	18	
CHRYSOMELIDAE			X			X			8
Cassidinae*			X			X			8
Eumolpinae					X	X			8
Alticinae				X					4
APIONIDAE			X						4
ANTHICIDAE					X	X	X	X	24
ALLECULIDAE				X		X			8
PHALACRIDAE*				X					4
HISTERIDAE**				X	X				8
DERMESTIDAE									
Dermestes maculatus				X	X		X		12
CARABIDAE*				X		X			8
STAPHYLINIDAE*				X	X	X			16
Bledius sp.									4
Philonthus spp*						X		X	8
BOSTRYCHIDAE						X			4
LEPIDOPTERA									
HETEROCERA				X			X		12
RHOPALOCERA				X			X		8
larvae				X					4
ORTHOPTERA									
ACRIDIAE				X					4
DIPTERA									
BOMBYLIIDAE			X	X			X		12
DROSOPHILIDAE		X	X	X	X		X	X	36
CALLIPHORIDAE						X			4
SEPSIDAE				X	X		X		12
TEPHRITIDAE			X	X					8
SPHAEROCERIDAE				X					4
SCIARIDAE				X	X				12
MUSCIDAE		X	X	X	X	X	X	X	56
HYMENOPTERA									
FORMICIDAE									
Cerapachyinae									
Simopone sp.			X	X					8
Myrmicinae					X	X	X		12
Messor capensis				X	X			X	12
Messor sp.			X	X					8
Pheidole sp.				X	X				8
Solenopsis punctaticeps				X					4
Tetramoruim spp.*				X		X	X		16
Triglyphothrix microps		X			X				12

Table 1 (continued)

Taxonomic group	1983/84 Months present							
	SEPT	OCT	NOV	DEC	JAN	FEB	MAR	% Occurrence
n	19	26	28	21	27	23	18	
FORMICINAE								
Amoplopelis custodiens			X	X		X		12
Anoplolepis sp.		X					X	8
Camponotus maculatus		X	X	X				36
Camponotus sp.			X			X		8
ICHNEUMONOIDEA*	X	X	X	X		X	X	24
POMPILIDAE	X		X	X				12
HALICTIDAE**	X	X	X		X	X	X	32
SPHECIDAE			X				X	8
Ampulicinae*		X	X			X	X	16
BRACONIDAE			X	X		X		16
Chelonus sp.			X					8
BETHYLIDAE*		X		X	X	X	X	24
CHRYSIDIDAE							X	4
CHALCIDOIDEA	X		X	X	X	X	X	28
CHALCIDIDAE								
Peltochalcidia sp.			X			X		12
PTEROMALIDAE			X			X		12
Pachyneuron sp.		X	X					8
EURYTOMIDAE								
Eurytoma sp.						X		4
EULOPHIDAE			X					4
Diclyphus sp.			X	X			X	12
ORMYRIDAE								
Ormyrus sp.			X	X				8
TORYMIDAE								
Megastigmus sp.				X	X			
HEMIPTERA								
CICADELLIDAE*			X			X		16
RHOPALIDAE			X			X		8
FULGOROIDEA*						X		4
CYDNIDAE			X		X	X	X	16
PENTATOMIDAE*			X		X		X	16
LYGAEIDAE			X	X	X	X	X	40
REDUVIIDAE					X	X		12
CICADIDAE			X	X				24
COREIDAE							X	4
DELPHACIDAE			X		X			8
CIXIIDAE			X	X				8
PSYLLIDAE			X	X	X			12
APHIDIDAE			X			X		8
TINGIDAE			X	X				12

Table 1 (continued)

Taxonomic group		1983/84 Months present							
		SEPT	OCT	NOV	DEC	JAN	FEB	MAR	% Occurrence
	n	19	26	28	21	27	23	18	
ISOPTERA									
TERMITIDAE									
Hodotermes mozambicus				X	X		X		16
PLECOPTERA			X	X					8
THYSANOPTERA			X						4
ARACHNIDA									
ARANEAE									
THOMISIDAE			X						4

