THE BIOLOGY OF THE LARKS (ALAUDIDAE) OF THE KALAHARI SANDVELD

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INTRODUCTION

No family of passerine birds has shown as great an adaptive radiation in the arid regions of the Old World as have the larks. One species, the horned lark *Eremophila alpestris*, probably has the widest range of any passerine (excluding introduced species), having a circumpolar distribution with numerous subspecies, and even one in northern South America (Meinertzhagen 1954). Of the world's 76 species of larks (Peters 1960) 25 occur in South Africa (McLachlan & Liversidge 1957) and of these, nine are found in the Kalahari sandveld. Eight of them are breeding species, while one, the red-capped lark *Calandrella cinerea*, is an irregular visitor in small numbers.

It is therefore surprising to find that little biological work has been done on the South African larks, although the systematists have argued long about the systematic position of museum skins (e.g. Macdonald 1952b, 1953, 1957; Verheyen 1958, 1959; White 1952, 1956a, b, c, 1957a, b, 1959a, b; Winterbottom 1962). Most of the biological work on larks has been done in regions where only one, or at most three or four, species occur regularly, such as North America (Du Bois 1935, 1936; Forbush 1927; Lovell 1944; Pickwell 1931), Europe (Abs 1963; Guichard 1960; Harrison & Forster 1959; Hartley 1946; Koffán 1960; Labitte 1958; Lebeurier & Rapine 1935; Wadewitz 1957) and Australia (Bourke 1947; Bravery 1962). In Africa the biological information is largely confined to works of a general nature (Andersson 1872; Etchécopar & Hüe 1964; Heim de Balsac & Mayaud 1962; Hoesch 1955; Macdonald 1957; McLachlan & Liversidge 1957; Meinertzhagen 1954; Smithers 1964; Valverde 1957), although a few more detailed studies do exist (Steyn 1964; Van Someren 1956; Winterbottom & Wilson 1959).

The present study is therefore a contribution to the biology of African Alaudidae; but perhaps even more important than that, it is a contribution to the biology of the Kalahari, an area rich in animal life almost untouched by the serious biologist. The work was done over a period of 19 months (October 1964 to April 1966 inclusive) in the Kalahari Gemsbok National Park situated in the south-western part of the Kalahari sandveld. The sandveld extends across southern and western Botswana, the northern Cape and eastern South West Africa. It consists of rolling red dunes with a sparse cover of grasses, bushes and trees. Detailed descriptions of this region are given by Leistner (1959a, b) and Smithers (1964).

Most of the observations which follow were done in the southern portion of the Park from Twee Rivieren northwards up the Auob and Nossob Rivers for about 25 miles, including the dunes between the rivers and for a mile or two on either side of the rivers (Fig. 1).

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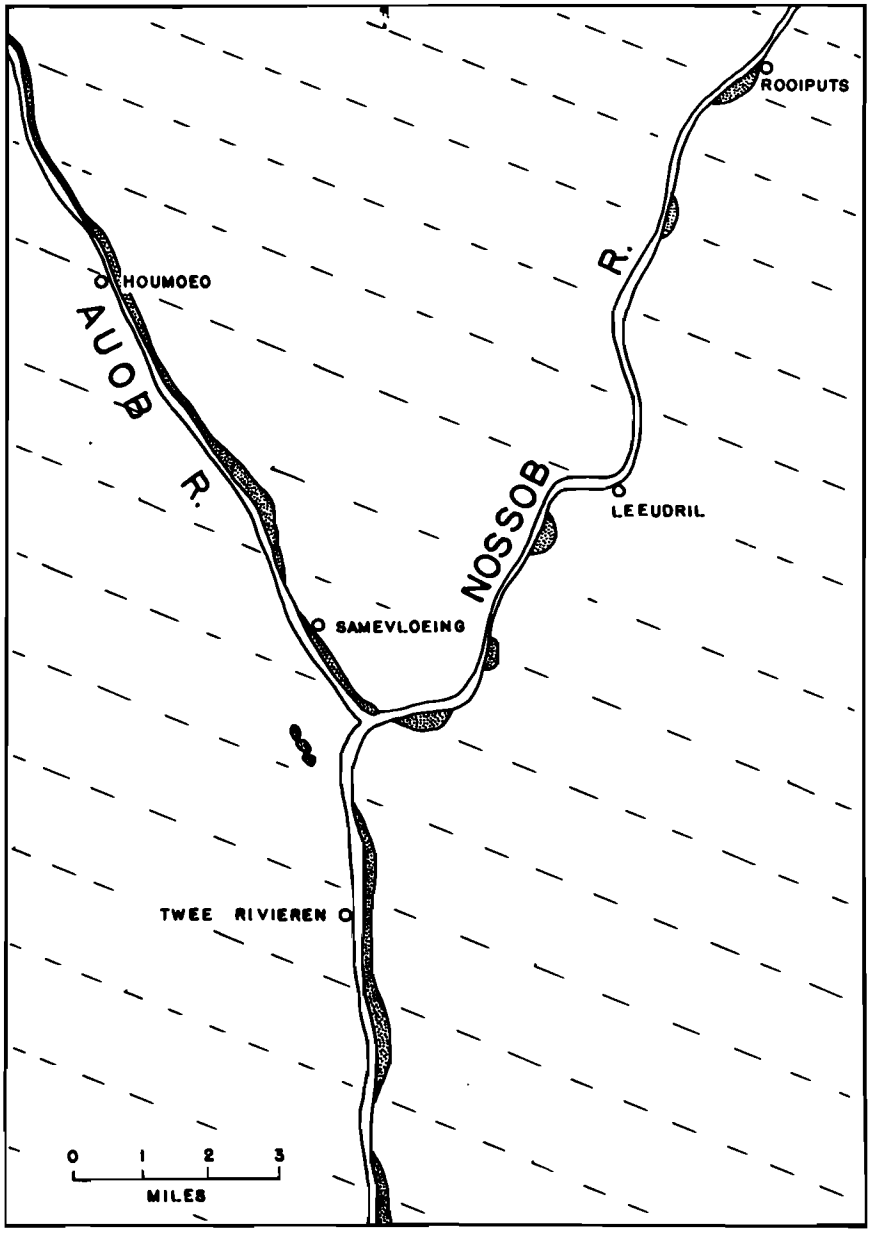

FIGURE 1
Map of the southern part of the study area. The broken diagonal lines indicate the direction of the dunes; the shaded areas on the east banks of both rivers represent the calcrete.

FIGURE 2
Typical dune trough with dense grass cover; this is the habitat of the fawn-coloured and pink-billed larks. The grass is mostly *Asthenatherum glaucum*.

The scientific names of the larks used in this paper are modified from those in McLachlan & Liversidge (1957) according to Harrison (1966) and White (1952, 1959b), except that the spike-heeled lark is retained in the genus *Certhilauda* for reasons which will appear in a later publication.

ECOLOGICAL ASPECTS OF THE SANDVELD

The study area included three distinct habitats: (*a*) the dunes, (*b*) the calcrete and (*c*) the river beds. Each of these can be further subdivided according to variations in the vegetation, partly the result of differences in the soil and partly the result of differences in rainfall. The mean annual rainfall for Twee Rivieren for the past five years is 226 mm. This figure increases northwards, but there are no actual weather records obtainable for other places within the study area.

The Dunes

The background colour of the dunes is the red of the sand. Throughout the area the crests and upper slopes of the dunes support a growth of tall, coarse grass (*Stipagrostis amabilis*), while widely scattered groups of thorny *Acacia detinens* bushes grow on the lower slopes. The dune troughs have a much more variable cover.

