A CONTRIBUTION TO THE BIOLOGY OF THE SOCIABLE WEAVER *PHILETAIRUS SOCIUS* (LATHAM)

by

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CONTENTS

Anyone who has travelled the dusty road in the bed of the Kuruman River from Kuruman in the Northern Cape to the South West African border at Rietfontein cannot fail to have been impressed by the large communal nests of the sociable weaver *Philetairus socius* which adorn many of the camelthorn trees along the way. One of the earliest reports of the bird and its nest is that of Sir Andrew Smith (1849) who passed that way through what was then Latakoo (the present day Kuruman), collecting birds which he described for the first time. To him we are indebted for the first published illustrations of the sociable weaver, its nest and egg, and a brief account, not entirely accurate to be sure, of the building and occupation of the nest. This account has since been quoted at length by Shelley (1905) and by Friedmann (1930a) who accepted Smith's statements as they stood.

Some years after Smith's travels, Anderson wrote (1872) that the flocks of sociable weavers

> ". . . . incubate their eggs under the same roof, which is composed by these birds of whole cartloads of grass piled on a branch of some kamel-thorn tree in one enormous mass of an irregular umbrella-shape, looking like a miniature haystack, and almost solid, but with the under surface, which is nearly flat, honeycombed all over with little cavities, which serve not only as places for incubation but also as a refuge against rain and wind".

This account gives some idea of the spectacular nests built by these birds which are hardly larger than a sparrow. But, living in the dry and thinly-populated western regions of southern Africa, the sociable weaver remained a remote curiosity, the subject of casual reports and some strange ideas.

Since Friedmann (1930a) studied the sociable weaver briefly in the western Transvaal, the only thorough field observations (mainly on nests and nest sites) up to the present have been those of Rudebeck (1953, 1956). Collias & Collias (1964) returned to the western Transvaal some 20 years after Friedmann's visit, but unfortunately had time for only a cursory study; their main interest was once again in the nest and its architecture.

Thus, in 1964 when I joined Dr. T.J. Cade, then of Syracuse University and now of Cornell University, on his desert biology programme, he suggested that the sociable weaver be the subject of special study in the Kalahari. Here was a bird, resident in a harsh environment, living throughout the year in an extraordinary nest, and almost completely unknown biologically. Among the questions to be answered were:

How is the nest started and how is it constructed ?

Which birds build, and how is the labour organized ?

What is the purpose of the elaborate nest: does it provide a micro-climate which enables the birds to survive better under arid conditions ?

How could such a communal nest have evolved ?

What is the social organization of the colony in and out of the breeding season ?

When do the birds breed and what factors induce breeding ?

What happens to the young birds after they become independent of their parents ?

Naturally many other questions arose as the work proceeded, but these were the main ones on which the project was initiated.

Acknowledgments:

This study could never have been completed without the kind help of a number of people and institutions. Financial support was provided by United States Public Health Service grant ES 00008 (Environmental Health) to Dr. Cade, to whom I am deeply indebted for introducing me to the interesting problem of the sociable weaver and for his help and encouragement throughout. It was due to the good offices of Dr. J.M. Winterbottom of the Percy Fitzpatrick Institute of African Ornithology, Cape Town, that Dr. Cade and I first became acquainted. My thanks go also to the National Parks Board of South Africa and its employees for allowing me to work unhindered in the Kalahari Gemsbok National Park and for assistance given. During the preparation of this paper I had fruitful discussion with, and much encouragement from, Prof. B.R. Allanson (Department of Zoology and Entomology, Rhodes University, Grahamstown, South Africa) and Dr. N.E. Collias (Department of

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Chapter 1

STUDY AREA AND METHODS

The study began in October 1964 in the Kalahari Gemsbok National Park, Cape Province, South Africa (Fig. 1) and it ran until the end of April 1966. The only break in the otherwise continuous observations was during September 1965. The study area extended from just South of Twee Rivieren up the Nossob River for a distance of just over 25 miles (Fig. 2) and for a short distance on either side of the Nossob River wherever sociable weaver nests were found. The entire area shown in Fig. 2 was studied for other purposes, but the number of sociable weaver nests in the dunes between the Nossob and Auob Rivers was very low and most of these nests were unoccupied. Nest counts were also done outside the study area northwards to Union's End at the northern tip of the Park, and southwards to Upington on the Orange River, a distance of 215 miles by road. Notes were also made on the occurrence of nests in South West Africa and in the Northern Cape and western Orange Free State for the purpose of constructing a distribution map of the sociable weaver.

The Gemsbok Park lies in the south-western Kalahari sandveld, a land of red sand dunes supporting a cover of grass, shrubs, bushes and (in some areas) trees. Leistner (1959a, b) has given a very adequate account of the physiography and vegetation of the Park itself, while Volk (1966) deals with the country to the west and Smithers (1964) to the east of the Park. The study area was divisible into three main habitat types, the extent of each of which can be seen in Fig 2.:

The River Beds

Within the study area, the Auob River bed is treeless except for a growth of bushy *Acacia haematoxylon* trees along the extreme western edge where the dunes descend to the river (Fig. 3). The bed of the Nossob River is also rather bare of trees south of Rooiputs, but the few camelthorn trees (*Acacia giraffae*) which do occur in this stretch are large, many of them quite suitable for sociable weaver nests. From Rooiputs northwards the trees increase suddenly in number. This is reflected in the greater number of sociable weaver nests in this area (Fig. 2) and is clearly shown by the tree-count in Table 25. Apart from trees, the vegetation of the river beds is sparse except after rain.

The Dunes

In the southern part of the study area, the dunes are almost treeless (Fig. 4); the few scattered *Boscia albitrunca* trees are usually too low for sociable weaver nests. North of Rooiputs, however, the *Acacia giraffae* trees form what may almost be termed "Wooded Steppe" (Moreau 1966), but which I prefer to call *Acacia* savanna, since the trees are rather sparse (Fig. 5).

The Calcrete

A narrow strip of rocky limestone flats on the east banks

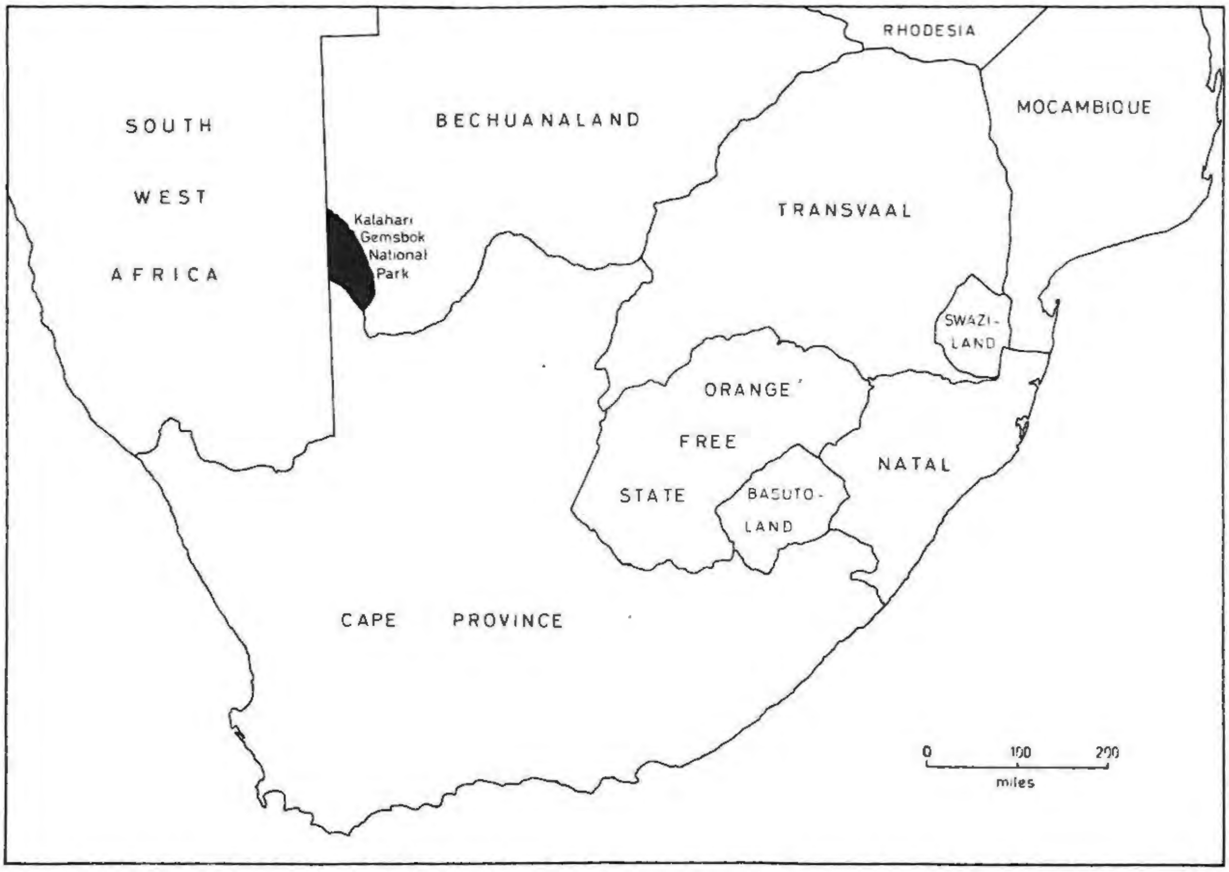

Fig. 1

Map of South Africa showing the location of the Kalahari Gemsbok National Park.

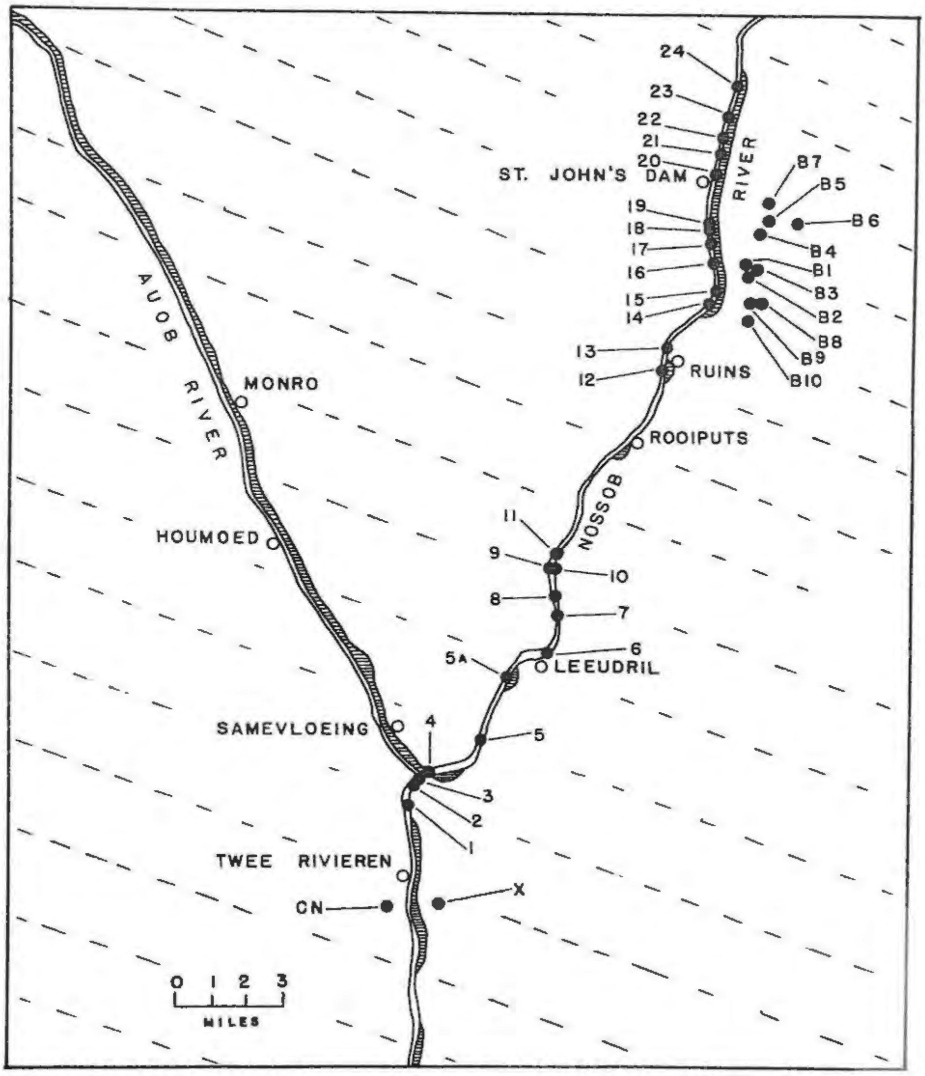

Fig. 2.

Map of the study area in the southern Kalahari Gemsbok National Park, showing the game wells (open circles) and the sociable weaver nests (solid circles with nest numbers). The broken diagonal lines indicate the extent and direction of the dunes; the hatched areas on the east banks of the two rivers show the extent of the calcrete.

Fig. 3.

The bed of the Auob River at Houmoed. The bushy trees on the right of the river bed are _Acacia_ _haematoxylon_; the left bank is calcrete. A blue wildebeest _Connochaetes_ _taurinus_ walks across the river after drinking at the water in the right foreground.

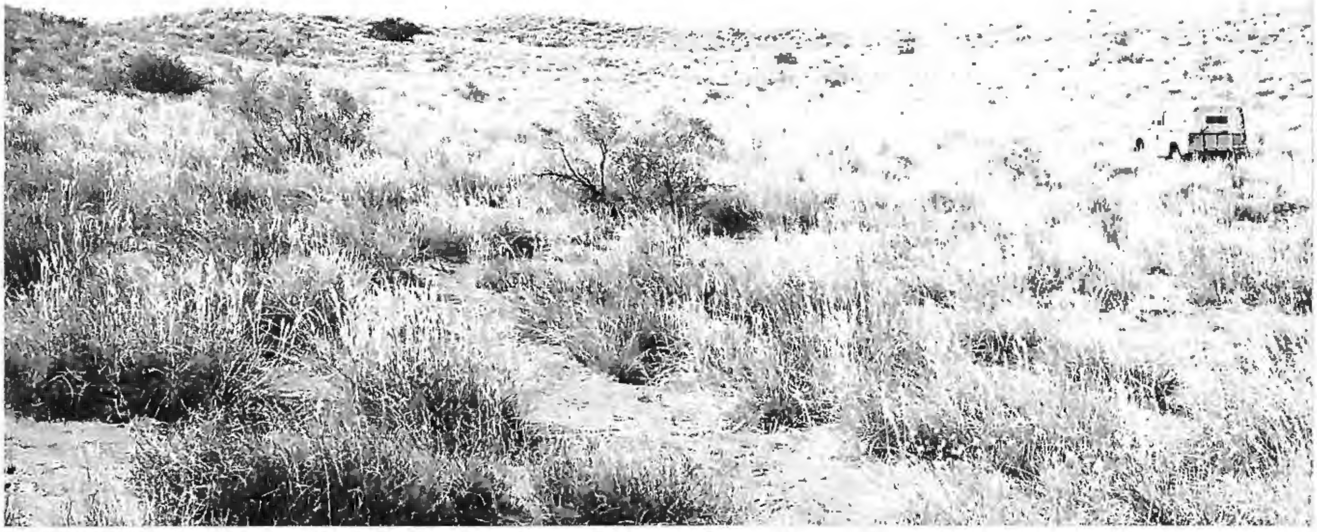

Fig. 4.

Typical treeless dune trough near Twee Rivieren.

Fig. 5.

Acacia savanna. Nest B5 is in the *A. giraffae* tree at centre left.

of the Auob and Nossob Rivers, the calcrete is a characteristic formation of arid regions. Wherever the Kalahari sand has been cleared away by wind, the calcrete is exposed. It supports a sparse growth of low shrublets and no trees (Fig. 6).

Methods

Daily weather notes were kept throughout the study period and weather data were available at the meteorological station at Twee Rivieren. All the sociable weaver nests in the study area, whether occupied or unoccupied, were plotted on a map (Fig. 2); riverine nests along the Nossob River were numbered from 1 to 24, while the few nests in Botswana (formerly Bechuanaland) included in the regular nest counts were prefixed with the letter B and numbered from 1 to 10. Two further nests near Twee Rivieren were Camp Nest (CN) and a nest in Botswana (X). A preliminary survey indicated which of these nests were suitable for regular examination for breeding studies and which were suitable as sites for trapping weavers for ringing.

Since each so-called "nest" contained several next chambers, the whole structure will be called the nest mass and each nest chamber will be referred to simply as a chamber. A single tree might contain more than one nest mass, so that each of the numbers assigned to the nest masses in Fig. 2 refers in fact to an occupied tree or a colony, rather than to a single nest mass.

Fig. 6.

The author on the calcrete; note the open nature of this habitat.

Within a single tree, each nest mass (if there were more than one) was designated by the colony number followed by a letter indicating the location of the mass in the tree. Thus 24W is the western mass of colony number 24, CNLM is the lower middle portion or mass of Camp Nest, and so on. Each chamber within each nest mass was numbered and in the text will be separated from the nest mass designation by a colon; thus 16E:24 is chamber number 24 in the eastern nest mass of colony number 16. I shall use this standard code throughout. All the chambers in each accessible nest mass within the study area were examined twice weekly during the breeding periods and once weekly at other times. Nest masses so examined were: CNLM, CNUM, CNSE, CNSW, X, 5L, 5U, 16S, 16E, 16N, 17E, 17S, 24E, 24W, B1, B2W, B3, B5, B7, B8, B9 and B10 (22 nest masses with a total of about 300 chambers between them).

Chamber contents were counted by hand using a rubber glove for protection against the sharp straws in the entrance tunnels; the fingers of the glove were cut off at the tips so that the eggs or young could be felt. Eggs could be counted easily in this way, but small chicks had to be carefully removed from the chamber for counting. The chicks did not appear to suffer in any way from this treatment. It was not possible to determine accurately the extent of desertion by parent weavers whose nests had been examined in this way, but it seemed not to be extensive once they had become accustomed to the routine. The lowest nests could be examined from the ground, higher ones from a step-ladder or from the top of the Land Rover, while the highest nests were reached by placing the ladder on top of the Land Rover (Fig. 7). Nest masses up to 20 feet above the ground could be examined by this method; those at greater heights were not examined (38% of the nest masses in the study area).

Nestling weavers were ringed at the age of two weeks at which stage they were well feathered but did not show any tendency to leave the nest. Adults were trapped for ringing and moult examination in three main ways:

funnel or drop-trapping with seed-baited traps;
mist-netting at the nests;
catching in the chambers at night.

The funnel trap was a simple rectangular cage of half-inch mesh wire netting over a stout fencing wire frame. At ground level on each of the two long sides was a short inward-facing funnel of wire netting. Trapped birds were removed through a door on top of the cage. The drop trap was similar but lacked the funnels; it was supported at one end by a stick attached to a string which when pulled removed the stick and allowed the cage to drop. Ordinary mixed commercial bird seed was used as bait.

Fig. 7. Method of examining nest masses of the sociable weaver. (Nest B7).

Mist nets were 24 mm. black nylon mesh, 12 metres long and 4-shelf (about 7 feet or 2.5 metres) high, supported at each end by an aluminium pole (Fig. 8). A net was suspended at right angles to a commonly used flight line, about 10 to 40 feet from a nest mass, and the birds chased out of the nest mass from the opposite side of the tree; occasionally incoming birds were also netted. For night-trapping in the chambers, the only equipment needed were several approximately 1 foot square pieces of sacking with which the chamber entrances could be plugged quickly before the birds took fright and flew out. After as many chambers as possible were plugged, each plug was removed slowly and a hand inserted into the chamber to catch whatever birds were inside; the birds were carefully extracted for ringing.

Coloured plastic rings and numbered aluminium rings were used, either separately or in combination. A ringing code was drawn up so that each bird had its own colour ring or rings and was individually identifiable in the field. Plastic rings of size 1a/B manufactured by the Greenrigg Works, England, were available in 7 plain colours (white, pink, red, yellow, blue, black and green) and 10 two-colour combinations (red/blue, red/white, orange/white, red/yellow, blue/white, blue/yellow, black/white, black/yellow, green/white and orange/yellow). Of the plain colours, blue and pink were the least suitable because of poor

Fig. 8. Mist netting sociable weavers at Nest No. 19.

visibility and a tendency to fade. For similar reasons blue/white and blue/yellow rings were less desirable among the striped rings. There was sometimes confusion between red/white and orange/white rings, but on the whole the colours were readily distinguishable and fading was minimal. Plastic rings became brittle with age, but loss of rings through breakage was small and did not affect the observations.

Altogether 1337 sociable weavers were ringed in the study area. No bird carried more than 3 rings (either 3 plastic rings, or 2 plastic and 1 aluminium). Of the total, 721 weavers were ringed as nestlings or juveniles, the rest (616) as adults. The distribution of ringed birds is shown in Table 1.

All retrapped birds were recorded, examined for moult and released. Most of the unringed birds were ringed and released, but some were killed for later dissection to study stomach contents, gonad development, ecto- and endoparasites, moult and measurements. Stomach contents and parasites were placed in 70% alcohol for later identification and examination. The number of samples of stomach contents was too small to allow of an adequate analysis of seasonal variation in feeding habits, but the number of weavers in the study area, although high, was not unlimited, so that it was thought inadvisable to kill too many birds. Moreover, it was not policy to kill ringed birds, particularly those at nests under regular examination, as this would have affected the breeding and population studies. Gonads were measured, but were not kept for histological study.

Field observations on the sociable weaver were conducted mainly at the nests, particularly Camp Nest where over 100 hours of watching were spent during the 19-month study period. A pair of 8 x 30 Zeiss field glasses was used at a distance of 30 feet from the tree and without a hide. The birds at Camp Nest soon became accustomed to my presence. For closer study of behaviour and nest-building, a small colony of 22 weavers, all trapped at the same nest, was kept in an aviary measuring 12 x 20 x 12 feet and placed in a dune trough about 150 yards from my laboratory at Twee Rivieren. A large tree trunk with a horizontal branch was placed in the middle of the aviary (Fig. 9). The birds were given mixed bird seed and water, and once daily were given a dish of "Pro-Nutro" (a commercial, high-protein cereal food) mixed into a porrige with water; from time to time they were also given harvester termites (Hodotermes mossambica) and grasshoppers. The aviary birds were all colour ringed.

A

B

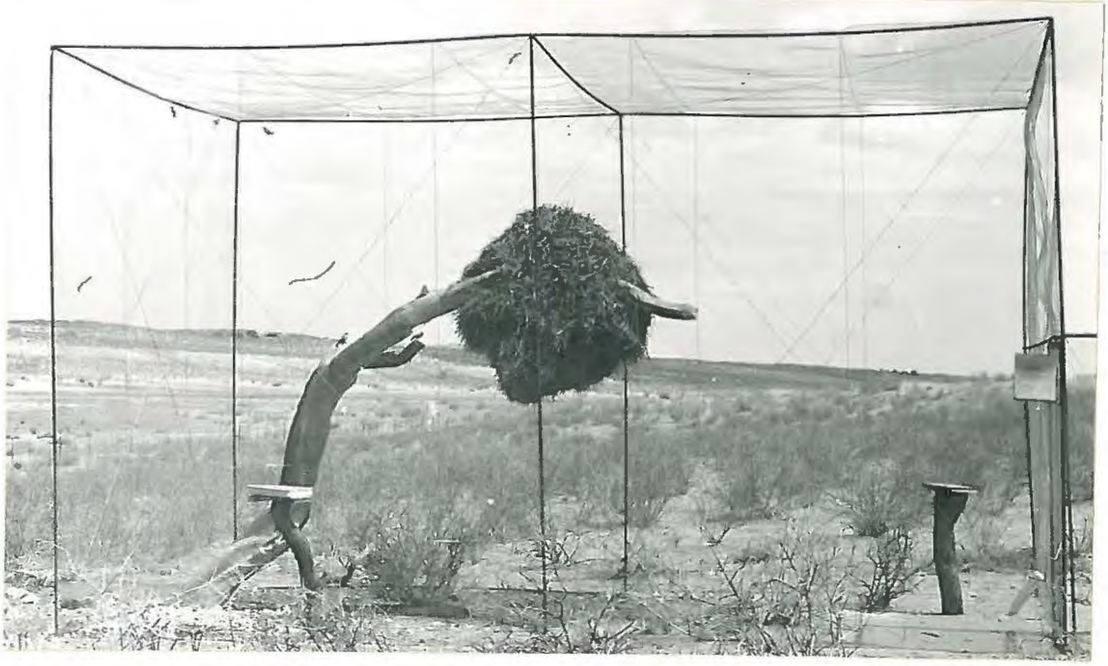

Fig. 9. A. The aviary a few days after the birds had been provided with a nest mass.

B. The aviary 3 months later, showing how the original nest mass was built on to by the birds.

Table 1. Numbers of adults and young sociable weavers ringed in the Kalahari from October 1964 to April 1966. All nests except Nos. 44 and 3M are in the study area. (Fig. 2).

NEST No.	ADULTS	YOUNG	TOTAL
Camp Nest	166	152	318
X	11	36	47
5	16	19	35
8	2	-	2
10	-	4	4
16	42	56	98
17	44	44	88
19	147	44	191
22	1	-	1
23	43	-	43
24	81	201	282
44	5	-	5
B1	15	48	63
B2	19	23	42
B3	2	6	8
B4	8	3	11
B5	3	14	17
B7	2	8	10
B8	5	38	43
B9	1	14	15
B10	3	9	12
3M	-	2	2
Totals	616	721	1337

Initially the aviary birds were given building material in the form of old pieces of nest mass from the field, but later on a portion of an old mass was suspended in the tree because the birds would not build there at first. They took to the old mass at once, however, and built freely on to it with nest material provided as before, either in the form of old nest portions or fresh green grass and herbs when these were available.

The aviary nest was also used for collecting data on temperatures and relative humidities inside the chambers. Ambient air temperatures were measured with an ordinary mercury thermometer; temperatures inside the chambers and in the nest matrix were measured with thermistors permanently inserted into the nest material and in use from 27 November 1965 until April 1966. Ambient and nest temperatures were taken simultaneously at irregular intervals day and night. Relative humidities of the air and of the chamber interiors were measured with an Atkins Psychrometer whose readings were used to calculate the RH from standard tables (Marvin 1934).

The sociable weaver proved fortunately to be a highly suitable subject for field studies, as the birds were fairly tame and easy to watch; they were hardy and survived handling well; they did not desert their nests readily in the breeding season; and they were easy to keep in the aviary on a simple diet. Furthermore it was one of the commonest birds in the Nossob River.

Chapter 2

THE BIRD AND ITS RANGE

The sociable weaver has been described and figured in general texts several times since Smith first did so in 1849. The description by Mackworth-Praed & Grant (1963) is probably the most recent:

> "top of head to nape earth-brown; sides of neck, mantle and scapulars blackish with buff edges to feathers giving a scaly appearance; rump and upper tail coverts earth-brown with buff edges; flight feathers, wing coverts and tail dusky with buffish edges to feathers; lores, at base of lower mandible and chin black; ear coverts and below buff-stone; patch of black feathers with white edges giving a scaly appearance on flanks; eye brown; bill horn; legs and feet yellowish grey. The sexes are alike".

This description, as well as that of McLachlan & Liversidge (1957) which runs "bill horn; legs light brown", have apparently been made from museum specimens, since in life the bill and legs are a light bluish grey. Otherwise the descriptions are adequate. There is some slight individual variation in the tone of buff on the ventral surface and feather edges.

Adult sociable weavers measure about 14 cm. in length. The measurements of individual parts of the body given by McLachlan & Liversidge (loc. cit.) are only very slightly larger than those made by me on 73 males and 43 females (Table 2). The sexes vary little in size. The only statistically significant difference between males and females is wing length ($P = 0.01$). The extreme similarity between the sexes made it impossible to distinguish between them in the field; the differences noted by Smith (1849) were not even detectable in the hand, nor was I able to notice any significant behavioural differences.

Young weavers lack the black face before their first moult; the top of the head is spotted dull blackish and the dark centres of the flank feathers are duller than in the adults. Some young birds had a slaty wash about the lores and chin and the scaly pattern of the back extending down the sides of the upper chest to give a half-collared effect.

Table 2. Weights and measurements of male and female sociable weavers (73 males and 43 females).

		Weight (gm.)	Lengths (mm.)				
			Culmen	Wing	Tarsus	Hind claw	Tail
Males	Maximum	31.9	16.3	77.8	18.7	7.6	45.5
	Minimum	23.8	13.5	68.1	15.8	5.4	36.7
	Mean	27.5	14.9	71.7	17.1	6.4	41.0
Females	Maximum	32.0	16.1	74.1	18.5	6.9	45.1
	Minimum	24.0	13.7	68.1	15.6	5.7	37.6
	Mean	27.3	14.9	70.7	17.0	6.3	40.8

The range of sociable weaver (Fig. 10) has been determined from a number of sources as well as my own observations (see Friedmann 1930a; Plowes 1943, 1946; Plowes & Cusack 1944; Rudebeck 1956; McLachlan & Liversidge 1957; Maclean 1960; Mackworth-Praed & Grant 1963; Smithers 1964). The species extends from north-western South West Africa at latitude 19°S, just west of the Etosha Pan, southwards along the eastern edge of the Namib Desert into northern Namaqualand, thence eastwards to about 23°E (a line just west of Kuruman) which is apparently the eastern limit of the main population. From south of the Orange River at this point, the range extends directly northward to the Molopo River and up along the Nossob to the South West African border, ending again at the Etosha Pan. There is a much smaller eastern population which ranges from the extreme western Orange Free State (the most easterly nest in the western Free State is 13 miles east of Kimberley), western Transvaal and the Vryburg District in the Northern Cape to a few miles north of Mafeking at Baralong Farms just inside the Botswana border. R.H.N. Smithers (in litt.) assures me that the sociable weaver does not occur along the northern border of the Molopo River and that the only other place in Botswana where the bird may be found is just along the eastern bank of the Nossob River (see also Smithers 1964).

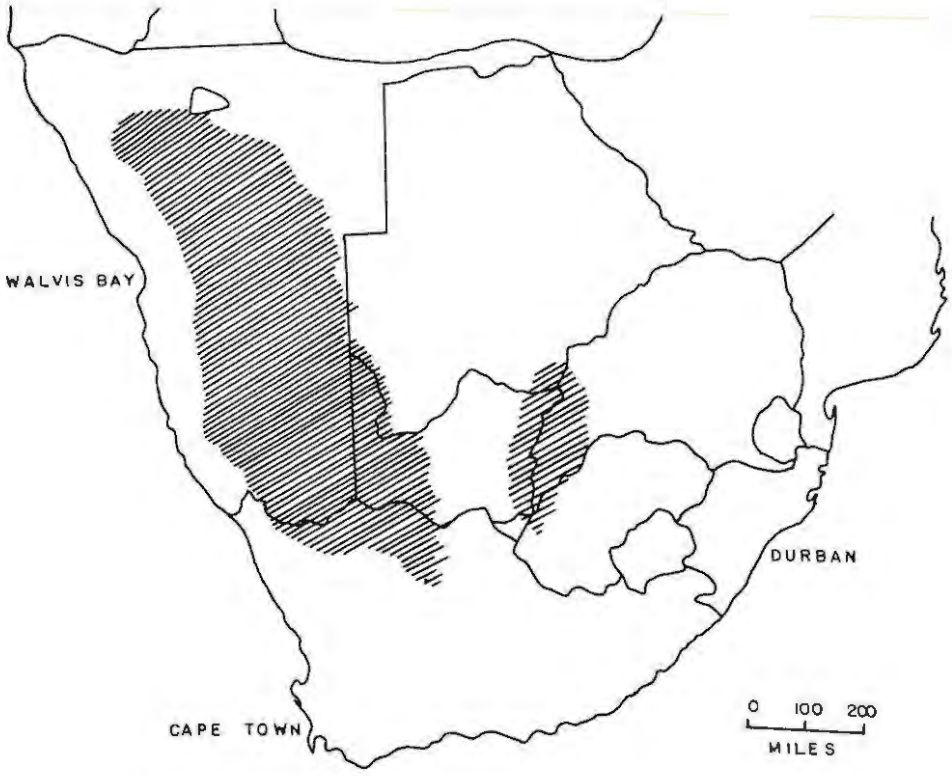

Fig. 10. Simplified map of southern Africa showing the range of the sociable weaver (cross-hatching) based on references in the text.

The rainfall within the range of the sociable weaver varies from about 80 mm. per year in the extreme western parts to about 600 mm. in the extreme north and east. At Twee Rivieren the mean annual rainfall for the years 1961 to 1965 was 226 mm. (8.8 inches). This agrees well with figures in the rainfall maps presented by Stengel (1966). The Kalahari is generally a summer rainfall region. (Fig. 11).

Geographically the area is highly variable ranging from the rugged mountains along the western escarpment and south of the Orange River to the flat stony plains of southern South West Africa and the rolling dunes of the Kalahari sandveld. Elevations within the area range from 500 metres in the Orange River valley at Vioolsdrift to 1500 metres around Okahandja and Kimberley; the study area was about 800 metres above sea level. The predominant tree over the whole range of the sociable weaver is the camelthorn *Acacia giraffae*. Associated tree-like plants include *Boscia albitrunca*, *Aloe dichotoma* (in the rocky western parts) and a number of other species of *Acacia*, notably *A. haematoxylon* in the Kalahari sandveld. Coarse *Aristida* grasses predominate over most of the area, which corresponds for the most part with the Karroo-Namib floral type, particularly the so-called "Gordonia-Zentrum" (Volk 1966), which seems to be the centre of the weavers' distribution.

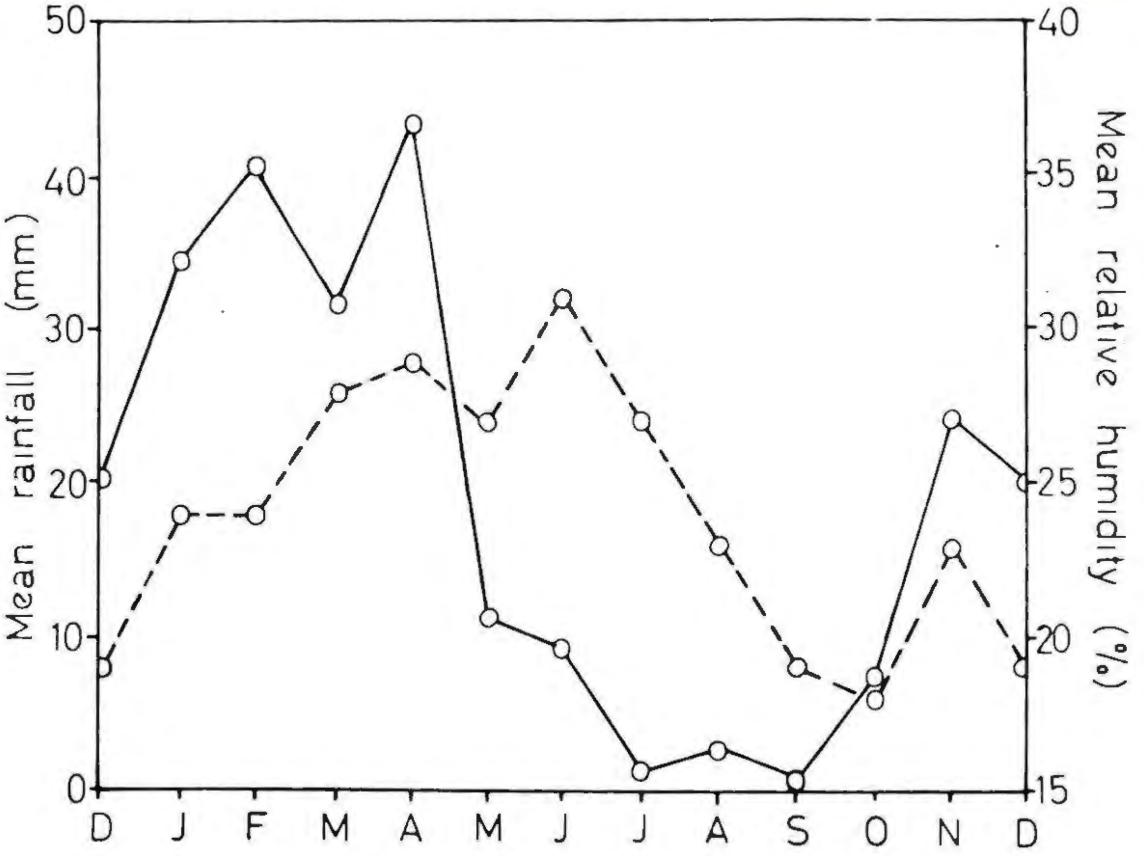

Fig. 11. A. Graph showing the mean monthly rainfall (solid line) and the mean minimal relative humidity (broken line) from weather records made at Twee Rivieren since September 1960.

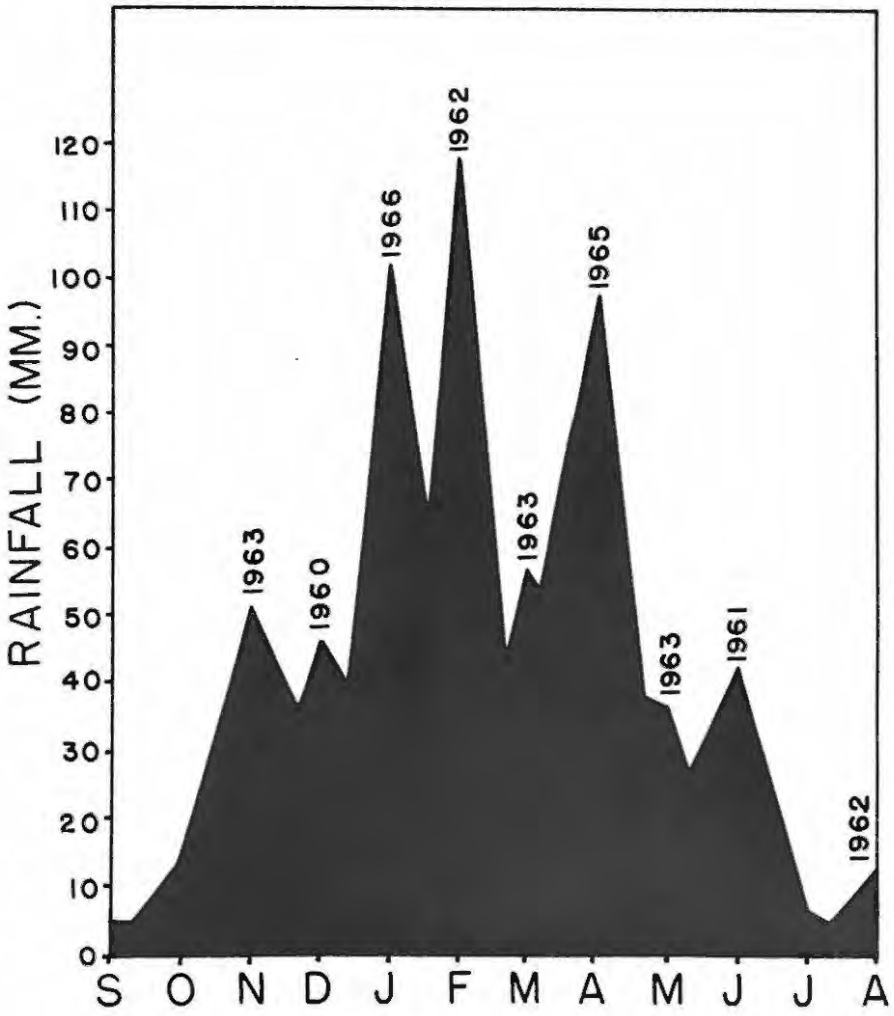

Fig. 11. B. Rainfall peaks at Twee Rivieren from September 1960 to April 1966.

