# BIOLOGY OF LARKS (AVES: ALAUDIDAE) IN THE CENTRAL NAMIB DESERT

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ABSTRACT

1. The biology of six species of larks in the Namib Desert near Walvis Bay, South West Africa, was studied in 1964, 1965 and 1966.
2. All species reproduced following rainfall in summer and autumn months, with the appearance of green grass and abundant insects on which the birds fed.
3. The primarily insectivorous species, *Certhilauda albofasciata*, shows no seasonality in moulting and testicular development, and reproduces whenever local rainfall results in favourable feeding and nesting circumstances, while the primarily granivorous *Spizocorys starki* and *Eremopterix verticalis* have markedly seasonal testicular and moulting cycles timed so that reproduction occurs only during the late summer and autumn months. *Ammomanes grayi* is intermediate in food habits and in timing of moulting and reproduction, and *C. albescens* and *Mirafra naevia* may also be intermediate in this respect.
4. *S. starki* and *E. verticalis* are the only larks that normally drink, but flocks of both species were observed that were independent of drinking water.
5. Larks avoid heat stress during daytime by keeping to the shade of stones, tufts of vegetation and mouths of rodent burrows; and nests are nearly always placed on the shady side of a stone or tuft of grass.
6. It is suggested that larks may be successful desert occupants because they have not become highly specialized and therefore can tolerate rapidly and severely changing environmental conditions associated with drought and irregular rainfall.

## INTRODUCTION

The desert environment, with its shortage of water, extremes of temperature, and paucity of food and vegetative cover, presents special difficulties for the survival of terrestrial animals. The Namib Desert in South West Africa is one of the driest, most barren regions on earth; yet it is inhabited by a number of avian species. Prominent among these birds are several species of larks, family Alaudidae, that live and reproduce successfully under these conditions. The purpose of my study was to learn something about the ways in which these larks are adapted to their desert environment. I gave special attention to the questions of how and where these birds obtain water, what they eat and how they obtain food, what their breeding habits are, and how reproduction and moulting are related to changing environmental conditions.

I did my field work at the Namib Desert Research Station at Gobabeb on the lower Kuiseb River, about 60 miles southeast of Walvis Bay, during July and August, 1964, and from July, 1965, to July, 1966. My approach was extensive rather than intensive, since very little is yet known about the avifauna and ecology of the Namib Desert, or about the biology of desert birds in general and larks in particular.

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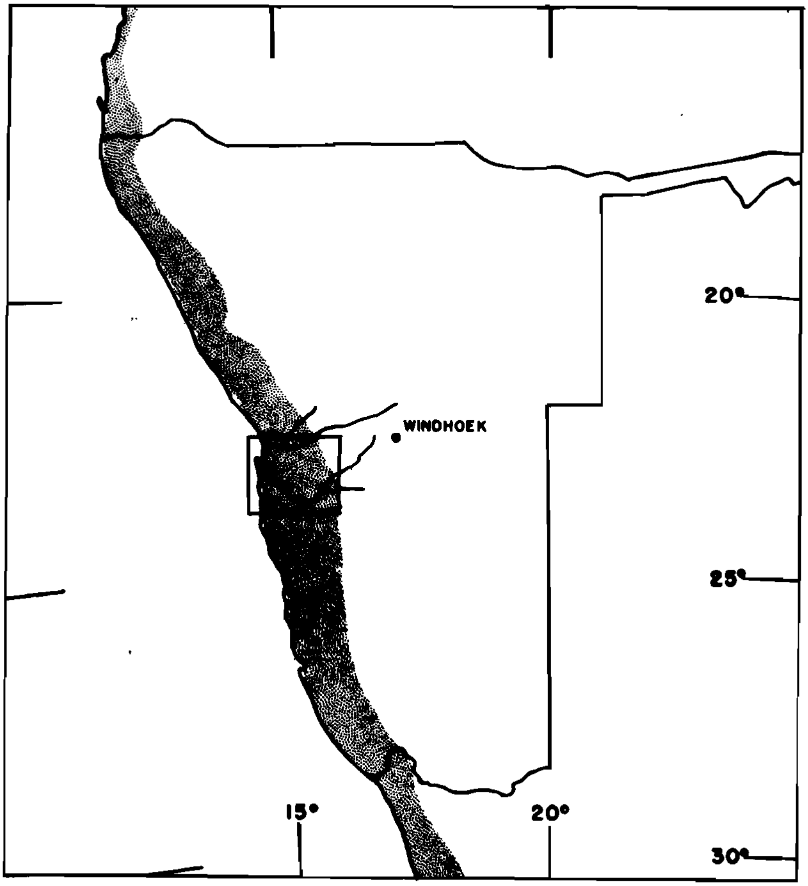


FIGURE 1
Map of South West Africa, with the geographic limits of the Namib Desert indicated by stippling. The rectangle encloses the study area. (From Willoughby & Cade 1967, with permission of Namib Desert Research Association.)

## THE NAMIB DESERT

The Namib Desert extends some 1 300 miles along the west coast of southern Africa, from near Mossamedes in Angola to the mouth of the Olifants River in the Cape Province. The geography of this desert has been treated in detail by Wellington (1955) and Logan (1960). The latter reference in particular has a wealth of information pertaining to the study area, and the terminology used here follows that given by Logan where applicable. In South West Africa, this arid coastal strip varies in width from about 60 to 100 miles (Fig. 1), merging on the east with the semi-arid continental highlands.

The study area includes all of Game Reserve Number 3 (Fig. 2), lying between the lower Kuiseb River and Walvis Bay on the south, the Swakop River on the north, and extending inland about 80 miles. The area centres at about the coordinates of 15°15′ E. and 23°15′ S. This area forms the geographic centre of the Namib and includes both of the major

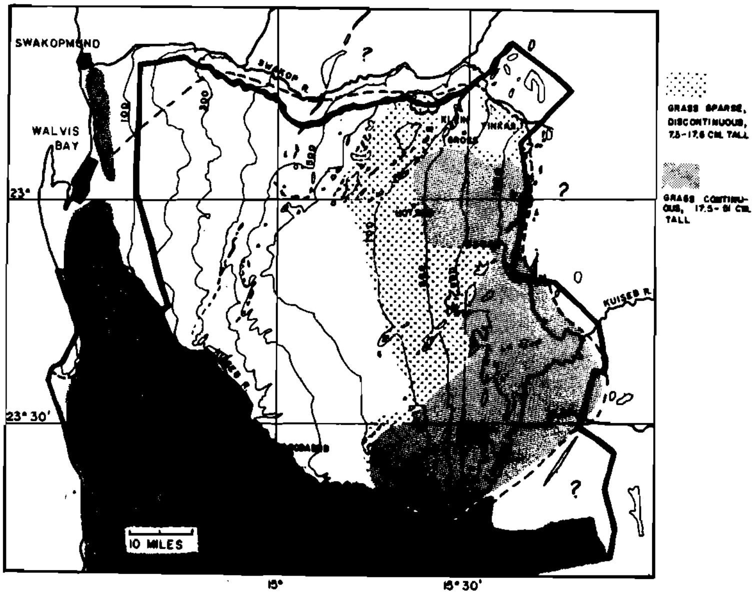


FIGURE 2
Map of the study area indicating 100-metre contour lines, and outlines (but not contours) of mountains and *koppies*. The heavy line is the border of Game Reserve No. 3 (also called Namib Desert Park); dark shading indicates areas of sand dunes; lighter shading indicates extent of occurrence and relative amounts of new grass resulting from rainfall in summer and autumn, 1965-66, as assessed in May; dashed line encloses the area directly observed and question marks indicate areas that were not observed.

geomorphic features of this desert. From the Kuiseb River southward about 400 miles to the Orange River, lies an expanse of high, barren dunes termed The Great Sand Dunes by Logan. North of the Kuiseb, the dunes extend to the Swakop River only along the coast (Fig. 2). Otherwise, stretching north from the Kuiseb is a vast, flat, gravel plain, The Namib Platform, which slopes gradually upward from the coast for about 80 miles to the foot of the western escarpment of the continental highlands at about 1 000 m elevation.