Diet

The presence of the different arthropod taxa in the stomachs of Cliff Swallows collected in the 1983/84 season is given in Table 1. The Cliff Swallow preyed on a wide variety of insects with the Coleoptera, Diptera, Hymenoptera and Hemiptera the most important orders. These orders were also most commonly trapped in the suction traps (Figure 3). The only other insect taxon often trapped in the suction traps, the Thysanoptera, are very small (± 1 mm in length) and was seldom found in stomach samples (Table 1). Dung beetles of the family Scarabaeidae and weevils of the family Curculionidae were the most important Coleoptera in the diet. In the Diptera, the families Drosophilidae and Muscidae were by far the most important. The Carabidae beetles are flightless and must have been taken on the ground or off vegetation, as must have been the Coleoptera and Lepidoptera larvae and workers of the *Hodotermes* termites. The spiders were all found in one stomach and could have been taken either from vegetation or while the spiders were drifting in the wind.

Small stones ranging in size from 1-5 mm in diameter were present in 11 % of stomachs examined. Stones were found in both males and females and even in the stomachs of chicks. The significance of these stones were not known. Captive chicks which were reared to study certain behavioural aspects were often fed impurities such as sand and pieces of grass, together with insects and these impurities as well as some insect chitin, were cast out in the form of pellets.

DISCUSSION

To date there has been no detailed information on the diets of any swallow breeding regularly in the Afrotropical region. The diets and foraging ecologies of several swallow species breeding in the Holarctic region have been studied. Beal (1918) reported on the diets of a number of North American species, while Stoner (1936) and Waugh (1979) studied the diet of the Sand Martin *Riparia riparia* on both sides of the Atlantic. The diets of two other species occurring in southern Africa during the summer months, the House Martin *Delichon urbica* and the European Swallow *Hirundo rustica*, have been well studied in Europe (Thomas 1933-39, Von Gruten 1961, Von Gruten & Schwarzenbach 1962, Schulze-Hagen 1970, Bryant 1973, Közená 1979). In all of these studies the identification of food items tends to be superficial. The food is often highly fragmented and identification can rarely be done in a quantitative way below the sub-family taxon. However, most authors have only used the family taxon (e.g. Johnson 1967, Turner 1983). This superficial identification would tend to make the different swallow species appear closer in their diet to one another and makes it difficult to detect seasonal differences in diet of individual species.

Although the suction trap samples probably gave a good indication of flying insects generally available to the Cliff Swallows, it probably underestimated the availability of poor or reluctant fliers such as Hemiptera. These insects most commonly only flew for short distances between plants and close to the ground as the vegetation is short karoo bushes. The bugs were surely available to the Cliff Swallows, as nearly 30 % of foraging is done less than 0,5 m from the ground (Figure 1). However, the suction traps sampled only at 1,3 m, which is higher than the bugs would tend to fly. The beetles, and especially Scarabaeidae dung beetles, are probably also under-represented in the suction trap samples as they tend to fly at dawn and dusk when no sampling was done. The ideal would be to sample continuously and at different heights. This was not possible in this study because of the portable generator used which only ran for five hours before it needed refilling, which could not be done because of logistical problems. The suction traps were all of the same size and because the area where sampling was done was private property, structures to sample at various heights could not be errected. The samples from stomachs and suction traps are not directly comparable, for instance in indicating prey selection. However, the suction traps trapped large numbers of very small insects, such as Thysanoptera and aphids, which were rarely found in Cliff Swallow stomachs (Table 1). Hespenheide (1971, 1975) described the food preferences of a number of insectivorous birds, including several of the family Hirundinidae. He concluded that the average size of prey taken is usually larger than the average that is available. This also seems to be the case with the Cliff Swallow. However, Turner (1982) found that it is profitable, in terms of net energy gain, for the European Swallow *H. rustica* to take a mixture of large and small items, even though optimal foraging theory would predict exclusive specialization on large items.