Troughs with dense grass cover: The taller, denser grasses are *Asthenatherum glaucum*

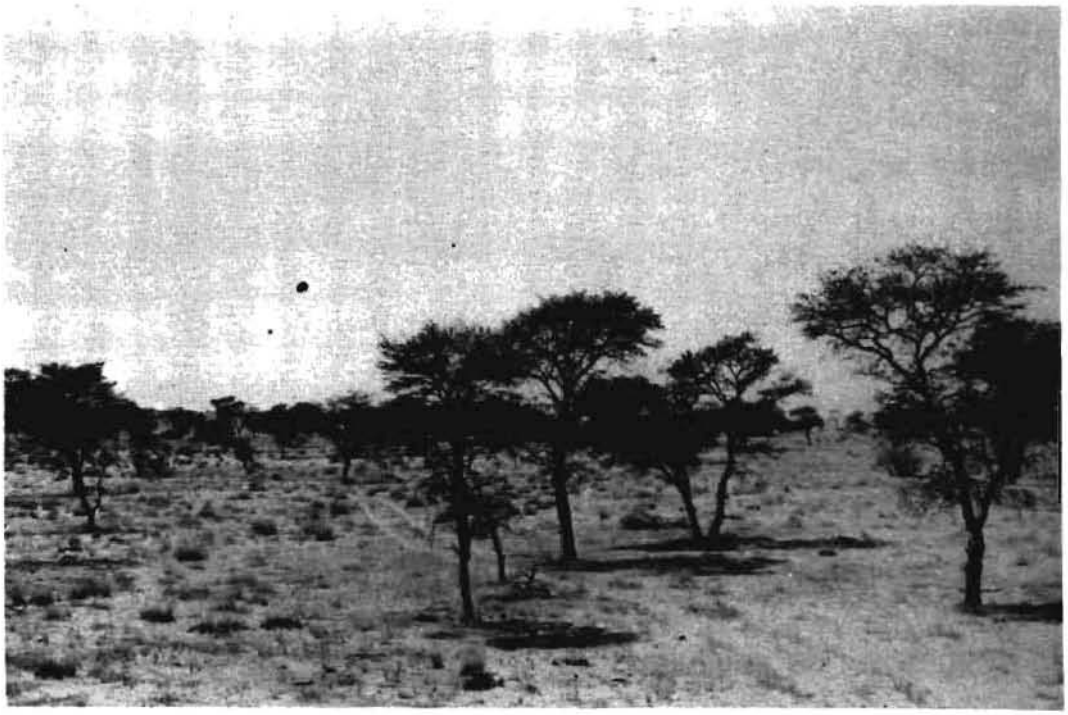

FIGURE 3
Acacia savanna about a mile east of the Nossob River to the north of Rooiputs.

and *Aristida ciliata* with an occasional admixture of *Stipagrostis amabilis*. They are characteristic of deep sand. Shrubs are sparse or absent (Fig. 2).

Troughs with sparse grass cover: The more open troughs usually consist of shallower sand in which the influence of the underlying calcrete or limestone is apparent in the short, tufty grasses such as *Aristida obtusa* and *A. uniplumus*. There are usually a few low shrubs present.

Troughs with shrubs: Many of the shallow sandy areas support an almost pure growth of the shrub *Rhigozum trichotomum* which favours a mixture of calcareous and sandy soil. Where the dunes and calcrete meet there are often extensive "*Rhigozum* flats" with little or no grass, even after good rains.

Troughs with Acacia *savanna:* From Rooiputs northwards, mainly east of the Nossob River, the dunes are covered with scattered *Acacia giraffae* trees increasing in size northwards and forming a parkland community. The trees reach just over 30 feet in height (Fig. 3).

The Calcrete

The restricted areas of calcrete (see Fig. 1) are rather uniform in appearance throughout the study area—flat, stony limestone with a sparce cover of low shrubs, not usually more than a foot high (Fig. 4). The general background colour of the calcrete is grey.

FIGURE 4
The calcrete showing the flat, open nature of the terrain. This is the typical habitat of the grey-backed finch-lark.

The River Beds

The Auob: Within the study area, the Auob is mostly bare with a few bushy *Acacia haematoxylon* trees at the very edges of the river bed; some of the bare areas have a thin cover of short grass, but mostly there are just a few dry *Geigeria pectidea* plants.

The Nossob: As in the Auob River, there are extensive areas sparsely covered with *Geigeria*, but the Nossob River has many more trees, mostly *Acacia giraffae*, particularly from Rooiputs northwards. Characteristic of parts of the Nossob River are dense growths of the shrubby *Galenia africana*, an evergreen standing two or three feet in height; these areas are referred to as "*Galenia* regions". The *Galenia* seems to act as a trap for wind-blown seeds.

The south-western Kalahari is predominantly a summer rainfall region (Fig. 5) with the bulk of the rain falling during the latter half of summer. Summer temperatures frequently exceed 40°C during the day, while in winter the temperature may drop as low as —11°C at night.

LARK HABITATS

Smithers (1964) has given a concise summary of the habitat of each species of lark in the sandveld. The Kalahari larks are broadly divisible into two main colour groups, "red" larks and

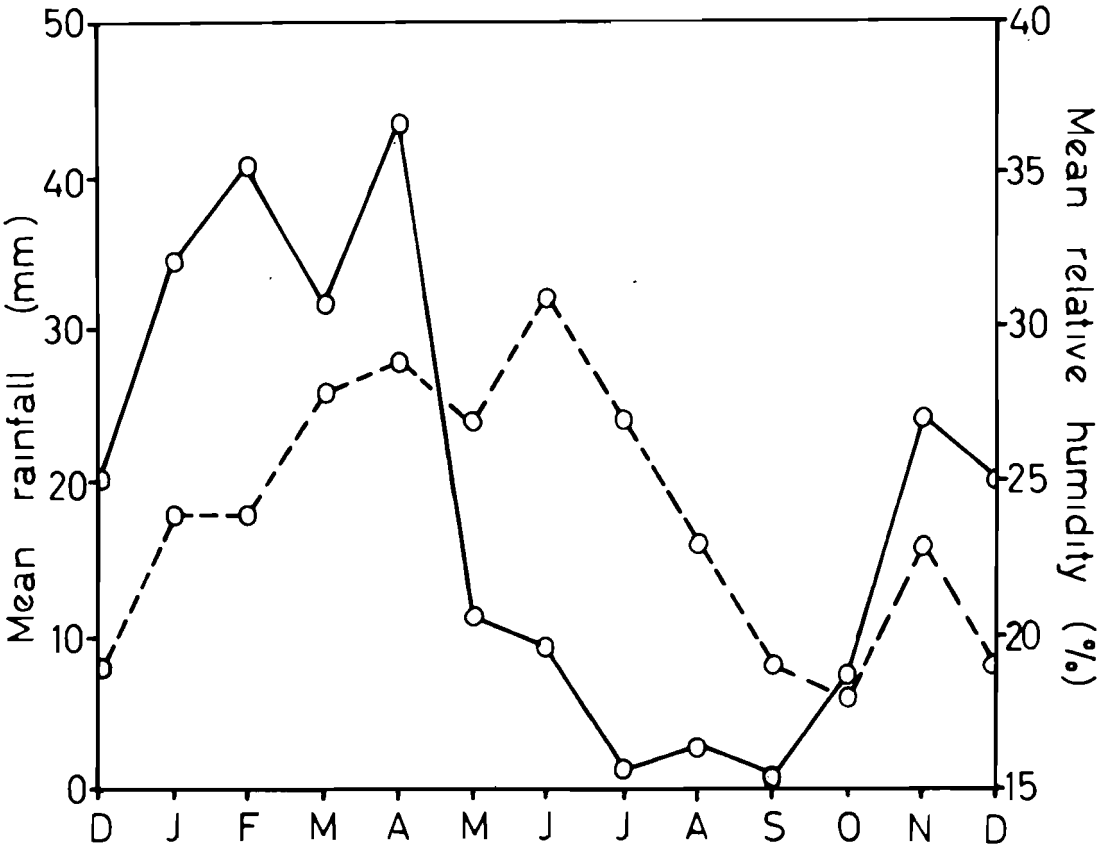

FIGURE 5
Graph showing the mean monthly rainfall (solid line) and minimal relative humidity (broken line) at Twee Rivieren over the past five years.

"grey" larks. The former occur mainly in the dunes, the latter mainly on the calcrete. Winterbottom (1967) indicates these same colour differences for the larks of the Karroo, including eight of the species dealt with in this paper.

I. *Breeding Species*

A. *The "red" larks*

1. Fawn-coloured lark *Mirafra africanoides*

The colour of the dorsal surface of this lark is generally a sandy red, varying from dull pinkish to bright rufous according to the individual. The fawn-coloured lark occurs only in the dunes in all types of dune habitat, but less commonly in the *Rhigozum*-covered troughs than in grassy troughs. It is the commonest, and sometimes the only, species of the *Acacia* savanna.