Chapter 3

THE NEST

Architecture

The nest mass can be divided into two main structural regions: the superstructure or roof, and the substructure or living area which contains the chambers (Fig. 12). A typical, well established nest mass which has been in use for several years consists of an extensive superstructure of small sticks 10 to 30 cm. in length and often thorny, and an even more extensive substructure of grass straws extending below the supporting branch on which the mass is built. The number of chambers varies with the size of the nest mass from 5 to 50. Each chamber consists of an entrance tunnel up to 25 cm. in length and about 6 or 7 cm. in diameter leading vertically into a nest chamber measuring some 15 cm. in diameter and set to one side of the tunnel (Fig. 12). The chambers are all separate and do not interconnect with one another inside the substructure.

The chambers in a new nest mass may sometimes be above the level of the supporting branch, but usually they are below it as in the diagram in Fig. 12. The size of the nest mass varies with age as it is continually being added on to by the birds; and it varies with the site upon which it is built.

Nest sites

The commonest nest site of the sociable weaver over most of its range is the stout horizontal branch of an *Acacia giraffae* tree (Fig. 13). Other species of trees used as nest sites include *A. haematoxylon*, *Boscia albitrunca* (Fig. 14) and *Aloe dichotoma*. I have never seen exotic species of trees used by the weavers, although artificial sites such as telegraph poles (Fig. 15) and tankstands (Fig. 16) are frequently used. Both natural and artificial nest sites usually have two properties in common: (a) a stout horizontal, or nearly horizontal, supporting structure and (b) free access from below, unobstructed by small branches, leaves and twigs.

A leafy, vertically branching tree will not be used as a nest site by the sociable weaver. This is why *Acacia giraffae* is the most suitable nesting tree in the bird's range. An interesting variation of the usual type of site may be found where even an *A. giraffae* tree does not provide a suitable site: two nests (Nos. 1 and 5A) in the Nossob were built on drooping, leafy camelthorn branches (Fig. 17) which limited the size that the substructure could attain, and which were liable to break before the nest mass was large enough to contain more than 4 or 5 chambers. Telegraph poles also impose size limitations on nest masses because of limited surface area.

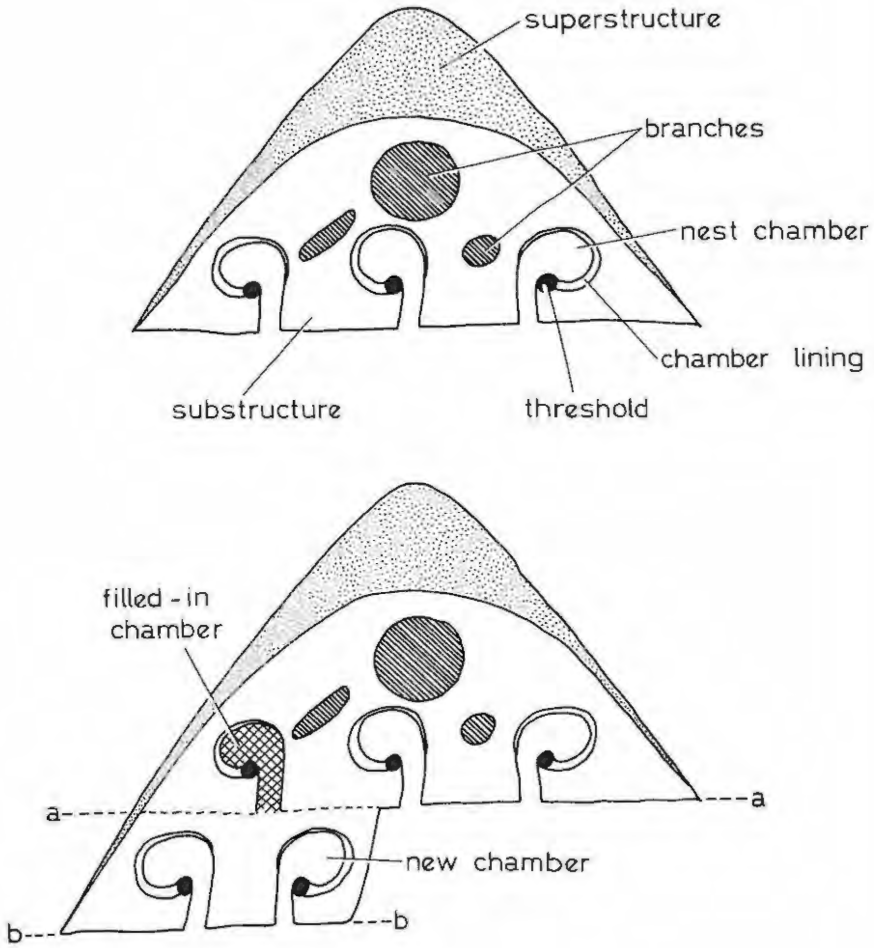

Fig. 12. Section through a mature sociable weaver nest mass (upper) and an old nest mass (lower) indicating the main structural features.

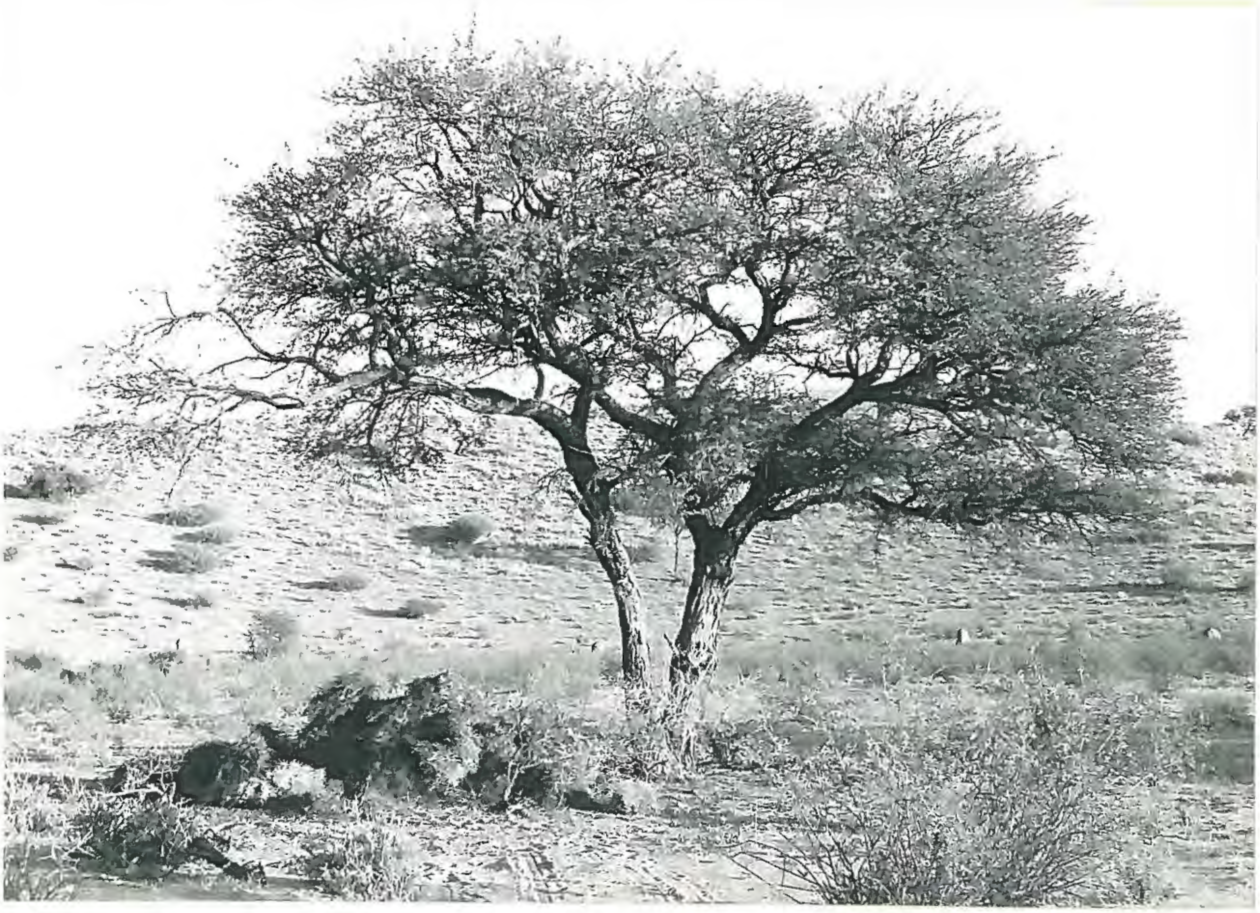

Fig. 13. A typical sociable weaver nest site: the horizontal branch to the left of the *Acacia giraffae* tree after removal of Nest B4.

Fig. 14. A low, abandoned nest mass of the sociable weaver in a Boscia albitrunca tree in the dunes. The field glasses hanging from the left hand part of the tree give an idea of the large size of the masses, the lowest of which are only 1.5 metres off the ground.

Fig. 15. A nest mass of the sociable weaver on a telegraph pole about 15 feet high, Loch Maree about 50 miles south of Twee Rivieren.

Fig. 16. A nest mass of the sociable weaver on a tankstand on the farm Straussennest between Aroab and Keetmanshoop, South West Africa. Note the small mass started between the upper triangular supports of the stand; this is the way in which the birds build on branches of Aloe dichotoma.

Fig. 17. Nest No. 1 in the Nossob River - an unsuitable site on a drooping *Acacia giraffae* branch.

Table 3 shows the different sites I have recorded in the Northern Cape and South West Africa and indicates clearly the weavers' preference for camelthorn trees as nesting sites. The height above the ground of nest masses varies from less than 5 feet (1.6 metres) to an estimated 50 feet (16 metres), but nests in the study area averaged about 17 feet (5.5 metres). Nest masses in *Boscia* trees were lower than those in *Acacia* trees, averaging around 7 feet above the ground. *Boscia* and *Acacia haematoxylon* are usually bushy in habit, providing inadequate access to potential nest sites from below; in the Molopo River between Kooppan Suid and Obobogorob where *A. haematoxylon* was more plentiful than *A. giraffae*, there were a number of new nest masses on telegraph poles right among the *A. haematoxylon* trees showing the importance to the birds of clear access below the nest. Several *A. haematoxylon* trees in this area had indeed been used and supported some very large nests whose size indicated that they must have been built before the telephone had been introduced into the Northern Cape.

Apart from support and clear access from below, a nest site should provide a means by which the initial straws can be firmly anchored when a nest mass is being started. The *Acacia* spp. have a rough bark into which straws can be inserted (Fig. 18). The larger branches of *Boscia albitrunca* are covered with numerous small vertical twigs which hold the grass in place. However

Fig. 18. Grass straws inserted into the bark of an *Acacia giraffae* tree by sociable weavers.

Aloe dichotoma and artificial sites provide little or no means of anchorage, so that nests started on these sites require a somewhat different building technique which will be described in the section on building methods.

Nest materials

The four structural regions of the nest mass (superstructure, substructure, thresholds and chamber lining) (Fig. 12) each require different building materials as well as different building techniques. Plant names are those of Leistner (1959a, b) with minor alterations.

(a) The substructure

The substructure comprises the main body of the nest and consists almost entirely of dry grass straws, mostly *Aristida ciliata*, a grass which occurs throughout the range of the sociable weaver. It is strong, thin and durable. Some *A. obtusa* (also a common grass in the sandveld) may be used, but it tends to be short and lacks the strength of *A. ciliata*. Straws are usually between 10 and 20 cm. in length, but at Camp Nest the birds were also using thin roots, some of which measured a metre in length, although this was unusual. The substructure of a large nest mass in the Molopo River consisted almost entirely of a dry dicotyledonous herb; the use of this plant instead of grass probably resulted from the overgrazing of the local grasses by domestic stock, as this area has been used for stock-farming for many years.

Table 3. Nest sites of the sociable weaver in the Upington and Keetmanshoop Districts of the Cape and South West Africa.

	Acacia giraffae	*Acacia haematoxylon*	*Aloe dichotoma*	Boscia *albitrunca*	telephone pole	tankstand
No. of colonies	120	26	4	16	6	3
Percentage	69	15	2	9	4	1

(b) The superstructure

The coarse material used in the superstructure consists mainly of sticks from woody plants (Table 4), usually *Acacia giraffae*. Collias & Collias (1964) also noted this and suggested that most of the superstructural material fell from the branches of the nest tree. That this is not the case is seen clearly in the fact that nests on telegraph poles also have a superstructure of sticks. A portion of superstructure from an occupied nest was analysed in order to determine the plant species used (Table 4). Only 51.5% of the sticks in this sample bore thorns, so there seems to be no selection by the birds for thorny sticks. The few grasses used in the superstructure are coarse species such as *Stipagrostis amabilis* and *Asthenatherum glaucum*.

(c) The chamber threshold

This rather specialized region of the nest requires flexible materials for its construction. Green grass stems are usually used, but after rain when green herbaceous plants are available, the weavers will also use these for the construction of the threshold; these plants include *Celosia linearis*, *Helichrysum argyrosphaerum* and *Tribulus zeyheri*. The grasses used include *Aristida ciliata* and *obtusa*, *Sporobolus parvulus*, *Eragrostis annulata* and *Schmidtia kalahariensis*. Certain colonies of weavers may use predominantly one or other of these plant species, depending on their availability.

(d) The chamber lining

The whole of the interior of the chamber is thickly lined with soft, dry materials. These include seed heads of grasses (particularly *Aristida* spp. which have silky flowers), the furry leaves of *Helichrysum argyrosphaerum*, shredded grass blades, an occasional feather and a variety of artificial fabrics when these are available, such as wool, cotton and woven pieces of cloth of either of these substances.

Collection of nest material

Building material may be collected by the weavers anywhere in the vicinity of the nest. Most of it seems to be collected within 100 yards of the nest tree, but when the birds return to the nest after a foraging expedition most of them bring back a straw, so that some grasses may come from as much as a mile from the nest (Fig. 41). Nest lining may have to be collected some distance from the nest, depending on the season. After rain there is usually plenty of soft material in the form of grass inflorescences, but during a drought the birds have to look further afield.

Much of the collection of materials at an old nest is done right under the nest itself where fallen straws and sticks accumulate. Any part of the nest mass which falls to the ground

Table 4. Plant materials used in the superstructure of the nest mass of the sociable weaver in the Nossob River. Plants marked (*) possess thorns.

PLANT SPECIES	NO. OF PIECES	PERCENTAGE OF TOTAL
Acacia giraffae*	523	43.0
Geigeria pectidea	125	10.3
Rhigozum trichotomum	110	9.0
Monechma australe	100	8.2
Stipagrostis amabilis	77	6.3
Argemone mexicana	70	5.8
Aptosimum marlothii*	52	4.3
Lycium spp.*	37	3.0
Acacia detinens*	6)	1.2
Acacia haematoxylon*	6)	
Acacia hebeclada*	3)	
Other spp.	108	6.3
TOTALS	1217	100.0

is collected straw by straw and built into some other part of the nest mass. In this way, substructural materials are retrieved very quickly, but superstructural materials (which are usually collected at a slower rate anyway) take longer to retrieve.

The birds appear to exercise some selection in the collection of straws, since they may pick up and discard several pieces before finally carrying one up to the nest mass. When a bird's building drive is at a low intensity it may drop a straw which it has carried up to the tree, before it builds it into the nest mass. There is much variation in the building drives of individual birds in a colony, some birds building infrequently, others doing so almost continually. For instance the most ardent builder at Camp Nest was bird No. 93 which once collected 6 straws (and built them in) in the space of two minutes.

Straws are always carried one at a time by one end. If there is still part of the inflorescence attached to a straw, it is carried by the lower end (Fig. 19). Straws are picked up as loose pieces of grass from the ground; I have never seen a bird nip off a straw either during collecting or building as noted by Collias & Collias (1964).

The collection of chamber lining materials is rather different from the collection of straws. A bird gathers pieces of soft material until it has a billful in the form of a wad, which is carried to the nest. After building the wad into the chamber, the bird emerges and wipes its bill on a branch in the same way it does after feeding young. The artificial fabrics collected near human habitations may prove a hazard to the weavers as the following observations show:

25 November 1964 - Bird No. 35 was found with one wing caught in a loop of thin string which had been built into a chamber. The bird hung in the tunnel entrance by the trapped wing, fluttering intermittently and pecking at one of the plastic rings on its leg. It finally fluttered free and flew to a perch, apparently unharmed.

16 January 1965 - An unringed bird brought a billful of cotton waste to the nest, but before it could fly into a chamber, it got tangled up in the threads of cotton around its body and head. It freed itself by preening and scratching.

25 February 1965 - Bird No. 28 was heard fluttering in the entrance to its nest chamber. I freed it and found that it had one toe firmly entangled with a piece of red thread in the chamber lining. The bird soon recovered after its release.

22 May 1965 - Three juvenile birds, the offspring of Bird No. 28, were all caught up by their feet in a tangle of string in the nest chamber (the same chamber as their parent had been caught in previously). The string was hanging from the chamber roof. The birds flew off unharmed on being released.

Fig. 19. A sociable weaver carrying a straw in the typical manner of the species (drawn from a photograph).

Material for the superstructure may also be collected around and under the nest tree, but much of it consists of plants which do not grow in the river beds or dunes where the weavers' nests are. For instance *Monechma australe* and *Aptosimum marlothii* are confined to the calcrete, while *Rhigozum trichotomum* and *Acacia detinens*, which grow mainly in the dunes, are often found on top of nests in the rivers. As in the case of grass straws, sticks for the superstructure are carried by one end.

Building methods

Most of the nest materials used by the sociable weaver are dry and non-pliable and cannot be woven in any way. Instead they are just pushed into place. Holding a straw by one end, the bird inserts the short end into the nest mass; then with a sideways shaking of the head, at the same time moving the bill along the straw towards its free end, the bird works the straw into the nest mass until it is firmly held in place by friction alone. The chamber lining material is also simply pushed into the floor, roof and sides of the chamber. The sticks in the superstructure are usually laid on top of the nest mass with a minimal amount of wedging movement on the part of the bird. The irregularities (twigs, thorns) on the sticks cause them to hold the mass together until the superstructure becomes a consolidated roof.

The technique of forming the threshold is only slightly different from that of building with dry straws. The bird perches in the partly built chamber facing outwards, and inserts the short end of the flexible piece of material into one side of the chamber near the floor. It then perches on the building material to bend it into the shape of the threshold and inserts the free end into the other side of the chamber near the floor. In this way a downward-curving bow of straws or herbs is formed. When these green materials dry, the threshold becomes a strong step at the chamber entrance.

Construction of nest chambers

For the sake of simplicity it is easier to describe the formation of a new chamber in an already established nest mass. Chambers are formed as part of the substructure as building progresses and are not excavated as suggested by Roberts (1940) and by Mackworth-Praed & Grant (1963). Starting at the periphery of the substructure or at a slight depression on the side of the substructure, the birds insert straws at a downward and outward facing angle to form an arched overhang below which the threshold and floor of the chamber are begun as the overhang grows. This is stage 1 of the chamber construction (Fig. 20 : 1).

Straws are added to the roof and walls. Pliable materials are used in the threshold, which grows outwards and upwards to form the basin-shaped floor of the chamber. The first lining material

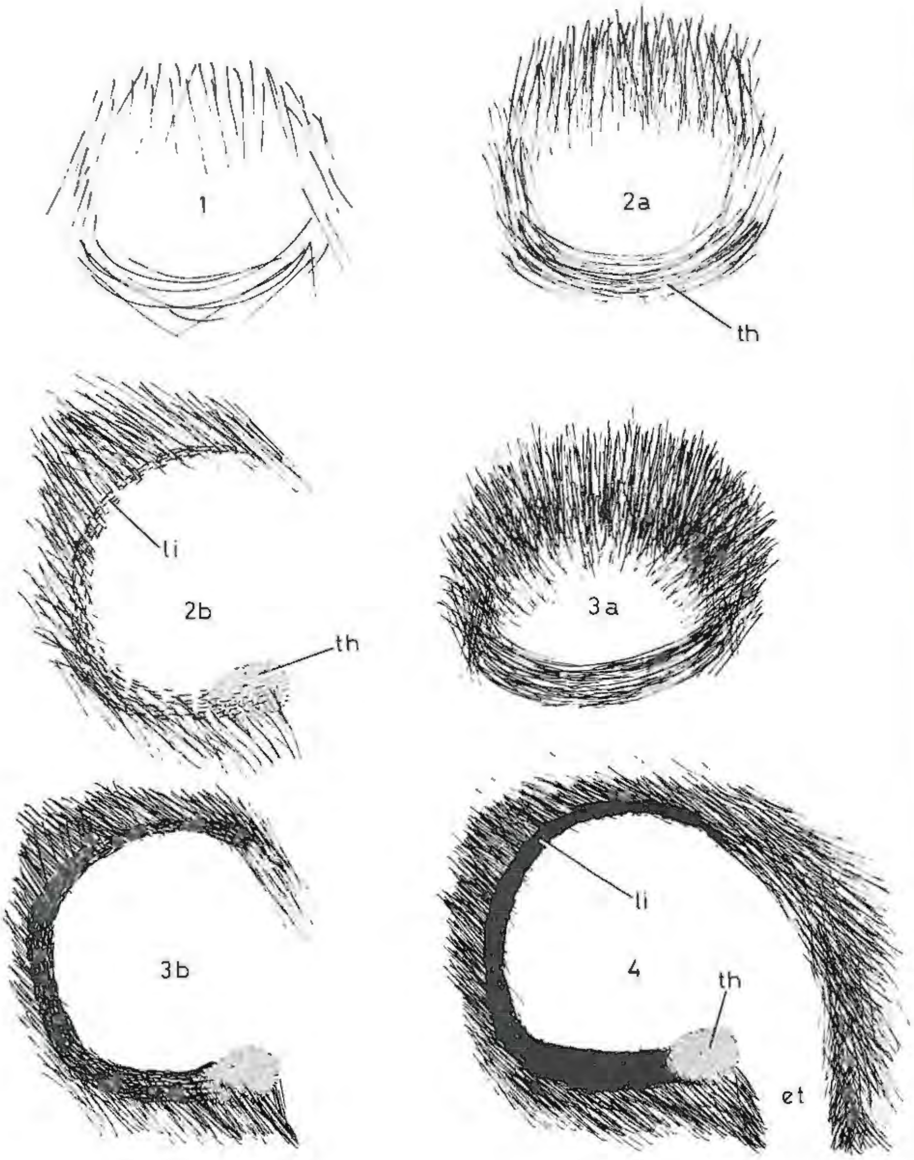

Fig. 20. The four stages in the construction of a nest chamber. Diagrams 1, 2a and 3a are seen in face view; 2b, 3b and 4 are in sagittal section.

is added. This is stage 2 (Fig. 20:2a, b). As the chamber grows, straws are added all around it and around any neighbouring chambers that are being built, so that they become enclosed and supported by a matrix of grass. The threshold materials slowly dry and harden to form a firm perch on which the birds building the chamber can now stand to build the roof and walls which grow downwards and forwards over the entrance of the chamber. This brings construction to stage 3 (Fig. 20:3a, b). By the end of stage 3 the chamber itself is virtually complete with a lining up to 10 cm. thick in the floor and about 3 cm. thick in the roof and can be used for breeding purposes if necessary.

The addition of the entrance tunnel, built entirely of dry straws, brings the chamber to stage 4 (Fig. 20:4). The straws are orientated inwards and downwards in the cavity of the tunnel. Stage 4 continues for the rest of the life of the chamber, although the tunnel grows slowly in length until it measures some 20 to 25 cm. after which it grows little, if at all. All further construction on the chamber is in the form of maintenance, especially of the entrance.

The end result, then, is a rounded chamber of dry straws in the roof and walls, green straws in the floor and threshold and an insulating layer of dry, soft material all around, leading via a vertical tunnel to the outside.

The start of a nest mass

The laying of the foundation of the nest mass varies slightly with the site chosen. Contrary to the statement by McLachlan & Liversidge (1957), the nest foundation is begun with straws and not with sticks or twigs. The first straws are either wedged into the rough bark (of *Acacia* trees) or between the upright twigs of a *Boscia* branch, but on a smooth site like an *Aloe dichotoma* or a telegraph pole or tankstand, the first straws are simply laid on the surface of the site. In the latter case, as might be expected, much of the initial material falls to the ground, especially in windy weather, when it is all but impossible to start a nest at all on such a site.

I have observed several attempts to start nests on telegraph poles in windy weather; there was usually a heap of fallen straws at the foot of the pole and only a few insecure straws on the pole itself. However, by continued effort, sufficient grass eventually accumulates to form the beginnings of a foundation and further construction can continue.

Aloe dichotoma is a rather more suitable site than a telegraph pole, since the forks formed by the bases of the branches close to the trunk can be filled in with straws for the nest foundation. Sometimes an artificial site may provide a few places into which straws can be wedged, e.g. the metal bracket of the telegraph pole cross-bar, or the spaces between the wires and the insulation cups. This latter is one of the most frequently used parts of the telegraph pole for starting a nest, particularly in the case of the thin metal poles sometimes found in the country north of Upington. Even so, there is still much trial and error involved in starting a nest foundation on an artificial site.

The laying of a nest foundation on a tankstand is again a simple process of placing enough straws on the flat surface of the platform supporting the tank, until the mass of straws becomes consolidated enough by its own weight to allow the birds to build on further.

The first few straws of a nest foundation are inserted into any crevices and other points of insertion that the site may offer. As construction progresses the foundation assumes a conical or pyramidal shape (Fig. 21 A) with the visible straws arranged at a downward and outward facing angle. The case of a nest on a tankstand is rather unusual. Initially only one corner of the platform is used (Fig. 21 B) but the nest mass gradually spreads all around the periphery of the platform and begins to hang over the edge, at which stage the chambers can be constructed (Fig. 16). With the construction of the first chambers in a new foundation, a young nest mass is formed.

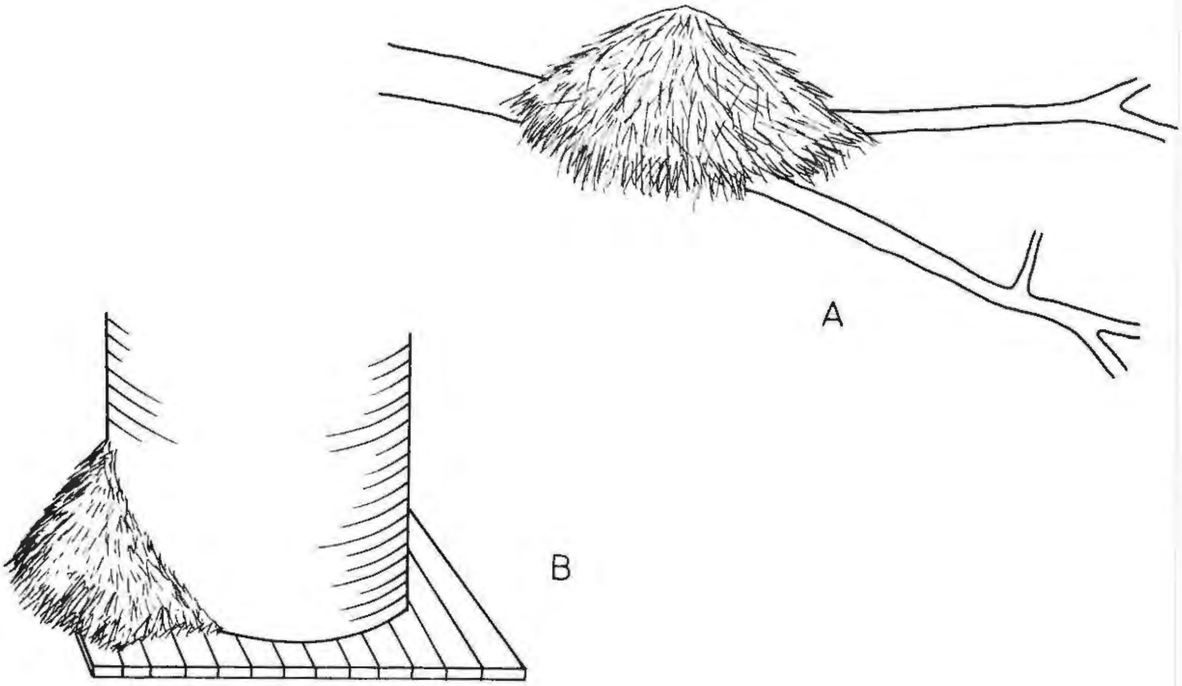

Fig. 21. The conical stage of nest foundations on (A) a horizontal branch and (B) a tankstand (cf. Fig. 16.)

Growth of the nest mass

The terms "young", "mature" and "old" used in the account which follows are relative only to the stage of the construction of the nest mass and not to its actual age, although in some cases the two may be synonymous. The meanings of these terms should become clear as the stages are outlined.

A young nest is one in which the first few chambers have been built. From this stage onwards, the nest mass grows in size as long as the nest site permits. On a fairly typical site consisting of a single, unbranched, horizontal limb of a tree such as that in Fig. 13, the nest mass grows in both directions up to the trunk of the tree on the one hand and to the tip of the branch on the other. Growth toward the tip of the branch continues until it becomes too thin to provide adequate support. During the process of growth of the nest mass, the birds begin to vary the materials they bring, in that they will now bring coarser materials for the superstructure which has hitherto consisted only of grass straws. More and more substructural construction is devoted to maintenance of the substructural matrix and of the chambers already formed, so that growth of the nest mass slows down as it gets larger.

Eventually a stage is reached where the nest mass occupies the maximal available space on the nest site; the superstructure is consolidated and consists mainly of sticks and twigs; and the substructure contains the maximal number of chambers which the site permits. The nest mass is now <u>mature</u> and usually consists of a single level of chambers (Fig. 12), unless the site is irregular in which case more than one structural level of chambers may result. This stage may last for a number of years and would remain thus if the birds confined their building drive to maintenance of the existing structure only. However, the building drive of the sociable weaver appears to be in excess of that required for mere maintenance, so that the nest mass is added on to.

The inhabitants of a mature nest have the curious habit every now and then of filling in one or more chambers (even though these may appear perfectly serviceable) with straws. Once the chambers have been filled to the tunnel entrances, the birds begin to build one or more new chambers below them. This usually happens only in one area of the substructure and results in the formation of two levels of chambers (Fig. 12). The process of filling in old chambers and adding on new chambers continues as long as the nest mass lasts. One nest in the Molopo River was 4 metres deep as a result of such additions, but this is exceptional. The substructure usually collapses under its own weight before such a depth is reached; in such an event the weavers merely retrieve the collapsed material straw by straw and rebuild the substructure. The branch supporting such a large nest may break under its weight, in which case the birds are forced to move.

A nest mass consisting of more than one layer of chambers (including those that have been filled in) is old. Most of the Philetairus nest masses in the Nossob study area are old. This term may apply to the actual age of the nest mass if the site allows much lateral growth. The dimensions of substantial old nests have been given by Friedmann (1930a), Rudebeck (1956) and Collias (1965). The largest nests recorded by Rudebeck had a long diameter of over 7 metres; the longest nest mass I have measured was 7.2 metres in length (Fig. 22). Further dimensions appear in Table 5.

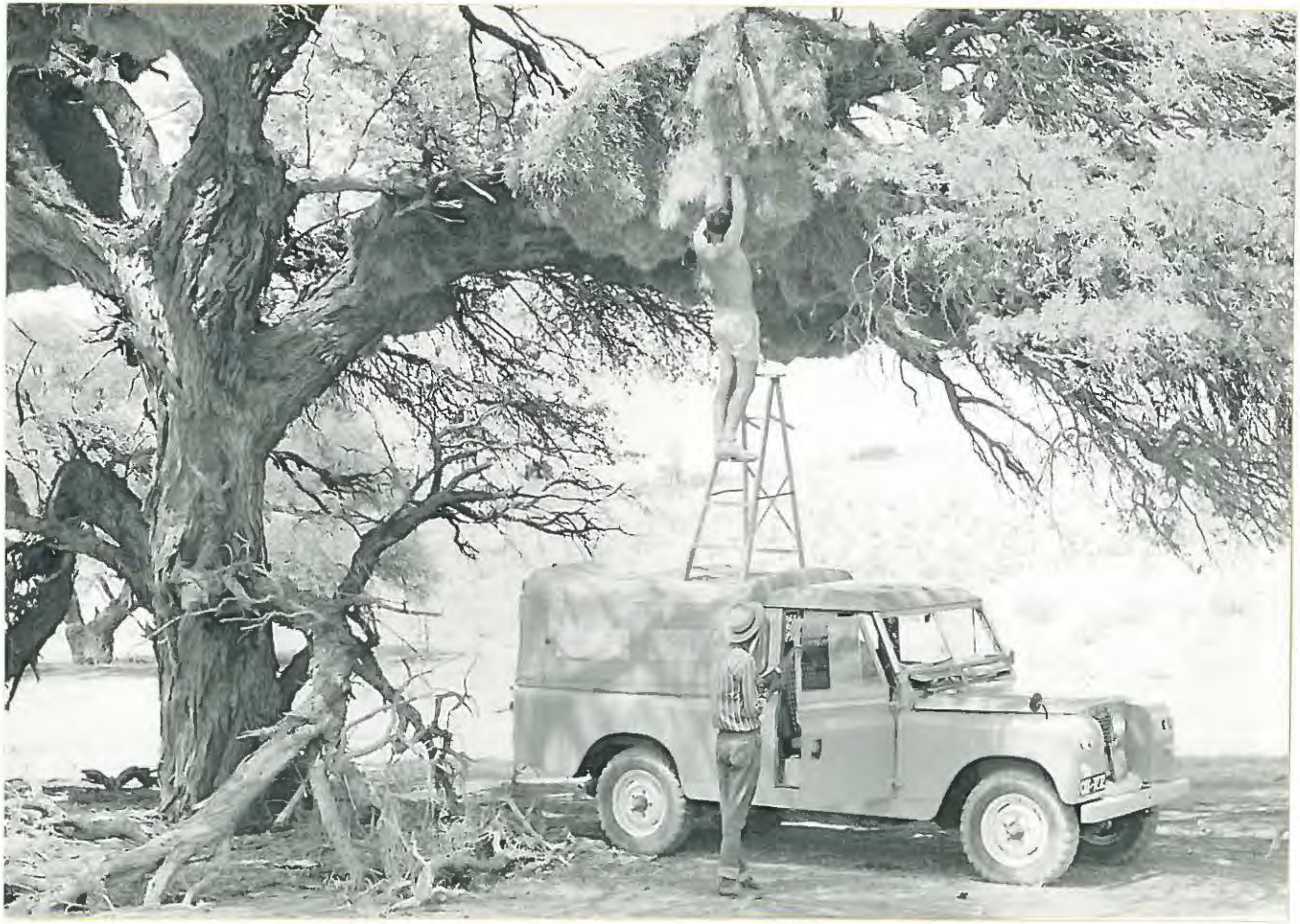

Fig. 22. Examining Nest 24E. Nest 24W in the background is the largest nest mass in the study area (see Table 5).

Table 5. Dimensions in metres of some nest masses in the study area.

NEST MASS	LENGTH	MAXIMAL DEPTH	NO. OF CHAMBERS
16E	2.4	1.5	16
17E	3.8	1.4	26
22	7.2	1.4	?
24E	2.1	1.6	40
24W	3.9	1.5	50
B5	1.5	1.2	11
B7	2.7	2.4	14

A further feature of old nest masses in the same tree is that their superstructures fuse as they are added on to by the birds. The substructures remain separate, however, as in the case of Camp Nest (Fig. 23) in which South and West masses are on branches on opposite sides of the main tree trunk; their superstructures have fused across the main fork, but their substructures are completely separated by the trunk.

The colony in relation to nest construction

The laying of the nest foundation and the construction of chambers is done cooperatively by all the members of a new colony of weavers. There seems to be no division of labour, but one bird usually concentrates on one particular chamber and on the substructural matrix immediately around this chamber. In this way the bird becomes restricted in its activities to a small area of the nest mass.

This restriction to a particular chamber was clearly illustrated by the aviary birds. At first, when no nest had been provided in the tree, the birds chose the highest point in the aviary in which to start a nest mass. This was in the northwestern corner of the cage itself. All the birds cooperated in building a chamber, wedging the first few straws into the wire netting and between the wire and the pipe framework. The site was such that not more than one chamber could be built, but all the birds worked together on it. However, when a nest was suspended in the tree, the birds began to fly in and out of the chambers in the mass, seemingly at random. After a few days, each bird had restricted its building activities to one or two chambers. In this way, maintenance of the nest mass was evenly distributed.

At first the aviary nest mass contained only 5 chambers. this meant a distribution of 4 or 5 birds per chamber. After 42 days, two new chambers had been added and two more had been started, but a number of different birds worked on these new chambers. There were finally 13 chambers in the nest mass, after which no new ones were added as the birds began to breed.

During the breeding period only the pair maintains the chamber. Outside the breeding season when the pair is no longer a social unit, more than two birds may build and maintain one chamber. I have seen up to four birds building one chamber, and sometimes there would be three birds in the chamber at one time. However, one bird may visit only those chambers within its own structural level (see Chapter 4). Any bird in the colony may build on to the superstructure at any part of the nest mass, since there is no division of the superstructure into structural or social regions. The superstructure is built on to at all times of the year.

Fig. 23. Camp Nest seen from the south west (cf. Fig. 25).

Nest maintenance and building drive

All the members of a colony build continually, even though some may build more than others. Young birds show signs of a building drive at the age of 80 days. This drive increases until it is so strong in adult sociable weavers that they build at all times except when resting, feeding or attending to eggs or chicks. This building activity continues throughout the year at a more or less steady rate, increasing only during a breeding period when nest chambers are re-lined and entrance tunnels are lengthened and narrowed by the addition of more straws.

The only structural region of the nest which is never added to after its completion is the chamber threshold. Since it becomes a single firm structure after it dries, it does not easily disintegrate as would the rest of the nest mass if it were not for nest maintenance, and it may last for years after the nest mass has collapsed (except that it is usually eaten by antelopes or harvester termites if it falls to the ground). (Fig. 24).