The Kuiseb River makes a remarkably distinct dividing line between The Great Sand Dunes and The Namib Platform. Although water flows at the surface of its bed only when summer rainfall in the highlands is substantial, there is a perennial subterranean flow of water supporting a dense forest of tall trees along its course. This forest forms an extreme contrast to the nearly vegetationless expanses stretching north and south from the banks of the river, and provides habitat for many bird species from the more mesic highlands (Willoughby and Cade 1967).

Lowman (1966, p. 658) has published a colour photograph of this region of the Namib taken from outer space by U.S. Project Gemini, which shows all the major geomorphic features of this area, including the Kuiseb River with its forest.

*Climate*

The works of Logan (1960) and Schulze (1966) provide descriptions of the climate of the Namib. Climatically, the Namib is divided into two regions, the Outer or Coastal Namib, and the Inner Namib. The Outer Namib is a fog desert, being influenced by the cold Benguela Current and within about 20 miles of the coast, fog is of very frequent occurrence, but rainfall is exceedingly scarce and averages only about 1·25 cm a year. Indeed, a large percentage of the total annual precipitation at the coast comes as condensed fog water and dew (Walter 1936).

About 40 miles from the coast the cool, foggy climate of the Outer Namib gives way to a climate that reflects somewhat the climate of the continental highlands. Dew and fog are unusual in the Inner Namib, and more than a month may pass without any condensation. Precipitation in the Inner Namib, however, is appreciably greater than in the Outer Namib and comes in the form of localised showers mainly in the summer and autumn months. Rainfall in the Inner Namib averages up to about 152 mm annually, but is highly unpredictable for any given locality.

*Precipitation.* In the year 1965–66 this part of the Namib probably had near normal rainfall, although just what the normal condition is has not yet been determined because weather observations between the coast and the interior highlands have been discontinuous or lacking until 1963, when an official weather station was established at the Namib Desert Research Station, which lies right on the transition between the Outer Namib and Inner Namib climatic regions. Logan (1960) gives a good summary of weather data existing for the study area to 1958. Figure 3 summarises rainfall data at locations from Walvis Bay at the coast to Windhoek in the interior highlands. Donkerhuk is located just outside the north-eastern corner of Game Reserve No. 3, about 20 miles east of the Tinkas water holes (Fig. 2), and represents rainfall conditions at the eastern edge of the Namib Desert. The data for mean monthly rainfall were obtained from the Weather Bureau of the Republic of South Africa (1963), and so were monthly rainfall figures for 1965 and 1966 (Weather Bureau, Department of Transport 1965, 1966). Figure 3 indicates that rainfall at Windhoek was near normal for both years, but rainfall at Walvis Bay was practically nil over the whole period and was well below the mean. Variability in occurrence of rainfall in the Namib is well illustrated by the data from Gobabeb (23°34′ S., 15°03′ E., 408 m), where slight but measurable rainfall came in January, February, March, April and September, 1965, and January, February, March, April and August, 1966. The data for Donkerhuk indicate the strong influence that the marked annual rainy period of the interior has on rainfall in the Inner Namib.

Except at Walvis Bay and Gobabeb, no rainfall figures are available for the study area during the period of this investigation; but periods of occurrence of rainfall within Game Reserve No. 3 were easily determined by observation. During this study, rainfall in all instances was very localised, so that some areas received several inches of rain (estimated) and others less than 25 mm or none at all. Figure 2 indicates general distribution of rainfall as assessed by the growth of new grass during the summer and autumn of 1965–66. The shading on the map indicates the relative density and height of the grasses resulting from the season's rainfall, as observed in May, 1966, and so gives an indication of the relative amounts and distribution of the precipitation. Periods when this rainfall was observed are indicated in Figures 5–8.

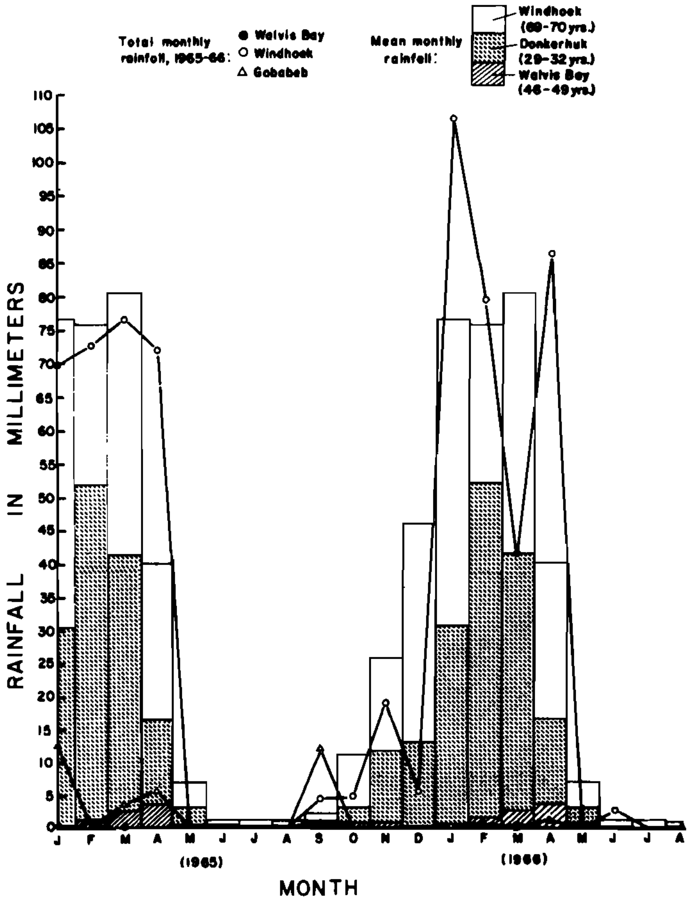


FIGURE 3
Monthly rainfall of localities in the central Namib and for Windhoek, located in the highlands of central S. W. Africa (Weather Bureau, Department of Transport, Republic of S. Africa, 1963, 1965, 1966).

*Vegetation and Habitats*

One of the most striking features of the Namib is its lack of vegetation, and large expanses of the Inner Namib Platform may have hardly a trace of vegetation after dry years.

Perhaps the best way to treat the vegetation here is as components of the major avian habitats already defined by Willoughby and Cade (1967). Table 1 summarises the habitats and their characteristics.