FIGURE 6
Typical dune scene looking east toward Twee Rivieren. The dune crest in the left foreground is covered with *Stipagrostis amabilis* and the dark areas in the dune troughs are *Rhigozum trichotomum* shrubs, the typical habitat of the black finch-lark.

2. Clapper lark *Mirafra apiata*

This shy and retiring species of lark (cf. also Macdonald 1957) is probably more common in the sandveld than it appears to be, as it is seen only when performing its spectacular display flights over its territory in the dunes. It is the brightest red of the sandveld larks and occurs only in dune troughs with a dense cover of long grass.

3. Spike-heeled lark *Certhilauda albofasciata*

Although red, the spike-heeled lark was also commonly found on the calcrete, but it seldom nested on a background where there was not at least some red sand, often apparently selecting a small patch of sand on the calcrete on which to nest. Smithers (1964) also noted that it was a bird of both dune and calcrete.

4. Pink-billed lark *Calandrella conirostris*

A nomadic, reddish lark of the dunes where there was a fairly dense grass cover, the pink-billed lark was found on the calcrete only where there was a patch of red sand with a good cover of grass. It may also occur in *Rhigozum* areas where there is little grass, but it appears to need good cover always.

5. Black finch-lark *Eremopterix australis*

Another nomadic species, the black finch-lark occurs almost exclusively in the *Rhigozum*-covered dune troughs (Fig. 6). Although it nests only in this habitat, it does feed commonly

in large flocks in the *Galenia* regions of the Nossob River in dry seasons when the birds are not breeding.

B. *The "grey" larks*

1. Sabota lark *Mirafra sabota*

More buffy than grey, but certainly not red, this lark is confined to the edges of the calcrete where they drop steeply into the river beds. Hoesch (1955) indicated clearly the habitat preference of the sabota lark when he said it lives "*an den Geröllhängen unserer Berge*" in South West Africa. It never occurs in the dunes.

2. Grey-backed finch-lark *Eremopterix verticalis*

Another nomadic species, the grey-backed finch-lark is the greyest of the Kalahari larks. It showed preference for the calcrete, but its vast numbers could not be accommodated on the limited area provided by the calcrete and many were forced into the dunes, even for breeding purposes. Some individuals even nested in the river beds.

3. Stark's lark *Alauda starki*

Stark's lark is also more buff than grey, but decidedly not red. Like the grey-backed finch-lark, it was nomadic and found only on the calcrete.

II. *Non-breeding Species*

1. Red-capped lark *Calandrella cinerea*

The red-capped lark occurred in the bare areas of the Auob River bed where there was a sparse cover of very short grass. It was recorded only twice: one bird on November 30 and again on December 1, 1964; and a small flock of nine to ten birds between April 7 and 21, 1966. These larks appeared to be in transit and did not show signs of breeding.

The habitat requirements of the nine species of larks are summarised in Table 1, from which it is seen that never more than three species occur in the same habitat and never more than two nomadic species occur in the same habitat.

FEEDING HABITS

On the basis of their food and feeding habits, the Kalahari larks can be divided into two groups: insectivorous and granivorous. However, these divisions are not rigid, particularly in the adults. The spike-heeled lark and the three species of *Mirafra* probably feed their young entirely on insect food, but the adults eat both insects and seeds. The granivorous larks include all the nomadic species. The adults of these species feed mainly on grass seeds and may even feed the young on green grass seeds. The grey-backed and black finch-larks appear to feed their young mostly on insects, however, and the same probably applies to the pink-billed lark.

TABLE 1

HABITAT PREFERENCES OF THE LARKS OF THE KALAHARI SANDVELD. OPEN TROUGHS HAVE LITTLE VEGETATION COVER; TALL GRASS MAY BE RATHER SPARSE. (+) INDICATES THAT THE HABITAT IS FREQUENTED, WHILE (++) INDICATES FIRST PREFERENCE

Species	*Habitats*							
	Dunes					*Calcrete*		*Rivers*
	Acacia savanna	*Dense grass*	*Tall grass*	*Open troughs*	*Rhigozum flats*	*Rocky slope*	*Stony flats*	*River beds*
M. africanoides	+	+	+	+				
M. apiata		++						
C. albofasciata				+	+		+	
C. conirostris			++		+			
E. australis					++			
M. sabota						++		
A. starki							++	
E. verticalis				+			++	+
C. cinerea								++

Stark's lark feeds considerable quantities of green grass seeds to its young even when newly hatched.

The bill structure of the different species reflects to some extent the different feeding habits (Fig. 7), from long and slender in the insectivorous larks to short and stout in the granivorous species.

BREEDING BIOLOGY

A. *Breeding Seasons*

Table 2 presents a full analysis of monthly nest counts for each of the breeding species of larks in the sandveld. These counts are shown in relation to rainfall in Fig. 8 from which it is clear that rain is the main factor initiating breeding, directly or indirectly, and regardless of whether the species is insectivorous or granivorous. The extent of the breeding period depends on the extent of rainfall, both in quantity and duration; also related to the extent of the rainfall is the lag period between the first shower of rain and the first eggs laid (Table 3). The heavier the first shower of rain, the shorter will be the lag period. Thus after a sharp downpour of 22 mm. of rain on January 18, 1966, followed by showers of 38·5 mm. and 21·5 mm. on the 19th and 27th respectively, the first eggs were found within a week after the first shower.

Up to a point, the greater the amount of rain, the more species of larks were found breeding. Although the third rainy season was the best in that the most rain fell in the shortest