The continuous building activity not only keeps the nest in good repair but also increases the size of the nest mass. Few chambers are added to a mature or old nest mass outside a breeding season, because the population is either stable or declining. This was clearly illustrated in the aviary when the birds ceased to build new chambers (unless existing ones collapsed) when the

Fig. 24. The detached threshold of a nest chamber showing how the straws are moulded into a bow-shape; note how the matrix straws are straight and simply inserted into the mass of grass.

number of chambers (13) allowed a ratio of roughly two birds per chamber. Unfortunately the captive weavers were not successful in raising any chicks, but at other nest masses in the field, during and immediately after a breeding period, new chambers were added where necessary as the population grew. At a large nest mass such as No. 24W (Fig. 22) in which there were a number of unoccupied chambers because of a low population level before the breeding period, there was no addition of new chambers, but rather a progressive occupation of the existing empty ones.

However, the number of chambers in an old nest mass does not change markedly at any time, for the following reasons:

(a) an old nest mass has usually reached its maximal size so the addition of new chambers is impossible;

(b) existing chambers are continually falling out due to structural weaknesses or the agency of predators, so the construction of new chambers is a process of replacement rather than addition;

(c) as long as juveniles are being fed by their parents or are helping to feed the young of subsequent broods, they usually roost with their parents in the breeding chambers. There is no foundation in the statement by Smith (1849) that roosting chambers are not used for breeding purposes;

existing chambers are used for breeding purposes as soon as adequate rains fall. The only time a new chamber is built for breeding purposes is when an existing chamber collapses or is pulled out; the breeding chamber is then used as a normal roosting chamber at the end of the breeding period.

Maintenance of the interior of a chamber consists mainly in the addition of soft lining materials as the old lining becomes compressed and matted with use. One interesting incident in this respect may be mentioned here: one day at Camp Nest a bird brought a billful of nest lining out of a chamber, shook it vigorously, emitting a cloud of dust, and then took the material back into the chamber. This seems to be a type of "nest sanitation" but it is probably not commonly employed.

The superstructure requires little maintenance, but is continually being added on to. If, however, it does begin to collapse, any holes or cavities are filled in by the weavers. This is probably the result of an endogenous drive to fill in cavities, but it serves the useful function of keeping owls and other potentially dangerous animals from occupying the cavities. A pair of barn owls *Tyto alba* moved into a large cavity in the superstructure of nest No. 16 and attempted to breed there. The weavers were unable to fill in the cavity as long as the owls were in occupation, but they did so as soon as the owls left. In the case of the giant eagle-owl Bubo lacteus which nests on the flattened top of the superstructure, the weavers appear not to object and do not necessarily fill in the depression after the owls have left.

Not all building activity results in the addition of material to the nest mass, and may in fact have the opposite effect. For instance, a weaver may remove a stick from the superstructure, mouth it briefly and drop it to the ground. A bird in a conflict situation (such as an individual from one nest mass attempting to establish itself in another one where the original occupants make it unwelcome) will repeatedly drop straws that it has collected. Bird No. 285 did this shortly after it arrived at Camp Nest from nest No. 5. These two instances are probably displacement activities and there is a considerable amount of "displacement building" going on all the time at a sociable weaver nest. Displacement building is almost certainly indicative of a low building drive, but the fact that the birds build at all at such times is in turn an indication that the building drive is strong. Some building-directed activity not resulting in the addition of material may, however, serve a useful function, such as when a bird pushes straws deeper into the nest mass, re-arranges a stick, or merely "fiddles" with the nest material by shaking it without dislodging it or re-arranging it in any way, in that it probably consolidates the structure.

The strength of the building drive is further shown by the reaction of birds to falling nest materials. Twice when a bird was on the ground below Camp Nest collecting straws, a single straw fell from the nest mass above; the bird immediately pounced on the fallen straw, carried it up to the nest mass and built it in. Similarly a bird perched in the tree will immediately retrieve a straw which it sees falling from the nest mass. The effect on the birds of a falling piece of substructure is even more dramatic. This happened once at Camp Nest. Several birds uttered alarm notes and flew to the ground to start retrieving the fallen material, one straw at a time. At nest No. 19 I removed part of a chamber and left it on the ground, whereupon a number of weavers descended to collect the material.

Effects of nest damage

The weavers' reaction to fallen material shows a tendency to reconstruct a damaged nest mass. This does not usually consist in rebuilding the damaged portion to restore it to its original appearance, although such a damaged portion will be restored in time. Damaged chambers are seldom rebuilt unless the birds are breeding. The material of two chambers removed experimentally from Camp Nest was used again by the birds, but the chambers were never rebuilt. If, however, the damage to a nest is extensive, as when bad weather or a predator destroys almost all the chambers in one nest mass (this happened to nest Nos. B2 and B5), the birds rapidly rebuild the whole structure, using the original materials augmented with new materials. In the case of total destruction (as at B4), the birds abandoned the site and built elsewhere.

Damage to the superstructure is infrequent and is usually the result of subsidence. As I have mentioned, any cavities resulting from subsidence are filled in by the weavers.

A partly damaged chamber is quickly rebuilt during a breeding period, but at other times it may never be rebuilt, even though some of the weavers may investigate it from time to time. It is of interest to note that such a partly damaged chamber in the aviary nest mass was never rebuilt even when accommodation was short; the birds built new chambers instead of renovating the old one. The selective advantage of this behaviour is probably to ensure the building of secure chambers and to preclude the use of a chamber which has previously been weakened by structural damage, since rebuilt chambers are never as strong as new ones.

Effect of nest masses on trees

All except two of the 53 separate nest masses in the Nossob study area were on living branches; one of the exceptions (at No. 15) was on the dead branch of a living tree, the other in a completely dead tree (No. 21). There were a few nest masses in the

Kalahari outside the study area which were also in dead trees, but by far the greater majority were in living trees. The question arises as to whether the presence of the nest can kill a tree or the branch on which it is built. Some sociable weaver nests in the western Transvaal are reported to be 100 or more years old (Friedmann 1930a; Collias 1965) and many of the Kalahari nest masses were surely at least as old as this, and yet the trees suffered no ill effects. Nests in dead trees were probably built there after the death of the tree, or else the tree died from other causes after the nest had been built.

A nest mass does not often become so heavy by the addition of material that the supporting branch breaks. The weight of the nest mass alone is seldom enough to break the branch without the aid of a strong wind, even if the branch is dead, since the wood of _Acacia giraffae_ is extremely tough when dry. The nest mass on the dead branch at No. 15 appeared to be of considerable age, and its supporting branch must have been dead for years, but it did not collapse until a violent gale snapped the branch.

Generally, the effect of a nest mass on a tree is negligibly small. This is to be expected. It is unlikely that this remarkable structure could have been evolved to its present state in which selection is for size, if it had had a widely adverse effect on the best available sites.

The internal environment of the nest

The nest is a living area. It is occupied by the birds at any time of the day and at all times of the year, both in and out of the breeding periods, by both old and young birds. It provides shade during the heat of the day in summer, and insulation against the cold in winter; it is waterproof and inaccessible to most predators. The question arises as to how much the internal environment of the nest chambers differs from that of the ambient environment, and if it does differ, whether or not the difference is large enough to be of advantage to the birds.

The results of the wet and dry bulb readings of ambient air and air in the nest chambers as determined with the Atkins psychrometer appear in Tables 6 and 7. When subjected to a *t* test, the difference between ambient air temperature and nest chamber air temperatures was found not to be significant ($P = > 0.2$). The relative humidities in the chambers were higher than the relative humidity of the ambient air at temperatures of less than 26.7°C, this difference being highly significant ($P = \ll 0.001$), but differences between the relative humidities of chambers and ambient air were not significant at ambient temperatures greater than 26.7°C ($P = > 0.05$). Thus at higher temperatures there is no significant difference between the environmental conditions with regard to temperature and relative humidity in the nest mass

Table 6. Ambient (Ta) and nest chamber (Tn) temperatures (°C), wet bulb depression (Ta - Ta'; Tn - Tn') and % relative humidities (RHa and RHn) at Ta < 26.7°C.

DATE	TIME OF DAY	AMBIENT			NEST		
		Ta	Ta - Ta'	RHa	Tn	Tn - Tn'	RHn
23.2.66	0630	11.4	5.6	40	11.4	5.6	40
23.2.66	0630	11.4	5.6	40	11.6	5.6	41
23.2.66	0630	11.4	5.6	40	11.6	5.6	41
23.2.66	0630	11.4	5.6	40	12.2	6.4	35
23.2.66	0630	11.4	5.6	40	12.8	6.7	33
19.2.66	0700	18.1	5.6	52	20.0	7.5	40
19.2.66	0700	18.6	5.8	51	20.8	7.8	40
23.1.66	1700	18.6	1.4	87	21.7	4.2	66
7.2.66	0645	18.9	0.3	97	21.7	2.2	81
19.2.66	0700	18.9	5.8	51	22.2	9.5	31
23.1.66	0645	19.2	1.7	83	20.8	3.6	70
23.1.66	0645	19.2	1.7	83	22.2	4.5	65
23.1.66	0645	19.2	1.4	87	23.1	5.0	61
19.2.66	0700	19.4	6.1	49	21.1	8.1	38
7.2.66	0645	19.4	0.3	97	22.5	3.3	71

23.1.66	0645	19.4	1.7	85	22.5	4.7	63
19.2.66	0700	19.7	6.4	47	20.3	6.4	48
7.2.66	0645	19.7	0.6	95	21.7	2.0	84
24.1.66	0630	20.6	2.0	83	24.2	5.8	56
24.1.66	0630	20.8	2.2	81	24.7	6.4	54
8.2.66	0645	21.4	2.8	77	25.0	5.8	57
8.2.66	0645	21.4	2.8	77	23.3	4.5	65
8.2.66	0645	21.9	2.8	77	23.9	5.0	62
1.2.66	0700	24.2	5.0	62	26.1	6.7	53
1.2.66	0700	24.2	4.7	64	25.8	6.1	57
1.2.66	0700	24.2	4.5	66	27.8	8.3	45
1.2.66	0720	24.4	4.7	64	29.4	7.0	57
22.1.66	1700	25.0	7.2	48	26.1	7.8	46
1.2.66	0720	25.3	5.3	61	25.8	5.8	58
24.1.66	1045	25.6	5.6	60	26.1	6.1	57
22.1.66	1700	25.6	7.8	46	26.7	8.1	45
22.1.66	1700	25.6	7.5	47	27.8	8.9	42
22.1.66	1700	26.1	7.8	46	26.7	8.3	44
22.1.66	1700	26.4	8.3	44	26.1	7.8	46
23.2.66	1245	26.4	12.2	23	26.4	12.2	23
MEANS		20.4		63	22.3		52

Table 7. Data as for Table 6 at ambient temperatures (°C) of >26.7°C.

DATE	TIME OF DAY	AMBIENT			NEST		
		Ta	Ta - Ta'	RHa	Tn	Tn - Tn'	RHn
24.1.66	1045	26.7	6.7	54	26.1	5.6	60
23.2.66	1245	26.9	12.8	20	25.8	11.7	25
23.2.66	1245	27.2	12.8	21	26.9	12.8	20
23.2.66	1245	27.2	12.8	21	26.7	12.5	23
23.2.66	1245	27.2	12.5	22	26.7	12.0	23
1.2.66	1015	27.2	7.2	51	28.6	8.3	46
1.2.66	1015	27.5	7.5	51	28.9	8.6	44
1.2.66	1015	28.1	7.8	48	28.9	8.6	43
11.2.66	1700	28.1	11.4	28	28.9	12.0	27
11.2.66	1700	28.1	11.1	30	29.2	12.2	26
11.2.66	1700	28.1	11.1	30	29.7	12.2	28
11.2.66	1700	28.1	11.4	28	28.9	12.0	27
5.4.66	1615	28.3	12.2	26	28.9	12.8	24
5.4.66	1615	28.3	12.0	29	28.9	12.2	26
20.1.66	p.m.	28.3	6.7	56	28.1	6.1	58
24.1.66	1210	28.3	8.9	43	27.8	7.8	48
24.1.66	1210	28.6	8.9	43	28.6	8.6	43
11.2.66	1700	28.6	11.7	29	31.1	13.1	26
5.4.66	1615	28.6	12.2	26	28.3	10.8	31
5.4.66	1615	28.6	12.2	26	29.2	10.3	35
5.4.66	1615	28.9	12.5	25	29.2	11.4	30
20.1.66	p.m.	28.9	7.8	49	27.2	6.1	58
24.1.66	1240	28.9	9.5	40	29.2	9.2	40

24.1.66	1240	28.9	9.2	40	30.0	9.7	42
24.1.66	1210	29.2	9.2	40	28.6	8.6	43
1.2.66	1130	29.4	9.5	41	33.3	11.7	35
1.2.66	1130	29.7	9.5	42	32.1	10.8	38
1.2.66	1130	30.0	9.7	40	32.5	11.1	36
23.1.66	1630	30.0	13.3	23	30.3	12.8	26
25.1.66	1100	30.0	10.0	39	32.8	11.7	35
1.2.66	1330	30.0	10.6	36	30.8	10.3	37
23.1.66	1630	30.3	13.1	23	32.1	13.9	24
7.2.66	1645	30.3	12.5	26	32.5	13.3	26
23.1.66	1630	30.6	13.6	23	30.6	12.8	26
23.1.66	1630	30.6	13.3	23	29.7	12.2	28
7.2.66	1645	30.6	12.5	27	32.5	13.3	26
7.2.66	1645	30.6	12.2	29	30.6	12.2	26
7.2.66	1645	30.6	13.1	26	30.6	11.7	31
24.1.66	1400	30.8	11.1	35	32.1	12.0	31
24.1.66	1400	30.8	11.1	35	30.8	10.8	35
1.2.66	1330	30.8	10.8	37	32.5	11.4	35
1.2.66	1330	30.8	11.1	35	34.4	13.1	30
7.2.66	1645	30.8	12.0	32	30.6	12.0	28
23.1.66	1630	31.1	13.6	22	31.7	14.5	22
25.1.66	1100	31.1	10.8	36	31.7	11.4	35
25.1.66	1100	31.1	10.6	37	30.3	10.0	39
25.1.66	1100	31.4	11.1	35	31.7	11.1	35
25.1.66	1100	31.4	10.8	35	32.1	11.7	34
24.1.66	1400	31.7	11.7	33	28.9	8.9	43
24.1.66	1400	31.9	12.0	31	32.1	11.7	34
24.1.66	1400	33.3	12.8	30	32.5	12.2	31
MEANS		29.5		33	30.0		34

and in the shade of the tree around the nest, except that there is less radiation inside the chambers than outside. The difference between chamber and ambient relative humidities at lower ambient temperatures is due to the higher temperatures in the chambers than outside, which in turn is caused by the presence of the birds in the chambers.

Chapter 4

SOCIAL ORGANIZATION

Most of the studies on social organization in the sociable weaver were done at Camp Nest which was an old nest mass consisting of a number of structural levels (Fig. 25) in two main nest masses. The Southern mass contained 5 levels: Upper Middle (UM), Lower Middle (LM), South Central (SC), South East (SE), and South West (SW). The Western mass contained 3 levels: Middle West (MW), Upper West (UW) and Lower West (LW). At any given time, it is the rule that the birds living and breeding in one of these levels do not attempt (nor are they permitted by their neighbours) to enter a chamber in another level, even in the same nest mass. I have already mentioned, however, that any bird may build on any part of the superstructure which appears to constitute a neutral area where all birds may come and go without eliciting any reaction from each other. But as soon as a bird from, say, LM attempts to land on the substructure of SC, even if it does not try to enter a chamber, it will be chased off at once by a resident of SC.

Thus a sociable weaver <u>in its own level</u> is dominant to any other weaver from another level. There are a very few exceptions to this rule. One noteworthy exception was bird No. 12 which was resident in SW and of a particularly aggressive nature; this bird could move with impunity to any level throughout the colony, even to the Western nest mass, and all other birds gave way before it. It frequently chased other birds, not only from SW but from other levels as well.

Not only are the birds usually confined to one level, but they are extremely faithful to their own levels from one season to the next. Any changes in level occupation occur usually at the beginning of a breeding period and probably involve females which have become mated with males from another level than their own (see Chapter 5). When this occurs, there is no apparent aggression towards the "foreign" birds from the original inhabitants of the level to which they have moved; this is rather comparable to the situation with the jackdaw peck order as described by Lorenz (1952).

When a portion of nest mass collapses, as did SW level at Camp Nest in October 1965, the inhabitants of that portion move to the nearest intact level where they immediately begin to build new chambers, or take over any old and unoccupied chambers. In this case again there is no aggression shown towards the newcomers by the original inhabitants, but the reason for the acceptance of these birds is obscure. A similar situation obtained at nest No. 15 in December 1964 after the nest mass on the dead branch collapsed after a night of gale force winds; the inhabitants of

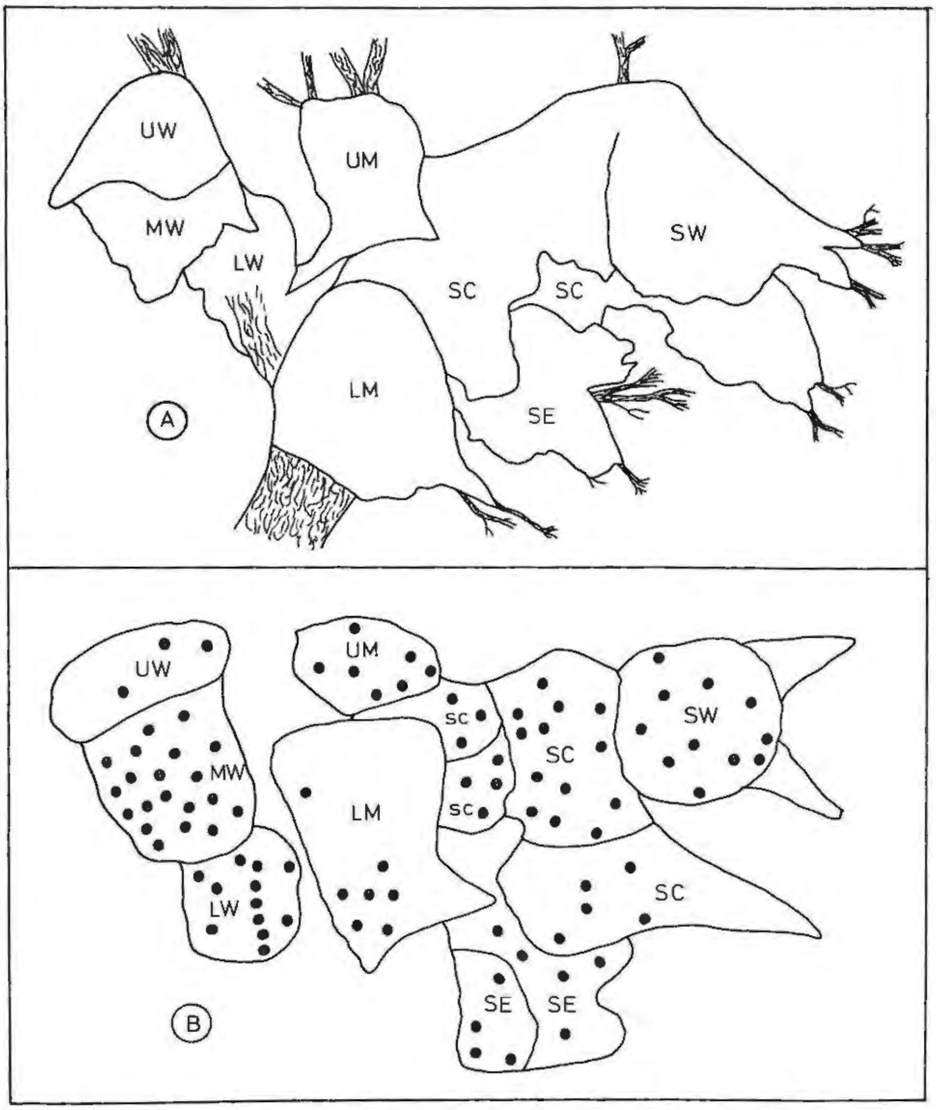

Fig. 25. A. The portions and levels of Camp Nest drawn from Fig. 23.

B. The lower surface of Camp Nest showing the positions of the chambers in each level. See text for an explanation of the lettering.

the collapsed mass apparently moved to the one mass that remained, since it was crowded with birds the day after the gale. Many of the birds were building new chambers on the sides of the remaining nest mass. Unfortunately none of the birds of this colony was ringed, so it was impossible to be sure about this.

The effect of the collapse of an entire nest mass on a whole colony was tested experimentally. The area chosen for the experiment included the Botswana colonies at nests B4, B5 and B6 (Fig. 2) which were constituted as follows on 1 March 1965:

B4: 14 chambers, 23 birds;

B5: 7 chambers, 8 birds;

B6: 50 chambers in 3 separate nest masses, birds not counted.

After nightfall on 1 March, 11 of the inhabitants of B4 were caught in the nest chambers, ringed and released. Three of the birds were immature. The B4 colony returned to roost in the normal way on the evening of 2 March, but it was decided not to attempt trapping again so as not to disturb the birds unduly. On the morning of 3 March, the entire B4 nest mass was demolished; that evening the following observations were made at the tree:

1852 hours: birds arrive, hop about in tree and depart in small groups.

1925 hours: almost dark, tree deserted.

After dark one of the ringed immature weavers from B4 was caught at B5 where it was sleeping next to another immature (which escaped) in a shallow depression on the side of the B5 nest mass. Unfortunately all the other occupants of B5 escaped.

At no time in the months that followed were any of the birds from B4 caught or seen at B5, but in December 1965 one of the ringed B4 birds (caught as an immature on 1 March) was seen building at a small, previously disused nest mass about half a mile south of B4, along with a small group of unringed birds. It was evident that any birds which may have moved to B5 on the night after the destruction of B4 did not take up permanent residence there, nor were B4 birds ever seen at B6.

Inter-nest movements are extremely rare (Table 8).

On 3 December 1964 bird No. 285 was ringed at Nest No. 5 in the Nossob River. It was one of a small party of weavers which had only recently moved to No. 5 from elsewhere. On 7 December this bird was seen at Camp Nest, some five miles to the south of nest No. 5, at 1700 hours. It tried to enter chambers in the SC level of Camp Nest but was continually harassed by the few resident Camp Nest birds that were present at the time. The residents actually uttered alarm calls when they encountered the interloper. The chasing continued for some time until the Camp Nest birds went off to feed. No. 285 stayed on at the nest and began some displacement building. Just before sunset at 1922 hours, all the birds at Camp Nest, including No. 285, were roosting in the chambers.

Table 8. Records of displaced sociable weavers for the whole study period. Nest No. 3M is just outside of the study area to the south of Twee Rivieren. (*) Ringed as a chick; all other birds ringed as adults.

BIRD No.	RINGED		RETRAPPED OR SEEN		
	DATE	LOCALITY	DATE	LOCALITY	DISPLACEMENT
58	12.10.64	Twee Rivieren	1.5.65	3M	3 miles south
66	14.10.64	Twee Rivieren	1.5.65	3M	3 miles south
82	17.10.64	Twee Rivieren	18.8.65	3M	3 miles south
268	27.11.64	24	11.2.65	19	3 miles south
285	3.12.64	5	20.1.65	Camp Nest	5 miles south
412	8. 1.65	16*	17.1.66	19	2 miles north
813	10. 6.65	B1	19.7.65	19	2 miles N-W

The next day No. 285 was still at Camp Nest, but was no longer being chased by the original inhabitants. The bird was seen again at Camp Nest on 20 January 1965 and again on 31 January and had almost certainly been there all the time in between these observations. When the next breeding period began in the latter half of April 1965, No. 285 was paired with one of the original inhabitants (No. 93) of Camp Nest, indicating its complete assimilation into the colony.

Within a single level, apart from the few cases of dominant birds already mentioned, there appears to be little or no peck-order among the birds. They come and go without any interference whether it be in or out of the breeding period, concentrating their attention on their own one or two chambers. However, all adults are dominant to all immatures; as soon as an immature bird attains its adult plumage at the age of four months, it becomes accepted as an equal throughout the colony. This feature will be dealt with further in Chapter 5.

Sociable weavers always roost in the nest chambers. Outside a breeding period, a bird may roost in any chamber in its own structural level. The birds return to the nest at about sunset and begin to fly into the chambers almost as soon as they arrive, sometimes trying one or two different chambers before finally settling into one for the night. The number of birds roosting in a single chamber seems somewhat haphazard. Actual counts have revealed up to five adults sleeping in one chamber, but this is probably not maximal. In the aviary nest mass, as many as 8 birds roosted in a chamber while the number of chambers was limited. From time to time only one bird may roost in a chamber, but the sociable weaver more often roosts in two's or more. Some chambers are more favoured than others for reasons which are not clear.

It is impossible to see the sleeping position of the birds inside the chamber, but some observations on the aviary birds provided part of the answer. When the birds were first put into the aviary, the only roosting place they had was a small piece of nest mass with three chambers, placed on the ground. As this mass disintegrated as a result of the depredations of harvester termites, the birds had less and less space and eventually crowded up to 12 together in what was left of the last two chambers, huddling together with their heads resting on their neighbours' backs. However, a bird sleeping alone would tuck the bill into the feathers of the upper back in the normal passerine fashion.

When more than three weavers roost in an intact chamber, they sleep in layers, the top birds completely covering the lower ones. When a chamber is full or nearly full of birds that have settled in for the night, any incoming birds leave again at once and try adjacent chambers until they find room to roost. However, since the birds usually go to the same chambers night after night, there is less confusion during retiring than might be expected to occur. A retiring flock alights in the top of the nest tree on arrival from the feeding grounds; the birds then filter down through the branches of the tree until they are at or below the level of the substructure, and then quickly fly into their chosen chambers.

Roosting patterns during a breeding period vary somewhat from that outlined above, since most of the chambers are occupied by pairs of breeding birds. Thus at the beginning of the breeding period, most of the chambers have only the pair roosting in them at night. Non-breeding birds usually roost in separate chambers from the breeding pairs, but this is not an invariable rule. I have seen non-breeding birds enter and remain in chambers in which the breeding pair may have eggs or chicks. During the day, however, such intrusion is not tolerated by the pairs. At night the aggression of breeding birds is probably less than during the day, but in any case it is not often that non-breeding birds roost in breeding chambers; it seems to occur most often in the case of late-comers who arrive at the nest as darkness sets in. The statement that a pair of birds roosts in each chamber throughout the year (McLachlan & Liversidge 1957) is untrue and is not even strictly applicable in a breeding period.

Calls and associated behaviour patterns

Most of the calls of the sociable weaver consist of staccato chipping notes, somewhat metallic in quality, but not harsh or unpleasant. The descriptions of the different calls which follow are accompanied by a system of diagrammatic notation (Fig. 26) invented by Saunders (1951); reference to Fig. 26 for each call should help greatly in understanding the actual sounds which the birds produce. Where a call is accompanied by a particular behaviour pattern, the two are described together. Ten basic types of call notes were noted and all except the threat notes were recorded on tape in the field.

1. Contact call

Although the name "contact" call implies a functional interpretation of the calls, this function is only assumed. The contact call is a simple "chip" note uttered singly or in short phrases of two or three syllables. When the aviary birds were in a rested state, after having fed and possibly done a lot of nest-building, they used to sit perched in the tree or on top of the nest mass, dozing or performing comfort movements (preening, scratching, stretching); they would occasionally utter a "chip" or "chip-chip", rather low and quiet. The birds were seldom absolutely silent unless they were asleep in the nest chambers. The fewer the birds outside the chambers and the less their

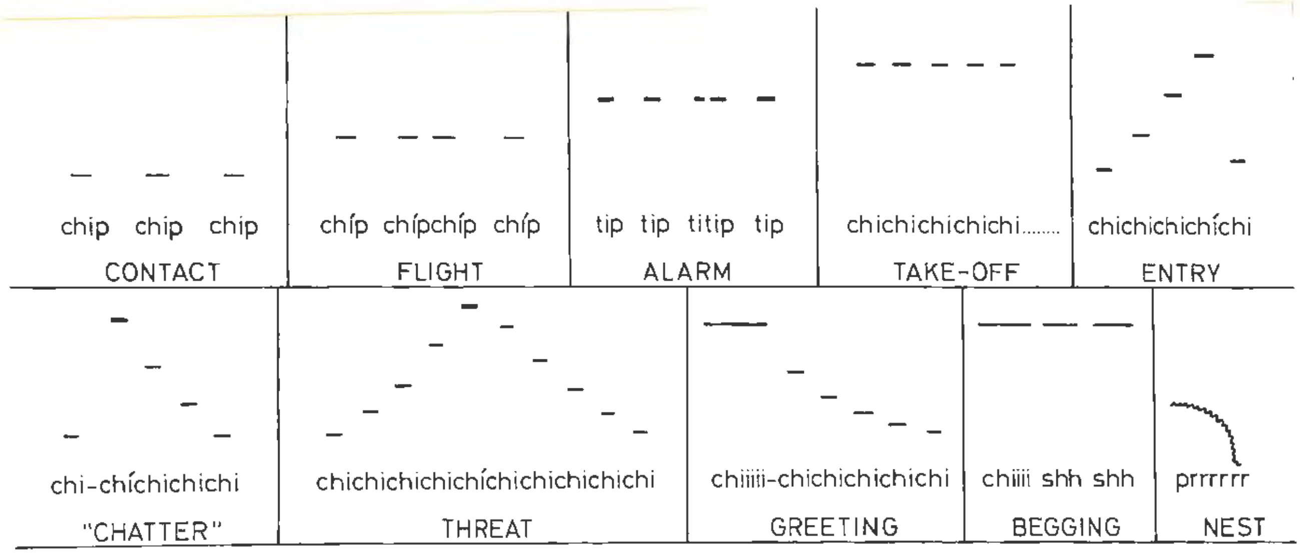

Fig. 26. The calls of the sociable weaver. The notation follows the system of Saunders (1951).

activity, the fewer and more subdued were the contact notes.

In a large colony, such as Camp Nest, when the birds were resting in the branches of the tree, there was a continual chippering due not only to the fact that many birds were uttering contact calls, but also because each bird was calling more frequently than in the small aviary colony. There appears thus to be a marked social facilitation involved in the intensity of the contact call, which increases as the number of birds present increases. The intensity also increases as the birds' activity increases, whether they are building or feeding young. Even at night when all the birds are in the nest chambers, an occasional "chip" may be heard; this usually elicits a reply from a bird in another chamber, but neither utters more than a single note, indicating a low intensity of contact calling.

The effect of social facilitation on the contact calls was clearly seen at rising time in the morning when the birds began to emerge from their roosting chamber. The first bird to emerge begins to utter "chip" or "chip-chip" notes every second or half second and as more and more birds emerge, the intensity of calling increases, reaching a peak just before the whole colony leaves the nest for the feeding grounds. Likewise at night, when the birds are going to roost, the intensity of contact calling decreases as fewer and fewer birds are outside of the chambers.

2. "Chatter"

During periods of great activity at the nest, the variety of calls is considerable and the contact notes themselves become very variable. The notes rise and fall running "into a metallic, not unmusical chatter or tinkling sound" (Collias & Collias 1964). Chattering is a series of phrases following one another in rapid succession, each phrase starting as a normal "chip" note and ending in a chatter of notes coming down the harmonic scale (Fig. 26). Since the chatter very often accompanies an encounter between two or more birds, it almost certainly has elements of threat notes in it, but is not accompanied by the threat display, nor by any noticeable advance or retreat on the part of either of the birds which have come together at the nest mass. Chatter is probably indicative of socially facilitated excitement.

3. Entry call

A brief phrase of about four notes running up the scale and ending in a single note at the bottom of the scale is uttered by a bird as it flies from a perch into the entrance tunnel of a nest chamber. This call is heard under no other circumstances and, for want of a better term, is called the entry call. It is very similar to the first part of the threat call (q. v.) and is probably indicative of approach on the part of the caller.

4. Threat call

Running first up, then down the scale, the threat call is accompanied by actual or incipient attack in which the caller advances towards another bird, bill open and sometimes also with the tail fanned. The note and the display are usually enough to drive off another bird, but if it fails to leave, the threatening bird will actually attack the other bird, usually by pecking at its head, but occasionally at some other part of the body.

Threat behaviour may be elicited by too close an approach of one bird by another either at the nest or on the feeding grounds; also by the arrival of a bird at a level not its own. Sometimes two birds may fall to the ground fighting, but they soon release their grip on one another and return to the tree where the fight is not normally resumed. A bird may take up a position in the mouth of an entrance tunnel and defend it against other birds which may try to enter. The threat notes are usually enough to prevent any intended entry by an incoming bird. If not, the defender will attack the arriving bird. In one such encounter, the defending bird held the other by the feathers of its head, from which it hung in a submissive attitude until released, when it flew off.

5. Greeting call

A weaver entering a chamber already occupied by another weaver is almost invariably greeted by the occupant with a rapid, chattery "chiiiii-chichichichichi" uttered as the bird looks down the entrance tunnel from the threshold of the chamber. The first note of the greeting call is very similar, if not identical to the begging call and the last part of the call is a descending chatter. The begging note probably indicates submission, or at least the very opposite of threat.

6. Begging call

The slightly drawn out and rather raspy "chiii" or "shhhh" of the begging call is uttered by chicks begging for food from their parents, and I have also seen it uttered by certain adults when begging for food from other adults. In the latter case, it appears to be part of pair formation or courtship feeding, although the sexes of the two birds were never satisfactorily determined. In any case the begging bird, be it adult or young, assumes a typical submissive posture, somewhat crouched on the perch, and with wings drooped and quivering.

7. Flight call

In open flight the sociable weaver gives an occasional "chip" note, slightly higher pitched than the basic contact call note. As with the contact calls, flight calls are more frequently uttered by birds in a large flock than by birds in a small flock or flying alone. In fact, a lone bird may not call at all in flight until it begins to approach the nesting tree.

8. Take-off call

On take-off a sociable weaver utters a very rapid burst of high pitched notes which become lower pitched and more widely spaced once the bird is in open flight and the flight call takes over. Before a bird actually takes off, it signals its intention to do so by uttering a sharp note, intermediate in pitch between flight and alarm notes, at increasingly frequent intervals until it leaves with the take-off call. This may be termed the flight-intention call, but all three calls associated with flight grade into one another as the bird proceeds from flight-intention to take-off to open flight.

9. Alarm call

The alarm call is very distinctive. It is intermediate in pitch between flight and take-off calls, but much louder than either and has a sharp, metallic quality which all other calls lack. It is uttered by the weavers in the presence of man, a snake, a hawk or any other dangerous animal either at the nest or elsewhere. The intensity of alarm is indicated by the loudness and rapidity with which the notes are uttered.

Alarm calls are not accompanied by any obvious display, although the birds hop rapidly back and forth while uttering alarm notes in the presence of a cobra at the nest. This may have some distractive function. As is commonly the case among most small birds, alarm calling by one species will often elicit alarm calling from another species. On one occasion a small flock of scaly finches *Sporopipes squamifrons* was hopping around the superstructure of B1 while the weavers were away feeding; a cobra suddenly appeared from the top of the nest mass and the finches began intense alarm calling immediately. This brought the weavers back from where they were feeding about 50 metres away and they took up the alarm calls as soon as they saw the snake. After one or two minutes of high intensity alarm calling, the weavers flew away to feed. Some of them returned again later and began alarm calling again as they saw the snake in the nest chambers. This happened three or four times until the weavers stayed away from the nest until the snake had gone.

An alarm note from one sociable weaver elicits alarm notes from any others which may be within hearing range. Any birds which may be in the nest chambers usually emerge and take up the alarm calls, which increase in intensity as the danger gets closer until finally the whole colony departs precipitately.

10. Nest call

I have taken the term "nest call" from Collias & Collias (1964) who describe it as "a not unpleasant, soft nasal single note heard while the birds were undisturbed in the nest and as they came and went when building". The nest call is a downward-slurred trill (Fig. 26) which can be heard only at fairly close range and may be uttered from inside a chamber or outside in the tree. When given outside the nest, the nest call is very often accompanied by the fanned-tail-flicking display in which the fanned tail is flicked once or twice at intervals of about one second and the call given less frequently. Nest calls and fanned-tail-flicking by one bird may release the behaviour in a number of others nearby and I have seen a group of four or five birds all displaying together.

I do not agree with Collias & Collias (loc. cit.) that the calls are uttered by undisturbed birds. A nest call is almost invariably a response to contact calls, "chatter", flight calls or even just the rustle of an arriving bird's wings and may in such circumstances serve to indicate that a nest chamber is occupied. But more than this, I get the impression that a nest call is indicative of mild anxiety, because the fanned-tail-flick is an anxiety display in the presence of an intruding animal which is not a predator. For instance, after a few minutes of alarm calling, the aviary or Camp Nest colonies would settle down to nest calls and fanned-tail-flicking in my presence, and any birds in the chambers would respond to the alarm calls of those outside with nest calls. Nest calling was also the reaction to a cow approaching the aviary nest too closely. Incubating birds in which the drive to incubate was greater than the drive to depart often gave nest calls in response to alarm calls from the rest of the colony.

The daily rhythm

Although the birds in the nest chambers may begin contact calling at dawn, they do not usually leave the chambers until sunrise time or a few minutes later (Table 9). On a cloudy morning, rising time may be somewhat later than actual sunrise time. On a warm morning when air temperatures are 20°C or more, the birds may leave the nest a few minutes before sunrise when the weather is fine. In winter, however, when the air temperature is less than 10°C, rising time may be considerably delayed with respect to sunrise. One frosty morning in South West Africa the birds were still in the nest chambers and quite quiet at 0900 hours in fine weather, that is some 2 hours after sunrise.

Once the first bird has emerged from a chamber and begins to give contact calls from a perch in the tree, four or five others may emerge and take up the contact calling which becomes general as the birds in the nest also join in. Quite suddenly one of the birds gives a few flight-intention notes and takes off with a burst of take-off notes; this is the signal for the whole colony to depart in a body and the volume of noise produced by all the take-off calls is quite spectacular. The flight calls of the colony are then heard to fade away in the direction of the feeding grounds. The colony may depart in two or three large groups, but there is little delay between the departure of the first and last birds.

While the majority of birds are feeding on the ground, there are usually two or three birds perched on nearby bushes or fence-posts. These birds act as sentinels, but whether this is incidental or not has not been established. A feeding flock is rather silent, except for an occasional "chip" or perhaps a threat call from a bird which has been too closely approached by another. The factors governing the length of the feeding periods are dealt with fully in Chapter 10. After the morning feed the birds return to the nest for the midday "siesta". I have termed this resting period siesta, as it is a more or less extended time of inactivity from about 1000 to 1400 hours in summer and much shorter in winter, during which the birds are all inside the nest chambers, completely silent, and possibly asleep.

If, as sometimes happens during a drought when food is probably scarce, the birds are feeding far from the home nest, they may spend the midday hours at an abandoned nest mass if it is closer than the home nest. Occasionally the birds will simply rest in the shade of bushes on or near the feeding areas.