*Sources of Drinking Water*

Fog is a possible source of drinking water for birds in the Outer Namib, as it tends

TABLE 1
AVIAN HABITATS IN THE CENTRAL NAMIB

| *Name of habitat*[1] | *General Description* | *Typical Vegetation* | *Characteristic Birds* |
|---|---|---|---|
| Outer Gravel Flats | Barren gravel plains of Outer Namib Platform | Nearly vegetationless, or widely-spaced halophytic bushes 30 to 60 cm tall, *Arthraerua leubnitziae* and *Zygophillum stapfii* | Layard's Chat *Oenanthe tractrac* |
| Inner Gravel Flats | Barren or sparsely vegetated gravel plains of Inner Namib Platform | Sparse annual or perennial grasses, mainly *Stipagrostis ciliata* and *S. obtusa*. Also *S. uniplumus* and *S. hirtigluma*. Some areas with widely-spaced low shrubs 15 to 60 cm tall, *Monechma arenicola*, *Salsola* spp., others | Gray's Lark *Ammomanes grayi*, Stark's Lark *Spizocorys starki* |
| Open Acacia Woodland | Narrow strips of forest of very open aspect along dry water courses on Inner Gravel Flats | Camelthorn *Acacia giraffae* (large tree) and various smaller trees and shrubs | Red-headed Finch *Amadina erythrocephala*, Sociable Weaver *Philetaïrus socius*, Fiscal Shrike *Lanius collaris* |
| Open Bush | Scattered bushes 60 cm to 3 m tall anywhere in Namib Platform, but mostly in Inner Namib (where ground water that is not too salty nears the surface) | Primarily *Acacia reficiens*, several other species of shrubs | Scaly-fronted Weaver *Sporopipes squamifrons*, Chat Flycatcher *Bradornis infuscatus*, Schlegel's Chat *Cercomela schlegelii* |
| Rocks | Large boulders, crevices and ledges with or without vegetation, anywhere in Namib Platform | In Inner Namib low scrub dominated by *Commiphora* spp. and cactus-like euphorbias. In Outer Namib, lichens and small succulents (see Giess 1962; Walter 1936) | Mountain Chat *Oenanthe monticola*, Familiar Chat *Cercomela familiaris*, White-throated Seed-eater *Serinus albogularis* |
| Sand Dunes | Shifting dunes, barren in Outer Namib, but with scattered tufts of perennial grasses in the Inner Namib | In Inner Namib the grasses *Stipagrostis sabulicola*, *S. lutescens*, *Eragrostis spinosa* | Karroo Lark *Certhilauda albescens* |

(Continued on next page)

| *Name of habitat*[1] | *General Description* | *Typical Vegetation* | *Characteristic Birds* |
|---|---|---|---|
| Kuiseb Riverine Forest | Dense forest of tall trees and brushy undergrowth along lower Kuiseb and Swakop rivers | *Acacia giraffae*, *A. albida*, *Ficus sycomorus*, *Tamarix austro-africana*, *Euclea pseudebenus*, *Salvadora persica* | Tit-babbler *Parisoma subcaeruleum*, Red-eyed Bulbul *Pycnonotus nigricans*, Red-faced Mousebird *Colius indicus* |

[1] Willoughby and Cade 1967.

to condense on solid objects and often gives rise to puddles on bare rock, and drenches vegetation with droplets. Scattered water holes and man-made wells occur along the lower Kuiseb River, and supply drinking water to many of the birds that live in the Kuiseb Riverine Forest (Prozesky 1963, p. 78; Willoughby and Cade 1967). However, these watering places are of minor importance to larks and other species of the Sand Dunes and Gravel Flats.

The few natural water holes in the Inner Namib are of much greater significance to this study. Two such water holes that supply water to many thousands of birds and game mammals are Gross Tinkas and Klein Tinkas (Fig. 2). These consist of places in a dry stream bed where water seeps out of the coarse sand. Mountain Zebra *Equus zebra* and Gemsbok *Oryx gazella* paw out depressions in the wet sand and drink the water that seeps in to fill the holes. Birds, including some species of larks, visit these places by the thousands in hot dry weather. Occasional salt-water seeps are to be found in the Outer Gravel Flats, but the water does not appear to be utilised.

The South West Africa Administration has erected three game-watering wells in Game Reserve No. 3 at Ganab, Hotsas, and Zebra Pan (Fig. 2). Each consists of a windmill that pumps water from a borehole into a watering trough, thus supplying water to thousands of birds and mammals from the surrounding Inner Gravel Flats.

*Avifauna*

The avifauna of the Namib Desert is relatively poorly known. Since the middle of the 19th Century ornithologists have made occasional collecting trips into or across the Namib, spending only a few days at a time there, and treating the avifauna of the Namib incidentally to a more general coverage of birds of southwestern Africa (see for example Andersson 1872; Hoesch and Niethammer 1940). Willoughby and Cade (1967) have listed the species of land birds found in Game Reserve No. 3 during my period of study, and have indicated their habitat associations. Our list includes 107 species, of which 81 species belonging to 28 families occurred in the Namib outside the Kuiseb Riverine Forest habitat.

*Mammals*

Potential mammalian predators of birds that were observed in the study area included the Chacma Baboon *Papio ursinus*, Bat-eared Fox *Otocyon megalotis*, Black-backed Jackal

*Canis mesomelas*, Striped Polecat *Ictonyx striatus*, Yellow Mongoose *Cynictis penicillata*, and Suricate *Suricata suricatta*. Herbivorous mammals in the study area include the Mountain Zebra, Steenbok *Raphicerus campestris*, Klipspringer *Oreotragus oreotragus*, Springbok *Antidorcas marsupialis*, Gemsbok, Cape Hare *Lepus capensis*, Rock Rat *Petromus typicus*, Cape Ground Squirrel *Xerus inauris*, Striped Mouse *Rhabdomys pumilio*, Namaqua Gerbil *Desmodillus auricularis*, Lesser Gerbil *Gerbillus paeba*, and Brush-tailed Gerbil *G. vallinus*, plus a number of other small mammals.

*Arthropods*

The insect fauna in the Sand Dunes and Outer Gravel Flats is dominated by beetles of the family Tenebrionidae, which are the most conspicuous animals in these regions (Koch 1962). The insect fauna in the Inner Gravel Flats, in addition to the Tenebrionidae and other beetle families, has conspicuous additions of ants, termites (chiefly the harvester termites, *Hodotermes* spp.), locusts and stick insects, and others. Insects are especially conspicuous and abundant for a few weeks after local rainfall, when they multiply and swarm in the grass and other vegetation that grow after the rain.

Other conspicuous arthropod groups are solifugids, scorpions, and spiders.

## METHODS

I made regular field trips into both Inner Gravel Flats and Outer Gravel Flats habitats to make observations and to collect specimens. I also made observations in small areas of the dunes on the south side of the Kuiseb River, but this work was limited by flooding of the Kuiseb during five separate occasions in February, March and April, which prevented crossing the river to get into the dunes. The observations reported here represent about 2 000 hr of field work.

Specimens were collected whenever time and circumstances permitted, with a single-shot ·22/·410 combination rifle and shotgun. I injected about 0·5 ml of 10 per cent formalin into the peritoneal cavity of each specimen as soon as it was secured to preserve the stomach contents and gonads for future inspection. In this way specimens could be collected over a period of up to three days in the field and prepared later upon returning to the Namib Desert Research Station. Whenever possible each specimen was preserved as a study skin and the whole stomach preserved in 70 per cent ethanol or 10 per cent formalin. Study skins are deposited in the Fuertes Bird Collection, Fernow Hall, Cornell University, Ithaca, New York.

The preserved stomach contents were later analysed for the percentage composition by volume of various food items. This was done, in the case of larger samples, by pooling the stomach contents of all the specimens collected during a given month, and manually separating the components into arthropod remains, seeds, and other vegetable matter under a dissecting microscope. The collected food items were then drained of excess fluid on filter paper, and their volumes determined by sinking them in a volume of 70 per cent ethanol in a small graduated test tube and recording the change in volume.