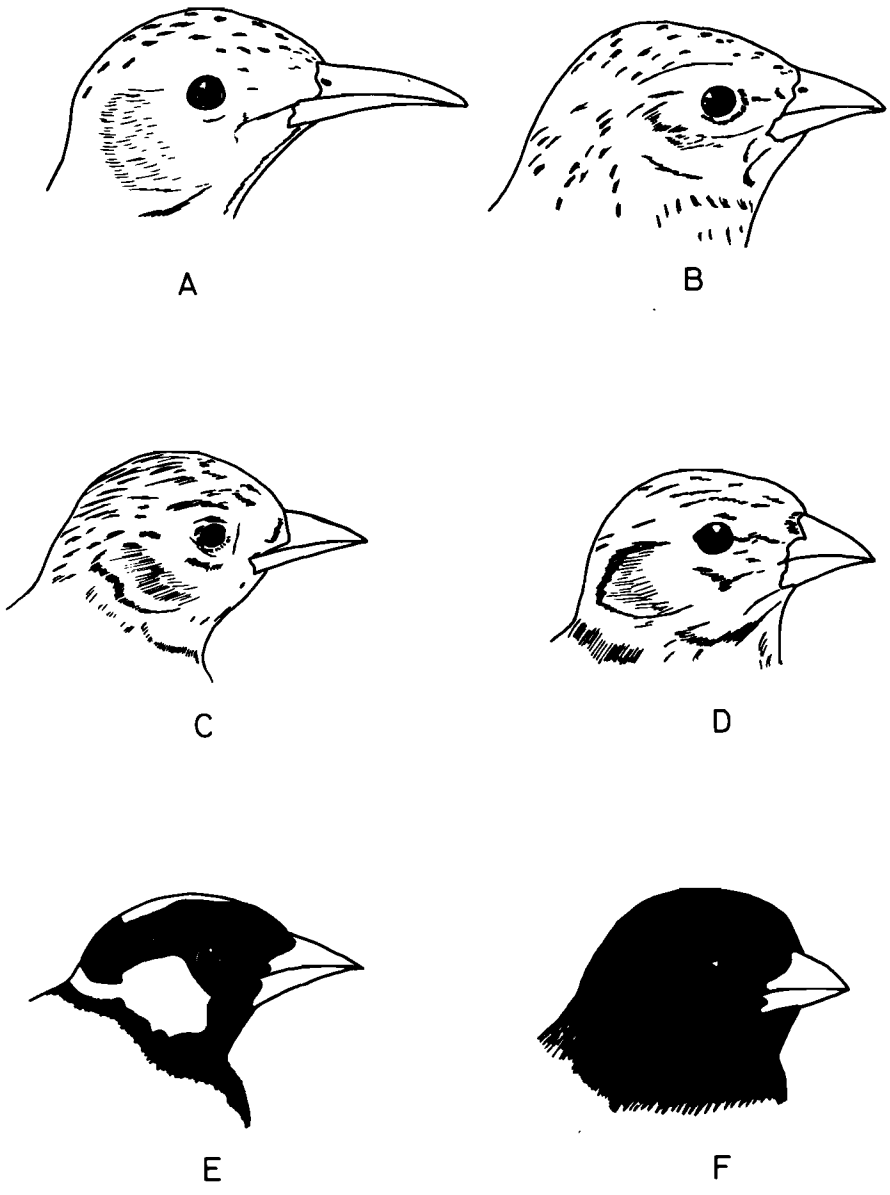

FIGURE 7
The heads of 6 species of larks of the sandveld, showing variations in bill structure: A. *Certhilauda albofasciata*, B. *Mirafra africanoides*, C. *Alauda starki*, D. *Calandrella conirostris*, E. *Eremopterix verticalis*, F. *Eremopterix australis*. These differences are associated with differences in diet (see text for explanation).

TABLE 2

TOTAL NEST COUNTS PER SPECIES PER MONTH OF THE LARKS OF THE KALAHARI SANDVELD

Species	1964						1965									1966			
	O	*N*	*D*	*J*	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*	*J*	*F*	*M*	*A*
M. africanoides							1					1		1		1	7	3	1
M. sabota								1									1		
C. albofasciata			2					6	1	4	3	3	6	1		3	6	3	1
E. verticalis				11			1	6	14	48	19	6	5			19	50	15	
E. australis								5	9	12	1						31		
C. conirostris								6	21	16	2	4	2				3	1	
A. starki									1	4	1								
Totals	0	0	2	11	0	0	2	24	46	84	26	14	13	2	0	23	98	22	2

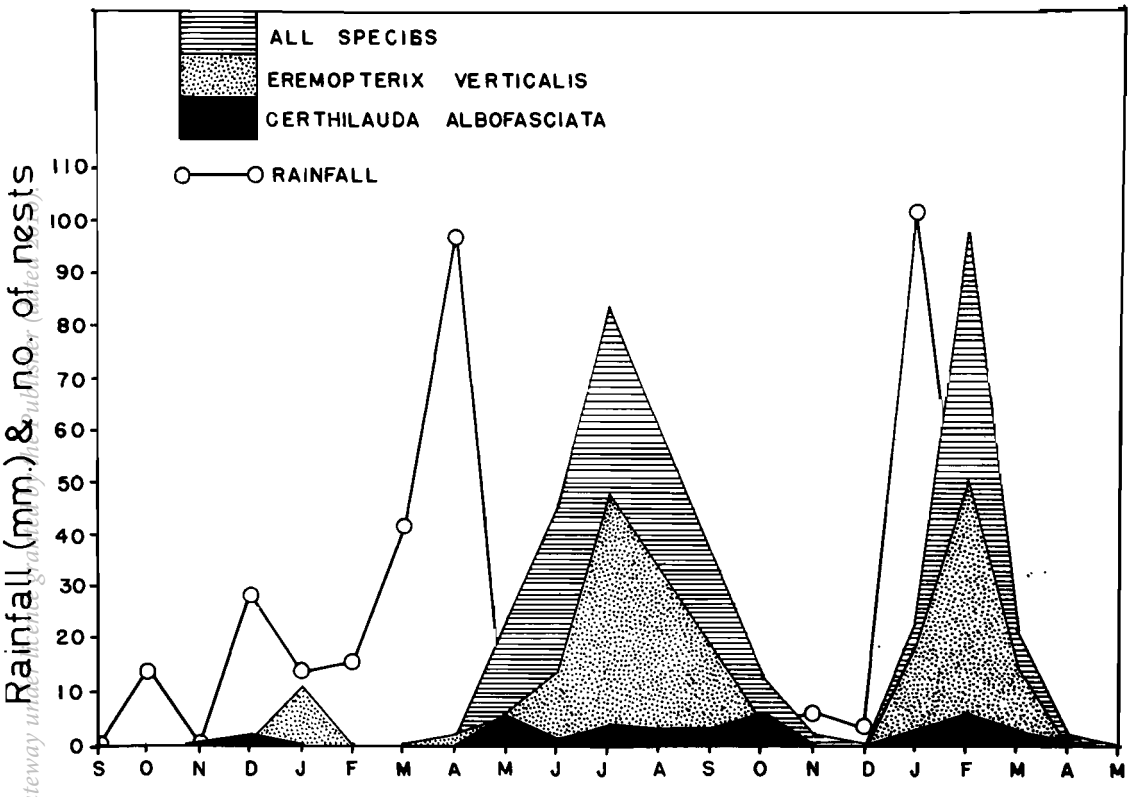

FIGURE 8

Graph showing the relation of nest counts to rainfall in the larks of the Kalahari sandveld.

TABLE 3

THE EFFECT OF THE DURATION AND AMOUNT OF RAINFALL ON THE LAG PERIOD BETWEEN FIRST SHOWER OF RAIN AND FIRST NEST, AND ON THE DURATION OF THE BREEDING PERIOD IN TWO LARKS OF THE KALAHARI SANDVELD

Breeding Period	*Duration of Rainy Season*	*Rainfall (mm.)*	*Lag Period between first Shower of Rain & First Nest*		*Duration of Breeding Period*
			C.albofasciata	*E.verticalis*	
December–January 1965	4 weeks	28·6	3 weeks	5 weeks	3 weeks
April–November 1965	4 weeks	139·0	6 weeks	8 weeks	30 weeks
January–April 1966	3 weeks	131·3	1 week	1 week	12 weeks

space of time, the pink-billed lark bred in very small numbers and Stark's lark did not breed at all. The reason for this is not immediately obvious, unless both these species are predominantly winter breeders over their entire range.

B. *Populations in Relation to Rainfall*

As with breeding, rainfall largely determines population fluctuations in the nomadic larks. The term *nomadic* is used instead of "migratory" for reasons given by White (1959a) and refers to those species which move about locally according to weather conditions and other factors which still need working out. Fig. 9 shows how the population of the four breeding nomadic species of larks increased after each rainy period; the population peaks correspond to the peaks of nest counts in Fig. 8.

The very high counts of *Eremopterix australis* and *Alauda starki* in February and March 1965 are interesting because neither species bred at the time; both occurred in flocks, a typical characteristic of non-breeding nomadic larks. These two months were very dry in the sandveld and it is possible that these larks (and also the few *Calandrella conirostris*) were concentrating in the National Park as a result of a food shortage in the overgrazed farming areas to the south. The same may be true of *Eremopterix verticalis* since it is unlikely from the low nesting success for that period that the peak in February could have been due to young birds augmenting the numbers of non-breeding birds flocking on the calcrete.