At the end of the siesta the birds leave the nest in a flock, much as they do at rising time in the morning, and fly out to feed again. Unless the birds were breeding, they did not usually return to the nest again before roosting time in the evening. As with rising time, roosting time varied with the

Table 9. Some rising and roosting times of sociable weavers at Camp Nest.
Approximate temperatures are:
"cold" = less than 18.0°C;
"mild" = between 18.0 and 25.0°C;
"warm" = between 25.0 and 35.0°C;
"hot" = over 35.0°C.

DATE	MORNING				EVENING			
	SUNRISE	RISING	TEMP °C	CLOUD (+)	SUNSET	ROOSTING	TEMP °C	CLOUD (+)
13.10.64		0610						
17.10.64						1730		
18.10.64		0630		+				
21.10.64						1845		
23.10.64						1755		
28.10.64	0557	0602	"cool"					
3.11.64		0600						
4.11.64		0605	17.5	+				
8.11.64						1830		
17.11.64		0540		+		1850		+
18.11.64					1852	1840		
20.11.64					1900	1810	19.0	
25.11.64						1830	"warm"	+
26.11.64	0542	0547	18.0					
2.12.64	0545	0615		+				
7.12.64					1908	1908		
21.12.64	0544	0535	15.0					
9. 1.65						1920		
13. 1.65						1907	"warm"	
14. 1.65	0600	0549	"warm"					

16. 1.65					1927	1920	"warm"	
20. 1.65	0605	0602	"mild"		1924	1930		
28. 1.65	0613	0600	23.0					
29. 1.65	0614	0600	"mild"					
2. 2.65		0609	"warm"	+				
3. 2.65	0616	0607	"cool"					
9. 2.65					1920	1922	"hot"	
10. 2.65	0627	0607		+				
26. 2.65					1908	1912	"cold"	
28. 2.65	0633	0645	17.0					
2. 3.65					1845	1857	"warm"	
3. 3.65					1845	1852	"warm"	
4. 3.65	0638	0634						
9. 3.65					1836	1838	"mild"	
10. 3.65					1836	1902		
12. 3.65					1835	1830		+
15. 3.65						1847		
16. 3.65						1852		
17. 3.65		0630						
21. 3.65					1823	1856		+
26. 3.65						1752		
27. 3.65		0633	18.5					
28. 3.65						1729		raining
9. 4.65					1825	1810		
13. 4.65					1821	1821	"cold"	
17. 4.65					1817	1830		
20. 4.65					1815	1830		
21. 4.65	0700	0635	14.5		1814	1830		

season and with the weather. "Roosting time" is necessarily a rather loose term, since the birds did not usually all enter the nest chambers at once to roost in the evening; however, it means here the time at which most of the colony entered the chambers (if they tended to do so in a large flock) or the time at which almost all the members of the colony were inside the chambers (if they had been entering in twos and threes at longer time intervals). It was found that silence began to descent upon the colony shortly after roosting time, whichever of the two above situations prevailed.

In winter when the temperatures at sunset were less than 15°C, roosting time coincided roughly with sunset time, but in summer the birds sometimes came to roost some minutes before sunset time (Table 9). On mild winter evenings (temperatures between 20°C and 25°C) roosting time was as much as 30 minutes after sunset, probably because the birds need to feed relatively later in the evenings on the short winter days than they need to do in summer. On a cloudy evening at any time of the year, roosting time is earlier than on fine evenings.

This outline of the daily routine is highly generalized. Even when the birds are not breeding, a few members of a colony may be found at the nest at almost any time of the day, except immediately after the initial departure of the colony at rising time in the morning.

Chapter 5

BREEDING BIOLOGY

During the study period it was possible to observe the sociable weavers in three separate breeding periods. The expression "Breeding Season" is avoided here, since the weavers did not breed seasonally. The difficulty of distinguishing between the sexes in the field made it impossible to do more than guess at which member of a pair of breeding birds was the male and which the female, but there were small behavioural differences on which a tentative separation was based. It was impracticable to kill birds at Camp Nest in order to confirm sexual differences in behaviour, since this would have defeated the purpose of having ringed birds under observation from one season to the next. However, it was not a serious drawback; the roles of the sexes are evenly divided, courtship is minimal and copulation seems to occur in the nest chambers, and so it did not matter unduly that the sexes could not be told apart.

Factors influencing breeding

Gonad measurements of both sexes throughout the study period show that there is a direct relation between an increase in gonad size and the occurrence of rain (Fig. 27). There were three rainy seasons during the study period: the first in December 1964, the second in March/April 1965 and the third in January/February 1966. Each of these resulted in a breeding period. not only in the sociable weavers but also in most of the Kalahari birds. In the sociable weaver, the extent of breeding taken as the number of clutches per month was found to be directly related to the amount of rain which fell each season, regardless of the time of the year when the rain fell (Fig. 28).

Rainfall is one of the main factors influencing breeding, but it may not be a direct proximate factor. Fig. 28 shows that 14.0 mm. of rain in October 1964 did not trigger of breeding activity, but 28.6 mm. of rain in December 1964 was followed by breeding, so that a certain minimal amount of rain is required before breeding will occur. This minimum is probably a little over 20 mm. within a month. Furthermore, the length of the breeding period is not entirely dependent on the amount of rain, but rather on the time of year at which the rain falls. Thus a total of 139.1 mm. of rain in March and April 1965 was followed by a breeding period lasting nine months, while a rainfall of 129.3 mm. in January and February 1966 was followed by a breeding period of little more than three months. Rainfall alone is thus not the limiting factor on reproductivity.

The effects of rain in the Kalahari are rapid and marked. There is a sudden increase in the visible insect life and the vegetation quickly produces flowers and leaves. The duration of green leaves and green grass depends on the time of year when rain

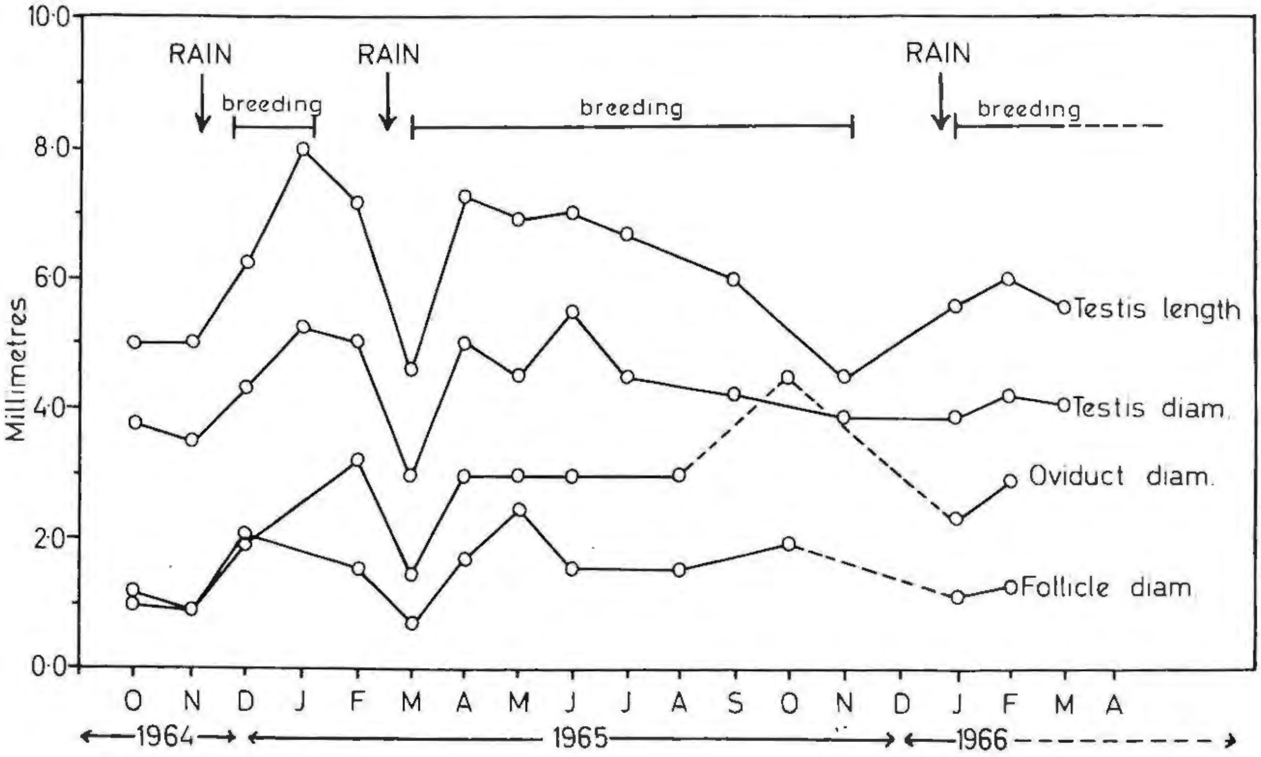

Fig. 27. The relation of mean monthly gonad size of the sociable weaver to rainfall and breeding periods (sample sizes as in Table 20).

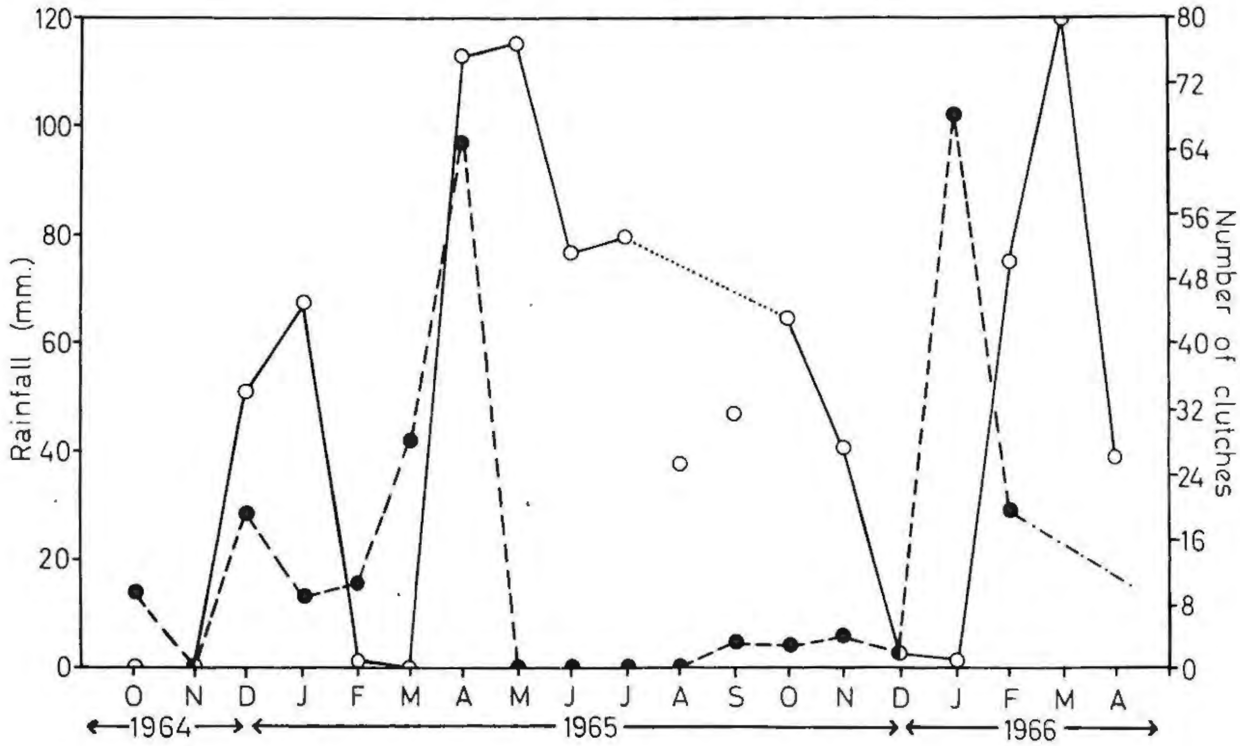

Fig. 28. The relation of the number of clutches per month (solid line) to the monthly rainfall (broken line). The dotted line joining counts for July and October omits the unreliable counts for August and September when I was away for part of the time.

falls; the effect of the December 1964 rain was short-lived because of the intense heat which prevailed for the rest of the summer, and also because the small amount of rain resulted in a poor growth of grass and leaves. The weather was already becoming cooler when the March/April 1965 rains fell, so that the shrubs were still in leaf at the end of November and they only lost them in December of that year. After the January 1966 rains fell in the space of one week, high temperatures and sunny days prevailed throughout February and March, so that the very luxuriant growth of grass, herbs and shrubs began to dry up by the middle of March. The duration of the breeding season in the sociable weaver seems therefore to be dependent, directly or indirectly, on the duration of green plant growth after rain.

The last egg of the first breeding period was laid on 1 February 1965 and the first egg of the next breeding period was laid 69 days later on 10 April. The last egg of the second breeding period was laid on 10 December 1965 and the first egg of the third breeding period was laid only 44 days later on 23 January 1966. Thus if there is a refractory period of the gonads, it is a short one.

Pre-breeding behaviour

During the first week or two of each breeding period, an occasional bird was seen to pick a small green leaf from the nesting tree and fly into a nest chamber with it. Shortly before the aviary colony began to lay eggs, some of the birds would offer harvester termites to other members of the colony which would accept the offering with quivering wings and begging calls. It was always the same birds which carried the insects and the same birds which begged; perhaps the former were males and the latter females. No courtship feeding was seen in free-living colonies. Leaf-carrying may be a form of ritualized courtship feeding. Nevertheless, courtship is almost certainly a simple performance and, apart from courtship feeding and leaf-carrying, no behaviour was seen which could be construed as courtship.

Copulation was observed only once at a distance of about 150 metres, as the pair sat on a fence, so that the two birds could not be identified. Since it was not seen more often, it is possible that copulation normally took place inside the nest chambers as has been shown for some Estrildidae (Immelmann 1965).

Unless part of a nest mass has been destroyed, there is little more building activity at the beginning of a breeding period than at other times; what there is, is devoted to narrowing the entrance tunnels with straws.

Sociable weavers do not pair for life, but because of their conservative attachment to structural levels within a nest mass, the same pair may re-form in a subsequent breeding period. At Camp Nest birds No. 12 and No. 25 were mated in two successive periods. but all other birds observed paired with different individuals in successive periods (Table 10). Table 10 shows that one member of each pair remained in the same chamber, or else in a nearby chamber (usually in the same level) for both breeding periods. It seems likely that this bird in each case was the male. Thus I would tentatively suggest that birds No. 4, No. 12 and No. 33 were males.

Clutch size

The clutch size of the sociable weaver varies from 2 to 6 eggs. The number of eggs per clutch varies with the season; the better the season (as determined by rainfall and temperatures), the larger the clutch size and also the more clutches laid, as shown in Table 11. A chi-squared analysis of the clutch-size data for the months of April to November 1965 as given in Table 11 shows that the differences are highly significant at the 0.01 level $[X^2 = 110.14;\ X^2\ 0.01\ (28df) = 48.28]$, based on methods given by McCarthy (1957). Most clutches consist of 3 or 4 eggs with the mean clutch size for all three breeding periods = 3.54 eggs. As the vegetation becomes greener and as the insect life increases (as judged by the enormous increase of insects around lights at night), so clutch size increases.

Changes in the food supply available to the weavers were not determined directly by measurement. However, the increase in green leaves on shrubs and bushes, and the increase in the ground cover of grass and herbs on what was normally bare sand or calcrete, were accompanied by an increase in the numbers of insects, scorpions and other invertebrates in evidence both day and night, so I am assuming on this somewhat subjective basis that the food supply of the weavers increased under such conditions, which prevailed after rain.

It has been shown for many passerine birds (e.g. Dunnet 1955) that second clutches, be they replacement clutches or true second broods, are smaller on the average than first clutches. However, in the sociable weaver, many second clutches were larger than first clutches, or at least the same size. A full analysis of replacement clutches is given in Table 12 which shows that the mean size of second clutches is greater than the mean for first clutches and that clutch size decreases in successive replacement clutches in the same way that clutch size decreases as the season progresses (Table 11) and almost certainly for the same reasons. More will be said about second and later broods subsequently.

Table 10. Mated pairs of birds at Camp Nest in the first and second breeding periods.

BIRD NO.	MATED WITH BIRD NO.		CHAMBERS	
	1st PERIOD	2nd PERIOD	1st PERIOD	2nd PERIOD
4	114	11	SW:9	SW:6
12	25	25	SW:7	SW:5
20	33	39	SC:4	UM:4
33	20	19	SC:4	SC:4

Table 11. Number of clutches and mean clutch sizes per month at colony Nos. 5, 16, 17, 24, B1, B2, B3 and Camp Nest of the sociable weaver in the study area, for the entire study period.

YEAR		CLUTCH SIZE					TOTAL CLUTCHES	MEAN CLUTCH SIZE PER MONTH
		2	3	4	5	6		
1964	October	-	-	-	-	-	0	0.00
	November	-	-	-	-	-	0	0.00
	December	1	17	16	-	-	34	3.44
1965	January	5	22	16	2	-	45	3.33
	February	-	1	-	-	-	1	3.00
	March	-	-	-	-	-	0	0.00
	April	5	18	41	11	-	75	3.77
	May	3	6	46	21	1	77	4.10
	June	6	11	25	9	-	51	3.73
	July	3	22	25	3	-	53	3.53
	August	2	13	8	2	-	25	3.40
	September	2	17	11	1	-	31	3.35
	October	5	28	9	1	-	43	3.14
	November	4	22	1	-	-	27	2.88
	December	-	2	-	-	-	2	3.00
1966	January	-	1	-	-	-	1	3.00
	February	1	26	23	-	-	50	3.44
	March	13	25	38	6	-	82	3.45
	April	1	9	13	3	-	26	3.69
TOTALS		51	240	272	59	1	623	MEAN 3.54

able 12. Analysis of replacement clutches of the sociable weaver in the study area for the second breeding period (April 1965 to December 1965). Clutches in parentheses were completely unsuccessful; those not in parentheses gave rise to at least one flying chick.

CHAMBER	1st CLUTCH	REPLACEMENT CLUTCHES 1st	2nd	3rd	4th	5th	6th	7th
5L:1	(4)	4	5	-	-	-	-	-
5L:2	(3)	4	(4)	5	(3)	(3)	(3)	-
5L:6	(4)	4	4	(3)	(3)	(4)	(3)	-
5L:8	(3)	(3)	(3)	-	-	-	-	-
5L:9	(3)	(4)	-	-	-	-	-	-
5U:4	(4)	6	4	(3)	(4)	-	-	-
16S:2	(4)	3	-	-	-	-	-	-
16S:3	(4)	(4)	3	(4)	(4)	(2)	(3)	(3)
16S:4	(4)	(4)	-	-	-	-	-	-
16S:5	(2)	3	3	(3)	(2)	(3)	-	-
16E:4	(5)	4	-	-	-	-	-	-
16E:5	(3)	(4)	(4)	-	-	-	-	-
16E:7	4	(3)	2	-	-	-	-	-
16E:8	2	(3)	(4)	(2)	-	-	-	-
16E:10	(3)	(4)	(4)	(2)	3	-	-	-
16E:11	(4)	4	(3)	(2)	-	-	-	-
16E:15	(4)	(3)	(3)	-	-	-	-	-
16N:1	(5)	(5)	(5)	-	-	-	-	-
16N:5	(3)	(5)	(4)	-	-	-	-	-
16N:6	(3)	(3)	(4)	-	-	-	-	-
16N:7	(4)	(3)	-	-	-	-	-	-
16N:11	(5)	(5)	-	-	-	-	-	-
16N:15	(3)	(4)	3	-	-	-	-	-
16N:16	(4)	3	(3)	(4)	(3)	-	-	-
16N:17	2	(4)	-	-	-	-	-	-
17E:1	(4)	(4)	-	-	-	-	-	-
17E:2	(4)	(4)	(4)	4	-	-	-	-
17E:18	(4)	5	-	-	-	-	-	-
17E:22	(4)	(4)	(4)	-	-	-	-	-
17S:6	(2)	(3)	-	-	-	-	-	-
24W:3	5	4	3	(3)	-	-	-	-
24W:7	4	5	4	4	-	-	-	-
24W:31	4	4	3	-	-	-	-	-
24W:35	4	4	3	(2)	(3)	-	-	-
24W:37	4	4	(3)	(3)	-	-	-	-
24W:39	5	5	3	(3)	-	-	-	-
24W:46	3	4	2	(3)	-	-	-	-

Occupation of breeding chambers

In the first breeding period, out of a total of 299 nest chambers under regular observation, only 105 chambers ever contained eggs. This was 34% of the total and may be expressed as 34% occupation. The percentage occupation in the second and third breeding periods was 46% and 35% respectively, but these differences are not statistically significant (Table 13). The higher percentage in the second breeding period is due in part to the fact that some females did not always lay subsequent clutches in the same chamber, and also that, over the long duration of breeding, some chambers collapsed and new ones were built.

It seems therefore that the number of breeding pairs does not increase significantly with increasing rainfall.

Egg-laying and incubation

Eggs are laid at 24-hour intervals, usually during the morning hours. The eggs are dull white in ground colour, more or less thickly covered with fine speckles of light grey, forming a denser cap at the thick end. The shell is smooth but not glossy. Measurements of 13 eggs from different nests give a mean of 20.9 x 15.1 mm. (19.5-22.6 x 14.8-15.8). These measurements compare with those of McLachlan & Liversidge (1957).

Incubation usually begins with the laying of the second egg of the clutch, although it may sometimes begin with the first egg. This is rather unusual for a passerine bird, since most species do not begin incubation until the clutch is complete. This means that the third and later chicks hatch at roughly one-day intervals after the first two and are visibly different in size up to the age of about two weeks (Fig. 29). After two weeks, the differences even out rapidly and the whole brood usually leaves the nest on the same day, or within two days.

The incubation period is between 13 and 14 days with a mean of 13.5 days. This period is comparable with that of most other passerine species of similar size.

Parental behaviour during incubation

Both sexes incubate. A mean attentive period of 14 minutes was obtained from 22 observed attentive periods, of which the shortest was only 2 minutes and the longest 40 minutes. Each member of a breeding pair takes an equal share in the incubation: for instance in the pair of birds No. 4 and No. 11, the same attentive periods were 22 and 18 minutes respectively, while in the pair of birds No. 99 and 108, the mean attentive periods were 12 and 13 minutes respectively. An incubating bird does not normally leave the chamber until its mate comes to relieve it, so that the eggs are seldom left uncovered at any time during incubation. This is also unusual for a passerine (cf. Rowan & Broekhuysen's observations on the warbler *Prinia maculosa* (1962)).

Table 13. Percentage occupation for breeding purposes of nest chambers by sociable weavers in the study area during the second and third breeding periods. (*) indicates that the nest mass was not occupied at all, or had collapsed, in the third breeding period.

	2nd PERIOD			3rd PERIOD		
NEST MASS	TOTAL CHAMBERS	BREEDING CHAMBERS	% OCCUPATION	TOTAL CHAMBERS	BREEDING CHAMBERS	% OCCUPATION
5L	12	9	75	10	5	50
5U	5	2	40	*	*	*
16S	14	10	71	8	2	25
16E	15	9	60	17	8	47
16N	30	17	57	16	6	38
17E	29	11	38	18	6	33
17S	6	6	100	*	*	*
24W	50	11	22	50	7	14
24E	30	7	23	32	5	16
B7	14	4	29	9	4	44
B5	11	5	45	6	3	50
B1	17	11	65	15	5	33
B2	13	6	46	7	5	71
B3	7	5	71	5	2	40
B8	40	20	50	13	10	77
B9	12	8	67	9	4	44
B10	11	6	56	6	4	67
CNLM	13	2	15	6	0	0
CNUM	4	2	50	7	2	29
CNSW	7	4	57	*	*	*
CNSE	7	4	57	9	4	44
X	13	7	54	13	7	54
TOTALS	360	166	46	256	89	35

Fig. 29. A brood of sociable weaver chicks from the same nest chamber showing the discrepancy in sizes. Note the prominent white gapes.

Why the sociable weaver should keep its eggs covered all the time, even though they are well protected and insulated in the closed nest chamber, seems difficult to explain and no attempt will be made to do so yet.

Nest relief is simple. The relieving bird simply flies into the chamber and the sitting bird leaves at once. It seems as if the incoming bird releases departure in the incubating bird, since even the entry of a bird which is not a member of the pair will cause a sitting bird to leave without delay. One member of each pair, but never both, usually brings either a small item of food (such as a lepidopterous larva) or a straw of grass to the nest when it comes to relieve its mate. This may have been the male in each case; in the two pairs consisting of Nos. 4 and 11 and Nos. 12 and 25, only No. 4 and No.12 brought food or grass to the nest at nearly every relief. Both these birds remained in their own levels in successive breeding seasons (Table 10) and I have already shown in Chapter 4 (p. 78) that No. 12 was of a very aggressive nature, which may further indicate that both these birds were males.

When a "strange" bird enters a nest chamber, causing the incubating bird to leave, it remains in the chamber until it is relieved in its turn. Whether it incubates the eggs or not is a matter of conjecture, but it probably does, since a non-breeding adult may help a breeding pair to feed their chicks. I would expect that, if the "strange" bird did not incubate the eggs, it would leave the chamber immediately after entering, and would not wait inside until relieved by one of the rightful owners. In such a highly sociable species of bird as the sociable weaver, this sort of adaptive and adaptable behaviour is not entirely surprising.

Hatching and subsequent parental behaviour

The percentage of eggs which hatched successfully varied with the three breeding periods (Table 14). The overall hatching success during the study period was 41.8%. Unsuccessful eggs were either robbed by predators or were infertile; a few were deserted by the birds, but it was not always possible to distinguish between robbed and deserted clutches. In only seven clutches were all the eggs infertile. Two of these clutches were laid by the same female in 24E:15; during the second breeding period this female laid an infertile clutch of four eggs followed by a fully fertile clutch of 5 eggs, a clutch of 4 eggs of which 3 were infertile, and finally a completely infertile clutch of 3 eggs, making a total of 10 infertile eggs out of 16 eggs in one season.

In the case of the seven fully infertile clutches, incubation lasted for 27, 24, 24, 23, 23, 20 and 18 days respectively,

Table 14. A comparison of breeding success in the sociable weaver for the three breeding periods under observation over the whole study area.

BREEDING PERIOD	EGGS LAID	CHICKS HATCHED	% HATCH	CHICKS FLOWN	% EGGS PRODUCING SUCCESSFUL CHICKS
First	371	140	38.0	19	5.1
Second	1841	874	47.5	328	17.8
Third	577	154	26.7	18	3.1
All periods	2789	1168	41.8	365	13.1

before the birds gave up. The 20 and 18 day counts are minimal, so that the birds probably sat for over 20 days in all cases, i.e. about a week longer than the normal incubation period. In six out of the seven cases, the infertile eggs were thrown out of the nest before a replacement clutch was laid. In one case the replacement clutch was laid with the infertile eggs and all were incubated together.

Seldom was more than one egg in a clutch infertile, however, and by far the greater majority of clutches were fully fertile. The overall figure of 41.8% hatching success is probably too low a figure, as there was a high mortality among very small chicks which meant that a chamber would contain a full clutch of eggs on one visit and on the next visit (when it should have contained young) it would be empty. It could not be established whether or not all the eggs hatched, so they were recorded as being unhatched. Why newly hatched chicks should so frequently have disappeared was not determined. Cobras certainly accounted for many of them, but this was not always the case, since a cobra would also have accounted for the larger chicks in the same nest mass, and they did not disappear at nearly the same rate. Although the common black skink Mabuya striata, which inhabited the Acacia giraffae trees and the superstructures of all the sociable weaver nest masses in the Kalahari, ate any small dead chicks which had fallen to the ground below the nest masses, it is not likely that it could have eaten any of the chicks in the nest chambers. None of these lizards was ever seen in the substructure of a nest mass. Some factor such as disease or parasites may therefore have caused many of the losses of small chicks.

After hatching, the parents dropped the eggshells to the ground. This is quite unlike the situation in most passerine birds (and indeed in most birds) which remove the shells to some distance from the nest before dropping them; the advantage is to remove these conspicuous objects from the immediate vicinity of the nest. Nothing could be much more conspicuous, however, than the nest mass of the sociable weaver and the accumulation of faeces and débris that lie on the ground below it. It would therefore be of little value to retain the eggshell-removal behaviour pattern, so that it has probably been lost in the sociable weaver.

Newly hatched chicks are brooded almost continually by the parents except sometimes in warm weather. Chicks are fed from the first day; the parent bringing food brooded the chicks after feeding them, while the mate went off in turn to forage. Initially the food brought to the chicks consists of very small insects and insect larvae. As the chicks get older, the food brought to them is larger both in the size of individual insects and in the quantity per feed. There is a gradual change from small, soft insects to large grasshoppers, moths, mantids and Neuroptera.

The cooler weather immediately after rain brings out large numbers of harvester termites during the day. These insects form a large proportion of the food given to the chicks at all ages. Chicks receive only animal food until they are independent of the parents. Both parents feed about equally, carrying the food in the bill. Out of 66 recorded intervals between feeds, the shortest was 1 minute and the longest 47 minutes with an overall mean of one feed every 15.4 minutes during the feeding times, which exclude the midday hours from about 1100 to 1400 hours.

Usually only the pair fed their own young, but in the first breeding period one or even two non-breeding adults assisted in feeding chicks in certain chambers at Camp Nest. Why these extra adults should have been tolerated by a breeding pair which usually drove off other birds from their breeding chamber is obscure, but the advantages of having added help in a season when food is scarce are obvious. During the second breeding period only one case of an extra adult feeding at a chamber was recorded. This adult had already mated with another bird and raised a brood successfully, so why it should have transferred its parental attentions to another brood is not clear.

Disposal of the chicks' faeces is not done by the parents. Instead, from the first day of their lives, the chicks deposit the faeces over the edge of the chamber threshold from where it drops to the ground. Only once did I see a parent remove a dropping from a chamber in which there were chicks; it wiped the dropping off on a branch in what seemed a rather awkward fashion. It is possible that the dropping in this one instance had become lodged in the entrance tunnel and was merely being removed from there. The faeces of young sociable weavers are not enclosed in a faecal sac as in most other passerines. The faecal sac enables the parent to remove the faeces without soiling the nest or its bill in the process, so that when the parents no longer perform this function, the need for a faecal sac is lost and so, ultimately, is the sac.

Development of the chicks

At hatching the chicks are naked and blind; the skin is pink. The gape is swollen and creamy-white in colour, showing up clearly in the dark interior of the nest chamber. The inside of the mouth is plain yellow. After three or four days the quills of the rectrices and remiges begin to show as purplish papillae and the eyes begin to open a little. The eyes are fully open after a week or ten days. By the age of two weeks, the chicks are large enough to be ringed. At this stage all the feathers have emerged from their sheaths, but are not fully open on the ventral surface.

As the chick grows, the gape swelling shrinks and darkens to yellow. By the time the chicks are 14 days old they come to the chamber entrance to be fed, so that the need for the white gape is less. By the time the chicks leave the nest at the age of between 21 and 24 days, the gape swelling has all but disappeared and remains only as a thin yellow line which disappears altogether about two or three weeks after the young have left the nest.

Before the eyes open and for a day or two afterwards, the chicks' reaction to a hand inserted into the nest chamber is to beg with the bill open vertically upwards and weak begging squeaks which later develop into the "chiiii" begging call (Fig. 26). Once the feathers begin to emerge from their sheaths, the chicks' intruder-reaction is to crouch flat on the floor of the chamber. At this age one may often hear a dull pattering sound from the chamber containing fledgling chicks; this sound is made by the chicks' feet as they retreat to the back wall of the chamber furthest from the threshold. The function of this foot-pattering may be to startle a predator, although it would have little effect in the case of a snake, other than to draw the snake's attention to the chicks by the vibration of their movement.

Somewhere between the age of 17 and 20 days a very different intruder-reaction develops, in which the chicks make a dash for the chamber entrance and attempt to escape in a body. This reaction has good startle effect and probably serves to get the majority of chicks safely away, even though they cannot fly well yet. In some chicks this reaction does not develop until the age of 21 days or more, but it seems to be latent in all chicks from the age of 17 days, since it needs only one chick to attempt an escape to cause the rest to follow at once. After the chicks have left the nest, whether naturally or after a disturbance, they return to the chamber for long periods for a further 3 or 4 days. They are still fed by their parents (but not by any other adults, although they beg from all adults) for about a week after their first departure.

Throughout the incubation and nestling periods, both parents roost in the nest chamber at night. Sometimes one or more other adults may also share an occupied breeding chamber at night, but not during the day. Feeding of chicks takes place mostly during the first part of the morning and in the late afternoon, although some chicks may be fed at any time of the day. Chicks are not normally brooded after the age of 10 to 14 days, but they are kept warm at night by the roosting parents.

After leaving the nest for the first time, the chicks are almost invariably found back in the nest chamber in which they were reared. How do they find their way back? Parents can distinguish their own chicks from all others, probably by facial characteristics; therefore chicks that have left the nest will be found by their parents anywhere in the vicinity of the nest tree. That the chicks recognise their parents is evidenced by the fact that, although they will beg from any adults, as soon as they hear or see their parents arriving at the tree, they fly towards them immediately with a marked increase in the intensity of begging calls and postures. Once the family is together, the parent flies into its nest chamber and the chicks follow. I have seen this many times. Thus the parents actually lead their young to the correct chamber. The following-reaction of the young is elicited by the parent's presence only, since a parent without food in its bill can lead its brood to the nest chamber just as effectively as one carrying food.

Once the chicks have been led back to their nest chamber two or three times, they can usually find their own way back, although they occasionally make a mistake by entering an adjacent chamber. In one case the chicks reared in chamber SW:5 of Camp Nest repeatedly returned to SW:4 after leaving their nest chamber; their parents flew to SW:5 to feed them, but on finding them absent would fly to SW:4 until they had become so used to SW:4 that they raised their second brood in this chamber !

Juvenile sociable weavers are distinguished from the adults by the lack of black on the face and the duller plumage. After they attain their adult plumage at 16 to 18 weeks they resemble their parents in every way and can be told apart only by their coloured rings. They do not appear to breed for about a year, even if suitable rains fall within this period.

Breeding success

Breeding success is probably best expressed as the percentage of eggs which give rise to chicks that leave the nest successfully. This percentage varied drastically in the three breeding periods, being highest in the second period and very low in the first and third periods (Table 14). Most losses of chicks were due to predators (notably the Cape cobra), as I shall show more fully in Chapter 8. Both hatching success and nestling success increased with increasing clutch size (Table 15; Fig. 30) and therefore, as would be expected, breeding success varied monthly as did the mean clutch size, except that the greatest breeding success was a month later than the highest mean clutch size (Table 16; Fig. 31). This is also to be expected, taking into account the incubation and nestling periods.

Table 15. The relation of breeding success to clutch size in the second breeding period of the sociable weaver.

CLUTCH SIZE	EGGS LAID	CHICKS HATCHED	% HATCHED	CHICKS FLOWN	% FLOWN OF EGGS HATCHED	% FLOWN OF EGGS LAID
2	72	15	20.8	4	26.7	5.6
3	459	195	42.5	64	32.8	13.9
4	968	480	49.6	184	38.3	19.0
5	330	173	52.4	72	41.6	21.8
6	12	11	91.7	4	36.4	33.3
All clutches	1841	874	47.5	328	37.5	17.8

Table 16. The relation of breeding success to month of breeding in the second breeding period of the sociable weaver.

MONTH	EGGS LAID	CHICKS HATCHED	% HATCHED	CHICKS FLOWN	% FLOWN OF EGGS HATCHED	% FLOWN OF EGGS LAID
April	368	156	42.4	69	44.2	18.8
May	485	250	51.5	92	36.8	19.0
June	303	197	65.0	89	45.2	29.4
July	280	129	46.0	38	29.5	13.6
August	31	3	9.7	3	100.0	9.7
September	104	666	63.5	18	27.3	17.3
October	182	58	31.9	15	25.9	8.2
November	82	15	18.3	4	20.0	4.9
December	6	0	0.0	0	0.0	0.0
All months	1841	874	47.5	328	37.5	17.8

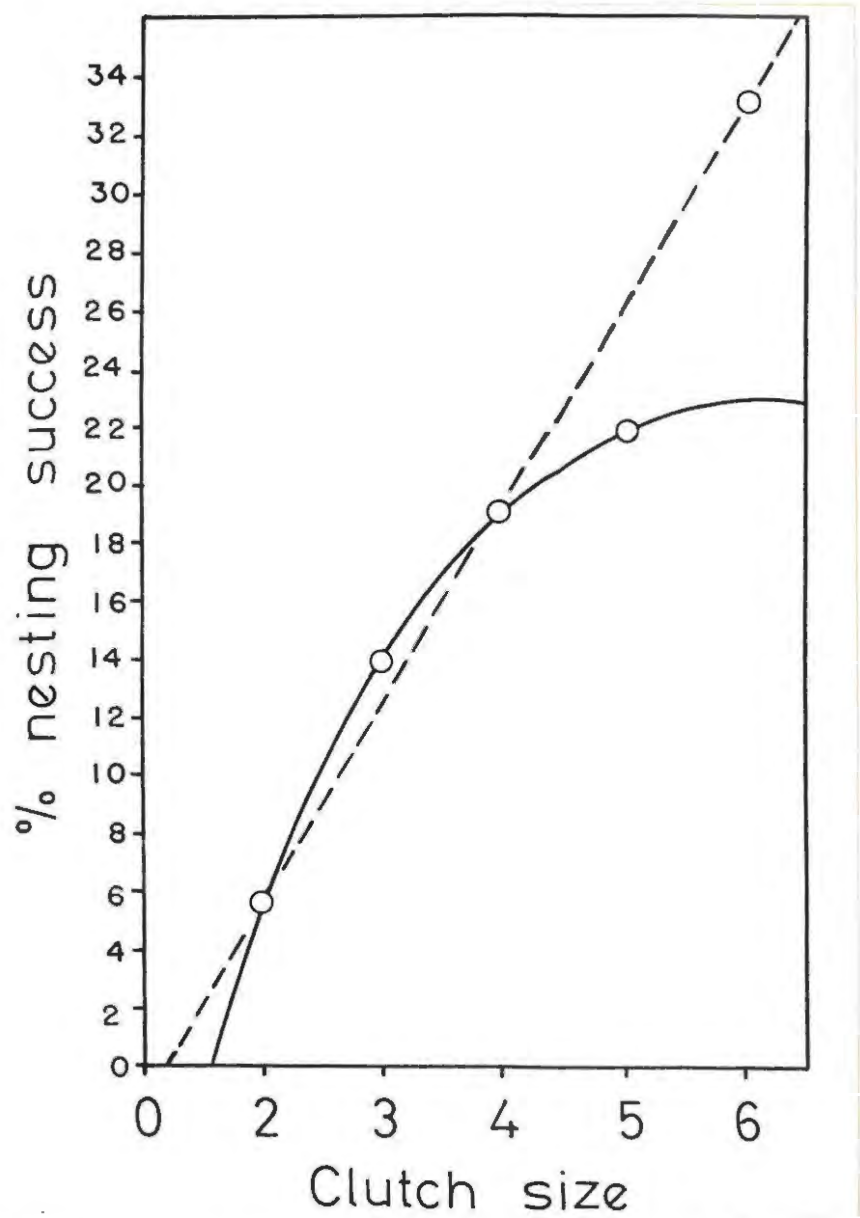

Fig. 30. Nesting success (expressed as a percentage of eggs that gave rise to flying young) related to clutch size. The solid curve is probably more reliable than the broken line, since data for clutches of 6 eggs were too few for adequate analysis.