Cliff Swallow prey was too fragmented to determine either size (such as by winglength)(Lewis & Taylor 1967, Turner 1982) or mass (for ash-free weight or calorific value). Food value of the diet was thus poorly understood, and even numerical values of food items were only available as indices of percentage occurrence.

Ground living arthropods such as the Coleoptera family Carabidae, were often found in the Cliff Swallow diet (Table 1) and ground foraging might have been more common than observed. Lepidoptera larvae and flower spiders were also found in the diet, indicating that food was also taken from plants.

Unusual prey items or foraging methods by Hirundinidae were reported often, such as *H. rustica* taking lepidopteran larvae (Brooke 1956, Turner 1981) or swallow species foraging on the ground (Bent 1942, p. 450, *H. rustica*, Weber 1980, *H. rustica, H. pyrrhonata* and *R. riparia*) or following ploughs (Winterbottom 1971). Some insect taxa which are not regular components of the aeroplankton are frequently found as prey items of certain swallow species. Közená (1979) thus hypothesized that *H. rustica* often preys on insects which it flushes itself. The method of flushing insects from vegetation as described for the Cliff Swallow is often used. One would then expect poor-flying insects such as bugs in the diet, which is the case (Table 1). The Cliff Swallow probably feeds on the ground more often than other swallows and the variety of terrestrial insects and spiders taken indicates this.

The casting of pellets by swallows have not been reported previously and there is also no record of swallows indigesting stones. Walton (1984) found Meadow pipits *Anthus pratensis* often had stones in their stomachs and Betts (1955) also reported on "grit" in the stomachs of four species of titmice (Paridae). The significance of stones in the stomach is not known at present.

OPSOMMING

Die Familieswael *Hirundo spilodera* voed in vlug gewoonlik naby die grond. Sowat 44 % van voedingsvlugte is minder as 1 m vanaf die grond. Prooi is dikwels deur die swaels opgejaag vanaf plante deur lugversteurings met hul vlerke te veroorsaak. Artropoda wat nie kan vlieg nie, soos die larwes van Lepidoptera en Coleoptera en spinnekoppe (Arachnida), het ook in die maaginhoude voorgekom. Alhoewel baie klein prooi soos plantluise (Aphididae) en veervlerke (Thysanoptera) soms in groot getalle beskikbaar was, het hulle selde in die Familieswael se dieet voorgekom. Kewers, veral van die families Scarabaeidae en Curculionidae, sowel as vlieë van die families Muscidae en Drosophilidae en wespes van die Chalcidoidea en Halictidae was die belangrikste prooi items.

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Time budget of South African cliff swallows during breeding

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The use of time by the South African cliff swallow was determined and use of energy calculated by using equations for predicting standard metabolic rate and the cost of flight. The highest daily energy expenditure was during the feeding of nestlings when 9,22 h were spent foraging. The cost of 127 kJ for building a nest is very low if it is considered that the nest is usable for a number of years.

S. Afr. J. Zool. 1986, 21: 57–59

Die benutting van tyd deur die familieswael is bepaal en die gebruik van energie is bereken deur middel van vergelykings vir basale metabolisme en vluglas. Die meeste energie word verbruik terwyl neskuikens gevoer word en tot 9,22 h is tydens hierdie periode aan die soek van kos bestee. Slegs 127 kJ is verbruik tydens nesbou en dit is baie laag indien in ag geneem word dat die nes vir 'n hele aantal jare bruikbaar is.