C. *Nests and Nest Sites*

1. *Mirafra africanoides*

The nest of the fawn-coloured lark is almost invariably a domed structure built under or against a tuft of grass or a herb such as *Hirpicium echinum* (Fig. 10). Only one nest out of 15 lacked a domed roof (Fig. 11), but the back of this nest was very slightly built up against

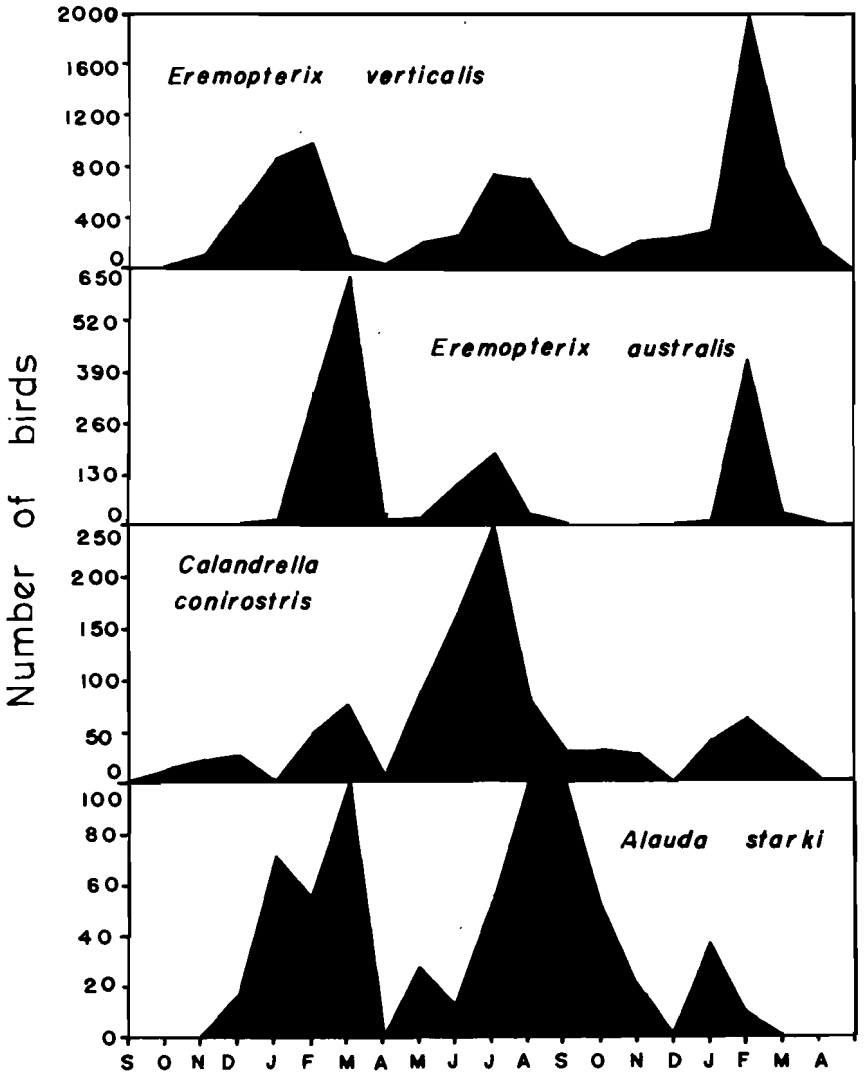

FIGURE 9
Population fluctuations of four nomadic species of larks in the Kalahari sandveld from October 1964 to April 1966.

the grass. Contrary to what Hoesch (1955) maintained, the dome and cup form a single constructional unit. Like all species of larks so far studied (Abs 1963; DuBois 1935, 1936; Guichard 1960; Koffán 1960; Pickwell 1931; Van Someren 1956) the fawn-coloured lark

FIGURE 10
Typical nest of *Mirafra africanoides* showing the domed roof. Note also the dark-spotted eggs.

first makes an excavation at the site. It then builds the roof of the nest, extending the bottom sides of the roof forwards to form the rim of the cup around the excavation, finally building the cup itself inside the excavation. The only materials used were grass and rootlets and no foundation was evident. Table 4 shows that the nests were mostly orientated towards the east and south.

FIGURE 11
An atypical, undomed nest of *Mirafra africanoides* at the base of a tuft of *Asthenatherum glaucum*; note how the back of the nest is slightly built up against the grass.

TABLE 4
ANALYSIS OF NEST ORIENTATION IN LARKS OF THE KALAHARI SANDVELD

Species	*Summer Nests*								*Winter Nests*								
	E	*SE*	*S*	*SW*	*W*	*NW*	*N*	*NE*	*E*	*SE*	*S*	*SW*	*W*	*NW*	*N*	*NE*	*Exposed*
M. africanoides	5	5	3		1						1						
M. sabota			2								1						
C. albofasciata	15	5	3					1	8		4		1		2		
E. verticalis	37	36	23	2	1		4	2	26	6	10	3	2	2	11	4	25
E. australis	19	4	7					1	11		2	1	3	1	2	4	3
C. conirostris	7	2							20	5	1				4	5	11
A. starki															4		2
Totals	83	52	38	2	2	0	4	4	65	11	19	4	6	3	23	13	41
Total Both Seasons									148	63	57	6	8	3	27	17	41

FIGURE 12
The domed nest of *Mirafra sabota* in a typical situation among the rocks of the calcrete slope.

2. *Mirafra apiata*

No nests of this species were found in the Kalahari, although the indications were that it bred there. It was apparently resident. McLachlan and Liversidge (1957) describe the nest of this species as being domed.

3. *Mirafra sabota*

The three nests of the sabota lark found on the calcrete slopes were all domed, exactly like the nests of *M. africanoides* (Fig. 12). Two were under shrubs and one against a rock. All faced south. One of the nests was set in a neat foundation of stones.

4. *Certhilauda albofasciata*

The nest of the spike-heeled lark is always a simple cup-shaped structure placed against a shrub or tuft of grass (Fig. 13), always on a soft, sandy substrate. Most nests had a small foundation ("pavement" of Pickwell (1931) and "glacis" of Meinertzhagen (1954) of stones or small earth clods and sometimes a stick or two. Of 39 nests, 35 (90%) had access from the

FIGURE 13
Typical nest of *Certhilauda albofasciata* at the base of a tuft *Asthenatherum glaucum* in the dunes. Note the foundation of sticks and the sandy spider web on the rim of the cup.

sector of the compass between east and south, most of them (almost 60%) facing east (Table 4). Twenty-four of the nests were on the calcrete and 15 in the dunes. The mean dimensions of 27 nests are: diameter 6.4 cm, depth 3.2 cm.

5. *Eremopterix verticalis*

The nest of the grey-backed finch-lark is a simple cup set in a foundation whose construction varies with the substrate on which the nest is built. In soft sand the foundation is minimal, consisting of perhaps half a dozen pieces of stone or earth. On hard calcrete where the bird cannot make any sort of excavation at all, the foundation is extensive and built up to the height required for the depth of the nest cup (Fig. 14). Most of the sheltered nests were placed against shrubs or grass tufts, but one was under a stone and another under an earth clod (Fig. 15).

Sheltered nests were usually placed on the east, south-east or south side of the object, but in winter the orientation is less strict (Table 4; Fig. 16). Out of 89 winter nests, 25 (28%) had no shelter at all. Of the total of 194 nests of the grey-backed finch-lark, 153 (78·9%) were on the calcrete, 33 in the dunes and only 8 in the river beds, showing clearly the preference

FIGURE 14
Typical nest of *Eremopterix verticalis* at the base of a woody shrublet on hard calcrete. The substantial foundation of stones and the inset grass cup are clearly visible. Note how much paler the eggs are than those of *Mirafra africanoides* in Fig. 11.

of this species for the calcrete. The mean dimensions of 125 nests are: diameter 5·3 cm, depth 3·0 cm.

6. *Eremopterix australis*

The nest cup of the black finch-lark is similar to that of *E. verticalis* but the foundation consists of sticks instead of stones or earth clods. A few clods may be used at times, but stones are generally not available in the normally sandy habitat of the black finch-lark. The sandy substrate also precludes the necessity of building the foundation above the level of the excavation to any extent, although the rim of the nest is usually a little above the substrate. Characteristic of all nests of this species in the Kalahari is a rim of mixed sand and spider web around the cup (Fig. 17). This feature was found on three nests of the spike-heeled lark, one nest of the pink-billed lark and four nests of Stark's lark.

Most of the black finch-lark nests faced east (Table 4) and exposed nests were found only

FIGURE 15
Nest of *Eremopterix verticalis* under an earth clod in the Nossob River bed; note how the foundation is built of pieces of earth instead of stones.

in winter. Only eight of the nests were on the calcrete, but all on patches of sand. Most of the nests (74·1%) were at the base of *Rhigozum trichotomum* shrubs; others were against other shrubs or occasionally grass tufts. The mean dimensions of 50 nests are: diameter 5·2 cm, depth 3·3 cm.