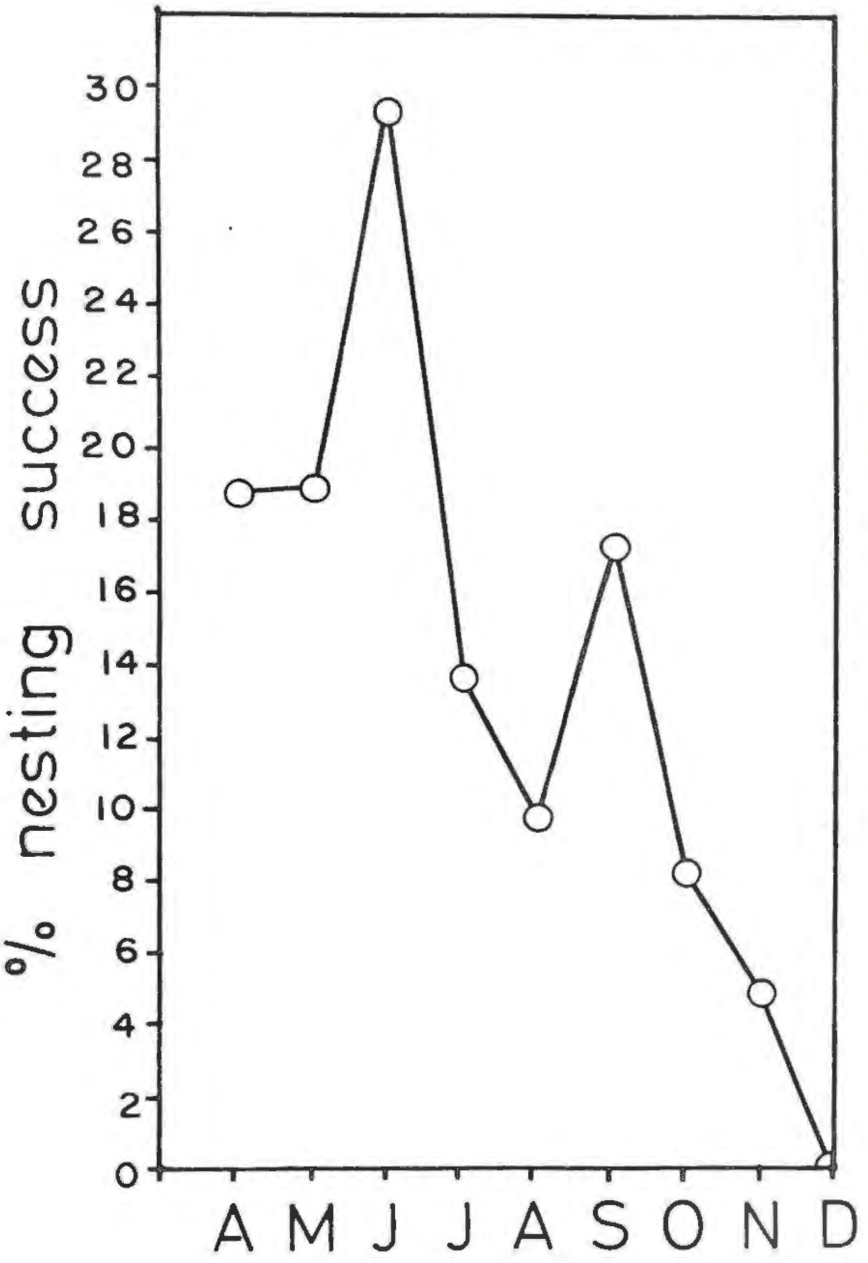

Fig. 31. Nesting success related to the month during the second breeding period (sample sizes as in Table 16).

Replacement clutches and later broods

Although not all replacement clutches are true second or later broods, it is probably as well to treat all types of replacement clutches together. Table 12 is a full analysis of replacement clutches in the second breeding period. All first clutches whether successful or not and which were not followed by a replacement clutch are not included in the table. From Table 12 it is clear that since only 28% of the first clutches were successful (i.e. gave rise to at least one flying young), 72% of the first replacement clutches replaced lost clutches and did not therefore constitute second broods. The success of the replacement clutches increases at the second replacement, most of which were laid by the time predation by cobras had ceased with the coming of winter. Subsequent clutches were decreasingly successful in the same way as breeding success declined as the breeding period advanced (Table 16) and for the same reasons. One of the main reasons for the decreasing breeding success was food shortage as evidenced by the starvation of many chicks, particularly the last of a brood to hatch, towards the end of the breeding period.

Table 12 shows that 16 pairs raised 2 broods, 12 pairs raised 3 broods and 4 pairs raised 4 broods. Four pairs raised 3 successive broods without any intervening unsuccessful clutches and all four of the pairs that raised 4 broods did so without any intervening failures. In the pairs nesting in the Camp Nest chambers SW:5 and SW:6, the last brood was lost because the whole of the SW nest mass collapsed in October 1965, just before the chicks were due to leave the nest. These chicks would otherwise almost certainly have been successful, in which case the pair in SW:6 would also have raised four successive broods without any intervening failures.

All the pairs which raised 3 or 4 broods (except one pair at nest X) lived in Camp Nest or No. 24, both large colonies with large nest masses, and the two largest in the study area. Most of the successful clutches in these pairs consisted of 4 or 5 eggs. I shall discuss the significance of these facts in Chapter 13.

The shortest time between the loss of a clutch of eggs and the laying of the first egg of the replacement clutch was only 2 days in the case of a weaver whose previous brood had been taken by a cobra. The time lag between the departure of a brood of successful chicks and the laying of the first egg of the next clutch averages longer (12.7 days, as opposed to 7.6 days after the loss of a clutch), although in two cases this time lag was only 5 days. It may, however, be as much as 20 days. The time lag between the abandonment of a clutch of infertile eggs and the laying of the first egg of the replacement clutch was 4 days in 3 instances and

6 days in another instance. All these periods of time lag between clutch replacement compare with the period of 6 days between the first shower of rain and the first egg laid in the third breeding period.

As soon as the chicks of a second or later brood have hatched, the chicks from the first brood or broods begin to help the parents to feed them. Young birds may therefore be only 25 to 30 days old when they start to feed the next brood. This happens with each successive brood, so that chicks of a fourth brood will be fed by their parents as well as the young of three previous broods. In this way I have recorded as many as 11 birds (9 young and 2 parents) feeding fourth-brood chicks in Camp Nest SW:6 and as many as 9 birds (7 young and 2 parents) feeding fourth-brood chicks in Camp Nest SW:3. This could mean that the parents need to do less work towards the end of a breeding period, by which time they are in highly worn plumage and possibly flagging a little from their exertion of several months' breeding activity. It is useful to have as many workers as possible at a time when food supply is dwindling.

During the incubation and nestling periods of second and later broods, the young of the previous broods continue to roost in the nest chamber with the parents until their numbers become too large. When there are as many as 6 young, the chamber becomes crowded and the young birds tend to sleep in adjacent chambers not occupied by breeding birds, although they do not usually move from the structural level in which they were raised, even after they have attained their adult plumage.

Post-breeding activity

As the breeding period draws to a close, fewer and fewer adults are caring for eggs or young. The pair bonds begin to break down and the birds begin once more to move rather more freely within their own nest levels. As more and more adults are freed from parental duties, the young birds bringing food to later broods are continually harassed by idle adults which often steal the food from them. In the struggle between a young feeding bird and a thieving adult, the food frequently drops to the ground, in which case the adult quickly flies down to eat it before the young bird has a chance to take any action.

Eventually there are no more chicks to care for and the last to leave the nests soon become independent. For the next four months, these last young birds are still in their juvenile plumage, but they finally moult into adult plumage and are "absorbed" into the activities of the community. They are no longer subordinate to the adults and the daily rhythm of a non-breeding colony are resumed. The pair ceases to be a unit. The disintegration of the pair bond may be accompanied by a decline in parental behaviour while the birds still have their last brood, and this could account for the starvation seen in some late-season chicks.

What is the fate of the young birds of the year after the end of the breeding period? Many of them get caught by raptorial birds, particularly the two goshawks Meliërax musicus and Micronisus gabar. The survivors stay on at the nest mass at which they were raised. Only one chick was ever found at a nest mass other than the one in which it was raised (Table 8), so it appears to be an uncommon occurrence for young birds to move from the home colony.

Chapter 6

INTERSPECIFIC RELATIONSHIPS IN THE SOCIABLE WEAVER NEST MASSES

In the foregoing chapters reference has been made from time to bird species other than sociable weavers, which use the weaver nests for purposes of breeding or roosting. The account which follows is a synthesis of the available information on these other species, both from the literature and from my own observations.

The pigmy falcon *Polihierax semitorquatus*

In many sociable weaver nest masses, one or more of the chambers may have a thick white deposit of pigmy falcon faeces on the threshold and possibly also in the entrance tunnel (Fig. 32). Of the 22 trees in the study area occupied by sociable weavers, 9 contained resident pairs of pigmy falcons; a further 3 nest masses unoccupied by weavers were occupied by falcons. The pigmy falcon (Fig. 33), a small member of the family Falconidae, has a widely discontinuous distribution in Africa. One population occurs in the Kalahari region where its range appears to be determined by the presence of the sociable weaver. The other population occurs in East Africa (Bowen 1931; Friedmann 1930b; Grant & Mackworth-Praed 1934; Mackworth-Praed & Grant 1952; Oberholser 1904; von Erlanger 1904) where it occupies the nests of other species of weavers.

Fig. 32. The under surface of Nest No. 19 showing the white faecal deposit at the entrance to a chamber occupied by a breeding pair of pigmy falcons <u>Polihierax semitorquatus</u>. The chamber to the upper left of the falcon nest contained young sociable weavers.

Fig. 33. A male pigmy falcon near its nest.

In the Kalahari, the pigmy falcons use the sociable weaver nests for roosting all the year round, and for breeding in summer (August to February). I have one record of a pigmy falcon roosting in a nest of the sparrow-weaver Plocepasser mahali. There is never more than one pair of falcons in a single sociable weaver colony, although adjacent colonies may be occupied by separate pairs of falcons if they are 1.5 Km. or more apart. Each pair takes over 2 or 3 chambers in a nest mass (cf. Hoesch 1935). One chamber is used for breeding and the other one or two for roosting. In winter the breeding chamber may also be used for roosting. Rarely, as in the case of nest No. 6, the falcons may take over so many chambers that the weavers will desert the nest mass. Normally, however, the two species live side by side and often breed in adjacent chambers.

In spite of this prolonged and enforced proximity, the weavers and falcons cannot be said to live in "harmony" together and the statement that "the Social Weavers do not seem to resent these little hawks" (McLachlan & Liversidge 1957) is quite unfounded. The falcons are essentially intruders and each time one of them appears in the nest tree, the weavers utter alarm notes and react as they would to a predator. The pigmy falcon is not, however, a frequent predator on the sociable weaver, and on the whole the two species probably derive some mutual benefit from one another: the falcons find suitable living quarters in the weavers' nests while the weavers must derive protection from the falcons' attacks on would-be predators, including man.

The giant eagle-owl Bubo lacteus

One of the commonest nesting sites of the giant eagle-owl in the Kalahari is the flattened top of the superstructure of a sociable weaver nest mass (Fig. 34). The weavers appear to ignore these large owls, which feed largely on small mammals and large insects in the Kalahari, although they will also take lanner falcons and chanting goshawks (Cade pers. comm.).

The barn owl Tyto alba

I have already mentioned that barn owls use cavities in the superstructure of sociable weaver nests, both for roosting and for breeding. Although the weavers evince some alarm when one of these owls flies to or from such a roosting place, I have no evidence to suggest that the owls eat anything but small mammals. As with the pigmy falcons, the weavers may derive some protective benefit from the presence of both species of owls, since owls would almost certainly not tolerate the activities of snakes or predatory mammals at the nest mass.

The martial eagle Polemaëtus bellicosus

In July 1963 Mr. Alec B. Daneel and I saw a martial eagle nesting on top of a sociable weaver nest mass in the Nossob River about 30 miles north of Twee Rivieren. This was probably an exceptional case, as I have not seen this species of eagle using such a nest site since then.

The pied barbet *Lybius leucomelas*

The pied barbet is the only member of the family Capitonidae which occurs in the Gemsbok Park. Like other South African barbets it is a summer nester, excavating its own nesting hole in a tree, but in winter it frequently roosts in the nest chambers of the sociable weaver where the ranges of the two species overlap. The pied barbet is uncommon in the Kalahari (probably because of the paucity of suitable fruit-bearing plants) but is common in South West Africa (Hoesch 1955; Maclean 1960).

The reaction of the weavers to the barbet's intrusion is one of intense alarm. The following account is taken from my field notes:

> "26 March 1965 - Camp Nest:
>
> 1639 hours: A pied barbet arrives at the tree. Weaver No. 285 at once tries to chase it off, but the barbet is dominant and chases the weaver instead. Each chase elicits a short "chewiii" fear call from the weaver. The barbet tries several times to enter a chamber but is chased by No. 285.

The barbet finally manages to enter and weaver No. 39 pops out of the adjacent chamber. Both weavers chase the barbet as it emerges again, but the barbet turns on them and they flee.

1648 hours: A small group of weavers arrives at the tree; the barbet chases some at the Southern nest mass, but the weavers prevent the barbet from entering the chambers. The barbet then flies to Western mass where there are no weavers. It enters a chamber (the weavers at Southern mass make no attempt to prevent it) and comes out again.

1653 hours: Weavers all depart.

1700 hours: Barbet enters a chamber and stays there.

1752 hours: About 70 weavers arrive; there is great excitement as the barbet is discovered. The weavers gather on a branch below it or hover just below the chamber entrance uttering alarm calls. The barbet emerges and the intensity of the weavers' alarm calls increases. The barbet scatters the weavers by chasing them to and fro.

1759 hours: The barbet enters the same chamber again and stays there. The weavers take turns hovering below the entrance and the whole colony utters alarm notes for 3 minutes. The weavers then resume normal activities.

1816 hours: All is quiet as the birds settle down for the night."

A barbet, possibly the same one, was seen at Camp Nest two days later, but that appeared to be its last visit to Camp Nest.

Why the weavers should resent the barbet's intrusion so violently is not at all clear. It is very unlikely that a frugivorous bird like a barbet would eat young sociable weavers even if it encountered them in the nest chambers. Perhaps the pied barbet resembles a pigmy falcon to some extent.

The red-headed finch *Amadina erythrocephala*

Throughout its range the red-headed finch (Fig. 35) uses old nests of other birds, usually Ploceidae, for breeding purposes. It is a common bird in the Kalahari where the sociable weaver nests provide eminently suitable nesting places. Of 30 red-headed finch clutches, about two-thirds were in nest masses unoccupied by sociable weavers, the rest in occupied nest masses. I have only one record of a red-headed finch evicting a pair of breeding sociable weavers from their nest chamber and subsequently laying a clutch of eggs in the chamber. Thus the red-headed finch does not seem to constitute any serious competition for nesting places with the sociable weavers when the weaver populations are low. It is interesting that the close proximity of

Fig. 34. A young giant eagle-owl Bubo lacteus on top of sociable weaver Nest No. 7. Note the coarse sticks of the superstructure.

Fig. 35. Male red-headed finch Amadina erythrocephala.

the sociable weavers nest chambers within the mass has led to the red-headed finch's becoming highly colonial in the Kalahari, whereas it is not usually colonial during its breeding season elsewhere in its range, although it is gregarious when not breeding.

Even when the finches and weavers are breeding side by side in one nest mass, there appears to be no animosity between the two species as a rule. Chambers occupied by breeding finches are recognizable by the fact that the finches build up the entrances until they are less than half the normal diameter; the finches also have pure white eggs and line the nest chamber thickly with grass and feathers. Furthermore the finches sit very tightly and can often be caught by hand in their nests. I have not found any evidence to suggest that the finches use the chambers for roosting in when they are not breeding.

The familiar chat *Cercomela familiaris*

Familiar chats (Fig. 36) use only deserted sociable weaver nest masses. I found three chat nests in two separate nest masses, one about 6 feet (1.8 metres) up in the *Acacia haematoxylon* tree, and the other lying partly on the ground where it had fallen when its supporting branch broke. The familiar chat builds a soft, neat cup of hair in the chamber and lays bright green eggs. However, these chats prefer to nest in the calcrete cliffs and use the weaver nest chambers only rarely.

Other species of birds

Plowes (1946) mentions four other bird species which have been reported as using sociable weaver nests for roosting or nesting purposes: Egyptian goose *Alopochen aegyptiacus*, rosy-faced lovebird *Agapornis roseicollis*, yellow-billed hornbill *Lophoceros* (= *Tockus*) *flavirostris* and lilac-breasted roller *Coracias caudata*. The Egyptian goose apparently uses cavities or depressions in the superstructure for nesting, as do the owls, but this seems to occur only in the extreme eastern part of the sociable weavers' range. Hoesch (1935) states that the rosy-faced lovebird uses sociable weaver nests both as living and breeding places. It is unlikely that either the yellow-billed hornbill or the lilac-breasted roller normally enter the nest chambers, but they may roost in the superstructure, although I have never seen them evince any interest in the nest masses in the Kalahari. Hoesch (1935) also includes the grey-headed sparrow *Passer diffusus* among the "guests" of the sociable weaver.

Species not directly associated with the sociable weaver nest mass

A tree containing a sociable weaver nest mass is seldom occupied by any other bird species not directly associated with the nest mass. One fairly common exception is the masked weaver

Fig. 36. The familiar chat Cercomela familiaris.

Ploceus velatus, itself a rather gregarious species, which may build its nests high up in a tree already containing a sociable weaver nest mass. There seems to be no antagonism between the two species. Although such birds as drongos, shrikes, tits, flycatchers, sparrows, bee-eaters and other small birds are often seen perched in a sociable weaver tree or feeding among its branches, even quite close to the nest mass (I have seen the grey tit *Parus afer* feeding right on a nest mass), they do not nest in the same tree as the weavers. They may, however, roost in the tree at night. Cape sparrows *Passer melanurus*, grey-headed sparrows *P. diffusus*, yellow canaries *Serinus flaviventris* and shaft-tailed widow birds *Vidua regia* all used to roost in the Camp Nest tree at night; any possible antagonistic behaviour towards these species by the sociable weavers was partly precluded by the fact that the weavers almost invariably went to roost earlier and left their nests later than did the other species.

Once a fiscal shrike *Lanius collaris* arrived at Camp Nest and showed some interest in the nest mass. The shrike's presence caused some alarm among the weavers, but it did not seem to try to enter any of the chambers.

Chapter 7

PREDATORS

The sociable weaver is preyed on by relatively few animal species, but predation is nevertheless high. The predators may be divided into two groups: (a) predators away from the nest and (b) nest predators.

Predators away from the nest

The predators in this category include species preying on adult weavers or flying young. The following are the most important:

yellow mongoose *Cynictis penicillata*
chanting goshawk *Meliërax musicus*
gabar goshawk *Micronisus gabar*
Falco spp.

I have found the remains of adult sociable weavers in a hole in the trunk of the Camp Nest tree where a yellow mongoose used to live. The mongoose probably captured the weavers on the ground below the nest mass as they came to collect straws for building. However, this mongoose does not normally live in holes in trees, being a burrowing mammal, so the extent to which it preys on the sociable weaver is difficult to estimate.

On the two occasions that I have seen weavers caught by avian predators, the weavers were handicapped. On the first occasion, a chanting goshawk took an adult weaver in the top of the Camp Nest tree where it had got caught on a thorn by a plastic leg-ring. On the second occasion, a gabar goshawk took a flying juvenile weaver which I had just released after ringing it; although the young bird flew well, it was probably a little bewildered and fell an easy prey to the hawk. The gabar goshawk is a common bird in the Kalahari where it hunts with great facility among the branches of the tree, so that it probably preys far more widely on sociable weavers than I have actually observed.

Although I have never seen any member of the genus *Falco* take a sociable weaver, it is very likely that these falcons will do so on occasion. My evidence is circumstantial. For instance, I have seen a rock kestrel *F. tinnunculus* take a young red-headed finch on the wing, after the finch had flown out of its nest chamber in a sociable weaver nest mass. I have also seen the red-necked falcon *F. chiquera* feeding on small passerines (e.g. larks). It is therefore possible that these two falcons as well as the lanner falcon *F. biarmicus* and the greater kestrel *F. rupicoloides* feed on sociable weavers from time to time. Pigmy falcons probably do not catch adult weavers, although these falcons can be trapped by using live adult sociable weavers as bait.

Nest predators

In the Kalahari there are only two predators that inflict heavy losses on the eggs and young of the sociable weaver, namely the Cape cobra *Naja nivea* and the honey badger *Mellivora capensis*. Cobras appear to be the only snakes in the region which are capable of invading the weaver nests; they are often found in the nest chambers and it is worthwhile to examine their method of nest examination, particularly since I have heard doubt expressed about their ability to do so.

On 29 March 1965 I arrived at nest B1 to find a Cape cobra on top of the superstructure of the nest mass. These snakes climb trees with great facility as I had previously seen in the field. The cobra slowly worked its way down the almost vertical side of the superstructure by burrowing with its head through the spaces between the stick, and anchoring its body against the sticks in the spaces so formed, until its head was at the level of the substructure. It continued downwards until its head and about a foot of the anterior part of its body hung in the air below the nest mass.

Then raising the head and testing the air with its tongue, the snake found a peripheral chamber, which it entered. The entire snake which was about five feet (1.5 metres) long just fitted into the chamber by rolling up in coils. Finding the chamber empty (as were all the others, since the weavers had not yet begun to breed), the snake emerged until a foot or more of the body hung down from the chamber entrance (Fig. 37). Raising the head again, it found and entered the adjacent chamber (Fig. 38). It continued to examine each chamber in turn, taking 2 hours to investigate 20 chambers. The long time taken to examine a nest mass reflects the laborious nature of the nest-examination process. The snake had to move with care so that it did not slip and fall, which it almost did once or twice. From time to time the snake would remain in a chamber for several minutes, apparently resting from its exertions.

Finally the snake emerged from the last chamber and moved back up the side of the superstructure (Fig. 39) in the same way as it had come down. After a few minutes it left the tree and disappeared. Eleven days later on 10 May, the same snake, recognizable by an asymmetrical black mark on its head (Fig. 38), was back at B1 which at that time had eggs in 5 chambers and chicks in two chambers. My next visit indicated that the cobra had eaten 12 eggs and 7 small chicks. The birds of B1 soon laid again, some within 3 days (see Chapter 5).

The depredations of a single cobra on a sociable weaver colony are considerable, and would be disastrous for the species if the weavers did not lay replacement clutches so soon after being robbed. A striking example of this was shown at nest B8. On 3

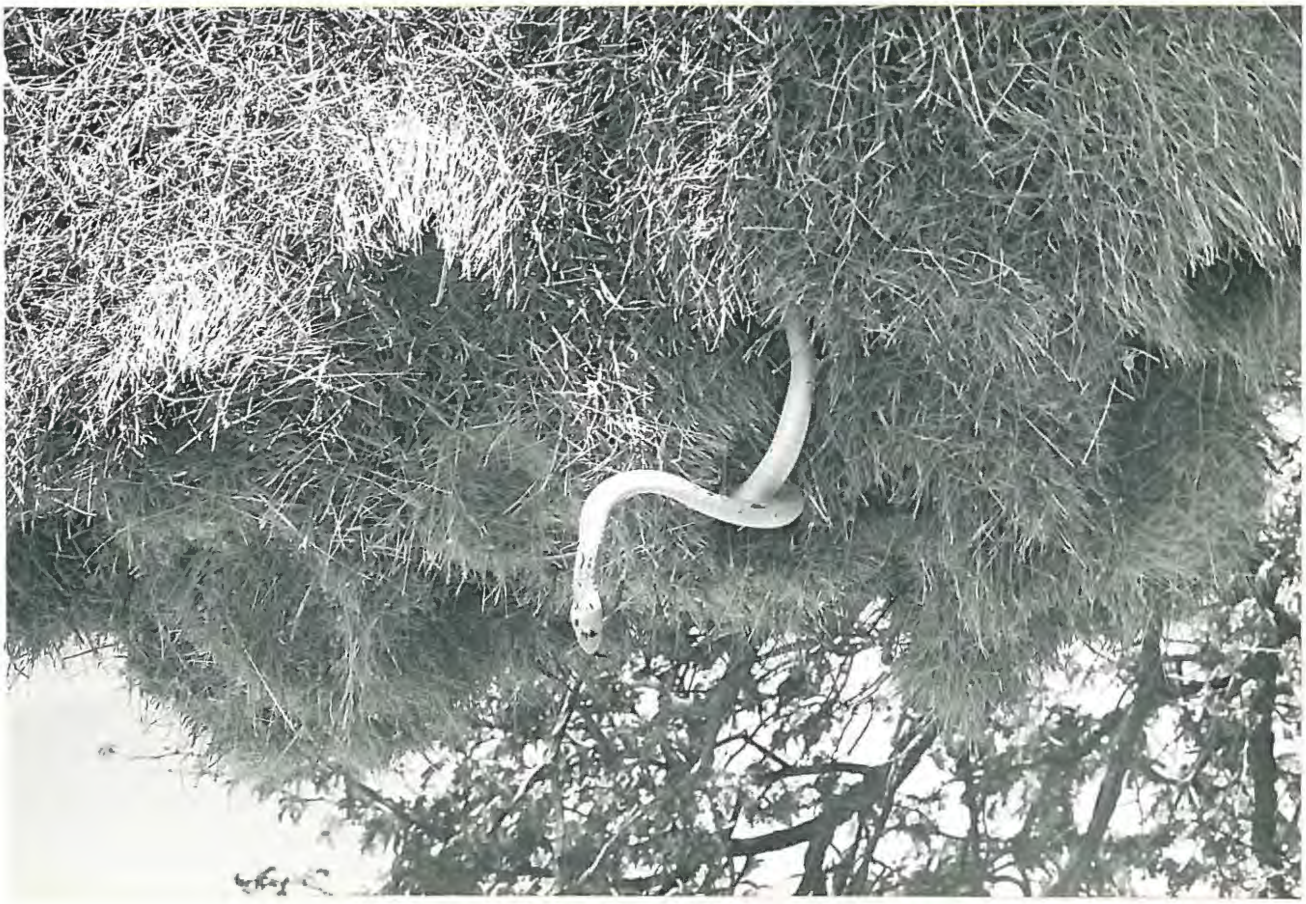

Fig. 37. A. A Cape cobra _Naja nivea_ hanging from a chamber of Nest B1.

Fig. 37. B. The same snake seen ventrally.

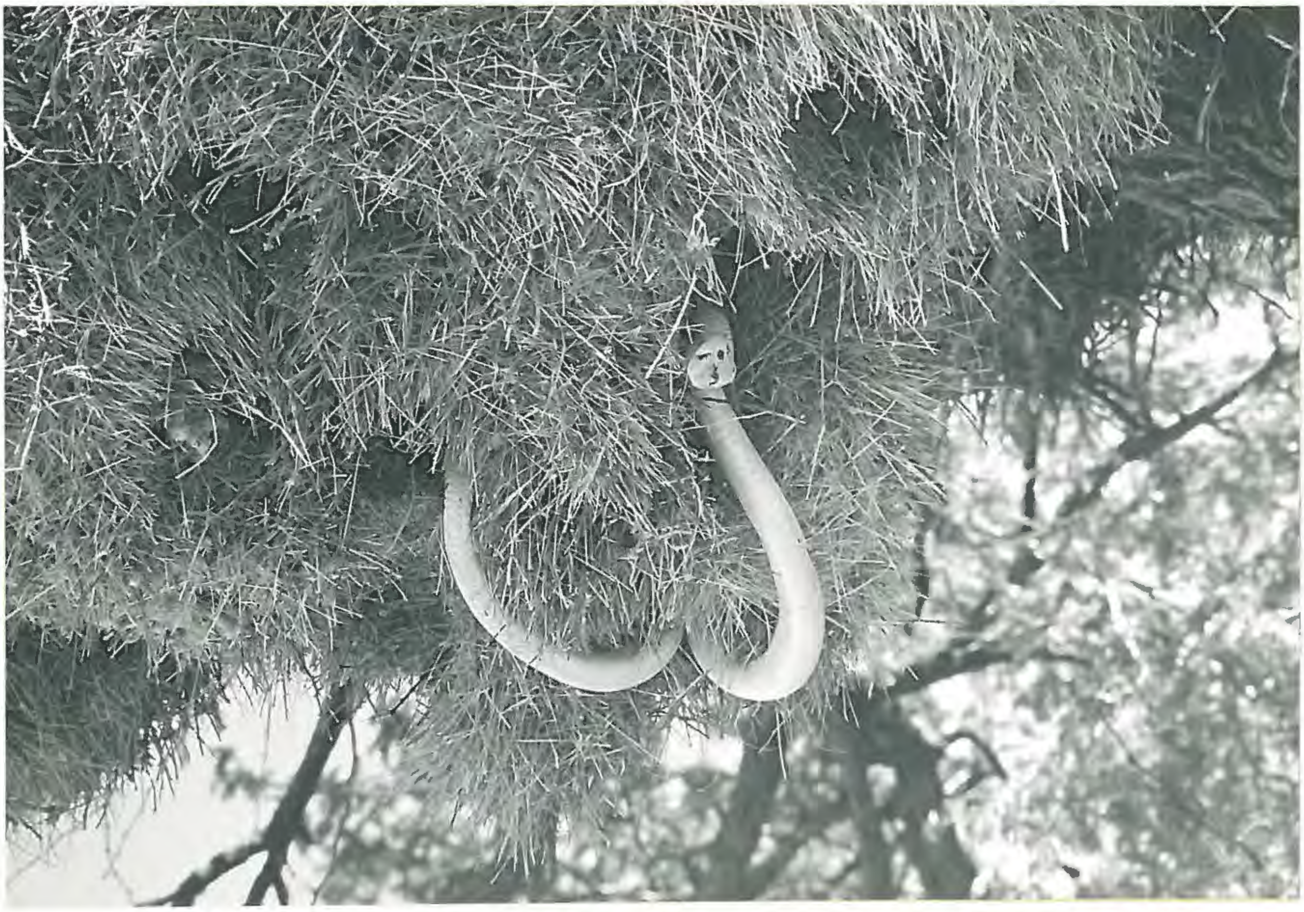

Fig. 38. The Cape cobra anchors itself in one chamber as it emerges to find the next chamber.

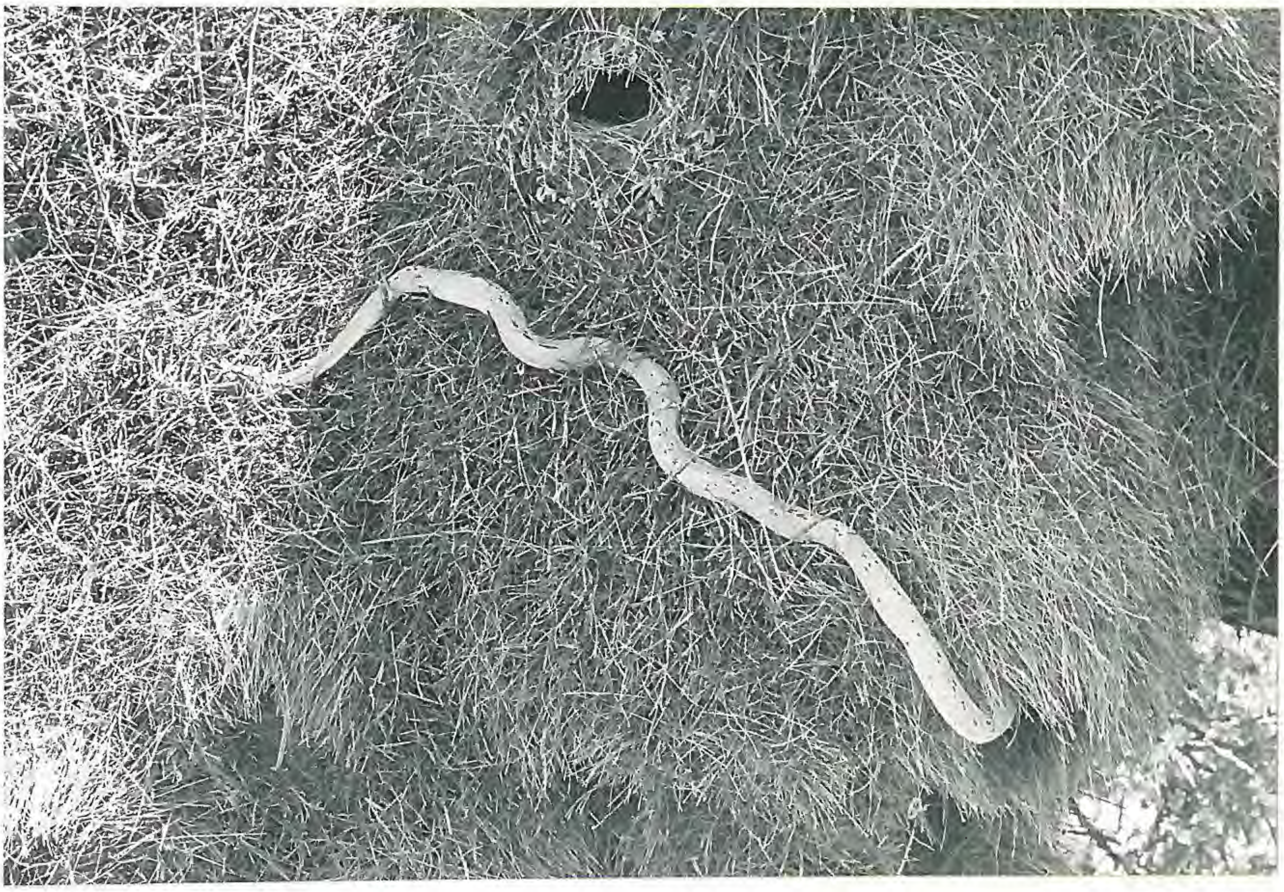

Fig. 39. After examining the entire nest mass, the cobra moves towards the superstructure of the mass.

May 1965 eleven chambers contained a total of 37 eggs, and five chambers contained a total of 16 chicks. On 6 May a large Cape cobra was seen examining the nest. Four days later when I again visited the nest, all the eggs and chicks had disappeared. Assuming no further predation between 3 and 10 May, this one snake had eaten about 36 chicks (calculated from estimated hatching dates of the eggs, plus the 16 chicks already present) and 17 eggs. In any case, the entire contents of the nest mass had been robbed.

However, new clutches had been started within 4 days of the snake's visit. Several chicks were then raised successfully, but between 19 and 22 July, during the same breeding period, a mammalian predator (almost without a doubt the honey badger) destroyed 10 chambers completely, accounting for 9 eggs and 25 chicks, most of them partly feathered already. After extensive reconstruction the weavers laid replacement clutches and raised numerous young successfully. Even after the reconstruction, however, the number of chambers was reduced from 23 to 17. The destruction of the nest had weakened the whole mass so that it began to fall apart and by the end of the breeding period in December 1965, only 11 chambers remained.

Predation by Cape cobras at B8 was again heavy during the following breeding period (January to May 1966). By March 1966 the number of chambers in the nest mass was up to 14. On 22 February a cobra took some 30 eggs and 2 chicks. Cn 1 March, 9 of the 14 chambers contained eggs and one contained chicks, and by 15 March only 3 chambers contained incomplete clutches. Since there was no nest damage, only a cobra could have been responsible for the robbery of a minimum of 22 eggs and 3 chicks. On 22 March a cobra was again found investigating the chambers of B8, but a week later there were replacement clutches in 6 chambers. On 5 April yet another cobra (at least 3 different cobras were involved at B8) was at B8 and a week later the chambers were still empty. By this time the weavers may have given up the unequal struggle. These data are summarised in Table 17.

Cape cobras were found at 7 of the 14 weaver colonies under regular examination at some time during the study period. All but one of these records were during the months of February to May, with most records in May (Table 18). No snake predation was noted during the winter months after 17 May, by which date the first frosts had probably driven the snakes underground for hibernation.

Table 17. Predation by Cape cobras *Naja nivea* and honey badgers *Mellivora capensis* on sociable weaver nest B8 in the second and third breeding periods.

DATE	EGGS TAKEN	CHICKS TAKEN
6. 5.65	17	36
20. 7.65	9	25
22. 2.66	30	2
1-15. 3.66	22	3
22. 3.66	6	0
5. 4.66	10	0
TOTALS	94	66

Table 18. Number of sightings of Cape cobras per month at sociable weaver nests throughout the whole study period.

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
0	1	2	3	5	0	0	0	0	0	1	0

No cobras were seen at the weaver nests during the first breeding period (December 1964 to February 1965), but there were numerous unaccountable disappearances of eggs and chicks. It seems likely that during the summer months the snakes are active only at night, in which case I would have overlooked them. The only summer record (other than late summer) was a cobra shot at Camp Nest in November 1965; this snake was dissected to reveal 6 sociable weaver chicks in its stomach.

It is unfortunate that there was little sociable weaver breeding activity during the breeding season of the pigmy falcons, as it would have been interesting to determine whether or not nests occupied by falcons suffered less snake predation than other nest masses. The fact that I have never seen cobras at nest masses occupied at the time by pigmy falcons is probably due more to the fact that the falcons breed in summer when the snakes are not so active during the day than to the fact that the falcons keep the snakes away (if indeed they do). There is no evidence, however, that a clutch of pigmy falcon eggs was ever taken by snakes in the study area.

The first sociable weaver breeding period did in fact coincide with the pigmy falcons' breeding season, but the survival rate of weaver chicks was so poor at all the nest masses that any attempt at correlating snake predation with falcon occupation is worthless. But to what extent do the pigmy falcons themselves prey on the weaver chicks ? That they do so at all is based on slender evidence; around 12 August 1965 a pair of pigmy falcons arrived at nest B1 where 3 weaver chicks disappeared on about that date. Possibly the same pair of falcons was responsible for the loss of 2 weaver chicks at nest B3 at this time. This was the very beginning of the falcons' breeding season in 1965 and the arrival of a female pigmy falcon at B3 was followed by the finding of the remiges of two large weaver chicks below the chamber in which the falcon had been roosting (as evidenced by droppings on the threshold and regurgitated pellets on the chamber floor). This same female (which was colour-ringed) had been investigating chambers in B1 and B3 and laid her first egg in a chamber of B1 on 18 August.

Similarly in July 1965, a pigmy falcon moved into B3 for roosting purposes at the height of the weavers' breeding period; a clutch of 5 weaver eggs was found lying on the ground below a chamber which contained fresh faeces and regurgitated pellets of the falcon. However, since the two species of birds have been found breeding successfully in adjacent chambers, it seems probable that a falcon will take weaver chicks (or evict the eggs) only if it is looking for a roosting or breeding chamber and happens to encounter the chicks in one of the chambers it has entered.