In this study the term *complete moult* is used to mean the replacing of both body and flight feathers. The term *partial moult* means the replacing of part or all of the body feathers alone.

## LARKS OF THE NAMIB

The larks, family Alaudidae, are typically small, brown or dull-coloured, ground-dwelling passerine birds of open, arid or semi-arid plains, and are found throughout the desert areas of Eurasia and Africa; but the family is not restricted to deserts or semi-deserts, and some species occur in alpine regions and on tidal flats and sand bars (Vaurie 1951). There are about 75 species (Van Tyne and Berger 1959, p. 502), with about 28 of them occurring in the southern third of Africa (Mackworth-Praed and Grant 1962). The nomenclature and systematics of the larks have been in considerable dispute, with most argument concerning generic relationships (Bianchi 1905; White 1957; Winterbottom 1962; Harrison 1966; Maclean 1969), and about all that is agreed upon is that the family is quite distinct and coherent.

Table 2 lists all the species of larks recorded in the study area together with their habitat associations. The status of each species during this study is given below.

*Large-billed Sabota Lark.* This species is considered conspecific with *M. sabota* by some authors. It is one of the so-called bush-larks—that is, it occurs in open bushy habitats and freely perches on top of bushes when not foraging on the ground. It occurred sparsely but regularly along the eastern edge of Game Reserve No. 3, and in places farther to the west where extensive areas of low, open scrub occur on rocky terrain, which is mostly above an elevation of 800 m. The species is found throughout South West Africa.



TABLE 2

THE LARKS RECORDED IN THE CENTRAL NAMIB DESERT AND THEIR HABITAT ASSOCIATIONS[1]

| *Species* | *Habitats* | | | | |
|---|---|---|---|---|---|
| | *GFO* | *GFI* | *OB* | *R* | *S* |
| Large-billed Sabota Lark *Mirafra naevia* .. .. | | | XXX | X | |
| Karroo Lark *Certhilauda albescens* .. .. .. | | | | | XXX |
| Long-billed Lark *Certhilauda curvirostris* .. .. | | | — | — | |
| Spike-heeled Lark *Certhilauda albofasciata* .. .. | | XXX | XX | | |
| Gray's Lark *Ammomanes grayi* .. .. .. | X | XXX | | | |
| Red-capped Lark *Calandrella cinerea* .. .. .. | — | — | | | |
| Stark's Lark *Spizocorys starki* .. .. .. .. | | XXX | X | | |
| Grey-backed Finch-lark *Eremopterix verticalis* .. | X | XXX | X | | X |
| Black-eared Finch-lark *Eremopterix australis* .. .. | | — | | | |

[1] GFO = Outer Gravel Flats; GFI = Inner Gravel Flats; OB = Open Bush; S = Sand Dunes; R = Rocks; XXX = primary habitat; XX = secondary habitat; X = marginal habitat; — = rare or status uncertain (see text).

FIGURE 4
Habitat of the Karroo Lark in sand dunes south of the Kuiseb R., about 10 miles southeast of Gobabeb, 20 April, 1966. The tall grass is *Stipagrostis sabulicola*.

*Karroo Lark*. The subspecies of the Karroo Lark found in the study area, *C. a. erythrochlamys*, was formerly known as the Red-mantled Lark *C. erythrochlamys* (Meinertzhagen 1951) because of its distinctive pale reddish-brown, unmarked back, and because it is restricted in distribution to the dunes from Lüderitz Bay and Aus northwards to the Kuiseb River. More recently it has been considered to be one of the eight or nine subspecies of the Karroo Lark that are scattered over the drier areas of the southwestern Cape Province and southern South West Africa (Lawson 1961). This lark appears to be the only avian species that permanently inhabits the sand dunes, where it lives in association with the tall, spiny dune grasses *Stipagrostis sabulicola* and *S. lutescens* (Fig. 4).

*Long-billed Lark*. A few long-billed larks were observed in open bush on rocky terrain, mainly around the Tinkas water holes in the northeastern sector of the study area. I secured only one specimen. Hoesch and Niethammer (1940) found the Long-billed Lark in the fog-free Namib and "Pro-Namib" between the Brandberg and Chuos Mountains, which lie north of the Swakop River, and in arid southern South West Africa. Taxonomists recognise about seven subspecies that are scattered throughout South Africa, South West Africa, and Angola (Mackworth-Praed and Grant 1962).

*Spike-heeled Lark*. The Spike-heeled Lark occurs sparsely all along the eastern edge of the study area, especially where the Inner Gravel Flats habitat has a scattered, woody scrub less than 33 cm tall. The species has a wide distribution in southern Africa, and as many as 16 subspecies have been recognised, primarily on the basis of divergencies in plumage colour (Winterbottom 1958). It is peculiar among the larks of this study in having an unusually long, straight hind claw, the function of which, if any, is obscure.

*Gray's Lark*. This lark is endemic to the Namib, and ranges from Aus and near Lüderitz Bay north into the Kaokoveld, at least as far as Orupembe. In the study area it occupied the more or less barren gravel flats, avoiding the sand dunes and sandy soils. Hoesch and Niethammer (1940, p. 223) considered it a characteristic bird of the fog desert, but in Game Reserve No. 3 during my study it occurred in greatest abundance eastward from about 600 m elevation to the eastern edge of the escarpment at about 1 000 m elevation. In other words, it was primarily a bird of the Inner Gravel Flats. Westward it was encountered with rapidly diminishing frequency, and appeared there presumably as transients that wandered into the Outer Gravel Flats from the east. This was most noticeable during strong east winds, when birds suddenly would appear near the coast where they otherwise could not be found.

*Stark's Lark*. Stark's Lark was one of the most abundant of the avian species in the study area, and was the most abundant of the larks. It is a small bird, with lengthened crown feathers that show as a crest when it erects them. Its habitat in the central Namib is Inner Gravel Flats where sparse grasses occur, and it is typically associated with gravelly or stony ground rather than sandy soil. Outside the study area Stark's Lark has a wide range in arid and semi-arid southwestern Africa. Hoesch and Niethammer (1940) found it in the Namib out to the beginning of the fog zone (Outer Namib), but not into it.

*Grey-backed Finch-lark*. The Grey-backed Finch-lark was the second most abundant lark in the study area, and in general habits and habitat it resembled the Stark's Lark, although it foraged on sandy ground more readily than the latter. The plumage shows a strong sexual dimorphism in colour, a type of characteristic that is lacking in most species of larks, but which is typical of the genus *Eremopterix*. Outside the study area, this species is widespread in southern and southwestern Africa.

*Black-eared Finch-lark*. I observed the Black-eared Finch-lark on only one occasion, 8 April, 1966, in grassy Inner Gravel Flats about 11 miles south of Ganab. Two birds in male and female plumage appeared briefly on the ground at close range, but I did not collect them. Outside the study area this species occurs in southern South West Africa, Botswana, parts of the Cape Province, Orange Free State, and western Transvaal (Mackworth-Praed and Grant 1962).