7. *Calandrella conirostris*

The nest of the pink-billed lark was completely different from the nests of any other sandveld larks. Always on sand, the nest cup of grass and rootlets was sometimes supported on a slight stick foundation, with the rim of the cup expanded on to the sand around the exposed side (Fig. 18). One nest built against a wall of earth at the foot of a large grass tuft lacked the back third of the grass cup, the sand serving as part of the nest wall. Even though most of the nests were found in winter, most of them faced east (Table 4). Eleven winter nests (about 24%) were exposed, while all summer nests were sheltered by plants. Only

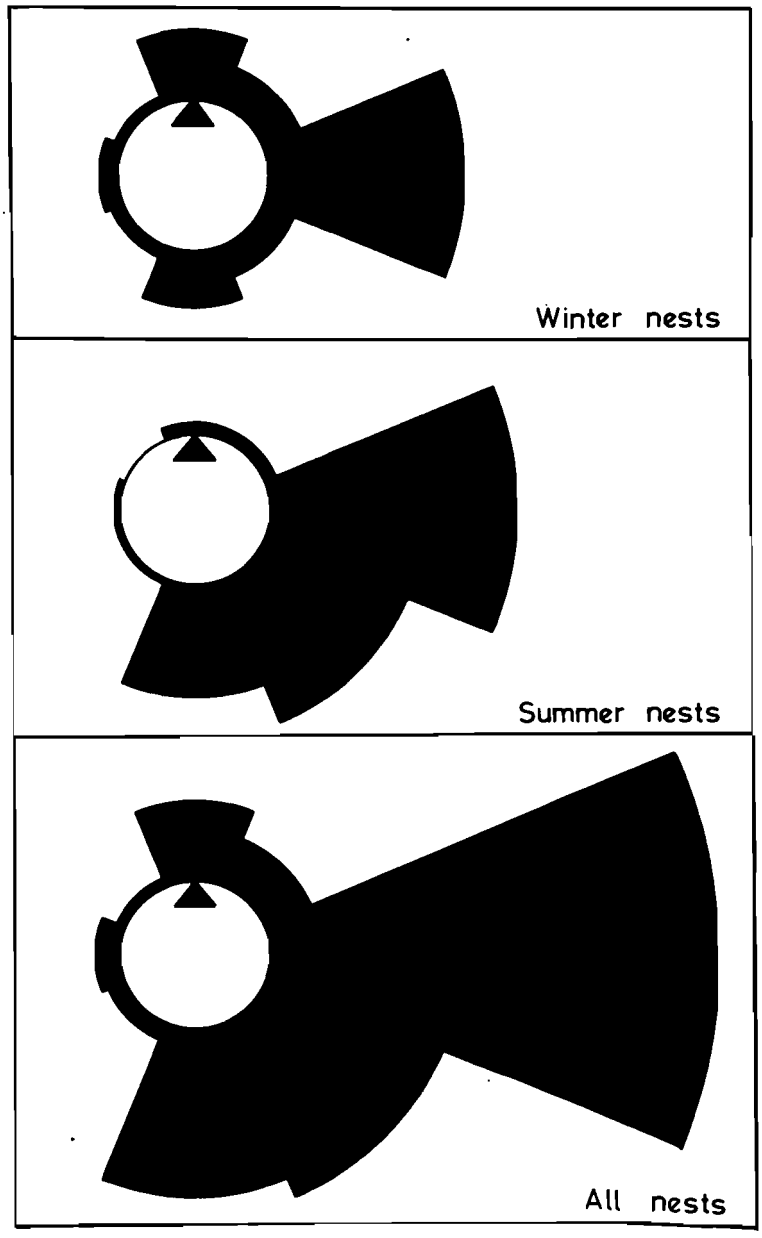

FIGURE 16
Compass diagrams showing the predominance of nests orientated towards the east, south-east and south. Winter nests are less clearly orientated for shade than summer nests.

FIGURE 17
Nest of *Eremopterix australis* containing a single chick. The thick rim of sandy spider web is clearly shown. This was a winter nest, hence the exposed site.

four of the sheltered nests were against shrubs, all the rest being against grass tufts. Mean dimensions of 54 nests are: diameter 5·3 cm, depth 3·5 cm.

8. *Alauda starki*

The six nests of *A. starki* were remarkably uniform in construction. Each had a foundation of pieces of earth and a few stones around an excavation on a sandy patch on the calcrete; the cup was made of white, silky flowers of *Aristida* grasses (Fig. 19). Shelter was minimal in each case, but only two of the nests were completely exposed. Four of the nests had a little sandy spider web around the rim, but not as much as in the case of the black finch-lark. Mean dimensions of six nests are: diameter 5·6 cm, depth 3·5 cm.

The orientation of the nests of all species showed a clear trend towards the east, south-east or south at all times of the year, but the summer nests showed this trend rather more markedly than the winter nests (Fig. 16). There were no exposed nests in summer at all.

FIGURE 18
Typical nest of *Calandrella conirostris* at the foot of stems of *Schmidtia kalahariensis* in the dunes. Note the "apron" of building materials around the exposed side of the cup.

D. *The Eggs*

General descriptions of eggs of larks (e.g. McLachlan & Liversidge 1957) are of little use in assessing the value of egg coloration within a single area. The eggs of seven species of larks breeding in the Kalahari sandveld are all white in ground colour, covered with underlying

FIGURE 19
Typical nest of *Alauda starki* on a sandy patch on the calcrete. Characteristic are the foundation of earth clods, the cup of silky grass flowers and the site among sparse *Sporobolus parvulus*. Note how very pale the eggs are.

grey spots and overlying brown spots. The main differences between the species lie in the different shades of brown which predominate within a species. There are three main shades of brown: a very dark chocolate, an intermediate yellow-brown and a pale pinkish brown which will be termed chocolate, yellow and pink respectively in the following account.

The eggs of *Mirafra africanoides* and *M. sabota* have rather large spots of chocolate and yellow, the former predominating to give a bold effect. The eggs of *Certhilauda albofasciata* are similar, but yellow predominates over chocolate and the spots are smaller, giving the egg a "speckly" effect. This speckly effect is found also in *Calandrella conirostris* but the spots are so dark as almost to be black. The eggs of *Eremopterix verticalis* are less heavily marked than any of the preceding species and yellow spots predominate over chocolate. The eggs of *E. australis* and *Alauda starki* are almost indistinguishable from one another, being spotted with pink to give an overall pale effect.

Dark-spotted eggs occur in species living in the most disruptive backgrounds, either tall grass or tumbled rocks (the two *Mirafra* species and *Calandrella conirostris*). Paler eggs

TABLE 5

ANALYSIS OF BREEDING SUCCESS IN LARKS OF THE KALAHARI SANDVELD

Species	*Clutches Analysed*	*Total Eggs*	*Chicks Hatched*	*% Hatched*	*Chicks Left Nest*	*% Chicks Left of Total Eggs Laid*	*% Chicks Left of those Hatched*
M. africanoides	13	33	24	72·7	10	30·3	41·7
M. sabota	1	3	0	0·0	0	0·0	0·0
C. albofasciata	28	69	34	49·3	21	30·4	61·8
E. verticalis	114	243	77	31·7	42	17·3	54·5
E. australis	37	78	25	32·0	8	10·3	32·0
C. conirostris	37	75	36	48·0	11	14·7	30·6
A. starki	6	12	4	33·3	0	0·0	0·0
Totals	236	513	200	39·0	92	17·9	46·0

TABLE 6

ANALYSIS OF CLUTCH SIZE IN THE LARKS OF THE KALAHARI SANDVELD FOR THE THREE BREEDING PERIODS. A CLUTCH OF 1 EGG OF *C. coinirostris* AND A CLUTCH OF 4 EGGS OF *M. africanoides* HAVE BEEN OMITTED FROM THIS TABLE WHICH SIMPLY SHOWS AN INCREASE IN THE INCIDENCE OF CLUTCHES OF 3 EGGS IN SUCCESSIVE BREEDING PERIODS

Species	*Breeding Periods*								
	Dec. 1964–Jan. 1965			Apr. 1965–Nov. 1965			Jan. 1966–Apr. 1966		
	c/2	c/3	% c/3	c/2	c/3	% c/3	c/2	c/3	% c/3
M. africanoides				2	1	33	6	4	40
M. sabota								1	100
C. albofasciata	2	0	0	14	10	42	5	7	58
E. verticalis	8	0	0	87	5	6	59	21	26
E. australis				25	2	8	24	5	21
C. conirostris				47	2	4	3	1	25
A. starki				6	0	0			
Totals	10	0	0	181	20	11	97	39	40

occur in the two species inhabiting more open country, mostly calcrete (*Certhilauda albofasciata* and *Eremopterix verticalis*). The palest, pink-toned eggs occur in the two species of open sandy country or sand on calcrete (*E. australis* and *Alauda starki*). There seems little doubt that the colour of the eggs is related to the habitat of the species of lark and probably can be classed as cryptic coloration.