From time to time I found a nest mass extensively damaged, sometimes by being torn open from the side, or by having a large hole a foot or more in diameter bored through the mass from top to bottom. It was long a puzzle as to what animal could be responsible for this destruction until one day I saw a honey badger climbing the trunk of nest tree No. 5. Twelve out of 22 separate nest masses under regular observation suffered some destruction. Many chicks and eggs were taken from these damaged nests, but any left in chambers that fell to the ground were simply left. It seems strange that a mammal such as a honey badger, which probably has a good sense of smell, would ignore any food so easily available, but it may be that the honey badgers do not recognise a nest mass on the ground as a potential source of food supply.

The seasonal effects of snake predation at the nests shows up in Table 16 (Chapter 5). Although the humber of eggs laid per month was highest in April and May 1965, the percentage of survival of the chicks was highest in June after snake predation had ceased. The subsequent decline in nesting success was due not to predation but to food shortage, as already mentioned in Chapter 5.

Other possible predators

There are a few other animals in the Kalahari which may take sociable weavers when they can get them. These include the caracal *Felis caracal*, the Cape wild cat *Felis lybica*, the red mongoose *Myonax ratlamuchi*, the fiscal shrike *Lanius collaris* and the puffadder *Bitis arientans*.

The two cats and the mongoose can climb trees, but it is doubtful if they can tear open the weaver nests to get at the young or eggs. By analogy with the yellow mongoose, they may catch the weavers on the ground when the birds are feeding or collecting nest material, since all three of these mammals are at least partly diurnal in their feeding habits in the Kalahari, particularly in winter.

I once saw a fiscal shrike at Camp Nest perch below the nest mass on a branch, and then fly to the side of the nest mass, but at no time did the bird attempt to enter a chamber. It may take fledglings at times, and may even take adults, as I have seen fiscal shrikes take birds as large as a Cape sparrow. It is, however, of little consequence as a predator.

The inclusion of the puffadder in this list of predators is based on a report in Rudebeck (1956) who quotes Farre (1954) as saying that "several fat puffadders" were found in a sociable weaver nest mass cut down by farmers for cattle feed. It seems to me unlikely that the puffadders could have climbed the tree, let alone get into the nest chambers. It is possible that the snakes were found among the nest débris if it had been left for a day or two after being cut down.

Effect of nest predation on breeding success

Obviously the observed predation in the field was a fraction of the total predation, since most of the losses of chicks in the study area were not accounted for. The heaviest predation observed was at B8 (Table 17) where almost a third of the total losses of eggs and chicks were due to accountable predation. Snakes do not damage the nest mass at all during feeding, so that most losses were probably due to cobras. The Cape cobra is the most important single predator of the sociable weaver in the Kalahari. To what extent this snake takes adult weavers in the nests at night is not known, but, because of the birds' habit of bursting out of the chambers in a body when disturbed, I would think that not many fall prey to snakes.

The effect of the honey badger on breeding weavers may be considerable when extensive damage is done to the nest mass, but it is not a very frequent occurrence. Honey badgers are wasteful predators where the weavers are concerned, almost half the losses of chicks and eggs being due to collapse of portions of the nest mass, and not to actual robbery. The honey badger does not climb trees easily because of its short legs and this may discourage more widespread badger predation.

Towards the end of the breeding periods, many juvenile weavers are lost after leaving the nest. Most of them are probably taken by the smaller raptorial birds already mentioned, while others may fall prey to small carnivorous mammals.

Predator-reactions of the sociable weaver

In Chapter 4 I dealt with the reactions of the weavers to snakes at the nest. The birds' reactions to pigmy falcons is very similar, but their reaction in the presence of goshawks is radically different. Should a chanting or gabar goshawk (or a falcon or kestrel) fly past a tree in which a colony of weavers is building or just sitting around preening, there is a sudden flurry of wings followed by dead silence; the weavers have in effect disappeared, although they have not entered the nest chambers. When the hawk has passed out of sight, a few tentative contact calls are heard from the weavers which gradually begin to re-appear from behind bunches of leaves where they have been hiding. Should the hawk land in the tree, the weavers flee panic-stricken to the opposite side of the tree and huddle together in bunches. They may utter alarm notes, but are usually silent. Should the hawk attempt to chase the birds, they flee again in close bunches, uttering the piercing "chwiiii" fear call, a single short note. This note may be uttered by birds caught in a mist net and has the effect of causing the rest of the colony to utter intense alarm calls.

I have already described the predator-reactions of chicks in the nest chambers (begging when still blind, crouching when only partly feathered, and bursting out of the chamber when fully feathered). It was unfortunately never possible to observe what effect this bursting out of the nest chamber had on a snake at the nest.

Chapter 8

PARASITES AND NEST FAUNA

The sociable weaver is remarkably free from parasites both as adult and nestling. The nest material is, however, inhabited by a large number of invertebrates, mainly arthropods, as well as the few vertebrates such as skinks (Lacertilia: Scincidae) which have already been mentioned.

Parasites of adult weavers

Ectoparasites

Adult sociable weavers are almost completely free from ectoparasites, and only a single feather louse (Mallophaga) was ever found on a weaver. The insect was on the bird's head, but was not recovered. Only three louse flies (Hippoboscidae) were found on adult weavers; these insects occurred on other members of the Ploceidae which were examined in the Kalahari and were not confined to the sociable weaver. It is again noteworthy that the degree of infestation was infinitesimal.

Endoparasites

Dissected weavers were examined only macroscopically for endoparasites. The only ones found were nematodes which occurred in the abdominal air sacs of the birds. These worms were identified as _Diplotriaena ozouxi_. The infection is summarized in Table 19. Females suffered a higher infestation (51.2%) than males (24.7%) and the left abdominal air sac of both sexes was usually more heavily infested than the right air sac. The reason for this was not evident.

The mean weight of infected weavers (27.5 g.) did not differ significantly from the mean weight of uninfected birds (27.3 g.); the weights of both infected and uninfected birds had a similar distribution about the mean. Even very heavily infected birds, such as one with a total of 19 nematodes in its air sacs, showed no loss of weight or other apparent ill effects, even though the air sacs were sufficiently distended by the worms to apply pressure to the liver and adjacent organs in the body cavity.

The nematodes are white and threadlike, averaging 31.4 mm. in length (mean of 20 randomly selected worms). Infected birds had a mean of 4 worms each (2.4 in the left air sac and 1.6 in the right air sac). How the worms get into the respiratory system was not worked out; dissection of lungs and other parts of the respiratory system revealed no sign of lesions or of further infestation.

Table 19. Infection of sociable weavers by the nematode <u>Diplotrisena</u> <u>ozouxi</u> in the right and left abdominal air sacs.

"F" = females

"M" = males

"nc" = not counted.

DATE	SEX	NUMBERS OF NEMATODES	
		RIGHT SAC	LEFT SAC
9.11.64	M	nc	nc
9.11.64	F	nc	nc
24.11.64	M	nc	nc
8.12.64	F	nc	nc
8.12.64	F	nc	nc
8.12.64	F	nc	nc
17.12.64	F	nc	nc
17.12.64	F	nc	nc
29.12.64	M	nc	nc
29.12.64	F	nc	nc
29.12.64	M	nc	nc
29.12.64	F	nc	nc
8. 3.65	F	nc	nc
23. 3.65	M	1	6
23. 3.65	M	0	1
31. 3.65	F	nc	nc

8. 4.65	F	2	1
8. 4.65	F	1	1
8. 4.65	M	0	3
8. 4.65	F	1	0
19. 4.65	M	3	2
19. 4.65	M	4	3
3. 5.65	M	0	3
17. 5.65	M	1	2
24. 5.65	F	0	1
14. 6.65	F	0	2
14. 6.65	F	9	10
24. 6.65	F	0	3
8. 7.65	M	2	0
15. 8.65	F	0	1
30. 9.65	M	0	2
11.10.65	M	2	2
22.11.65	M	8	3
17. 1.66	F	0	4
24. 1.66	F	0	1
1. 2.66	F	4	2
1. 2.66	M	1	3
22. 2.66	F	0	3
22. 2.66	M	1	1
TOTAL	40	40	60
Mean		1.6	2.4

Parasites on nestling weavers

Ectoparasites

The only ectoparasites of nestling weavers was a blood-sucking dermestid larva of the genus Dermestes (Coleoptera). These larvae are up to 6 mm. in length, light brown in colour and occur on the toes and tarsometatarsi of the young birds; I once found a larva on a bird's flank. The insects are ventrally concave so as to fit over the contour of the bird's legs and feet where they lie longitudinally orientated, with the mouthparts embedded in the skin or scales of the host. If a larva was pulled off (and this required some force), a drop of blood or plasma would ooze from the small wound on the bird's foot.

There were not usually more than one or two parasites per nestling, and never more than three. The nestlings appeared to suffer no ill effects from the parasites, although it is possible that, in a poor season when food is scarce, these parasites may have debilitated the young birds and thereby contributed towards the death of starving chicks, which were probably doomed already.

Endoparasites

No endoparasites were found in the few sociable weaver chicks which I examined.

Nest fauna

Sociable weaver nest masses are crawling with invertebrates which inhabit the substructural matrix and, to a lesser extent, also the superstructure. In about 1.5 cu. feet of the substructure of a part of Camp Nest, there were 143 arthropods of which 32% were roaches (Dictyoptera), almost certainly the same as those found in the western Transvaal by Collias & Collias (1964). 31% were larval beetles of the family Dermestidae, subfamily Attageninae, but these were never found on the birds in the nest chambers. 14% were adult Dermestidae of the genus Dermestes, almost certainly the adults of the ectoparasitic larvae on the weaver nestlings. Pseudoscorpions of the species Diplotemnus segregatus formed 8% of the nest fauna: these were the only adult arthropods that were occasionally found in the nest chambers of occupied weaver nest masses. The rest of the nest fauna consisted of some incidental insects which were not normally associated with the nest masses, with the possible exception of some adult and larval beetles of the genus Anthrenus (Dermestidae).

Chapter 9

FOOD AND FEEDING

The main questions to be answered in relation to feeding in the sociable weaver were:

(a) Where do the birds feed in relation to the nest ?

(b) When do they feed ?

(c) How do they find their food ?

(d) What do they eat ?

(e) On what do they feed their young ?

Most of the observations on feeding areas and feeding times were done at Camp Nest. Stomach contents of weavers trapped all over the study area were analysed. Feeding methods were observed at various localities whenever the opportunity presented itself. The aviary birds also provided much useful information on feeding.

Feeding areas

The map in Fig. 40 shows the feeding areas of the Camp Nest weavers. The birds seldom fed more than a mile (1.6 Km.) from the nest tree. Within the feeding area, they had certain favourite sites, the main ones being the camp itself, the Bushman settlement and the kraal where the goats were usually housed at night. The calcrete on the eastern bank of the Nossob River appeared to be the limit of the weavers' feeding range to the

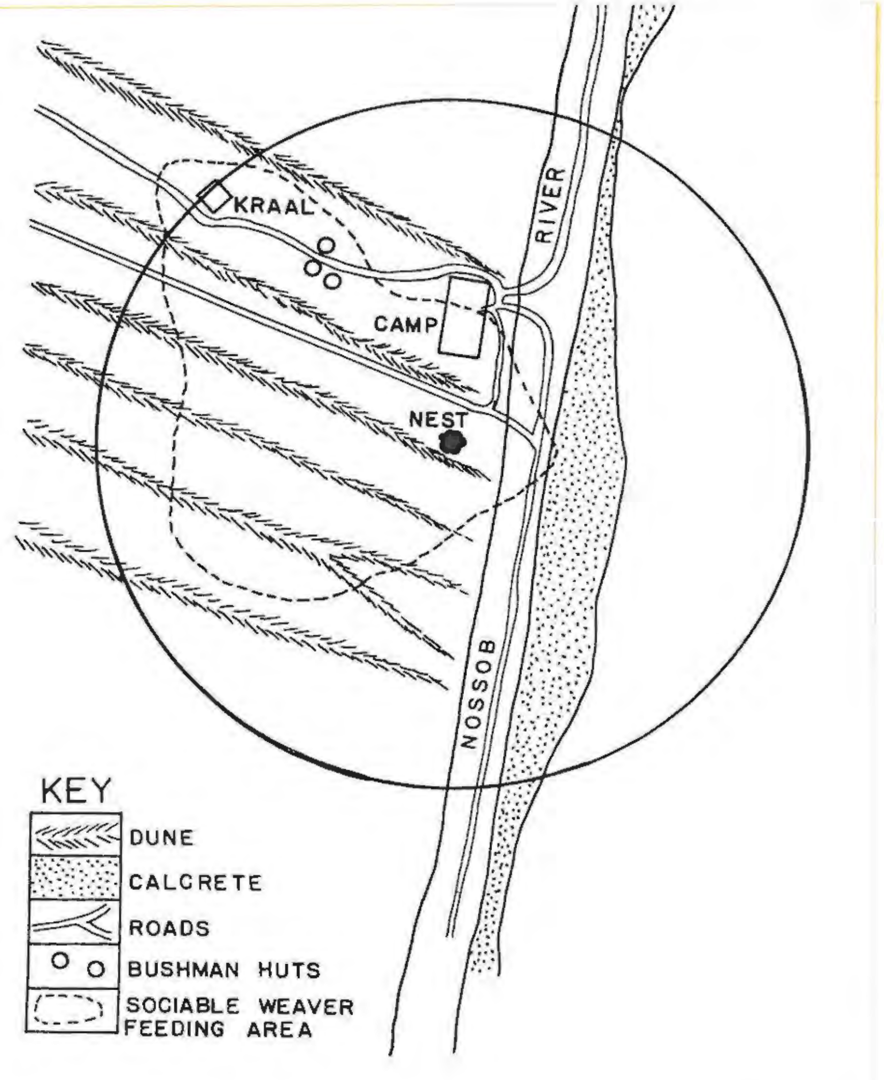

Fig. 40. Map showing the normal feeding area of the sociable weavers at Camp Nest. The large circle is 1 mile (1.6 Km.) in radius. Only a few of the relevant dunes are shown in the diagram.

east. The birds were very seldom seen outside the feeding area enclosed by the broken line. It is therefore unlikely that the 3 weavers trapped initially at Twee Rivieren and subsequently retrapped at nest 3M (3 miles south of Twee Rivieren) between 7 and 10 months later (Table 8) had originally come from nest 3M. More probably they were originally inhabitants of Camp Nest and later left the area for 3M, possibly as a result of having been caught for ringing purposes in the first place. All other birds recorded feeding at Twee Rivieren were from Camp Nest. There were never any weavers from nest X a little over a mile to the east. At other nests in the study area the birds have always been feeding within a mile of the nest. The feeding grounds around a nest or group of nests are more or less exclusive to the inhabitants of those nest masses, but not as exclusive to one colony as the nest mass itself.

Feeding times

Although sociable weavers can be found feeding at any time of the day from before sunrise to just after sunset, their main feeding times are during the first half of the morning and the latter half of the afternoon. The birds start to feed as soon as they arrive at the feeding grounds after leaving the nest in the morning at rising time (Table 9). The length of the morning feed will depend on various factors, namely:

(a) food supply;

(b) weather conditions;

(c) the breeding condition of the weavers;

(d) air temperatures.

In the summer when air temperatures in the shade reach 35°C and more, the weavers usually return to the nest by 1000 hours, provided that the food supply is adequate. During a severe drought, they may stay away much longer in the morning, probably because food is harder to find; their feeding is usually confined to the shade of trees when temperatures are high, since the desert sand can reach as much as 70°C in the sun. In cool or mild weather (between about 18° and 25°C) during a drought, the birds may remain away from the nest all day.

However, after good rains when food is abundant, the birds return to the nests by mid-morning, even in winter when the days are cool and the birds do not need to seek shade. If the temperature is less than about 10°C (which is really cold for the Kalahari during the day), the birds return to the nest for shelter. But the weavers feed under most weather conditions except when it is raining. Even a strong gale does not drive them back to the nests when they are feeding.

During a breeding period, food is apparently abundant, but adults have to find extra food for the young and will continue feeding until late morning (about 1100 hours) and will resume feeding in the early afternoon (about 1400 hours). In mild weather the siesta may be very short, or the birds may not even take a siesta, particularly when they have large chicks to feed. The somewhat shorter days in winter may necessitate their having to feed all day if late summer rains are followed by a winter breeding period as happened in 1965.

It is not a rule that non-breeding birds take a siesta break in the midday hours. For instance, on 10 February 1965, the hottest day of the month, 10 weavers from Camp Nest were feeding at Twee Rivieren at 1430 when the temperature was 40°C in the shade. The birds sat in the shade of a small tree about 2 metres from a feeding station supplied with dry birdseed on the sand in the sun; every few seconds one or more of the birds flew or hopped to the seed, quickly took a few, and always <u>flew</u> back to the shade of the tree where they sat panting in the heat. It seemed as if the sand was uncomfortably hot to their feet, but these birds continued to feed throughout the hot afternoon. None of the other seed-eating species of birds was feeding at the time.

The apparent food shortage during the hot dry weeks of February and March 1965 was reflected in the difficulty of trapping weavers at their nests, and in the fact that at least 18 of the February chicks starved to death in the nest chambers. The adults were away from their nests feeding for most of the day and seemed to be feeding well over a mile from their nests. The Camp Nest birds were found at deserted nest masses up to 2 miles from Camp Nest at midday. Even when feeding at camp, the Camp Nest weavers could be found resting at midday in the shade of *Lebeckia* bushes right at the feeding grounds, probably to avoid flying back to the nest in the hot sunshine.

Food

The food of the sociable weaver was determined both by stomach content analysis and by observation in the field of food eaten by adults, and taken by them to their young. The contents of 120 weaver stomachs were sorted into animal and plant remains; the samples were drained thoroughly and weighed wet. Animal food formed an overall 78.9% of the food, the rest consisting almost exclusively of seeds.

The animal food consisted almost entirely of insects, mainly harvester termites *Hodotermes mossambica*, lepidopterous larvae, and small grasshoppers. There were also a few Coleoptera, Hymenoptera and adults Lepidoptera (moths only). Harvester termites formed 48.9% by weight of the animal food, and 34.2% by weight of the total food. It may be noted in passing that the harvester termite appears to be the most important single source of food for numerous vertebrates in the Kalahari; it is readily eaten by all insectivorous birds and is even taken by jackals and eagles when it occurs in large numbers after good rains. Lepidopterous larvae were mostly those of the common white butterfly *Belenois aurota* which occurs in vast numbers in the Kalahari after rains, particularly in summer.

Plant food consisted mostly of green grass seeds, which could not be identified. Probably most were of *Aristida* species. Other seeds present were of the cyperaceous *Fimbristylis hispidula* which grows widely in the dunes. There were also some hard leguminous seeds. There were very few seeds of the common chenopod *Lophiocarpus burchelli* which forms the mainstay of the diet of the sandgrouse (Pteroclidae) in the Kalahari. The weavers preferred green grass seeds; these had a much higher water content than the dry *Lophiocarpus* seeds.

The number of samples of stomach contents collected during the study period was too small to allow of an adequate analysis of variations in the ratio of plant to animal food with changes in season, rainfall and other factors. There was some very slight indication that the proportion of animal food taken was higher in dry periods than wet periods, i.e. the proportion of animal food was higher at the beginning of the study period than at the end (Table 20). This may, however, be a reflection of the greater abundance of green grass seeds in the wet periods. During the first summer of the study period (October 1964 to February 1965) there was little rain (Fig. 28) and an almost negligible growth of green grasses of any sort. After the rains in March and April 1965 a good growth of grass was evident, but it consisted mostly of *Schmidtia kalahariensis*, an acid grass whose seeds were not often eaten by the weavers.

In the spring (September) of 1965. the moisture still remaining in the soil permitted a small growth of summer grasses such as *Aristida* and *Eragrostis* species which the weavers ate avidly. The heat of midsummer and the increasing dryness caused these grasses to die off, but the January 1966 rains brought on a tremendous growth of summer grasses which covered the veld. It is significant that this rain did not result in the growth of *Schmidtia* which appears to be a winter grass (cf. Leistner 1959a, b). After this rain, the weavers' stomachs were almost half full of green grass seeds (Table 20).

The proportion of plant food in the diet of the sociable weaver is, however, seldom more than 50% by weight. Only in the case of the Camp Nest birds was this figure ever as high as 100%, but these birds had access to an artificial supply of seed at camp.

Water

No matter how hot and dry the weather, I never saw a sociable weaver from any nest other than Camp Nest drinking at any source of water in the study area, even if the nest was only 90 metres from the water. Sociable weavers do not normally drink in the wild. The highest percentage of seed by weight found in a truly wild population of weavers was 91.6% in one bird, and in only two other cases was this percentage higher than 50% (63.6% and 74.2% respectively) (Table 20), but even these high percentages of plant food consisted of green grass seeds. The aviary birds seldom drank, probably because of the "Pro-Nutro" in their diet was mixed with water. The aviary birds also ate any vegetable matter with a high water content, such as fresh apples, tomatoes and the soft nodes of green grass stems; such foods were so sought after by the birds, that they would readily eat fresh apple out of my hand after only a week in captivity.

Feeding methods

Sociable weavers usually feed in flocks. Except when feeding on Rhigozum flowers or flying insects, they feed on the ground. The flock moves forward in a "leap-frog" fashion, the birds behind flying over those in front to land at the head of the flock. The flock is usually silent during feeding, except for an occasional muted "chip" note or a mild threat note when

Table 20. Weights (gm.) of animal and plant components of stomach contents of the sociable weaver, showing percentage of animal food.

DATE	Number of stomachs	Weight of animal food (gm.)	Weight of plant food (gm.)	Percentage animal food
16.10.64	6	3.00	0.07	97.6
29.10.64	6	3.91	0.92	80.9
9.11.64	8	6.46	3.28	66.3
15.11.64	5	5.44	1.63	76.9
18.11.64	2	1.71	0.04	97.7
24.11.64	6	3.73	0.15	96.2
24.11.64	1	0.32	0.23	57.3
8.12.64	5	3.17	0.88	78.2
14.12.64	4	4.57	0.23	95.3
17.12.64	4	1.31	0.01	99.1
28.12.64	3	1.73	0.14	92.5
28.12.64	4	2.12	0.52	80.2
28.12.64	4	1.18	1.09	52.1
30.12.64	4	3.82	0.10	97.3
30.12.64	4	3.17	0.11	96.7
11. 2.65	4	3.31	0.23	93.4
8. 3.65	3	5.38	0.69	88.6
23. 3.65	2	1.36	0.01	99.0
25. 3.65	2	1.48	0.003	99.8

[illegible]	[illegible]	[illegible]	[illegible]	99.0
25. 3.65	2	1.03	0.00	100.0
31. 3.65	2	1.03	0.01	98.8
5. 4.65	2	0.71	0.11	86.2
8. 4.65	2	4.01	0.00	100.0
8. 4.65	2	1.01	0.03	97.3
19. 4.65	2	0.90	0.25	78.4
3. 5.65	2	0.63	0.14	81.7
17. 5.65	2	0.13	1.23	9.4
24. 5.65	2	0.80	0.12	86.8
14. 6.65	2	0.88	0.08	91.8
21. 6.65	1	0.35	0.05	88.5
24. 6.65	2	1.25	0.43	74.6
7. 7.65	1	0.00	0.27	0.0
8. 7.65	2	0.38	1.08	25.8
30. 9.65	1	0.20	0.02	90.7
11.10.65	2	0.81	0.81	50.0
11.11.65	2	0.71	0.61	53.8
22.11.65	2	1.64	1.23	57.1
17. 1.66	2	0.93	0.83	52.8
24. 1.66	2	0.63	1.10	36.4
1. 2.66	2	0.16	0.12	58.0
22. 2.66	2	0.86	0.94	47.8
22. 3.66	2	0.90	0.84	51.5
TOTALS	120	77.12	20.63	78.9

two birds get too close to one another. The actual feeding actions of each bird depends on the type of food being taken.

Seeds

Seeds are often simply picked up off the ground. Grass seeds are usually husked before being swallowed. I have not seen sociable weavers take grass seeds from standing flowering grass inflorescences, but to judge by the large quantity of green grass seeds in the dissected stomachs, it seems as if they must do so; certainly the aviary birds ate green seeds from the grass that they were given as building material. Larger leguminous seeds with a hard testa are swallowed whole or are first cracked. Seeds lying in the sand are uncovered by flicking the sand aside with quick lateral movements of the bill.

Other vegetable food

Sociable weavers and several other seed-eating passerine birds, including masked weavers and yellow canaries, eat the ovaries of the flowers of *Rhigozum trichotomum* (Bignoniaceae) by nipping the flower off at the pedicel, nibbling off the ovary and dropping the petals to the ground. Soft fruit was pecked at and swallowed in chunks. Soft grass nodes were eaten in the same way as the *Rhigozum* flowers by nibbling them off and dropping the rest of the stem.

Harvester termites

Termites gathering food in the open are simply picked up by the weavers and swallowed alive. These insects are burrowers and bring the excavated sand grains or soil particles to the surface of the ground where they are deposited at the burrow entrance until a cone builds up to about 7 or 8 cm. high; in the centre of the cone, the particles are cemented together to form a tube through which the termites continue to bring more particles. The weavers have learned that the termites occur in the little soil cones, particularly in the early morning and after rain, and get at the insects by flicking the cones open with their bills. A weaver will hop from cone to cone until it has exhausted the supply in one area, after which it will move on to the next. I have seen this cone-flicking behaviour in such widely diverse avian species as crowned plovers *Vanellus coronatus*, hornbills, rollers, larks and other passerines.

Larger terrestrial insects

Adult grasshoppers are caught on the ground and killed by beingbeaten on the ground before swallowing. Large grasshoppers are held by the abdomen and beaten until the head and thorax are pulped or completely separated from the abdomen. Young weavers are usually fed only the abdominal region of large grasshoppers.

Insect larvae

Lepidopterous larvae are probably obtained as they drop off the bushes before pupating. Large larvae are pulped by "mouthing" in the bill, small larvae are swallowed whole. Coleopterous larvae are usually obtained by digging at the base of small plants with the same rapid side-ways flicking movements of the bill as are used to expose termites in their cones. Large beetle larvae are dismembered before being swallowed.

Flying insects

Alates of the harvester termites are eaten by the weavers as readily as the workers, usually by being picked up off the ground after they have shed their wings, but the weavers can catch them flying in the air. They are not very adept at this aerial hunting and miss frequently. The moths found in the weavers' stomachs may have been caught in the air. Aerial feeding is not a very common hunting method of the sociable weaver.

Chapter 10

MOULT

All the data on moult were obtained from an examination of live sociable weavers mist-netted in the field. Most of the netting was done at one nest colony (No. 19) to ensure as many retraps as possible so as to obtain as complete a picture as possible of each bird's moult pattern. Even so, only 47 birds were retrapped once or more (Table 21).

The feather regions of each bird were divided as follows:

1. Wing (right and left wings examined separately)
    - (a) Primaries 1-9;
    - (b) Secondaries 1-6;
    - (c) Axillaries and scapulars;
    - (d) Wing coverts
        - (i) dorsal
        - (ii) ventral.
2. Tail
    - (a) Left rectrices 1-5;
    - (b) Right rectrices 1-5.
3. Body
    - (a) dorsal
        - (i) Crown
        - (ii) Nape
        - (iii) Mantle

    - (iv) Upper back
    - (v) Lower back (including rump);
- (b) Ventral
    - (i) Chin
    - (ii) Neck
    - (iii) Breast
    - (iv) Abdomen
    - (v) Flanks
    - (vi) Under-tail coverts.

Old and new primary remiges were easily distinguishable, but the difference between old and new feathers was not so clear in the other feather regions. Rectrices were particularly difficult to determine, since they were always subjected to considerable wear as the birds entered their nest chambers. The method of wing examination is shown in Fig. 41. Body plumage was examined by blowing the feathers anteriorly to expose new feather tips. It was sometimes possible to tell whether the body plumage was new or old, but this was of less importance than a determination of which feather regions were undergoing replacement.

The results of moult examination were noted down in extensive tables in which each trapped bird was listed and all the details of its moult noted. Examples of the method of recording

Fig. 41. Examining a sociable weaver for moult.

Table 21. Weavers trapped more than once for moult studies at nest No. 19.

No. of times trapped	No. of birds
2	35
3	10
4	2
Total retrapped	47

moult are shown in Table 22.

Wing moult

Right and left wings moult simultaneously, or nearly so, so that the feather arrangement on both sides is symmetrical. The sequence of moult in the primary remiges is proximo-distally with the focus at No. 1 (Stresemann & Stresemann 1966), or in descending order from 1 to 9 (the innermost primary is No. 1). Primaries are replaced at the rate of about one feather a month. The shortest recorded period for primary replacement in adult weavers is 3 weeks; in immature weavers, this period is 2 weeks. In six cases a primary feather took more than a month for replacement; in all these cases the delay reflected the interval between the replacement of the 9th (outermost) primary and the start of the next descending cycle. This interval was between one and three months, but usually little more than one month. In no cases was there any overlapping of primary moult cycles (Staffelmauser of Stresemann & Stresemann 1966). The 9th primary was always fully developed before the 1st was dropped at the beginning of the next cycle. This usually applied to all the primaries but very occasionally the next ascending primary was dropped before the previous one had fully grown out.

There were four interesting cases of delayed moult in which the delay was not between cycles. In each case the delay occurred between April and June 1965, a period of intense breeding activity. In three of these cases, the period of feather replacement was extended to two months; in the fourth case the growth of primary No. 7 was arrested about half way for one full month. During this month, however, the bird underwent a full body moult.

Like the primaries, the secondary remiges are moulted symmetrically on both wings. Because of the smaller amount of wear on these feathers, the differences between old and new feathers were less clear than in the primaries; also the sequence of feather replacement was rather less regular. Therefore the moult pattern of the secondaries was not as well defined as that of the primaries. Generally however, the sequence is in ascending order (i.e. disto-proximally). There were usually 6 easily distinguishable secondaries, the innermost ones (from No. 7 inwards) grading indistinguishably into the tertiaries and scapulars.

The replacement period for a secondary was a mean of 1.4 months. This was only very slightly longer than the mean replacement period of 1.1 months for a primary. The cycles of primary and secondary replacement do not necessarily run simultaneously and may begin quite independently of one another. The

Table 22. Method of recording remex moult in the sociable weaver.

Symbols: O = old feather
N = new feather
- = missing feather
* = growing feather.

BIRD No.	DATE	LEFT WING		RIGHT WING	
		PRIMARIES	SECONDARIES	SECONDARIES	PRIMARI
		9 8 7 6 5 4 3 2 1	1 2 3 4 5 6	6 5 4 3 2 1	1 2 3 4 5 6
163	14. 6.65	N N N N N N N N N	N N N N N O	* N N N N N	N N N N N N
	22.11.65	O O O O O N N N N	O O O O O O	O O O O O O	N N N N O O
	15. 2.66	O O N N N N N N N	N N O O O O	O O O O N N	N N N N N N
	22. 3.66	O N N N N N N N N	N N N N O O	O O N N N N	N N N N N N
175	3. 5.65	O * N N N N N N N	N N N N N O	O N N N N N	N N N N N N
	14. 6.65	* N N N N N N N N	N N N N N O	O N N N N N	N N N N N N
	11.10.65	O O O O O O * * N	O O O O O O	* O O O O N	N * * O O O
	22.11.65	O O O O O * N N N	O O O O O O	O O O O O O	N N N * O O
190	3. 5.65	O O O N N N N N N	N O O O O O	O O O O O N	N N N N N N
	5. 7.65	O * N N N N N N N	N * O O O O	O O O O * N	N N N N N N
	30. 9.65	N N N N N N N N N	N N * O O O	O O O N N N	N N N N N N
628	3. 5.65	O O O O O * N N N	O O O O O O	O O O O O O	N N * O O O
	5. 7.65	O O O * N N N N N	O O O O O O	O O O O O O	N N N N N *
	15. 8.65	O * N N N N N N N	N * O O O *	O O O O * N	N N N N N N
431	3. 5.65	O O O N N N N N N	N N N N O O	O O N N N N	N N N N N N
	1. 2.66	O O * N N N N N N	N N N * O O	O O * N N N	N N N N N N
441	27. 5.65	O O * N N N N N N	N O O O O O	O O O O O N	N N N N N N
	15. 2.66	O O * N N N N N N	* O O O O O	O O O O O O	N N N N N N
626	26. 4.65	* N N N N N N N N	N N O O O N	N O O O N N	N N N N N N
	17. 1.66	* N N N N N N N N	N O O O O O	O O O O O N	N N N N N N
1224	11.11.65	O O O O O O - * N	O O O O O O	O O O O O O	N * * O O O
	24. 1.66	O O - * N N N N N	* O O O O O	O O O O O *	N N N N N *
1266	17. 1.66	O O O O O * N N N	O O O O O O	O O O O O O	N N N * O O
	1. 2.66	O O O O * N N N N	O O O O O O	O O O O O O	N N N N - O

sequence of secondary moult was determinable in 26 cases. Of these, 16 were in regular ascending order. In all except two cases, the first secondary dropped was No. 1. In the two exceptions, No. 1 was dropped second. In the ten cases of irregular secondary moult order (Table 23), the same order of moult occurred on both wings. This was usual but not invariable.

In juvenile weavers the primaries begin to moult before the secondaries. The first secondary is dropped when the 6th or 7th primary is being moulted. The 2nd secondary and the 9th primary are usually moulted at the same time in the young birds.

Moult of wing coverts, axillaries and scapulars occurs in conjunction with the rest of the body plumage.

Tail moult

The moulting pattern of the rectrices is totally obscure. In some individuals the sequence seems to be from the centre outwards, in others from outwards to the centre, while in most it shows no regularity at all. In most cases it is not even symmetrical on the two halves of the tail. Any pattern of moult which may exist is masked by the wear on the rectrices. The rate of tail moult was also not determinable.

Body moult

The sequence of body moult is antero-posterior, both dorsally and ventrally. The entire body moult occurs within the space of one month. The posterior feather regions of the body start to moult before or immediately after the completion of head moult. Moult of the dorsal plumage is usually slightly in advance of the ventral plumage, so that the last body feathers to undergo moult are the ventral tail coverts. There appears to be only one body moult a year. The peak of moulting during the study period was in May and June 1965, tapering off to the end of the breeding period in November (Table 24). The cycle of body moult is not regular and appears to depend to some extent on rainfall, occurring after good rains. Thus bird No. 652 moulted in May 1965 and again in February 1966.

The onset of body moult does not appear to affect wing moult in most sociable weavers, but it may slow it down a little as I have suggested.

Table 23. Ten examples of irregular secondary moult sequence in the sociable weaver. Secondary numbers in parentheses are those whose actual order of moult was not recorded, but whose order has been inferred from information obtained from other birds.

BIRD No.	SECONDARY No.					
A	1	2	3	4	6	5
B	1	2	4	6	(3)	(5)
C	1	2	5	(3)	(4)	(6)
D	1	2	5	(3)	(4)	(6)
E	1	3	2	(4)	(5)	(6)
F	1	4	(2)	(3)	(5)	(6)
G	1	6	(2)	(3)	(5)	(4)
H	1	6	5	2	3	4
I	2	1	(3)	(4)	(5)	(6)
J	4	1	6	2	3	5

Table 24. Counts of sociable weavers in full moult per month throughout the study period, showing the peak of body moult in May.

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
1	1	1	1	7	6	2	2	3	2	1	0

Chapter 11

GENERAL BEHAVIOUR

There are a number of behavioural aspects of the sociable weaver not directly connected with social organization or with breeding biology, although certain of the behaviour patterns to be described may have acquired signal function (McKinney 1965) and therefore affect the social life of the birds to some extent.

Locomotion

(a) Terrestrial

The sociable weaver always hops on the ground, except when progressing very slowly while feeding, in which case it may take a short shuffling step or two. The bird normally hops with both feet together (Fig. 42) but during rapid progression the feet are out of phase, so that one is a little in front of the other and the individual hops are longer (Fig. 43).

(b) Aerial

The flight of the sociable weaver is highly characteristic. Over a short distance (say 90 metres or less) the flight is fast and straight with rapidly beating wings in the manner of a small *Euplectes* (e.g. *E. orix* or *E. afer*). Over longer distances the bird uses what I have termed an "open flight" pattern of flying in which a burst of rapid wing-beats is alternated with a dip in the flight path as the wings are closed. The open flight pattern

Fig. 42. Footprints of a sociable weaver hopping slowly with both feet together.

Fig. 43. Footprints of a sociable weaver hopping fast with feet out of phase. Note how the bird's right foot touched the ground more lightly than the left foot.

is much the same as that of weavers of the genus Ploceus.

The sociable weaver displays considerable manoeuvrability when flying from a perch into a nest chamber. With the characteristically rapid wingbeats the bird is able to fly vertically upwards with the body held horizontally; at the last moment before entering the tunnel to the chamber, the body is orientated vertically and the bird shoots into the entrance. Despite this manoeuvrability, the sociable weaver cannot hover for more than a second or two.

Comfort movements

The terminology used in this section is that of McKinney (1965), except where I have found it necessary to modify it to suit a passerine bird. I have also included here sunbathing and sleeping postures and the movements associated with the adoption of these postures.

(a) Shaking movements

Body-shake is the only shaking movement I have observed in the sociable weaver. The plumage is erected before the whole body is shaken. The wings remain in their "pockets" (flank and breast feathers) during the movement. Wing-shake, head-shake and tail-shake do not occur as separate movements in the sociable weaver. Body-shake may be performed at any time;

it is frequently seen in birds which have just emerged from a nest chamber and probably serves to re-arrange the plumage and to rid it of dust and other loose particles. The movement does not appear to have signal function.

(b) Stretching movements

Wing-and-leg-stretch: This is a common stretching movement in the sociable weaver, as in most birds, in which the leg and wing on one side are stretched simultaneously.

Both-wings-stretch: This is another common stretch movement in which the wings are both raised over the back with the carpal joints flexed. At the same time the head is lowered and the neck stretched forward. Both-wings-stretch frequently follows wing-and-leg-stretch.

Jaw-stretch: Jaw-stretch or "yawning" occurs infrequently in the sociable weaver, but may be overlooked quite often as it is of very short duration. It is performed usually when the bird is in a state of rest and is accompanied by complete or partial closing of the eyes.

(c) Cleaning movements

Scratching: Scratching of the head with a foot is indirect in that the foot is brought up over the wing. The cleaning function of scratching was clearly shown in the case of the weaver that got tangled up in strands of cotton waste which it had brought for nest-lining. Scratching commonly accompanies preening.

Preening: There appeared to be nothing remarkable about the preening movements of the sociable weaver when compared with similar movements in other passerine birds. The weavers spent much of their time preening while perched in the nest tree during the siesta hours and in the evening just before going to roost.