*Red-capped Lark*. The Red-capped Lark was observed only three times during the study. A female was collected by Dr. Tom J. Cade about 33 miles southeast of Walvis Bay on barren Gravel Flats habitat on 3 August, 1964. It was in a flock of about six birds. Subsequently, I observed one at Zebra Pan on 18 September, 1965, where it drank at the watering trough, and another one on Outer Gravel Flats on 13 January, 1966, near Rooibank about 20 miles southeast of Walvis Bay, where it was foraging among scattered saltbush *Arthraerua leubnitziae*. Hoesch and Niethammer (1940) found this species on the coast between Cape Cross and Swakopmund in February, 1939. Outside the study area it is widely distributed in the drier regions of Africa and Asia.

## RESULTS

The following accounts of the species vary in completeness according to the abundance and accessibility of the species. The birds listed above that are omitted from further consideration because of insufficient observations are the Long-billed Lark, Black-eared Finch-lark, and Red-capped Lark. Table 3 summarises specimen data for the Large-billed Sabota Lark, and

TABLE 3
SPECIMEN DATA FOR *Mirafra naevia*

| *Specimen number* | *Sex*[1] | *Date* | *Body weight* | *Gonad measurements*[2] | *Moult* |
|---|---|---|---|---|---|
| 282 | M | 11 Sept., 1965 | — | 1·5 mm | Late stage of complete moult |
| 729 | M | 18 March, 1966 | 26·7 g | *ca.* 6·0 mm (testes damaged by shot) | Early stage of complete moult |
| 807 | F | 7 April, 1966 | 24·1 g | 1·0 mm | Heavy complete moult |
| 876 | M | 14 May, 1966 | 25·3 g | 7·1 mm | Complete moult just starting |

[1] M = male, F = female
[2] length of left testis or diameter of largest follicle

Figures 5–8 summarise specimen data for the Spike-heeled Lark, Gray's Lark, Stark's Lark, and Grey-backed Finch-lark.

BODY WEIGHT

*Karroo Lark*. The mean weight of eight males was 29·4 g (range 26·3 to 33·1), and of 10 females, 26·8 g (range 24·8 to 28·9).
*Spike-heeled Lark*. There was no apparent seasonal change in body weight. The data reflect the marked sexual dimorphism in body size, with males averaging about 5 g heavier than females.
*Gray's Lark*. There was no seasonal change of weight. There was definite sexual size dimorphism, reflected in the heavier body weights of males, which averaged about 3 g more than females.
*Stark's Lark*. Body weight varied little with sex or season.
*Grey-backed Finch-lark*. As in Stark's Lark, body weight did not vary much with season or sex.

BREEDING

*Large-billed Sabota Lark*. I found no nests. Andersson (1872) described the nest as being of the domed type with a side entrance. Reproduction very likely occurred during summer months.
*Karroo Lark*. I found no nests, but the enlarged testes of males collected in January and April, and a fully-developed egg yolk and oviduct in a female collected on 28 February indicate that egg-laying was occurring during that period. On 15 November, I observed

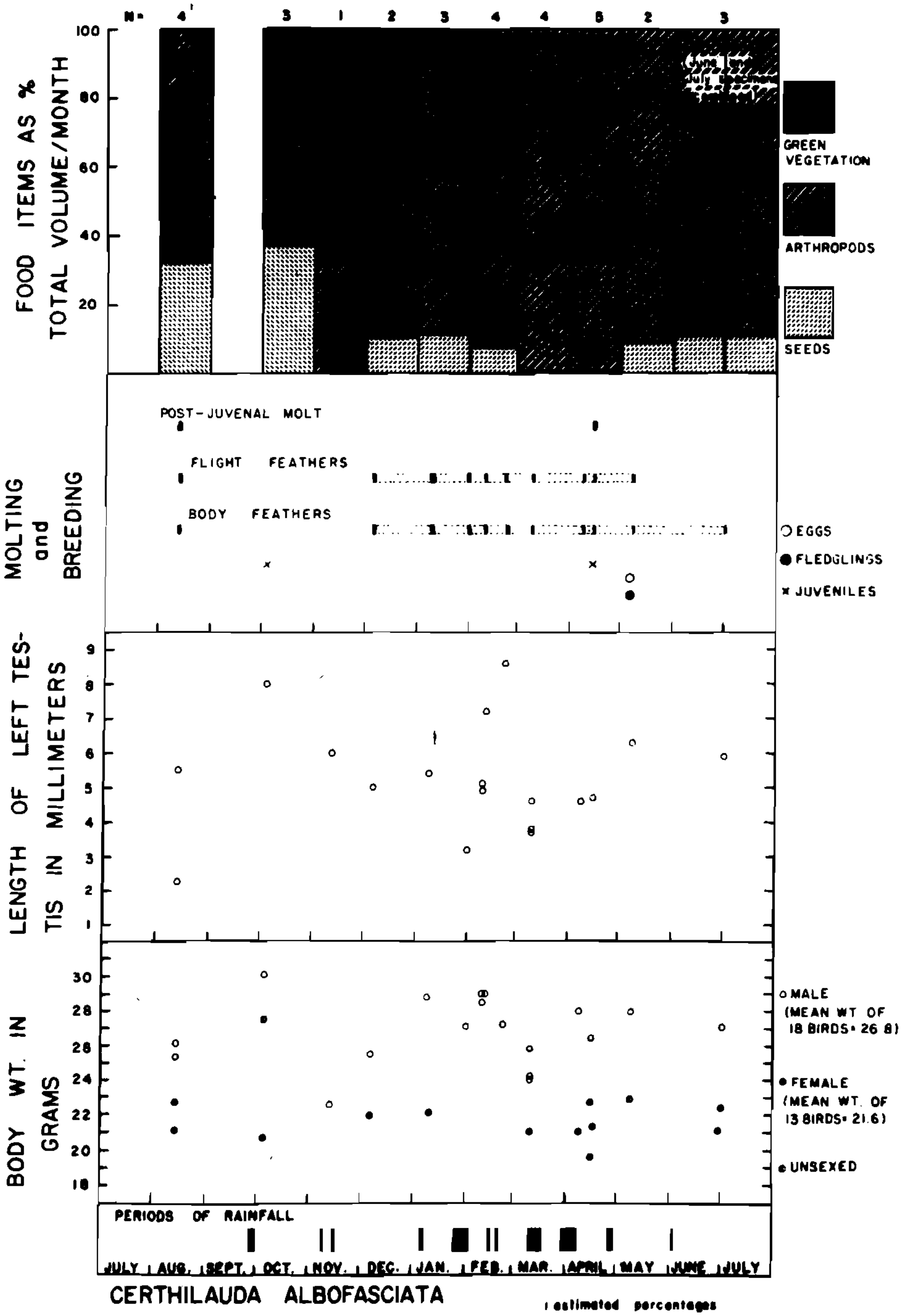


FIGURE 5

**Specimen data for the Spike-heeled Lark in Game Reserve No. 3, 1965-66. Vertical bars for moult indicate observed moulting; broken lines connecting observations indicate periods when at least a part of the population was in moult.**