E. *Clutch Size*

The data on clutch size appear in Table 6. Clutches of two eggs predominate in all species (with the possible exception of *Mirafra sabota* for which the count of one clutch is useless for analysis), but the incidence of clutches of three eggs increases with increasing rainfall. Increasing clutch size with increasing rainfall has been found in other bird species in the Kalahari (Maclean, unpublished), but the differences in the larks are rather small. For instance in *Eremopterix australis* it is safe to say that clutches of three eggs are exceptional, even after good rains.

The only clutches of other than two or three eggs were a single clutch of one egg in *Calandrella conirostris* and a single clutch of four eggs in *Mirafra africanoides*, both of which have been omitted from Table 6.

F. *Breeding Success*

Table 5 shows the percentages of breeding success expressed both as a percentage of eggs which gave rise to chicks that left the nest, and of hatched chicks which were successful. These figures are based only on those nests whose fate was reasonably well determined and includes nests which were totally unsuccessful. The nest counts of *Mirafra sabota* and *Alauda starki* are too small to consider reliable, but they have been included in the overall nesting success for the whole family.

PREDATORS

The only predation that was actually witnessed was a red-necked falcon *Falco chiquera* feeding on an adult spike-heeled lark. It is probably reasonable to assume therefore that the other species of *Falco* which occur in the Kalahari (*F. biarmicus*, *F. tinnunculus* and *F. rupicoloides*) may take larks from time to time. Other small birds of prey such as the gabar goshawk *Micronisus gabar* may be included as lark predators too and it is highly likely that the chanting goshawk *Meliërax musicus* takes young larks as it does much of its feeding walking about on the ground.

Among the mammals, the bat-eared fox *Otocyon megalotis* is probably the commonest predator on larks, mainly on eggs and young. I have seen this animal sniffing along from the base of one bush to the next as though looking for nests; one was actually seen to flush a sandgrouse from its nest in this way and then eat the eggs, so many lark nests may be robbed thus. The silver fox *Vulpes chama* may account for many lark nests along the edge of the calcrete. Other carnivorous mammals which are almost certainly responsible for losses of eggs or nestlings are the yellow mongoose, black-backed jackal and Cape wildcat.

The Cape cobra *Naja nivea* is also to be regarded as a potential predator on larks; it certainly eats the young of arboreal birds in the Kalahari (Maclean, unpublished).

One interesting case of nestling loss in the black finch-lark occurred in a nest containing two small chicks; one of the chicks had been killed and eaten by a large burrowing spider whose burrow had opened into the floor of the nest cup, while the remaining chick was still alive but badly injured from what appeared to be a spider bite.

DISCUSSION

It is fairly clear that the red larks live in the dunes and the grey larks on the calcrete, although one red lark, the spike-heeled, is found as often on the calcrete as in the dunes; and the grey-backed finch-lark is found in the dunes when populations on the calcrete get overcrowded. I do not believe that dust-bathing in soil of a particular colour was a major factor in the matching of the larks to their background (cf. Hoesch 1958a). The differences between the red and grey larks of southern Africa have already been pointed out by Hoesch & Niethammer (1940) and by Macdonald (1953).

The situation of overcrowding on the calcrete obtained in another terrestrial passerine, the lark-like bunting *Emberiza impetuani*, which was also nomadic in the Kalahari sandveld. This bunting is normally a bird of rocky areas, but moved into the sandveld after the January 1966 rains; the only rocky habitat was the calcrete slopes inhabited by the sabota lark. The buntings began to breed on these slopes, but so many moved into the area that the calcrete could not accommodate them all. They then moved into the dunes to breed under shrubs and grass tufts instead of under rocks as they usually did.

There is a certain amount of ecological separation of the various species of larks both in the dunes and on the calcrete. *Mirafra africanoides* is the most ubiquitous of the dune larks and usually the only one found in the *Acacia* savanna. *M. apiata* and *Calandrella conirostris* overlap to a slight extent, but the former occurs only in the very thickest grass cover, while *C. conirostris* will inhabit sparser growth as long as the grass is tall. The diets of these two species will serve to separate them in the non-breeding periods.

Certhilauda albofasciata being a bird of very open country as a rule overlaps only occasionally with *Mirafra africanoides* in the dunes and its different diet from that of *Eremopterix verticalis* serves to keep these two species from competing on the calcrete to any marked extent. *E. verticalis* is usually only present after rains anyway, at a time when food is abundant.

The degree of overlap among the three "grey" larks is probably insignificant. *Mirafra sabota* does not compete with *Eremopterix verticalis* on the flat calcrete. Numbers of *Alauda starki* are usually too small to constitute serious competition for food, and its nesting areas differed slightly from those of *E. verticalis* which probably obviated a lot of territorial competition. In any case, all the nomadic species of larks had very small territories, nests of the same or different species occurring as little as nine or ten feet apart.

The habitat of *Eremopterix australis* is such that few other larks occur in the same area; only *C. albofasciata* and *C. conirostris* may be found breeding in very small numbers in the *Rhigozum* habitat.

In summary then, the dune larks and calcrete larks are fairly well separated from each other and from other species within the dunes and calcrete by small differences in vegetation cover. *Certhilauda albofasciata* occurs in most of the sandveld habitats except where cover is very dense.

It is interesting that all the nomadic species of larks are granivorous. It may be because the seeds on which the young are fed (to augment their insect food) must be green, presumably for their high water content. However, it seems as if *Eremopterix leucotis* in Rhodesia feeds its young on dry seeds; this species is exceptional too in that it breeds before the rains (Steyn 1964). Those species of larks whose food seems to be largely animal in origin are all resident. All appear to eat seeds at times, but the fact that they do not drink water seems to indicate that the proportion of seeds eaten is considerably smaller than of insects. This is the main advantage of being insectivorous in an arid environment. Four seed-eating species of larks of the sandveld are quite frequently seen at water, but *Eremopterix australis* does not appear to drink at all. A study of its diet may show that even the adults are largely insectivorous. The differences in the drinking habits between the insectivorous and granivorous larks of the sandveld have been clearly shown by Irwin (1956) who was, however, in an area where *E. australis* unfortunately did not occur.

An examination of Fig. 7 will show that there is some overlap in the bill shapes of the so-called granivorous larks and insectivorous larks. For instance the bills of *Mirafra africanoides* and *Alauda starki* are rather similar in shape and intermediate between the heavy conical bill of *Calandrella conirostris* and the slender bill of *Certhilauda albofasciata*. This may indicate an overlap in feeding habits; it is certainly true of *M. africanoides* but to what extent *A. starki* eats insects has not yet been established.

There is little doubt that breeding in all species of larks in the Kalahari sandveld is initiated directly or indirectly by rain. This is a common adaptive feature of birds of arid areas (Keast & Marshall 1954; Serventy & Marshall 1957; Winterbottom & Rowan 1962; Immelmann 1963a, b) particularly where rain may fall at any time of the year. The reason for the long lag period between the first shower and the first eggs after the March-April 1965 rains is obscure, but it may have been due to the long duration of the rainy season which extended to April 20th. Perhaps the birds can sense the end of a rainy season and wait until then before nesting to avoid the hazard of flood. Bad weather seldom affects nesting larks in the Kalahari because most rainy seasons are so short, but it is a real hazard in temperate regions (DuBois 1936).

It seems as if more than 20 mm. of rain over a month's period is necessary to trigger off breeding. A small but concentrated shower of 10 mm. in October 1964 failed to induce breeding, but little more than twice that amount in December of that year resulted in a small number of breeding attempts in two species of larks. The opportunistic nature of the larks shows up particularly well in the nomadic species in which increases in population usually coincide with periods of breeding activity.