Bill-cleaning: Bill-cleaning consisted in wiping the bill quickly on alternate sides on a branch. The number of wiping strokes seldom exceeded 5 in one operation, but the number of wiping operations might be 2 or 3 in quick succession. Bill-cleaning was usually indulged in after the birds had fed on moist and "messy" food such as apples or large insects which had been dismembered; and also after an adult had just fed chicks or had built some lining into a nest chamber.

Social preening: Social preening, allopreening or mutual preening (Harrison 1965) is the preening of one bird by another. It seems unusual that, in a species as sociable as the sociable weaver, I saw allopreening only once when one bird briefly preened the chin, neck and breast feathers of another bird which sat quite still during the performance and made no attempt to preen the first bird in return. Harrison (loc. cit.) has found allopreening in only 3 other species of Ploceidae.

(d) Bathing

Bathing in water was recorded only once on a cold day in May 1965 when some of the aviary weavers bathed briefly in water dripping from the over-filled drinking tray. The bathing movements did not appear to be unusual when compared with those of other passerines, but were of such short duration that it was not possible to make much comment on the movements themselves. The birds soon lost interest in the water and were never seen to bathe again. Since wild sociable weavers do not drink, it may be assumed that they do not normally bathe in water. I have never seen sociable weavers dust-bathing, although their freedom from ectoparasites seems to indicate that they may do so.

(e) Sunbathing

In the morning shortly after sunrise, the weavers sometimes sun themselves by sitting on the topmost branches of the nest tree with their plumage fluffed out. They may do this at any time of the year, but it is most commonly seen in the winter months. Sunbathing, as opposed to the simple sunning mentioned, was noted only in cold weather.

I have recorded two sunbathing postures, both adopted to expose the maximal surface area of the exposed side of the body to the sun's rays. The first posture was a straightforward squatting on the ground, the feet covered by the abdominal feathers, back feathers slightly erected, wings drooped to the ground and the tail slightly fanned (Fig. 44C). In this case the sun's rays were shining directly on to the bird's back.

In the second posture (Fig. 44D) the bird had placed itself at right angles to the sun's rays. From a sitting position, it slowly raised the body on the sunny side by extending the leg slightly on that side. Both wings were drooped, the one on the shaded side being used to support the body. The tail was fanned to expose the ventral surface to the sun. The bill was opened a little, although the bird did not seem to be panting. The body feathers were slightly raised and the eyes almost closed.

(f) Sleeping postures

During the afternoon siesta when a few birds might be sitting in the tree instead of entering the nest chambers, some would doze for short periods on their perches; a resting bird would slowly relax until the head was drawn into the shoulders and the bill pointed slightly upwards. Its eyes would then close for several seconds. The bird would rouse briefly from time to time, subsiding into its dozing posture after each arousal. Only once did I see a weaver tuck its head into its back feathers: it did this twice, but only momentarily.

When the aviary birds slept together in old nest chambers on the ground, they did not tuck their bills into their back feathers, but rested them on a neighbour's back or simply held the bill up and pointing straight in front in the manner of a hummingbird (Greenewalt 1960).

Thermoregulatory behaviour

(a) Heat loss

Panting is a common heat-loss mechanism in the sociable weaver when air temperatures exceed 35°C. Panting is accompanied by depressing the plumage and holding the wings out at the wrists (Fig. 44A) possibly for radiative and conductive heat loss. The birds also tend to stand high on their legs.

(b) Heat conservation

At air temperatures below 20°C the heat conservation posture shown in Fig. 44B is adopted. The body plumage is erected, the wings are enclosed in their pockets and held close to the body, and the legs are covered by the abdominal feathers.

At extreme temperatures, whether high or low, the weavers repair to the nest chambers for shelter. I have already mentioned that, if they are far from the nest or if the weather is hot, they will as readily sit in the shade of bushes either perched low or on the ground.

Intention movements

The only clearly evident intention movements in the sociable weaver are flight intention movements. At low intensity, the weaver merely crouches, droops the wings a little and points the head in the direction in which it intends to depart. This is most clearly seen in a bird which is about to fly vertically upwards to its nest chamber. At a higher intensity, the drooped wings may be quivered as in a begging posture; this most often happens in a bird intending to fly into a chamber whose entrance is already occupied by another weaver, so that the movement may be displacement food-begging in the conflict situation of thwarted take-off.

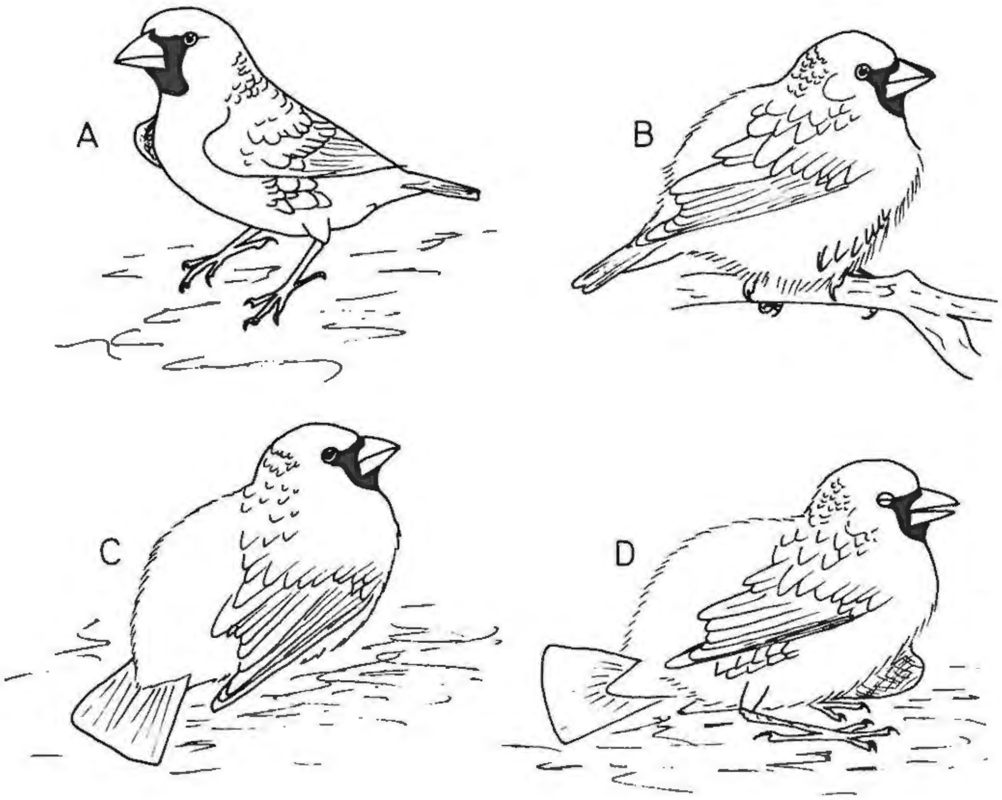

Fig. 44. A. Heat loss posture with compressed plumage, wings held out at wrists and legs exposed.

B. Heat conservation posture with fluffed plumage and legs covered by ventral feathers.

C. Sunbathing posture with sun shining directly on to the bird's back.

D. Sunbathing posture with the sun shining on to the bird's right side; note how the body is supported by the left wing, and that the bird is panting.

Chapter 12

LOCAL DISTRIBUTION AND POPULATIONS

Distribution

The distribution of sociable weaver nests in the study area is shown in Fig. 2; distribution of nests along the whole Nossob River from Twee Rivieren to Union's End at the northern end of the Gemsbok Park is shown in Fig. 45A. Both these figures show that the nest colonies often occur in small groups; these groups may consist of nest masses in neighbouring trees, a fact also noted by Rudebeck (1955). A similar distribution of nests was found along the road from Twee Rivieren southwards to Upington (Fig. 45B), where the presence of nests was dependent on the presence of trees. One might infer from this fact that the number of nests (and therefore the number of birds) would increase proportionately with an increasing density of trees. However, this is not so. There is an inverse relation between the number of trees and the percentage of trees occupied by sociable weavers in the study area (Table 25; Fig. 46). Where there is only one tree per mile, it is almost sure to be occupied if it provides a suitable nest site (100% occupation), but as the number of trees increases northwards to a maximum of 49 trees per mile, the percentage occupation falls to less than 3%.

Only 11% of all the trees in the Nossob River within the study area show evidence of having been occupied at one time or another by sociable weavers (Table 25). At present only 15 trees out of a total of 303 trees (about 5%) are occupied, since not all the nest masses are inhabited by sociable weavers. The determination of what constitutes a suitable nesting tree is at best rather subjective, but I estimated that suitable trees in the study area, including those already occupied, form 29% of all the trees (83 out of 303 trees), so that many of them are not being used by the weavers. Within the study area the maximal number of nests per mile is four, while the greatest number of nests per mile in the Nossob is 9 (Fig. 45A). However, the maximal number of occupied nests per mile is at present only 3 within the study area, and 4 elsewhere along the Nossob. There is an overall distribution of just over one nest mass or occupied tree per mile in the study area, and of 0.6 nests per mile along the Nossob between Twee Rivieren and Union's End. Such a sparse distribution may be expected in parts of the Nossob where trees are scarce, but north of Rooiputs in the Acacia savanna there must be other factors affecting the weavers' distribution.

There are two possible reasons to account for the distribution of sociable weavers in areas with may more suitable trees than are in fact occupied by the weavers: (a) inter-

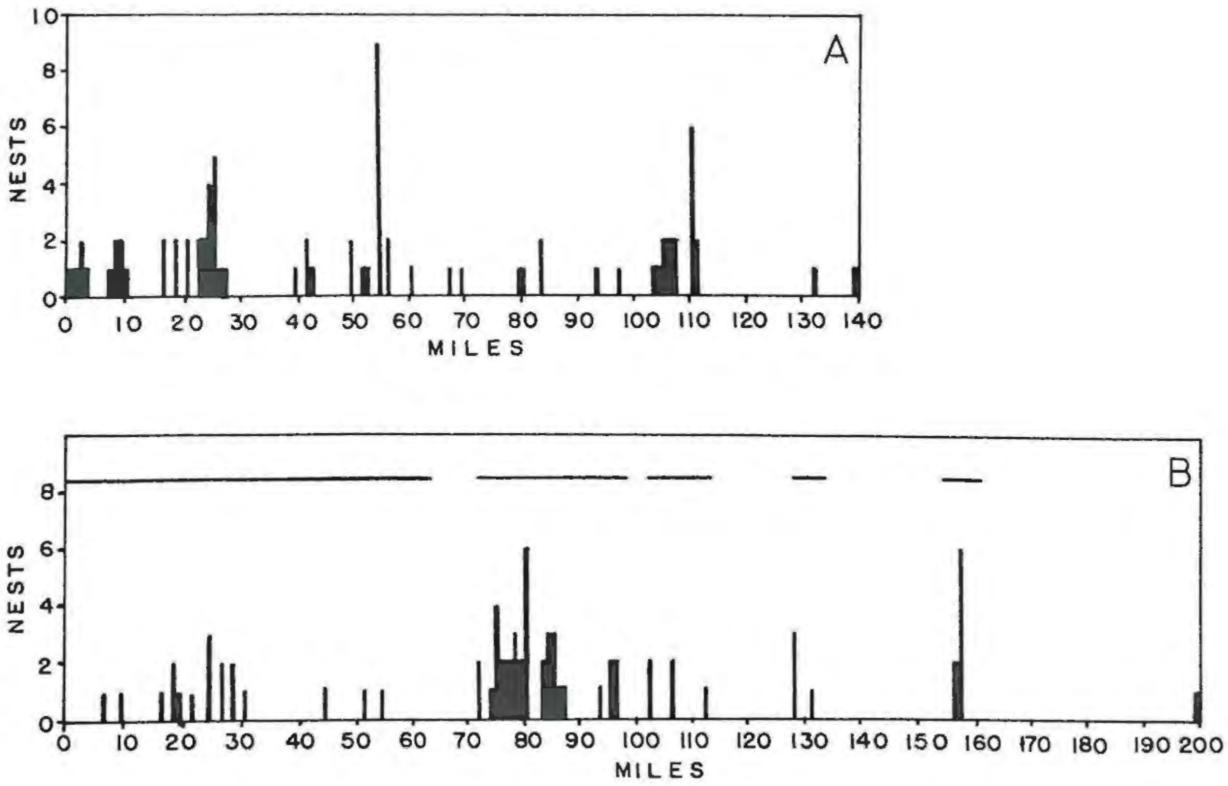

Fig. 45. A. Distribution of all sociable weaver nest colonies along the Nossob River from Twee Rivieren to Union's End, except for the last 30 miles from which these birds are absent.

B. Distribution of all sociable weaver nest colonies along the main road from Twee Rivieren to Upington. The horizontal lines above the histogram indicate the presence of trees.

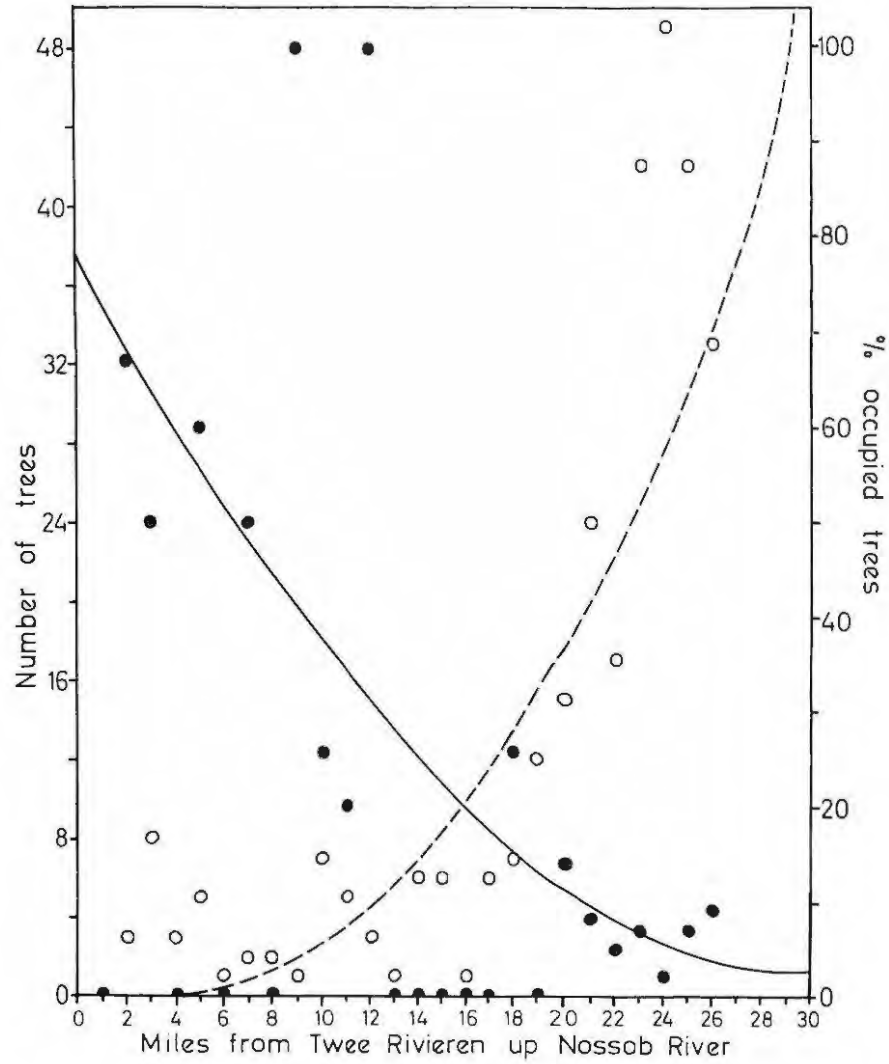

Fig. 46. Graph showing the inverse ratio between the number of trees (broken curve) and the percentage occupation of the trees by the sociable weaver (solid curve) in the study area. The curves have been fitted by eye and are necessarily very approximate.

Table 25. Occupation of trees in the Nossob River within the study area by sociable weavers. Total occupied trees are all trees with nest masses; present occupied trees are those with nest masses inhabited by weavers during the study period.

MILES NORTH OF TWEE RIVIEREN	NUMBER OF TREES	NUMBER OF SUITABLE TREES	OCCUPIED TREES		TOTAL % OCCUPATION	
			TOTAL	PRESENT	ALL TREES	SUITABLE TREES
1	0	0	0	0	0	0
2	3	2	2	0	67	100
3	8	4	4	1	50	100
4	3	0	0	0	0	0
5	5	3	2	1	40	67
6	1	0	0	0	0	0
7	2	1	1	0	50	100
8	2	0	0	0	0	0
9	1	1	1	1	100	100
10	7	2	2	1	26	100
11	5	1	1	1	20	100
12	3	3	3	3	100	100
13	1	0	0	0	0	0
14	6	0	0	0	0	0
15	6	0	0	0	0	0
16	1	1	0	0	0	0
17	6	2	0	0	0	0
18	7	3	2	0	26	67
19	12	2	0	0	0	0
20	15	2	2	0	14	100
21	24	5	2	2	8	40
22	19	6	1	1	5	17
23	42	10	3	1	7	30
24	49	11	1	0	2	10
25	42	13	3	1	7	23
26	33	11	3	3	9	27
WHOLE AREA	303	83	33	15	11	40

specific territoriality and (b) intraspecific intercolonial territoriality. These two reasons are not mutually exclusive and may both be operative.

With regard to interspecific territoriality, Orians & Wilson (1964) have the following comments:

> "Most birds defend territories against conspecific individuals but some species also defend territories against individuals of other, usually closely related species. . . . . interspecific territoriality among birds may be much more common than currently recognized. Abundant evidence indicates that in the absence of a normal component of a community another species often occupies the habitat, suggesting that most species are prepared to expand ecologically, but are continually held in check by competition with other species."

From Rooiputs northwards, not only do the _Acacia giraffae_ trees increase, but also the number of arboreal bird species. In the Nossob south of Rooiputs there are only 16 species of arboreal birds (small Falconiformes, all Coraciiformes and all arboreal Passeriformes), while north of Rooiputs there are 38 species. This increase in the number of these species may result in an increase in interspecific territorial competition for nesting trees. A tree currently occupied by sociable weavers is avoided by other arboreal birds (except the masked weaver) for nesting purposes. This excludes of course those species actually using the sociable weavers' nests for nesting. All other arboreal species, notably the drongos (Dicruridae) and flycatchers

(Muscicapidae sensu stricto), are highly territorial.

The rather even distribution of nests or groups of nests of the sociable weaver in the Nossob River seems also to suggest some sort of intraspecific intercolonial territoriality, assuming that the inhabitants of a group of nest masses in neighbouring trees originated from the same parent colony. The territory of a colony may well be equivalent to the feeding area such as I have indicated for Camp Nest (Fig. 40), although this is not always sufficient to account for the wide separation of almost ten miles between colonies in some cases (Fig. 45A), even though suitable trees occur in the intervening distance. However, the idea of intercolonial territoriality is supported by the very low percentage of inter-change of individuals between colonies, and the hostility shown to those birds which do make such an intercolonial movement.

Other factors such as food supply may also affect the weavers' distribution, but too little is known about these factors to allow of further profitable discussion at this stage.

Populations

A colony may be defined as a group of sociable weavers living in the same nest mass (if there is only one nest mass in the tree) or in the same tree (if there are more than one nest mass in the tree). This definition is based on the fact that the birds from one tree feed together and that the nest masses in one tree tend to fuse after a time, if the site allows. It is quite possible that nest masses in adjacent trees may house birds derived from the same parent colony, since these birds may also feed together (e.g. the birds at B1, B2 and B3 (Fig. 2)). Nest masses in groups of trees, such as the Botswana nests, tended to be smaller than nest masses not occurring in groups; although the large nest masses (such as Nos. 22, 23 and 24) may occur within half a mile of each other, they were never in adjacent trees. Thus the term "colony" may well apply to the inhabitants of a group of nest masses in adjacent trees. Further evidence is needed to support this idea.

The number of birds per colony is highly variable. The smallest colony I have recorded consisted of only 2 birds (at nest No. 8), the largest of an estimated 500 birds (nest No. 24). The study area contained an estimated 2500 sociable weavers, a distribution of about 100 birds per mile. Since the study area was about 26 miles long and half a mile wide, there were about 180 weavers per square mile.

The maximal size of a colony is limited by the number and size of the nest masses which can be accommodated by the nest sites provided by one tree or a group of trees. When a tree has more than one branch suitable for a nest site, the colony will grow until all available sites have been used up, after which some of the birds may move to a neighbouring tree if it is also suitable and if it is not already being defended by another species of bird. This is why nests tend to occur in groups, particularly when a tree can support only one rather small nest mass; this is very clearly seen when the weavers build on telegraph poles. I have seen up to 14 consecutive poles with sociable weaver nests on them, the central nest mass being the largest, the others grading down in size to the smallest at the ends of the row. This is in effect an extended colony and the large number of nest masses in the group is correlated with the very small size of each individual mass. How far afield the weavers will move in the absence of suitable nest sites in the immediate vicinity of the parent colony has not been determined.

Since the availability of nest sites in a small area is limited, the birds must move further afield as the colony expands. In this way they become dispersed. This is borne out by the spread of birds into otherwise unsuitable areas when artificial nest sites are provided. There is a thriving colony on a tankstand on the farm Straussennest (Fig. 16) between Keetmanshoop and Aroab in South West Africa in a region where there are no other sociable weavers for miles around because of the lack of nest sites in this treeless region. It would be interesting to know whether or not the nest on a windmill tower on the neighbouring farm (van der Merwe) (1966) was started by members of the Straussennest colony as it grew too large for the present site; unfortunately van der Merwe does not mention the distance apart between the two colonies.

Considering the number of unoccupied nest masses in the study area, most of which were in a state of good repair, it can be assumed that the populations of sociable weavers in the area was at one time larger than it was during the study period. There may have been severe competition for nest sites at such a time, a fact evidenced by some of the nest masses on marginal sites in _Acacia_ _giraffae_ trees (Fig. 17) and in low _Boscia albitrunca_ trees in the dunes (Fig. 14), most of which are now abandoned. These nest masses are no doubt occupied by birds that are supernumary with respect to the riverine nest masses in exceptionally good years. It is also possible that there may always be more nest masses than existing populations can occupy; a colony may simply shift "headquarters" from time to time, as was the case at nest No. 6 and probably also at nest

No. 5.

The years 1956 to 1959 were very dry in southern South West Africa, so much so that I found no breeding at all among the sociable weavers in this area at about 100 colonies during these three years. The drought which lasted for 6 years altogether must have affected the weaver populations of the whole of western South Africa, including the Kalahari, since I have shown (Chapter 5) that breeding in the sociable weaver is dependent on rainfall. Unfortunately I do not know what happens to a colony as its numbers fall, but I would suggest that those colonies in marginal nest masses probably amalgamate with colonies in more favourable sites, particularly in the river beds in the Kalahari. The dune birds would thus act as a reservoir to keep the optimal riverine habitat "saturated" in poor years. There were very many more deserted nest masses in the dunes than in the rivers.

Occasionally an abandoned nest mass in the Nossob River would be occupied for a few days by what seemed to be a transient group of sociable weavers. These birds may have come from the dunes. Only one such transient group settled long enough to become established at nest No. 5, which was completely deserted at the beginning of the study period. On 24 November 1964 five birds were in occupation and several more moved in until there were at least 15 birds by 28 January 1965 (Fig. 47). Breeding at No. 5 began on 12 April 1965 and the colony increased in size until there were about 50 birds in April 1966.

Another unsolved problem was the origin of the sociable weavers seen building on telegraph poles along the road to Upington. Many of these birds had only just started to build. Where did they roost at night ? That sociable weavers can survive temperatures as low as 3°C without the shelter of a nest chamber was shown by the aviary birds in May 1965 when they slept on the ground huddled together without any nest. Perhaps the birds near Upington slept in groups perched on the telegraph pole or in nearby bushes, because there were certainly no nest masses for many miles around which they could have used as roosting places.

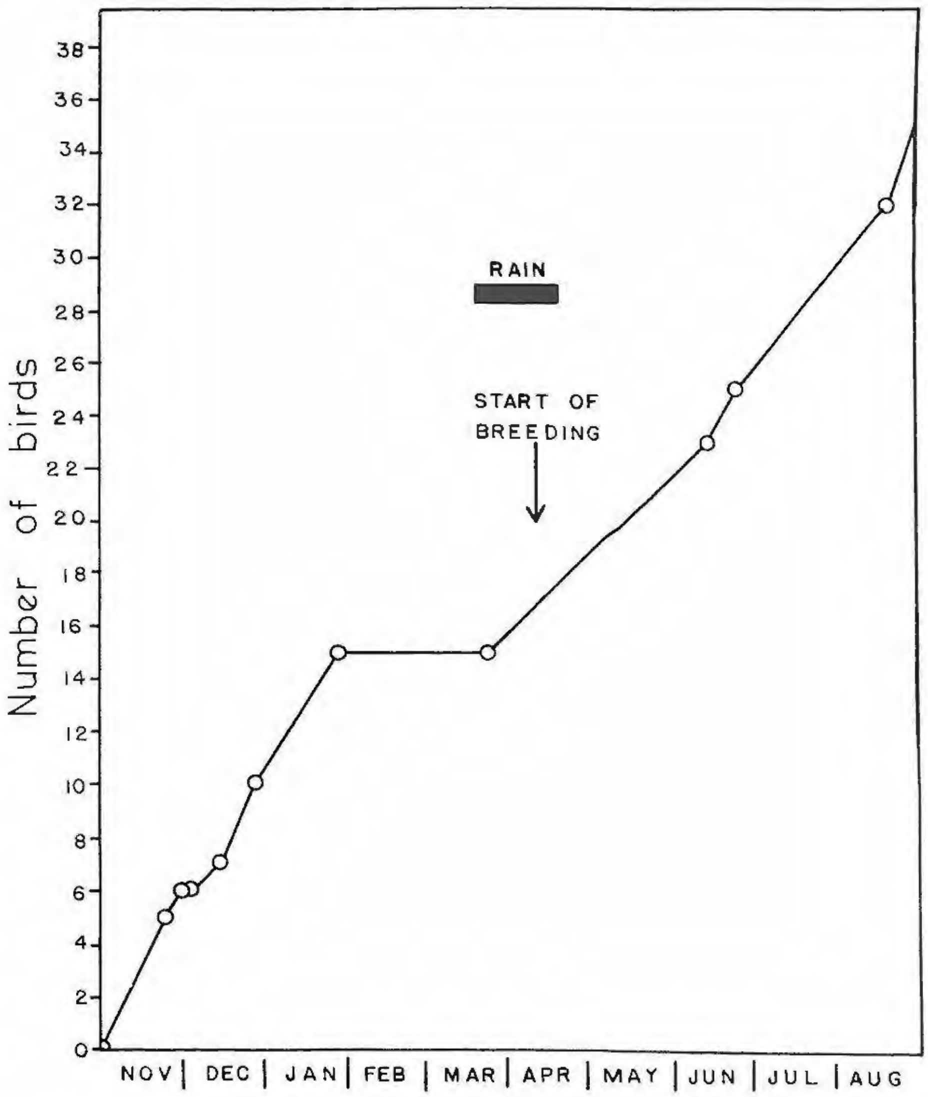

Fig. 47. Growth curve of the colony at Nest No. 5 in the Nossob River from the time the first bird was seen there, until August 1965 towards the end of this colony's first breeding period in the study area.

Chapter 13

DISCUSSION

Most of the initial questions regarding the biology of the sociable weaver have been answered at least partially. As with most scientific investigation, however, many more questions have arisen as a result of this work than were at first thought of.

The nest

The methods of nest building in the sociable weaver are adapted to the architecture of the nest and occur in no other member of the family Ploceidae (Collias & Collias 1964; Crook 1960). Only the lining of the chamber interior with grass heads resembles somewhat the nest lining habits of the Ploceinae (*op. cit.*). Otherwise building techniques are adapted to the dry materials available at all times of the year (cf. Friedmann 1950). Even the threshold could be built with fairly dry straws, since it requires only a small degree of flexibility to bend a straw to fit the requirements, but green material is still better because of its greater durability and cohesion after it has dried in the form into which the bird has moulded it.

Collias & Collias (1964) have discussed the ways in which the nest construction of the sociable weaver differs from that of other weavers and have emphasized the absence of "weaving", a fact already mentioned by Friedmann (1950). Collias & Collias (1964) say that the "minute structure of the nest in Philetairus resembles that of the nests of other Plocepasserinae more than it does those of any other subfamily of weaverbirds", but the structure seems nevertheless different enough to make it a doubtful criterion for indicating a close relationship between the sociable weaver and other members of this subfamily. The two groups are behaviourally very different; the sparrow-weavers are not colonial, while the other so-called "sociable weavers" (Dinemellia and Pseudonigrita) of East Africa seem to be no more sociable than most of the Ploceinae. The only other communal nesters among the Ploceinae are the buffalo weavers (Bubalornithidae) whose nest architecture differs widely from that of the sociable weaver in that the herbaceous chambers are added after a shell of thorny twigs has been built, and their openings are lateral or ventrolateral; moreover, Bubalornis is probably polygynous (Collias & Collias 1964).

The specialization in the sociable weaver's nest-building requirements is further reflected by its range, which appears to be governed almost exclusively by the availability of grasses of certain genera, mainly Aristida. Even where the birds occur in regions where other grasses predominate (as in the western

Transvaal), they build with "grasses more typical of arid country" including Aristida, Sporobolus and Eragrostis (Collias & Collias 1964). I have recorded sociable weavers in the Kalahari using species of all three of these genera of grasses. The importance of grasses in the distribution of the sociable weaver is shown by the fact the birds use telegraph poles as nest sites in country where trees are absent, as long as the right kinds of grasses occur.

The habit of building on telegraph poles has been ascribed by Sclater (1928) to the cutting down of Acacia giraffae trees, but this is probably not the case. I have seen nests on telegraph poles in areas where camelthorn trees are abundant, as well as in areas where these trees almost certainly never grew at all. It seems more likely that the poles have facilitated the spread of the sociable weaver into treeless areas where the birds did not occur before, as suggested by Rudebeck (1956). It is also possible that the weavers have learned that telegraph poles cannot be climbed by nest predators such as snakes and arboreal mammals. These nests are, however, not immune from destruction by Post Office officials who periodically remove them from the poles, particularly in rainy weather when the wet nest material causes deterioration of the wires and woodwork at the top of the pole.

Rudebeck (1956) confirms my observations on tree nest sites of the sociable weaver as being mostly in "acacias or trees of similar habitus". Nests in Aloe dichotoma are common in South West Africa and have been known for some time (Hutchinson 1946, p. 175; Macdonald 1957; Newby 1943; Reynolds 1950, p. 493). A photograph in Reynolds' book shows how the nest mass incorporates numerous branches of the Aloe. Nests on artificial sites have also been widely reported in the literature (Clancey 1950; Farre 1954; Gill 1950; Hutchinson 1946, p. 431; Rudebeck 1953; van der Merwe 1966). It is noteworthy that there is not a single published record of a sociable weaver nest in an exotic species of tree, confirming my own observations.

Distribution

The distribution of avian species in relation to vegetation has been discussed by Pitelka (1941), who states that certain species agree with the limits of biotic communities, particularly species confined to climax associations. Few undisturbed desert vegetation communities are not climax associations, so that the sociable weaver probably falls into this group of "certain species". Pitelka (op. cit.) goes on to say that "birds apparently do not respond to any specific differences among the dominant plants of a climax or any of its stages". This is certainly true of the sociable weaver. This implied flexibility in the adaption of a bird species to a different plant species within one life form is shown by the weavers' use of different indigenous trees as well as artificial nest sites within its range. There is some specificity, however, in the types of grass used in nest construction, although more than one species of Aristida or Sporobolus may be used. Moreau (1966, p. 20) has also mentioned the importance of vegetation as a factor in the distribution of the birds of Africa.

The sociable weaver is thus confined to a vegetation type in which desert grasses and some desert trees are the controlling life forms. This does not explain, however, the discontinuous distribution of the bird. Smithers (1959) found the sociable weaver absent between Mafeking and Tsabong in Botswana, in country which seems to be suitable for it. While there are extensive areas of calcrete with its characteristic vegetation, unsuited to the weavers' requirements, between the eastern and western populations, these areas are not continuous. They are bridged in places by dunes and river beds with Acacia giraffae, in which the weavers might be expected to occur. Perhaps there is a lack of suitable grasses. Hoesch & Niethammer (1940) mention the "sehr ungleichmässiger Verteilung" of the sociable weaver in South West Africa. The problem of distribution in this bird needs further study.

I have already shown that the statement by de Villiers (1958) that the sociable weaver's abundance in the Gemsbok Park "does depend on the availability of suitable nesting sites" is only partly true, in that the birds are absent where there are no nesting sites, but that their abundance is not directly related to the abundance of suitable trees. The idea of dispersal of nesting colonies being effected by interspecific territoriality and by intraspecific intercolonial territoriality was outlined in Chapter 12. Orians (1961) has a further suggestion to explain the "peculiarly spotty distribution" of breeding colonies of tricoloured blackbird Agelaius tricolor (Icteridae) in California, namely the fact that a colonial system is more exacting of high concentrations of food supplies. However, the situation in the blackbirds and the weavers may not be exactly comparable, since the former nest in marshes, which themselves constitute a discontinuous habitat, unlike the apparently uniform habitat of the Acacia savanna in the Kalahari. While it is true that most interspecific territoriality occurs between members of the same genus (Simmons 1951), this is not always the case. Hall (1964) tells of a nesting blacksmith plover Vanellus

(= "Hoplopterus") armatus chasing a stilt Himantopus himantopus from its nest, and I have seen nesting coursers and sandgrouse chase larks from their nests when the larks came too close; these may not be cases of territoriality as such, but the nest is clearly defended against a wide variety of species. Gannon's statement (1953) to the effect that "with birds territory is only proclaimed against members of their own kind" is in any case patently untrue. The matter of dispersal in the sociable weaver is obviously dependent on a number of factors, not one of which is well understood.

Evolution of social behaviour

Within the confines of its own colony the sociable weaver is "probably as social as any bird could possibly be" (Friedmann 1950). Friedmann (1935) also made the pertinent comment that "the truly social aspect of these birds' mode of life is confined to actual nest-building". The only other birds that construct truly communal nests are the buffalo weavers (Collias & Collias 1964), the palm-chat Dulus dominicus (Friedmann 1935) and the monk parakeet Myiopsitta monachus (Naumberg 1930; Wetmore 1926). The smooth-billed ani Crotophaga ani nests communally but in a single nest (Davis 1940). Van Tyne & Berger (1959) distinguish between three types of social nesting habits:

(a) Communal nesting in which all the adults share parental duties as in Crotophaga and Guira.

(b) Co-operative nesting in which the adults share in the building of the nest but not in the care of the young as in Philetairus, Bubalornis and Myiopsitta.

(c) Colonial nesting in which there is no assistance between the pairs in the colony.

How does such social behaviour develop ? Crook (1965) maintains that communal behaviour involving reproductive activities appears to have evolved under two types of circumstance:

"(a) where colonialism has led to a marked reduction in territory size consequent upon the advantages of crowding as many birds into protected sites as possible.

(b) where extension of parent-child bonding has led to the participation of the latter in brood care in a succeeding generation and such behaviour improves the chances of survival of the chicks, selection may favour an increase in mutual participation, especially if the breeding season is long and the breeding is staggered".

Assuming that nest building in the sociable weaver began as an essentially reproductive activity in an already colonial species, the circumstance (a) above is not at all improbable as an explanation of the evolution of the nest mass. But in the case of the sociable weaver, circumstances (a) and (b) are not mutually exclusive, since the first broods do in fact participate in the care of the later broods. It seems likely therefore that the situation progressed from (a) to (b) as the birds' nest building became increasingly co-operative.

However, this is an oversimplification. The present nest mass is not built on a "protected site", but has become itself a protective device. The ancestors of the sociable weaver may have built on protected sites such as drooping branches, as some still do (Fig. 17), but the choice of site must have been greatly modified as the structure evolved into its present bulky form. The nest mass is protective in that only two nest predators commonly invade the chambers (snakes and honey badgers). Although the snakes cause considerable losses of eggs and chicks, there is some evidence suggesting that the larger the nest mass the better protected are the nest contents. The breeding success of the birds at Camp Nest and nest No. 24, the two largest nest masses in the study area, was higher than at any of the other colonies as Table 12 shows clearly. Selection probably favours an increase in the size of the nest mass now that the site itself is not particularly well protected.

Presumably as the co-operative nest evolved, the co-operative building drive increased until the nest mass became the focal point of the birds' existence. The nest mass takes a long time to build and even longer to attain the size of Camp Nest or 24; it also takes considerable building activity at all times to maintain the structure in good repair. The birds could therefore not afford to leave the nest mass in between breeding periods. Thus it becomes a living area which served as a breeding place after rain. The function of the nest as a breeding place is now no more important to the survival of the species than it is as a place of shelter from the elements and protection from predators.

The suggestion by Collias (1965) that the compound nest of the sociable weaver may have evolved as a result of nesting in association with "noxious insects" is probably without foundation, since the Kalahari _Acacia_ species are not inhabited by such insects, as the _Acacia_ species of East Africa are.

As the nest mass evolved into an increasingly larger structure, the birds would have been able to use simpler straws as building material. They probably began by using similar materials to those used today by the sparrow-weavers, but can now use straws without any inflorescences to hold them together. The "haystack" proportions of the nest mass provide sufficient friction to hold the straight straws in place.

Whether the sociable weaver evolved its present nest structure before or after it became semi-desertic in habitat is not clear. If it was already a bird of arid areas, a paucity of trees, such as occurs over most of its range today, would have favoured the evolution of a communal nest so as to fit as many pairs as possible into the limited number of available nesting sites. If, however, conditions became arid after the birds had already evolved their present nest structure, this very structure would have been instrumental in ensuring their survival in the progressively drier conditions. Further speculation along the lines is not profitable for, as Moreau (1966, p.60) has pointed out for Africa, "a species need be only some 20,000 years old to have witnessed the full range of the continent's ecological visissitudes" because of the rapid and recent succession of changes in the ecology.

Although the nest mass has aided the survival of the sociable weaver in arid conditions, it does not provide the birds with any other microclimate than insulation in cold weather and shade in hot weather. These provisions are nevertheless important. The main function of the midday siesta is probably to escape the intense solar radiation of the desert sunshine;

the nest chambers provide more effective shelter than the shade of a bush. It is hardly surprising that the nest chambers do not differ significantly in temperature or relative humidity from the ambient air, since the nest material is sufficiently porous to allow air to circulate through to the chamber interior. Furthermore, there is no reason to suppose that sociable weavers would require a special environment for survival in a climate in which other small birds manage very adequately without modifying their environment in any way.

One point mentioned by Crook (1965) in connection with brood care of chicks by a previous brood is the survival value of such behaviour if the breeding season is long and breeding staggered. This was very definitely the case in the sociable weaver. The second breeding period was 9 months long and the help provided by the young of the first broods must have contributed substantially to the survival of later broods; some experimental work involving the removal of these first broods after they leave the nest would be useful in determining their value as helpers, particularly towards the end of a breeding period when food is growing scarce. This kind of assistance is found in other bird species also, e.g. the smooth-billed ani (Davis 1940) and several others (Skutch 1961). Davis (1940) claims that the behaviour of young anis suggests that they are mimicking the adults; I would think this to be highly likely in the sociable weaver too.