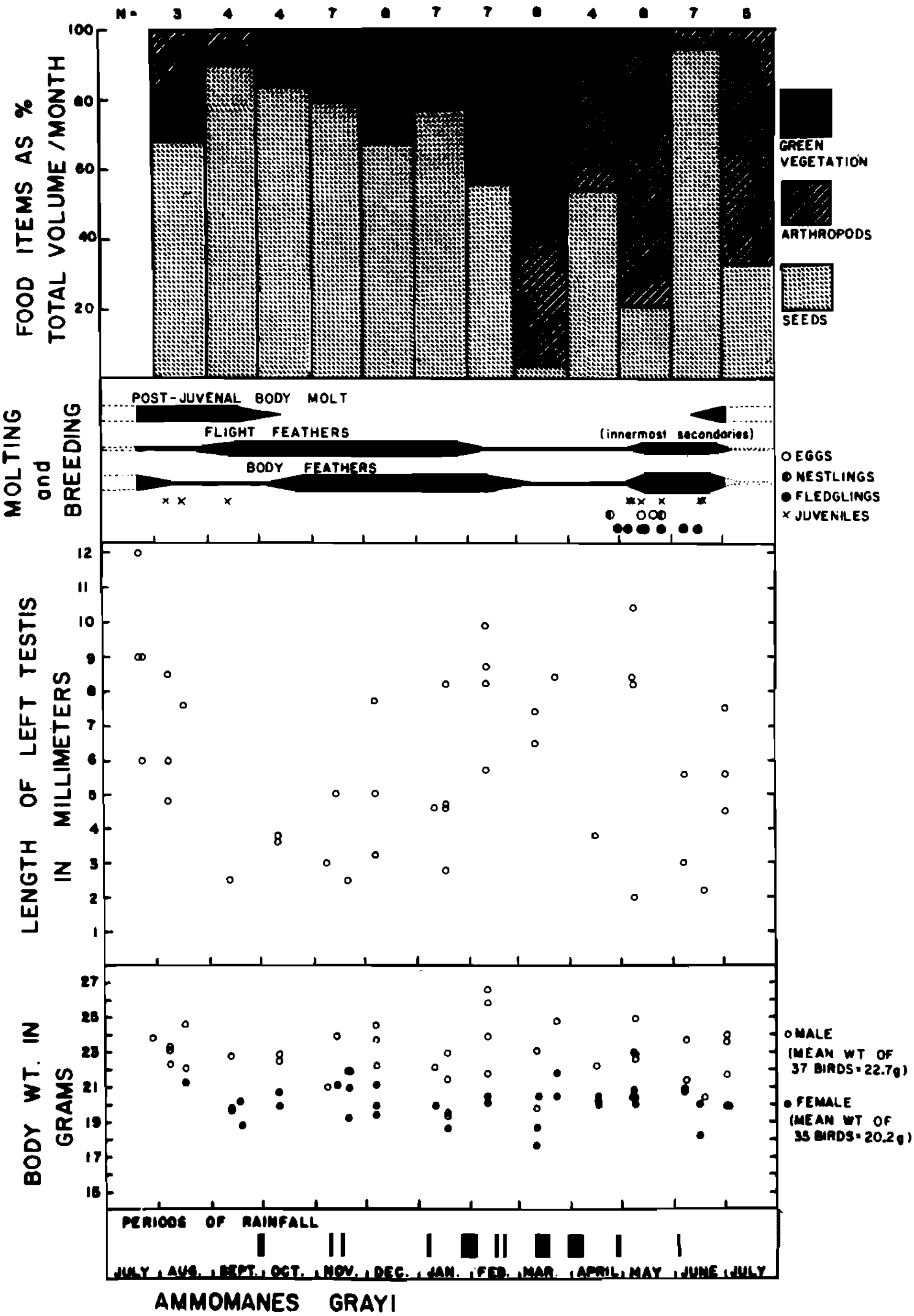


FIGURE 6

Specimen data for Gray's Lark in Game Reserve No. 3, 1965-66. The length of the black lines for moulting indicate known duration of moulting in the population, and the width of the bar indicates the relative intensity of moulting within the population (*i.e.* the narrow bar indicates that a few birds were moulting, and the wide bar indicates that most of the birds were moulting). Broken lines indicate probable moulting, extrapolated from the data.

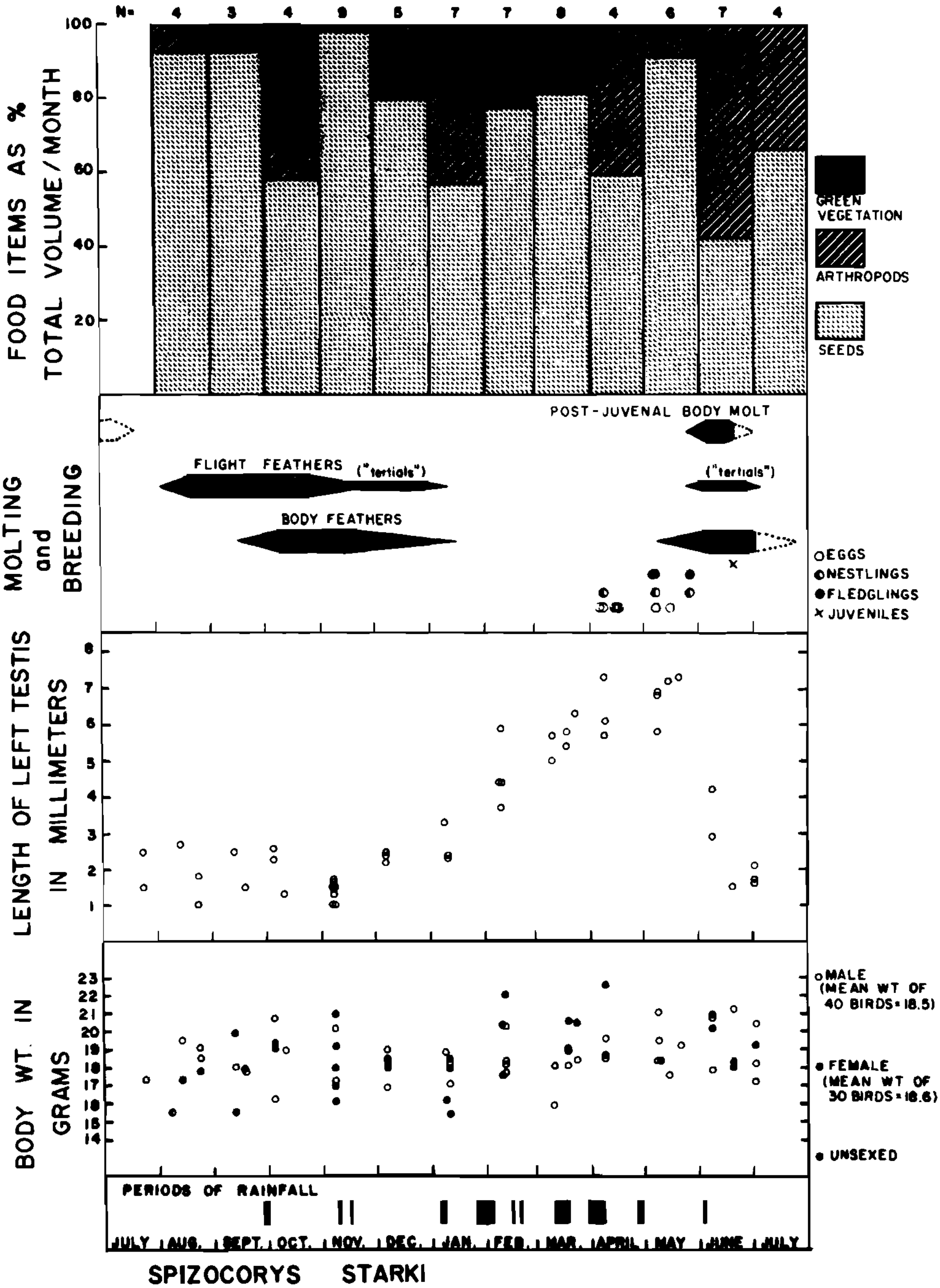


FIGURE 7
Specimen data for Stark's Lark in Game Reserve No. 3, 1965-66. Symbols for moulting as in Fig. 6.