The architecture of the nest within a species is on the whole well adapted to its environment, particularly to the texture of the substrate and the available materials. Thus the foundations of the nests of *Eremopterix verticalis*, *Alauda starki* and *E. australis* consist mainly of stones, clods and sticks respectively, although there is a certain amount of flexibility in the

birds' choice of foundation materials. For instance, the nest foundation of *Certhilauda albofasciata* consists of stones and earth when the bird is nesting on the calcrete, and of sticks when it is nesting in the dunes.

The function of the foundation is most clearly demonstrated in the case of *Eremopterix verticalis*; the harder the substrate, the more substantial the foundation in order to provide sufficient depth for the grass cup. Van Someren (1956) reports much the same thing in *E. leucopareia* in East Africa. Another function of the foundation may be for mechanical strength. On one occasion the wheel of a Land Rover passed over a nest of *E. verticalis* set level with the ground in a stone foundation; neither the nest nor the two small chicks it contained suffered any injury. This may be of limited protection against the hooves of the larger antelopes, such as gemsbok and wildebeest. Furthermore the foundation may prevent subsidence of the nest cup if winds undermine the sand around it. This is probably the function of the grass "apron" around the nest cup of *Calandrella conirostris* which always nests on a sandy substrate in the Kalahari.

The domed nest of the genus *Mirafra* presents an interesting problem. One might suggest that the roof is for protection against the sun, but this is probably not the whole explanation as nests of *Mirafra* species may lack the roof. There is a strong generic trend towards the building of domed nests by members of this genus: among those which do so are *M. africana*, *M. rufocinnamomea* (McLachlan & Liversidge 1957), *M. affinis* (Henry 1955), *M. cantillans* (Meinertzhagen 1954), *M. javanica* (Bourke 1947; Bravery 1962; Serventy & Whittell 1962; Cayley 1963) and *M. woodwardi* (Cayley 1963), as well as the three species which occur in the sandveld. Hoesch (1955) also mentions the domed nests of *M. africanoides* and *sabota* and as early as 1872 Andersson described the "round and dome-shaped" nest of *M. sabota*.

Although some species of *Mirafra* appear not to build domed nests, at least sometimes (e.g. *M. fischeri* (Van Someren 1956) and *M. albicauda* (Vesey-Fitzgerald 1957)), the only other larks for which I can find mention of domed nests are the woodlark *Lullula arborea* (Ash 1951), the crested lark *Galerida cristata* (Clancey 1944), Gray's lark *Ammomanes grayi* (Hoesch 1958b), the long-billed lark *Certhilauda curvirostris* (McLachlan & Liversidge 1957) and the Karroo lark *Certhilauda albescens* (Maclean 1957). Hoesch's description of the nest of Gray's lark rests almost without a doubt upon a misidentification as shown by the recent findings of Willoughby (pers. comm.); the two species of *Certhilauda* should certainly be included in the genus *Mirafra* as claimed by White (1959b) and as I hope to confirm in a later paper.

The orientation of most lark nests in the Kalahari towards the east, south-east or south (Fig. 16) is a function of shade requirements. This sector of the compass around the base of a bush or other object is the one that receives the greatest amount of shade in the southern hemisphere, so that nests so sited receive shade during the hottest hours of the day. The complete absence of north-west facing nests in summer reflects the fact that this sector receives the sun during the hottest part of the day (i.e. mid- to late afternoon). Similar orientation for maximal shade has been shown for lark nests in the northern hemisphere where they face in a northerly direction (DuBois 1935, 1936; Hartley 1946; Chappell 1946; Labitte 1958; Harrison & Forster 1959; Guichard 1960; Koffán 1960; Abs 1963), although in temperate

regions the nests may be orientated more for protection against prevailing winds than against the sun (Forbush 1927; Bravery 1962). Meinertzhagen's (1954) statement that the horned lark of the North African desert builds "usually on the south side of a tuft or stone" is surely a curious one in view of the high irradiation that the nests would receive from the south.

Clancey (1944) says of nests of crested larks in Italy that "the dome was always so constructed as to give the nestlings the maximum protection from the fierce solar rays". It is clear that nest orientation in larks is highly adaptive. The greater number of exposed or randomly orientated nests in winter bears this out further, since the need for protection against the winter sunshine of the Kalahari is slight. The large number of north-facing nests in winter may reflect the need to shelter from the cold southerly winds.

The adaptiveness of egg colour also seems to be clear, but it is not easy to test experimentally in the field. How far clutch size in the Kalahari larks is adaptive can only be assumed at this stage of our knowledge, although the validity of the assumption is partly justified by Lack's (1966) information on the adaptiveness of clutch size in other species of birds. The overall breeding success of the Kalahari larks is low when compared with figures for the red-capped lark (Winterbottom & Wilson 1959) and the crested lark (Hartley 1946), probably because predation under the natural conditions of the Kalahari was much greater than in the settled areas where the other studies were made.

Why the breeding success of the resident and largely insectivorous *Mirafra africanoides* and *Certhilauda albofasciata* is greater than that of the nomadic species is not altogether obvious. The comparison may not be a good one because of the low sample numbers in the insectivorous larks. Could the domed nest of *Mirafra* have a protective function against predators? Or it may be that the insectivorous larks do not nest as close together as the more numerous nomadic species and are therefore less heavily preyed on. The fact that the insectivorous species do not build in exposed sites may have a bearing on the matter also. This is partly borne out by the fact that only one exposed nest of *Calandrella conirostris* was successful, all other successful chicks of this species coming from concealed nests. More data and much larger samples for all species are needed further to clarify the situation and more observation is needed to determine the causes of losses of eggs and young.

SUMMARY

Nine species of larks occur in the Kalahari sandveld, 8 of them as breeding species and one as an irregular and uncommon visitor. The 8 breeding species can be divided into two colour groups, "red" and "grey"; the red larks live mainly in the red dunes and the grey larks on the grey calcrete. They can also be divided into two groups on the basis of diet (insectivorous and granivorous), particularly as regards the food fed to the young in the nest. All the granivorous larks are nomadic. Populations of nomadic larks increased after rain. Rain or associated effects is the principal *Zeitgeber* (Immelmann 1963a) for breeding in all the larks.

Nest architecture is adapted to the environment of each species. Members of the genus *Mirafra* tend to build domed nests, the function of which is uncertain, but which show a strong generic trend, regardless of habitat. Most nests of all species are orientated towards the sector

of the compass between east and south so as to obtain maximal shade, especially in summer. Breeding success expressed as the percentage of eggs producing young which left the nest was 17.9% for the family. Most losses were probably due to predation.

Egg colour appears to be adapted to the respective backgrounds on which each species nests. Clutch size varies little, being two eggs in most cases for all species, but the incidence of three-egg clutches increases with increasing rainfall.

ZUSAMMENFASSUNG

Neun Lerchenarten kommen in der Kalahari-Wüste (dem Sandveld) vor, acht als Brutvögel und eine als seltener Wanderer. Die acht Brutarten können aufgrund ihrer Färbung in zwei Gruppen ("rot" und "grau") geteilt werden; die roten Lerchen wohnen in den roten Sanddünen, die Grauen auf den grauen Kalkflächen (=calcrete). Die Lerchen können auch in zwei Nahrungsgruppen geteilt werden (Insektenfresser und Samenfresser) hauptsächlich wo es sich um das Futter der Jungen handelt. Die Samenfresser sind alle Wandervögel, deren Populationen sich nach Regen vermehren.

Regen (oder zusammenhängende Zustände) ist der Zeitgeber der Brutaktivität. Die Nestform jeder Art ist seiner Umgebung angepaßt. *Mirafra*-Arten bauen überdachte Nester, dessen Funtion nicht ganz deutlich ist, die aber dieser Gattung charakteristisch sind. Die meisten Nester aller Arten wurden gegen Osten, Südosten oder Süden gerichtet, so daß sie gegen die Sonne geschützt waren. Eifarbe scheint der Bodenart angepaßt zu sein.

Gelegegröße und die monatliche Anzahl der Nester jeder Art steigerten mit steigerndem Regenfall. Bruterfolg der ganzen Familie Alaudidae war 17,9%. Offenbar konnten die meisten Verluste Raubtieren zugeschrieben werden.

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