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The South African cliff swallow *Hirundo spilodera* breeds in dense colonies, usually on man-made structures such as concrete road bridges (Earlé 1985). Nests are built with mud and are gourd-shaped with a short entrance tunnel and a nestpad consisting of soft materials. South African cliff swallows re-occupy old nests and, if broken, repair these during the breeding season. Both sexes incubate and feed the young in about equal proportions (Earlé in press). These swallows mostly feed on the wing. The time spent on the three activities during the South African cliff swallow breeding season were calculated from three 24-h watches at three different nests on different occasions. Nests were observed from 04h30 to 19h30 and it was assumed that the specific individuals watched spent the other 9 h during the night in the nest, which was found to be the case as the individuals only left the nests after observations started. Unless disturbed, South African cliff swallows sleep in their nests at night. Nest building was observed on 12 October 1983 at a colony where mud was collected from a temporary pool 20 m from the nest. Incubating birds were watched at another colony on 29 November 1983, while birds feeding 20-day-old nestlings were observed on 16 October 1984.

A sample of 36 adult cliff swallows was captured by mist net at a colony in October 1984 and body weight, wing span and wing length measured. To calculate the time spent flying it was assumed that the swallows only perched at the nest. Flight velocity was determined on a calm day over a 100-m course by timing 30 birds with a stopwatch. Times required to collect a mud pellet, carry it to the nest and pack it into the nest were also measured.

The equation of Lasiewski & Dawson (1967) was used to predict standard metabolic rate (SMR) of the South African cliff swallow and the cost of flight was estimated from aerodynamic theory of flapping flight as given by Pennycuick (1969) and Tucker (1973) (see Appendix).

The South African cliff swallow spent most of the 24-h day in the nest (Table 1). This included about 9 h spent sleeping in the nest at night. Nest building was a minor component of total activity during the incubation and nestling periods, while most time was spent foraging during the nestling period (Table 1).

Flight velocity was determined to be 9,2 m s^{-1} (range 8,3–11,6) (33,1 km h^{-1}). At this velocity the metabolic cost of flight for a 21,7-g bird is predicted to be 2,59 W (or 6,8 SMR) (Tucker 1973). Measurement of flight velocity was made on a calm day so that there was no need for correction because of ambient wind velocity. Existence metabolism in the nest was taken to be 1,5 SMR (0,57 W) and metabolic cost of nest building (i.e. packing mud and collecting mud) was assumed to be 2 SMR (0,76 W). These SMR figures were similar to those used for the American cliff swallow *Hirundo pyrrhonota* by Withers (1977), who also pointed out that an error as much as 50% in these two assumptions would only result in a 7% error in the daily energy expenditure because of the large contribution of flight relative to non-flight activities.

The highest daily energy expenditure was during the feeding of nestlings when 0,062 W g^{-1} was expended, in comparison to nest construction and during incubation when 0,059 and 0,053 W g^{-1} was expended respectively. The highest food harvest rates (24-h day/time spent foraging) were obtained during incubation when only 7 h per day was spent foraging (Table 1). The harvest rates given in Table 1 are probably an underestimation as some time on the wing is probably spent in social activities and not foraging but no estimation of the time spent in social activities was made.

Table 1 Daily time and energy budgets of *Hirundo spilodera* during nest construction, incubation and nestling periods

	Nest construction		Incubation		Nestlings	
	Hours	kJ	Hours	kJ	Hours	kJ
Foraging	8,21	76,5	7,00	65,2	9,22	85,9
Nest building	3,69	10,1	0,11	0,3	0,03	0,1
In nest	12,10	24,8	16,89	34,6	14,75	30,3
Total[a]	24,00	111,4	24,00	100,1	24,00	116,3
Harvest rate (Total[a]/h foraging; W)	3,77		3,97		3,51	
Daily energy expenditure						
W g^{-1}	0,059		0,053		0,062	
× SMR	3,37		3,03		3,54	

[a] Conversion of time to energy assumes flight cost (foraging) = 2,59 W, cost of nest construction = 0,76 W, and existence metabolism = 0,57 W.