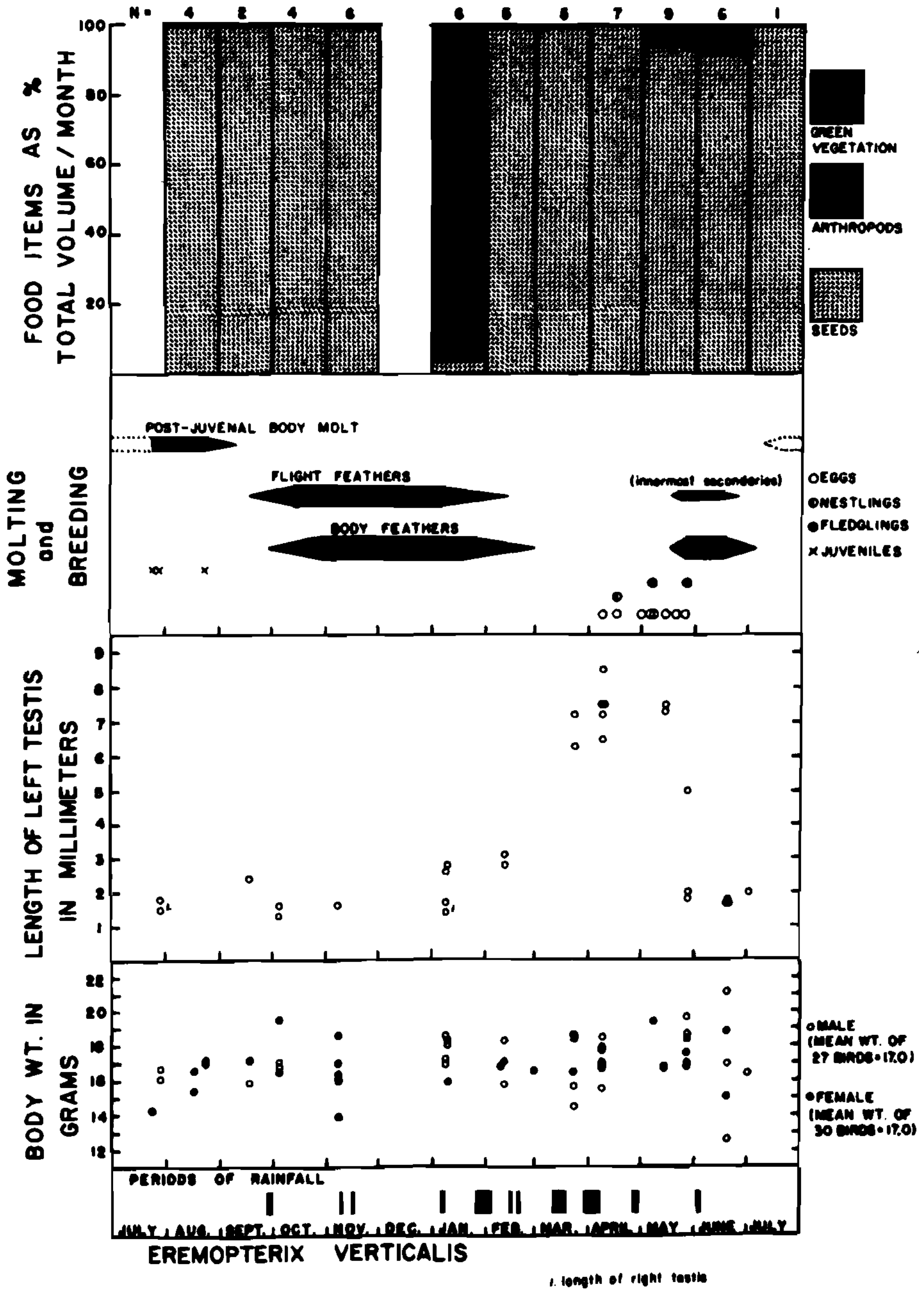


FIGURE 8
Specimen data for the Grey-backed Finch-lark in Game Reserve No. 3, 1965-66. Symbols for moulting as in Fig. 6.

FIGURE 9
Nest of Spike-heeled Lark at the eastern border of Game Reserve No. 3 at Farm Onanis, 6 May, 1966.

birds chasing each other vigorously and associating in pairs, and heard loud advertising song, all of which indicate that breeding activity was starting by the middle of November. By the middle of June, there was no evidence of breeding. Probably, then, the period during which reproduction occurred was from late October to early May, and so coincided with the rainy season of the Inner Namib.

The nest of the subspecies *C. a. erythrochlamys* evidently has not been described as such. The nests of other populations of the Karroo Lark often have a dome or bower of stems over them, and are usually placed under bushes (Vincent 1946, pp. 466–467; Maclean 1957; McLachlan and Liversidge 1957; Macworth-Praed and Grant 1962). In the Sand Dunes, nests probably are placed under the bush-like tufts of the dune grasses. The nest discovered by Hoesch (1958) among vegetation on the sandy margin of the lower Kuiseb River and described by him as the nest and clutch of *Ammomanes grayi* was most likely that of *C. a. erythrochlamys* instead. Hoesch described that nest as being roofed over with dry grasses; and thus it is consistent with descriptions of the nests of the other subspecies of the Karroo Lark.

*Spike-heeled Lark*. The fact that enlarged testes were observed throughout the year indicates that at all times of year the population had individuals that were probably capable of reproduction under the right circumstances; and it is reasonable to assume that this species breeds whenever environmental conditions are propitious, without strict seasonality. A juvenile bird which was collected in October may have hatched the preceding August. Another juvenile which was secured in April probably had hatched in February or March. A nest with two eggs was observed on 6 May, 1966. These observations indicate that actual breeding did take place during both dry and rainy periods.

The one nest that was observed contained two eggs which were chalky grey finely speckled with brown. It was an open cup of old, weathered grass leaves and plant fibres with a few twigs

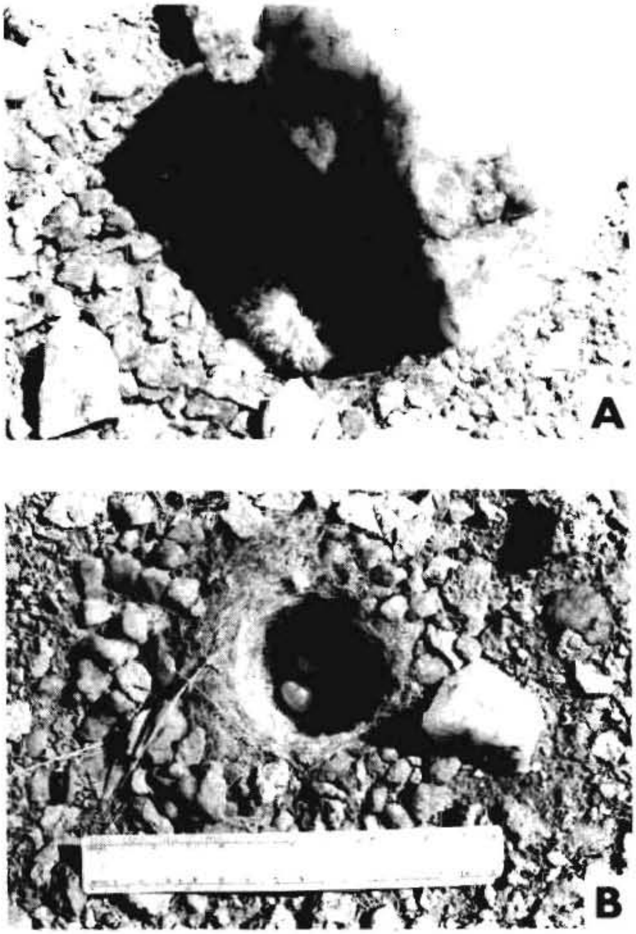

FIGURE 10
Nests of Gray's Lark. A, eight miles west of Zebra Pan, 26 April ,1966, a scrape measuring 13 × 7·5 cm. B, one mile west of Zebra Pan, 14 May, 1966 (the scale is 15 cm long).