The situation involving "nonbreeding adult intraspecific helpers" (Skutch 1961) is less clear, but the same explanation could hold good for them as for the young birds. Skutch (*op. cit.*) mentions 4 species in which adult helpers occur, possibly as a result of the larger number of males than females. This could be the case in the sociable weaver. If the birds netted in the study area can be regarded as a random sample, the ratio of males to females was 8:5 (76 males and 47 females). This is one instance in which it would have been useful to have been able to distinguish between the sexes in the field.

Although it is not possible to know how long the sociable weaver has inhabited arid regions, it has probably done so for a long time in evolutionary terms. This raises the question of what adaptations, other than the nest mass, the birds have evolved to suit its environment. Naturally the evolution of the nest mass was accompanied by the evolution of associated behaviour patterns, apart from building methods and breeding behaviour. The most important of these is probably the siesta. Most Kalahari birds rest up in the shade of bushes, trees, stones or burrows during the midday hours, but the sociable weaver is probably the only one that uses its nest for this purpose. A few species such as the scaly finch Sporopipes squamifrons use their nests for roosting at night, but I have never seen scaly finches in their nests during the day, unless they were actually breeding. But the siesta habit is not just a protection against the heat of the summer sun, since the birds shelter in the nest during rain or cold weather too. It must also protect the birds to a great measure from birds of prey and other predators that cannot invade the nest chambers.

Associated with the social life of the birds are the various calls, postures and displays that constitute the "language" of the species. The 10 calls recorded for the sociable weaver include 5 of the calls listed by Thorpe (1961, p.17), assuming that my "contact" and "threat" calls correspond to his "flock" and "aggressive" calls respectively. Thorpe's list includes "distress calls" which I have not included in the 10 calls in Chapter 4, but the sociable weaver does have a fear trill which it uses very occasionally in the wild and which is a form of distress call. Thorpe's term "pleasure calls" probably correspond to what I have called "chatter", or else it may be the muted "chip" notes heard from resting weavers. I have, however, not heard anything in the sociable weaver that could be classed as "territorial-defence" or "feeding" calls. Instead of "specialized alarm" calls for ground and air predators, it seems as if the weavers use the general alarm call for ground predators, and a single alarm note followed by hiding in complete silence for a flying predator; this single note may in fact have a particular quality that distinguishes it from other alarm notes, but I have failed to notice it. If so, it can be classed as a "flying-predator" call. The sociable weavers had no notes which could be classed as song.

Among the postures with signal function were fanned tail-flicking (anxiety ?), threat or attack, begging and flight-intention. The flight-intention posture serves the purpose of informing the rest of the colony of the bird's intention to fly, so that the other birds do not take off also. Much the same situation is well known in gannets, duck and other gregarious birds.

The rarity of allopreening as part of the social life of the sociable weaver is interesting. Harrison (1965) suggests that allopreening may be a ritualized displacement activity resulting from the non-departure of an attacked bird which instead assumes an appeasement posture which may result in displacement preening on the part of the attacker. He goes on to say that, in some birds, allopreening has been replaced by special greeting ceremonies. This may explain a curious piece of behaviour in the sociable weaver, which I have so far not been able to explain. It is a simple ceremony which I have called "close inspection" in which two birds encountering one another on the same perch at close quarters will, instead of threatening each other, sit quite still, bill-tip to bill-tip, apparently staring at one another. I have even seen 3 birds involved in the display, the middle bird "close-inspecting" the outer two by turns. If this is in fact a greeting ceremony replacing allopreening, which in turn replaces attack, it is extremely useful in avoiding frequent clashes in a colony of birds living in such close proximity as does the sociable weaver. Under normal circumstances, fights are rare in the colony.

Heat-loss mechanisms are similar to those found in many other birds. The sleeping posture has undergone modification as a result of the highly sociable roosting habits in that the bill is not tucked into the bird's back feathers when it is sleeping with a group of other birds in the same chamber. Presumably the interior of the chamber is kept warm enough by the group to preclude the necessity to insulate the bill with the back feathers. The habit of tucking the bill into the back feathers has, however, not been lost and is probably employed only if a bird happens to be roosting by itself in cold weather.

Feeding

The sociable weaver's independence of drinking water is an adaption to arid conditions associated with its predominantly animal diet, a source of food with a high water content. The only wild weavers that drank water were those feeding on 100% dry seeds. This is probably why the birds normally feed on green grass seed when it is available. A more comprehensive study of the diet of the sociable weaver is needed to show more clearly the seasonal differences in food, particularly those associated with dry and wet conditions. Fleck (1894) and Smith (1849) both mention insects in the diet of these birds, although Smith says that they feed on "seeds, and occasionally small insects".

The sociable weaver feeds almost exclusively on the ground where it is extremely well camouflaged by its coloration; as Friedmann (1930) said "like most denizens of dry regions it is subdued and sandy in coloration . . . ." Associated with this is its comparative silence when feeding, contrasted with its noisy "chatter" at the nest. Only the sparrow-weavers, sparrows and scaly finches among the South African Ploceidae, seem to do as much of their feeding on the ground. They are not, however, as cryptically coloured as the sociable weaver.

Breeding Biology

It is in its breeding biology that some of the most striking desert adaptations of the sociable weaver are found. The most obvious of these is its complete dependence on rain or associated phenomena as the Zeitgeber for breeding. This is a feature of many desert birds, particularly in areas of erratic rainfall (Immelmann 1963a, b; Keast & Marshall 1954) and Moreau (1950) has pointed out that ". . . . 'semi-arid' birds are notably sensitive to rainfall . . . ." This is reflected in the short time lag between a good shower of rain and the laying of the first eggs in the case of the sociable weaver and other desert birds (Immelmann 1963a; M'Gilp 1919). That such birds may not breed for several years if rain does not fall has also been noted in Australia by Keast & Marshall (1954); they also showed that the sexual "cycles" respond quickly to rainfall or its effects. This quick response is a function of "tonic gonadotrophic activity" (Immelmann 1963b) and is indicated in the sociable weaver by the small differences in gonad size in breeding and non-breeding birds. There is only a 50% decrease in testis size between breeding periods. Similar readiness for breeding has been shown by Marshall & Serventy (1958) in some Australian desert birds.

Further evidence for the dependence of the sociable weaver on rainfall as a Zeitgeber was obtained from information kindly supplied to me by Mr. O.P.M. Prozesky (in litt.). On a visit to the Gemsbok Park from 3 to 10 January 1967 after a total of only 12.1 mm. of rain in December 1966, he found no breeding among the weavers in my study area (the colonies can all be identified by plastic numbers on the trunk of the tree). But on a second visit from 27 February to 3 March 1967, the birds were found breeding after a total of 104.1 mm. of rain between 12 January and 9 February, the first big shower of which fell on 18 January (33.0 mm.). Most nests contained eggs or small chicks.

If the rainfall in an arid region were regular, it would seem as if the birds' breeding periods were seasonal. This might obscure the effect of rain on the breeding of birds in such regions, e.g. the south-western deserts of the United States, although even here there may be more variability than is generally recognized.

The effect of environmental conditions on clutch size was better seen in the second breeding period of the sociable weaver, than during the other two breeding periods. The information nevertheless needs augmenting with further studies. Firstly, no measurements of monthly food supply were made; this is in any case not an easy matter. It is probably reasonably safe in this case, however, to draw some conclusions on the circumstantial evidence alone. It seems that the largest clutches were laid when the food supply might be expected to be greatest, just after the rains (i.e. during May and June 1965) and that the mean clutch size decreased as food supply decreased with progressively drier conditions towards the end of the breeding period. Lack (1954, p. 36) has claimed that food supply is not usually a proximate factor influencing clutch size. What the proximate factor in the case of the sociable weaver could be (if it is not food supply), I do not know, but Hoesch (1936) has also shown that clutch size in these birds is greater in years of good rainfall than in poor years. Moreau (1944) has shown the same phenomenon in other African birds.

Just how ultimate a factor food supply is, is not clear, but it seems in some birds to be more of a proximate factor than is generally realized. For instance Schmaus (1938) showed very clearly that the food supply was highly influential on clutch size in some European birds of prey, particularly in the barn owl which raised its two largest broods in the best mouse year, while it normally attempted only one brood in other years. Similar effects have been found in North American owls by Pitelka, Tomich & Treichel (1955), while Lack & Lack (1951) have shown variations in clutch size with seasonal variation in the swift Apus apus.

The size of replacement clutches must also be considered when discussing decreasing clutch size. Replacement clutches in the sociable weaver tended to be smaller than first clutches only towards the end of the breeding period; the mean clutch size of the first replacement clutches was larger than that of the first clutches. The size of replacement clutches is therefore probably influenced by food supply. The same may apply to other species of birds in which replacement clutches are smaller, as in the starling <u>Sturnus</u> <u>vulgaris</u> (Dunnet 1955) and the swift (Lack 1966, p. 6).

The optimal clutch size of the sociable weaver (as of other birds) must vary with varying environmental conditions. Thus smaller clutches may be more successful than larger clutches in poor seasons. This applies in the case of the swift (Lack 1966, p. 4), but the data on the sociable weaver are not sufficient to allow further conclusions to be drawn. There seems little doubt, however, that clutch size is adaptive as claimed by Lack (1954, p. 22). The largest brood that can be raised successfully in a good season seems to be 5 young. There were too few clutches of 6 eggs to allow of an analysis of the comparative success of such a large clutch, but 6 young would probably be maximal for a single pair of weavers to feed in a good season, even with the help of previous broods. Only 3 other species of passerine birds in the Kalahari lay clutches of 6 eggs or more: the penduline tit Anthoscopus minutus, the rufous-eared warbler Malcorus pectoralis and the red-headed finch Amadina erythrocephala. All the others lay 5 eggs or less, and most lay only 2 or 3. A clutch of 6 eggs is therefore about maximal for any passerine bird in the Kalahari. The red-headed finch occasionally lays 7 eggs, but it augments the diet of the young with green grass seeds, unlike the other species mentioned, which feed their young entirely on insects and other animal food.

Clutch size seems therefore to be a product of natural selection as Lack (1954) has suggested. In a highly colonial nester "group selection" (Wynne-Edwards 1962) may also be a factor determining clutch size. Wynne-Edwards (1962, p. 4) is surely correct in maintaining that "the critical resource, as far as population density is concerned, is food"; Crians (1961) on the other hand says that "territorial behaviour cannot limit the sizes of breeding colonies but several lines of evidence suggest that colony size is nonetheless adjusted to the capacities of the environment". Taking these two statements together, it is possible to suggest that the ultimate density of a population may depend on the clutch sizes laid by the original population whose mean clutch size was in turn determined by group selection, in that the clutch size is one way in which the colony size is adjusted to the environment. Thus in good years the mean clutch size will be larger than in poor years. This will be particularly noticeable in desert birds. Of the tricoloured blackbird Orians (1961) says "apparently an assessment of the environment is made during the period of colony establishment by means of mass feeding flights but the exact mechanism remains obscure". This sounds very much like the sort of "epideictic displays" postulated by Wynne-Edwards (1962, p. 16).

Wynne-Edwards (1962, p. 159) mentions two factors which can limit population density; territorial dispersion system and a ceiling on colony membership. The territorial dispersion system of the sociable weaver is very limited, even within the nest mass. In any case, Orians (1961) has said that territorial behaviour is not a limiting factor on the size of the colony, at least in blackbirds. This means that a ceiling on colony membership is probably the more important factor. In the sociable weaver this ceiling is imposed only by the nest site and the size to which the nest mass can grow. Only in very good years will a nest mass of maximal size be fully populated; in other years, breeding birds will tend to lay the largest clutches which can be cared for by each pair since over-population of the nest mass will be no problem. What the situation would be with regard to clutch sizes at times of maximal occupation is not known. If clutch size tended to be smaller at such times, then group selection would be operative.

It is therefore not possible at this stage to discard the theory of group selection, as Crook (1965) and Lack (1966) have done. As Wiens (1966) has said: "where Wynne-Edwards' theory seems to apply it may be quite useful". It seems as if it could apply to certain colonial species of birds, but only under exceptional circumstances. In any case, it seems as if group selection must be regarded as a form of natural selection; the two concepts need not be mutually exclusive.

The sociable weaver's habit of starting incubation with the first or second egg of the clutch is a further adaptation to its arid environment. In a poor season or towards the end of a good breeding period when food is becoming scarcer, only the larger young in a brood usually survive. The smaller and weaker young survive only if food is sufficiently abundant to supply the larger young to the point of satiety, at which they cease to beg and allow the others to be fed. If all the young were of an age, they might all succumb in a period of food shortage. This asynchronous hatching is in effect a mechanism of regulating the brood size more directly and effectively than regulating clutch size. Asynchronous hatching has also been found in the later broods of the great tit Parus major (Gibb 1950), which Lack (1966, p. 33) suggests has the function of reducing the brood size quickly when food is sparse.

The number of broods reared in succession appears to be almost indefinite. As long as conditions suitable for breeding last, the birds continue to breed. The maximum of 4 successive broods in the sociable weaver is about the limit for any passerine in one season. Keast (1959) mentions 3 broods for the "wagtail" Rhipidura leucophrys (Muscicapidae), while Greenhow (1948) mentions four successful broods in the thornbill Acanthiza chrysorrhoa (Sylviidae) in the space of four months; both these birds tend to live in arid country. Lack (1954, p. 53) mentions up to 3 broods per season in some birds and adds: "just as clutch-size normally corresponds to the greatest number of young that can be raised, so the number of broods appears to be the largest possible for the species in the region in question", emphasizing, however, that the evidence for this is largely circumstantial. Nonetheless, the sociable weavers continued to breed for 9 months during the second breeding period; this seems to be rather more than circumstantial evidence that the birds breed as long as suitable conditions last. This was also shown in the persistence with which the birds laid replacement clutches. The largest number of clutches laid by one weaver (including the first clutch) was 8. The largest number of breeding attempts by any other passerine seems to be 5 consecutive nests in one season by a song sparrow Melospiza melodia (Berger 1951). The sociable weaver is thus a good example of an opportunistic breeder.

Why breeding success should have increased with increasing clutch size was probably attributable to the fact that the larger clutches were laid by older birds with more experience in rearing chicks. An increase in clutch size with increasing age has been shown in the great tit (Kluijver 1951) and in the redstart Phoenicurus phoenicurus (Ruiter 1941), so that it is not at all unlikely to find the same thing in the sociable weaver. If this is in fact so, it may mean that the older females are to be found in the larger nest masses, indicating that the nest mass has a protective function against predators on adult weavers, as well as on nestlings. Selection would therefore favour an increase in the size of the nest mass.

For a number of reasons it was not possible to follow the clutch size of a single female from one season to the next. At Camp Nest, for instance, the females did not always nest in the same levels; also the collapse of the SW nest mass terminated observations on a known group of birds which had been selected for special study. In any case, the smaller mean clutch size of the first breeding period was as much the result of poor food supply as of the age of the birds. The environmental conditions would tend to mask the effects of age on clutch size, so that this problem would need to be subjected to controlled experimental conditions.

There was no direct correlation of nesting success and clutch size with the height or size of the nest mass in the study area, although the data suggested that this may have been so. The mean clutch size differences between the different nest masses were not significant. Nevertheless the fact that most of the successful large clutches came from Camp Nest and No. 24, the two largest colonies with some of the highest nest masses, and collectively the largest nest masses, is suggestive. I have seen cobras feeding on chicks at both of these colonies, so that they seemed no less accessible than other nest masses which were more heavily preyed upon. These colonies may simply have been in areas of lower cobra populations.

Crook (1965) draws attention to some interesting facts concerning a colonial (but not co-operative) nester in the Ploceidae, the quelea Quelea quelea: this species is monogamous, males breed in their first year, males participate in parental care to a greater extent than other Ploceinae, and the birds live in "arid savanna with a very short rainy season". These are all features found to a greater or lesser extent in the sociable weaver. Could the similarity of habitat have led to this kind of convergence in their breeding biology ? It is clearly advantageous for birds in arid conditions to breed in their first year and for both sexes to participate in parental care. There is only one breeding Ploceine in the Kalahari, namely the masked weaver Ploceus velatus; it would be interesting to know whether the Kalahari populations of this species have modified their breeding biology from that of the eastern population in more temperate regions.

Although sociable weavers make solicitous parents, I found no basis for the statement by de Villiers (1958) and perpetuated by Labuschagne (1959) that the sociable weaver ". . . continues to breed in its apartments even when the huge structure has fallen to the ground". All fallen nest masses, whether or not they contained eggs or young, were abandoned and the young left to starve or die of exposure.

Predation

Apart from food supply, the main limiting factor in the breeding success of the sociable weaver in the Kalahari is predation by the Cape cobra. Hoesch & Niethammer (1940) mention other snakes as predators on these birds, namely the boomslang *Dispholidus typus*, the spitting cobra *Naja nigricollis* and the Egyptian cobra *Naja anchietae* (= *N. haje anchietae* (Fitzsimons 1962)), but these three snakes do not occur in the sandveld. They remark: "Seltsamerweise reagieren diese Weber nur wenig auf den Anblick einer Baumschlange . . . . " This seems to be generally the case, probably because the birds become quickly habituated to the presence of snakes, which occur so commonly in the nests. Hoesch (1935) bears this out by saying that weavers continue to feed young in chambers adjacent to one in which a boomslang is lying coiled up after feeding; he adds: "die Weber machen keinerlei Versuche die Eindringling zu vertreiben". Friedmann (1930) also mentions the boomslang as "the chief enemy of the social weaver".

Pitman (1958) mentions the bird- and egg-eating propensities of the Egyptian, Cape and spitting cobras, but claims that all three are terrestrial. Perhaps the situation in western South Africa is unusual, but in the Gemsbok Park the Cape cobra is highly arboreal and does much of its feeding in trees, not only on birds and their eggs, but on skinks and probably geckos too. Since skinks and Geckos are commonly found in the weaver nest masses (Hoesch & Niethammer 1940), the snakes may be seeking these as much as young weavers.

Elgood & Ward (1963) have put forward a hypothesis about snake predation to the effect that, in the tropics, where nesting occurs in all months, specialized predators may become attached to a colony of nesting birds which cannot defend actively against the snake; the birds therefore "defend" passively by laying synchronously and limiting the breeding time; the appetite of the predator is then the limiting factor on predation. This might apply to some extent in the sociable weaver, but I have seen more than one snake preying on a colony at different times, thereby eliminating the appetite factor in the case of each individual snake. Although the weavers lay more or less synchronously at the beginning of a breeding period, laying becomes highly asynchronous later on, much as in the red-winged blackbird Agelaius phoeniceus (Orians 1961). Moreover, breeding time in the sociable weaver is not limited. Perhaps in the more tropical part of its range in South West Africa this hypothesis might apply. In the Kalahari sandveld it is the onset of winter that causes a cessation in snake predation.

The percentages for the breeding success of the black-and-white manakin Manacus manacus of 40% for hatching and 19% for fledging (Snow 1962) compare very closely with the corresponding percentages of 47.5% and 17.8% in the sociable weaver. Both these species of birds are heavily preyed on by snakes. Female manakins may attempt up to 5 broods a season; Snow (op. cit.) correlates the low reproductive rate (the normal clutch is 2 eggs) in manakins with low adult mortality. Perhaps this is also true of the sociable weaver. I hope that return visits to the Gemsbok Park in the future will answer this question from an examination of weavers ringed during the study period.

Moult

Closely associated with the arid environment and with breeding biology is the pattern of moult. The slow wing moult is unique among passerines so far studied, but approximates the time taken for wing moult in the pin-tailed sandgrouse Pterocles alchata (Stresemann & Stresemann 1966), also a bird of arid country. Perhaps this protracted wing moult reduces the metabolic drain on the bird. Body moult, however, occurs within a short space of time when food supply is good; a similar, but seasonal, moult occurs in Steller's jay Cyanocitta stelleri in which it appears that "molt is as closely linked in its timing with summer food abundance as that interval of breeding when parents are feeding young in the nest" (Pitelka 1958). In northern Alaska where food is apparently abundant in summer, Passeriformes and Charadriiformes may complete both nuptial and post-nuptial moults in the period between the beginning of June and the middle of August (Johnston 1961); at one of these two moults all the remiges are replaced and this is also the birds' breeding season. Moult cycles are thus highly adaptive and may be modified according to the environmental conditions.

Evolutionary ecology

Lack (1965) listed 10 points which should be considered in a study of the evolutionary ecology of a species. I should now like to review what has been said on the ecology of the sociable weaver with regard to each of these 10 points:

1. It must be made clear as to which features of a species or population are evolutionary adaptations and which are merely consequences of population dynamics. The evolutionary adaptations of the sociable weaver include the nest mass and associated building methods, feeding methods and food, coloration, and almost all aspects of the breeding biology, including clutch size. It is difficult to draw the line between social organization developed in conjunction with the evolution of the nest mass, and social organization that is a consequence of population dynamics.

Both factors must have concurrent influences on the evolution of the social life of these birds.

2. Adaptive features must be divided into proximate and ultimate factors. It seems that adaptive features are the results of proximate and ultimate factors and are not factors in themselves.

3. The over-riding agent of evolution is natural selection. Of this there can be little doubt, but I have already indicated that I do not agree with Lack's statement that ". . . there is no need whatever to bring in the concept of group-selection , as Wynne-Edwards (1962) has done, to explain such features as clutch-size, the age of first breeding, or territorial behaviour in birds". Group-selection is simply a rather specialized form of natural selection.

4. It is important to study evolutionary ecology in the natural habitat of a species. Those aspects of the sociable weaver which have been studied hitherto could only have been studied in the field, but there are some physiological aspects such as water-relations and heat tolerance which can only be studied adequately in the laboratory. I hope that some day this will be done

5. The problem of associated adaptations: once an adaptation has been evolved, others tend to be evolved in

conjunction with it. In the sociable weaver one of the clearest examples of associated adaptations is that of the nest mass and the siesta habit. The siesta could not have evolved as part of the daily rhythm without the evolution of the nest mass as a living area. There are no doubt other examples, but none as striking as this.

6. *One of the difficulties in interpreting ecological adaptations is that one normally finds only the successful end-results of evolution and not the eliminated failures.* This is particularly true of birds in which the fossil record is so fragmentary, but it is nevertheless usually possible to determine what features of a species allow it to be successful in its particular environment. A study of the eliminated failures would have been interesting, but not altogether pertinent.

7. *The existence of adaptive modifications (e.g. modification of clutch size from season to season, depending on conditions) may complicate and obscure measurement of survival value of clutch-size or the behaviour being studied.* The modification of clutch size with season in the sociable weaver does indeed obscure any effect of age on clutch size, for instance. The same may well be true

of the effect of population density within a colony on clutch size. There are a number of such problems which can only be solved with time, and with very large sample numbers.

8. Because ecological adaptations do not usually vary in members of the same species, their significance may have to be assessed by comparisons between different species. This has already been done for the sociable weaver, but it is not always easy or valid to make comparisons between such a highly specialized animal and species less specialized. It is unfortunate that so little is known of the biology of such birds as the palm-chat and the monk parakeet, both of which should make good comparative studies from the standpoint of convergent evolution.

9. There is an urgent need to conserve natural habitats, because it is only here that some of the fundamental problems of biology can be studied. It was fortunate for the purposes of a study of the sociable weaver to have had at my disposal such a large area of relatively untouched natural habitat where the birds probably occur today under the same conditions as they did before the advent of man into the Kalahari.

10. Speculation on evolutionary ecology is dangerous unless

checked by first-hand observations in the field. I would go even further than this by saying that speculation on evolutionary ecology may be dangerous even if checked by first-hand observation in the field. Caution must be exercised always.

Populations

The gaps in aspects of populations of the sociable weaver are accounted for in a pertinent statement of Lack's (1966, p. 271): ". . . the study of breeding biology is relatively simple, whereas that of adult numbers is much harder and requires much longer". Nineteen months was not nearly long enough for a definitive population study.

Nest associates

Among the points which remain to be discussed, that of "guests" or nest associates in the sociable weavers' nests is perhaps the most important. Certainly the most interesting avian guest is the pigmy falcon. This bird has become almost entirely dependent on the sociable weaver for its survival in southern Africa. The claim by Roberts (1940, p. 49) that the weavers desert their nests during occupation by the pigmy falcon is normally untrue. He probably concluded this from the fact that so many pigmy falcons occupy nest masses which were abandoned by the weavers before the falcons moved in. Equally erroneous are the claims by Friedmann (1930) and by Hoesch & Niethammer (1940) that the two species live together without hostility "in gutem Einvernehmen". The presence of the pigmy falcons may well be of benefit to the weavers, even though the weavers resent the intrusion. Hoesch (1935) says of the two species: ". . . es besteht vielleicht sogar eine Art Symbiose, gegründet auf die Gewährung einer bequemen Brutstätte einerseits und dem Fernhalten nesträuberischer Reptilien andererseits". He substantiates this idea to some extent by his observation that no reptiles were ever found in nest masses occupied by pigmy falcons in South West Africa.

The presence of other bird species nesting in sociable weaver nests is probably neither detrimental nor beneficial, as long as the weaver populations are so low that there are unoccupied chambers available for the "guests". What happens when all the chambers are occupied by weavers was not established, since this situation did not arise during the study period. The only mammalian "guest" recorded in the nest masses is the dormouse Claviglis griselda (Hoesch & Niethammer 1940).

The invertebrate nest fauna, with the exception of the larvae of Dermestes beetles, seemed not to affect the weavers in any way. Very possibly such reptiles as the skink <u>Mabuya striata</u> and the gecko <u>Pachydactylus</u> <u>bibronii</u> feed largely on certain members of the invertebrate nest fauna.

Chapter 14

SUMMARY AND CONCLUSIONS

The sociable weaver *Philetairus socius* (Latham) is a passerine bird about the size of a sparrow (*Passer*), cryptically coloured buff and black, and confined to the dry western regions of southern Africa. Its range appears to be governed by the presence of certain xerophilic grasses, mainly species of *Aristida*, as well as the availability of nest sites in such trees as *Acacia giraffae* and artificial sites like telegraph poles and tankstands. Exotic trees are never used as nest sites.

The nest is a co-operatively built structure reaching as much as 7.5 metres in length and 3.6 metres in depth, consisting of a substructure of grass straws and a superstructure of sticks, on a stout horizontal branch. The substructure is more or less flat below and contains the nest chambers, which open on to the lower surface through tunnels about 20 cm. long. Each chamber is lined with soft plant material such as leaves or grass inflorescences. Only dry materials are used in the nest construction, except in the chamber threshold, which is built of green grass or herbs which dry to form a firm step. None of the nest material is woven as in the Ploceinae.

The main functions of the nest include protection from predators, shelter from rain and extremes of heat or cold, a roosting place at night, and a breeding place after rain. The extraordinary nest and the extreme sociability of the birds are unique in the family Ploceidae. Associated with the social life of these birds is the evolution of a number of calls and postures with signal function, serving as "language" within the colony. The upper limit to the size of a colony is imposed by the nest site or sites insofar as they limit the size of the nest masses. A colony may consist of from 2 to 500 birds in one or more nest masses in a single tree, or in a small group of nest masses in neighbouring trees. There is a strict social organization within the nest mass, not associated with peck-order, but with structural levels. Groups of nest masses are widely scattered. This dispersal is attributed to interspecific territoriality, intraspecific intercolonial territoriality and possibly food supply.

Rain, or associated phenomena, is the principal _Zeitgeber_ releasing breeding. The birds do not breed in the absence of rain. The same chambers are used for breeding as are used for roosting throughout the year. The birds are monogamous. The clutch size varies from 2 to 6 eggs, larger clutches being more common after good rains than in poorer years.

Food supply, as influenced by rainfall, may be the proximate factor regulating clutch size. Replacement clutches are not necessarily smaller than first clutches. The mean clutch size within one breeding period decreases with increasing time after rain, and presumably with decreasing food supply. The parents share parental duties about equally. Up to four successive broods may be raised in a single breeding period; a breeding period may last up to nine months and may occur at any time of the year according to the somewhat erratic rainfall which averages about 226 mm. per year in the south-western Kalahari.

First broods help their parents to feed later broods; fourth brood chicks may therefore be fed by as many as 11 birds (9 young and 2 parents). This is undoubtedly of survival value towards the end of a breeding period when food becomes scarcer. Of similar value is the habit of starting incubation with the first or second egg; in a poor season the older chicks will survive while the younger ones succumb from starvation, thereby effectively and quickly reducing brood size. Young birds moult into adult plumage at 4 months, but do not leave the home colony. The sexes are indistinguishable at all ages.

Wing moult is slow. Each remex takes about a month for replacement. Body moult occurs within the space of a month, usually after rain. Primary remiges are moulted proximo-distally from 1 to 9; secondaries are moulted disto-proximally from 1 to 6. Body moult is antero-posterior with the dorsal surface slightly in advance of the ventral surface.

The main nest predator is the Cape cobra Naja nivea in the Kalahari. This snake causes great losses of eggs and chicks; one cobra may eat the contents of an entire nest mass at one feed. Another nest predator which causes fewer losses of eggs and chicks but great destruction to the nest masses, is the honey badger Mellivora capensis. These are the only two nest predators in the Kalahari. Predators on adult sociable weavers include several birds of prey and some small carnivorous mammals.

The food of the sociable weaver during the study period consisted of 78.9% animal material; the rest was mainly seeds, mostly of green grasses. The young are fed entirely on animal food. The most important single source of animal food in the Kalahari is the harvester termite Hodotermes mossambica. Sociable weavers are independent of drinking water under natural circumstances. Members of a colony do not usually feed more than 1.5 Km. from the nest tree.

Some of the chambers in a sociable weaver nest mass may be taken over by other species of birds. Most of these, such as red-headed finches Amadina erythrocephala, use the chambers for breeding purposes only, but the pigmy falcon Polihierax semitorquatus is a permanent resident, roosting in the chambers at all times of the year. The presence of the falcons is resented by the weavers, although it may be beneficial in keeping snakes away from the nests. Adult sociable weavers are not normally preyed on by the pigmy falcons, although the falcons may occasionally take young weavers in the chambers.

Adult sociable weavers have few ectoparasites and no Mallophaga. A common ectoparasite on the legs of the chicks is a blood-sucking Dermestes larva which is not usually harmful. The only endoparasite found was the nematode Diplotriaena ozouxi which infected the abdominal air sacs. The nest material housed a wealth of invertebrate fauna (including the adults of the parasitic Dermestes larvae) as well as a few harmless reptiles such as skinks and geckos. The tops of the nest masses were often used as nest sites by the giant eagle-owl Bubo lacteus, while barn owls Tyto alba sometimes occupied cavities in the superstructure. Neither of these owls appeared to prey on the weavers.

There were an estimated 180 sociable weavers per square mile in the study area, but population density was low during the study period. There were many abandoned nest masses, particularly in the dunes, and many unoccupied chambers in the occupied nest masses. The dune populations may form a reservoir augmenting riverine populations in poor years when the birds' numbers are decreasing. Normally, however, intercolonial movement is negligibly small. Population density is not directly related to the density of trees and available nest sites, since the colonies are rather widely dispersed. The factors regulating dispersal and colonial movements are poorly known. The study period was too short for an adequate assessment of population dynamics.

ZUSAMMENFASSUNG

Der Siedelweber Philetairus socius (Latham) ist ein schutzfarbener, sperlingsgrosser Vogel des trockenen südlichen Afrikas. Sein Verbreitungsgebiet ist scheinbar von der Anwesenheit einiger xerophiler Gräser als auch von Nistplätzen (hauptsächlich Acacia giraffae Bäumen) abhängig. Exotische Bäume werden nie als Nistplätze benutzt.

Das Nest ist ein grosse, gemeinsam gebaute, bis 7,5 M. lange und 3,6 M. tiefe Struktur, die in einen aus trockenen Grashalmen errichteten Unterbau und einen aus groberen Stöcken konstruierten Oberbau geteilt werden kann. Es wird auf einem dicken waagerechten Baumast oder einer Telegraphenstange gebaut. Der Unterbau ist unten fast eben und enthält die Nistkammern, die sich durch ungefähr 20 cm. lange Eingangsröhren auf die untere Oberfläche öffnen. Jede Kammer wird von weichem, trockenem Pflanzenmaterial ausgepolstert. Ausser der Schwelle des Kammereingangs wird nur trockenes Material gebraucht; die Schwelle besteht aus grünen Grashalmen oder Kräutern, die langsam austrocknen und eine starke Treppe bilden. Das Material wird keineswegs gewebt, wie es bei den Ploceidae der Fall ist.

Die Funktionen des Nestes schliessen ein: Schutz gegen Raubtiere, Schutz gegen Regen oder übermässige Hitze und Kälte, Schlafplatz nachts, und Brutstätte nach Regen. Aufgrund des ausserordentlichen Nestes und der höchst gesellschaftlichen Lebensweise der Vögel unterscheidet sich der Siedelweber sehr viel von den anderen Ploceidae. Abhängig von der gesellschaftlichen Lebensweise ist die Entwicklung einiger Rufe und Gebärden, die als die "Sprache" dieser Vogelart dienen. Die Grösse einer Siedlung wird nur durch die Grösse des Nestes beschränkt und kann aus von 2 bis 500 Vögeln bestehen. Es entsteht eine strenge Gesellschaftsorganisation innerhalb eines Nestes, die nicht von der Rangordnung der Mitglieder der Siedlung, sondern von den Baustufen des Nistbauwerkes bestimmt ist. Nahestehende Bäume mögen benachbarte Nistbauwerke enthalten, diese Gruppen sind aber weit auseinander. Die Verbreitung dieser Gruppen oder Siedlungen wird der interspezifischen Territorialität, intraspezifischen interkolonialen Territorialität und dem Nahrungsvorrat zugeschrieben.

Regen, oder verbundene Erscheinungen, ist der Hauptzeitgeber der Brutzeit. Die Vögel sind monogam und brüten nur nach Regen, sonst gar nicht. Dieselben Nistkammern, die als Schlafplätze dienen, werden als Brutnester benutzt. Die Gelegegrösse variiert von 2 bis 6 Eier. Grössere Gelege kommen nach gutem Regen vor, Kleinere in schwachen Regenjahren. Der Nahrungsvorrat scheint der unmittelbare bestimmende Faktor der Gelegegrösse zu sein. Ersatzgelege sind nicht notwendigerweise kleiner als das erste Gelege; die Mittelgrösse der Gelege vermindert sich proportionel, so wie sich der Nahrungsvorrat vermindert. Die Eltern nehmen in Gleichem Masse an dem Brutgeschäft teil. Bis 4 aufeinanderfolgende Bruten werden in einer Brutzeit erzogen. Eine Brutzeit kann bis 9 Monate dauern und mag dem Regen zufolge zu irgendeiner Zeit des Jahres eintreten. Der durchschnittliche Regenfall in der Kalahari ist 226 mm. im Jahre.

Die Jungvögel der ersten Bruten helfen ihren Eltern mit dem Füttern späterer Bruten, so dass die vierte Brut von 11 Vögeln (9 Jungen und 2 Eltern) gefüttert werden kann. Dies ist wohl von höchstem Überbleibenswert gegen Ende der Brutzeit, wenn die Nahrung nicht so häufig ist. Mit 4 Monaten mausern die Jungvögel ins „Brutkleid", verlassen aber die Heimatsiedlung nicht. Die Geschlechter sind zu allen Altern ununterschiedlich. Jede Schwungfeder nimmt einen Monat für ihre Ersetzung; diese langsame Mauser ist eine Anpassung an die trockene Umgebung. Die Handschwingen mausern sich descendent von 1 bis 9, die Armschwingen ascendent von 1 bis 6, nicht aber so regelmässig wie die Handschwingen. Die Körpermauser findet binnen einem Monat statt, gewöhnlich nach Regen.

Das wichtigste Raubtier der Eier und Jungen des Siedelwebers ist die Kobra Naja nivea, die grosse Verluste verursacht. Eine dieser Schlangen kann den Inhalt eines ganzen Nistbauwerkes verschlingen. Ein anderes Raubtier, das die Nester zerstört aber nicht solche grossen Verlust verursacht, ist der Honigdachs Mellivora capensis. Diese beiden Tiere sind die einzigen Nesträuber des Siedelwebers. Die erwachsenen Vögel werden durch einige Raubvögel und kleinere Säugetiere gefangen.

Die Nahrung des Siedelwebers ist 78,9% tierischen Ursprunges. Der Rest besteht meistens aus grünen Grassamen. Die Jungen werden ausschliesslich mit Insekten und anderer tierischer Nahrung versehen. Die wichtigste einzelne Nahrungsquelle tierischer Art in der Kalahari ist die Termite Hodotermes mossambica. Unter natürlichen Umständen sind Siedelweber völlig wasserunabhängig. Die Vögel finden ihre Nahrung gewöhnlich nicht weiter als 1,5 Km. vom Nest.

Einige Nistkammern im Nistbauwerk werden von anderen Vogelarten übernommen. Die meisten dieser „Gäste" benutzen die Kammern nur zum Brüten, der Zwergfalke aber als Wohn- und Brutstätte das ganze Jahr hindurch. Die Webervögel verübeln diesen Eindringling, der die Weber aber nicht als Beutetier betrachtet. Die Weber gewinnen scheinbar von der Gegenwart der Falken Schutz gegen Schlangen.

Erwachsene Siedelweber haben wenige Aussenparasiten und keine Mallophaga. Ein häufiger Aussenparasit der Jungvögel ist eine blutsaugende Larve der Gattung *Dermestes* (Coleoptera), die aber gewöhnlich nicht schädlich ist. Der einzige Innenparasit ist *Diplotriaena ozouxi* (Nematoda), der in den Bauchluftsäcken vorkommt. Das Nistmaterial wird von einem Haufen Arthropoda bewohnt (einschliessend die *Dermestes*-Adulten) als auch ein paar unschädlichen Eidechsen und Geckos. Die Oberfläche des Nistoberbaus wird ab und zu als Nistplatz von Milchuhus *Bubo lacteus* benutzt. Schleiereulen *Tyto alba* werden manchmal in Löchern im Oberbau getroffen. Keine dieser Eulenarten scheint ein Raubtier des Webers zu sein.

Während der Studieperiode waren die Populationen der Siedelweber ziemlich klein; es waren viele unbewohnte Nistbauwerke und Nistkammern, hauptsächlich in den Dünen. Die Populationen in den Dünen bilden scheinbar eine Art „Reservoir", die in schwachen Jahren in die Flussbett-Nester übersiedeln. Gewöhnlich aber geschehen interkoloniale Bewegungen sehr selten. Der Populationsbestand ist nicht direkt von der Anzahl Bäume abhängig, denn die Siedlungen sind weit auseinander. Die Bestimmungsfaktoren der Verbreitung und der koloniale Bewegungen sind unbekannt. Die Studieperiode war überhaupt zu kurz eine Analyse der Populationsökologie zu erlauben.

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