To calculate the cost of building a nest the time spent on the three actions which constitute a nest-building trip was measured for a number of individual birds and the mean times spent on the mud-gathering site, on the nest site and travelling between the nest and mud source were used to calculate energy expenditure while building a nest. A single mud pellet was assumed to have a mass of 0,54 g [mean nest mass was 804 g, mean number of pellets was 1550 per nest (Earlé 1985)]. By carrying this mud pellet about 1% is added (Withers 1977) to the metabolic cost of flying which was considered a small enough extra cost to be ignored in further calculations. The number of trips required to build a nest was about 1550 if it is assumed that each pellet in the nest required a trip.

During each 60-s period of nest building 11,4 s was spent on the mud-gathering site, 28,6 s was spent on the nest site packing mud and 20 s flying between the two sites (Earlé 1985). The metabolic rate during such a 60-s cycle was found to be 3.6 SMR

$$\left[= \left(\frac{11.5}{60} \times 2\right) + \left(\frac{28.6}{60} \times 2\right) + \left(\frac{20}{60} \times 6{,}8\right)\right]$$

and the total cost of nest construction was thus:

$$\begin{array}{ccccccccc} \text{Mean cost of whole cycle } (\times \text{SMR}) & \times & \text{SMR (W)} & \times & \text{number of trips} & \times & \text{length of whole cycle} & = & \text{kJ (Withers 1977)} \\ 3.6 & \times & 0.38 & \times & 1550 & \times & 60 & = & 127\,\text{kJ} \end{array}$$

As the nest of the cliff swallow is usable for a number of years and up to four broods can be raised in a single nest per year (Earlé in press), the amount of energy spent in building a nest, namely 127 kJ, is very small. The remarkably similar energy output for nestbuilding in the American cliff swallow (122 kJ) (Withers 1977) indicates a very similar strategy in breeding and probably colonialism. The daily energy expenditure in raising nestlings of 3,54 SMR is higher than that of both the American cliff swallow (Withers 1977) and the purple martin *Progne subis* (Utter & LeFebvre 1973) where the costs are 3,05 and 3.02 SMR respectively. This higher cost to South African cliff swallows in raising chicks is probably related to food availability especially as observations were made in exceptionally dry years which resulted in a relatively low biomass of food being available (Earlé, unpubl. data). Although time-budget estimates of daily energy expenditure in birds can be in error by 20–40% (Weathers, Buttemer, Hayworth & Nagy 1984), the methods used were the same as those used by Withers (1977) for the American cliff swallow and are thus directly comparable with that study.

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Appendix

(i) Measurements and formulae used in calculating time and energy used by the South African cliff swallow during the breeding season

Measurements of *Hirundo spilodera* for energy estimates: Body weight 21,7 ± 1,4 g ($n = 36$)

Mean flight velocity 9,2 m s^{-1} ($n = 30$) (range 8.3–11,6 m s^{-1}).

All units are S.I. and the conversion factors are 1 watt (W) = 0,86 kcal h^{-1} and 1 kilojoule (kJ) = 0,239 kcal.

Weight (W) is measured in newtons and mass (m) in kilograms. $W = mg$ where $g = 9{,}81$ m s^{-2}.

Formulae used for:

Standard metabolic rate (SMR)
$P_{ib} = 6{,}15\,m^{0{,}724}$ (Lasiewski & Dawson 1967) where
P = power
i = input
b = basal
m = mass (kg)

Metabolic cost of flight
$P_i/(WV) = 0{,}896\,W^{-0{,}227}$ (Tucker 1973) where
W = weight (N)
V = flight velocity

Estimating daily energy expenditure (DEE)
Total kJ (converted to watt) ÷ 24 (h) ÷ weight of bird (g) = $\mathrm{W\,g^{-1}}$
Estimating food harvest rate
Total kJ (converted to watt) ÷ total hours foraging = W

(ii) Ambient temperatures during observations

(a) Nest building 12 October 1983 max. 27,9°C; min. 13,9°C; mean 29,9°C.
(b) Incubation 29 November 1983 max. 23,2°C; min. 14,6°C; mean 18,9°C.
(c) Nestling 16 October 1984 max. 23,8°C; min. 7,5°C; mean 15,9°C.