about 0·25 cm in diameter and 6·5 to 15 cm long around the rim, set in coarse sandy soil against the south-southeast side of a tuft of grass (*Stipagrostis* sp.) which was 30·5 cm tall and 4·2 cm wide at the base (Fig. 9). The nest had an inside diameter of 6·6 cm, and a depth of 2·3 cm.

*Gray's Lark*. There was no clear-cut seasonal gonadal cycle in males, although the data suggest that there was a period from August to December when testes were mostly small and reproductively nonfunctional. This period coincided with the main complete moult. But there was no well-marked synchrony of gonadal recrudescence and regression, and partly-

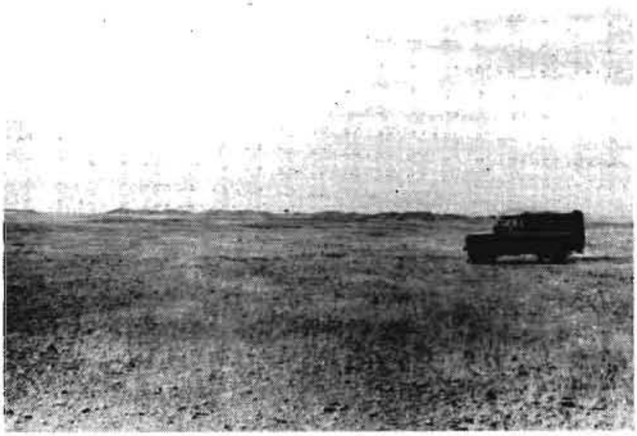

FIGURE 11
Nesting habitat of Gray's Lark, Stark's Lark, and the Grey-backed Finch-lark, 1 mile west of Zebra Pan, 14 May, 1966. The grass is primarily *Stipagrostis obtusa*.

enlarged testes occurred all year long. This suggests that there may be some individuals in the population ready to breed at all times of the year, as in the Spike-heeled Lark, given the needed environmental circumstances. Actual breeding was detected during my study only in March, April and May, which coincided with the summer-autumn rainy season.

The three nests that I found are described as follows: Nest number 1 was located eight miles west of Zebra Pan on 26 April, when it contained two nestlings estimated to be seven to nine days old (Fig. 10A). The "nest" was a bare scrape in the gravelly earth on the southeast side of a white quartz stone about 25 cm in diameter that shaded the nestlings during the afternoon. Sparse green grass (*Stipagrostis ciliata*) up to 30 cm tall, which had germinated after rainfall about the middle of March, was growing on the surrounding gravel flats. There was very little other vegetation, and probably the eggs had been laid before suitable nest materials in the form of dry grass leaves and seed awns were available.

Nest number 2 was located one mile west of Zebra Pan on 14 May (Fig. 10B), and it contained a full clutch of two eggs. The nest was a deep, thickly-felted cup of very fine, dry grass fibres, stems, and feathery *Stipagrostis* seed awns on bare gravel with a small quartz stone at the north rim, which, however, provided little shade for the nest. The nest cup had an inside diameter of 5·7 cm, and a depth of 5·1 cm, and had been built in a little depression with a surrounding apron of small pebbles so that its rim was nearly flush with the level of the surrounding ground. The sitting bird sank deeply into the cup so that its back was level with the ground, and in such a position the bird was invisible from just a few feet away because its dorsal coloration matched that of the ground perfectly. The habitat in which this nest was situated was Inner Gravel Flats, with sparse green grass (*S. obtusa*) growing about 30 cm tall in patches with much bare gravel surface between (Fig. 11).

Nest number 3 was found on 20 May, eight miles north-northeast of Zebra Pan. It then

TABLE 4

SUMMARY OF NESTING DATA OF *Spizocorys starki*

| *Date* | *Number of eggs or nestlings*[1] | *Nest dimensions (inside diameter × depth, cm)* | *Protective object* | *Compass direction from protective object* |
|---|---|---|---|---|
| 6 Apr. | 3 e. | 5·1 × 3·8 | Tuft of *Stipagrostis ciliata* 30 cm tall | SSE |
| 8 Apr. | 2 n. | 4·5 × 3·8 | Tuft of *S. ciliata* 30 cm tall | S |
| 8 Apr. | 2 e. | — | Small *Zygophillum simplex* | S |
| 8 Apr. | 2 e. | — | Small *Z. simplex* | S |
| 14 Apr. | 2 e. | 6·4 × ? | Stone *ca.* 13 cm diameter | SSE |
| 15 Apr. | 3 e. | 5·8 × 3·8 | Tuft of *S. ciliata* | S |
| 15 Apr. | 3 e. | 5·1 × 3·0 | 3 tufts of *S. ciliata* | S and E |
| 16 Apr. | 3 e. | 6·4 × ? | Small *Z. simplex* | (Surrounded by branches) |
| 16 Apr. | 2 e. | 5·4 × ? | Small *Z. cylindrifolium* | SE |
| 7 May | 1 e., 1 n. | 6·3 × 2·5 | Tuft of *S. ciliata* 33 cm tall | SSE |
| 8 May | 1 e., 2 n. | 5·5 × 3·7 | Small *Z. simplex* | SE |
| 15 May | 2 e. | 5·5 × 2·5 | Tuft of *S. ciliata* 51 cm tall | S |
| 25 May | 2 n. | — | Stone 10 cm × 18 cm | SSE |

[1] e. = eggs, n. = nestlings.

contained three eggs, one of which was very small and turned out to have no yolk. This nest was constructed just like nest number 2, and was set into gravelly soil at the south side of a tuft of *S. obtusa* that stood 18 cm tall and afforded the nest some shade during the afternoon. It had a built-up apron of small (0·6 to 1·5 cm diameter) pebbles around it so that the nest rim was a little higher than the surrounding ground level. The inside diameter of the cup was 5·7 cm, and the depth was 3·8 to 4·5 cm, a little shallower on the south side away from the tuft of grass. The habitat was Inner Gravel Flats with sparse but fairly evenly-distributed tufts of grass, *S. obtusa*, 14 to 30 cm tall and spaced 8 to 80 cm apart.

FIGURE 12
Stark's Lark feeding young at nest, 8 miles northeast of Zebra Pan, 25 May, 1966. One nestling had just tottered from the nest, and the other was still in the nest on the shady side of the stone.

*Stark's Lark.* There was a definite seasonal testicular cycle, with reproduction occurring near the end of the rainy period from late March to late May. Nesting occurred in areas where green grasses had grown after rains and had begun to mature and set seed (Fig. 11). Thirteen nests were observed. They were all simple open cups made of fine, dry stems, leaves, panicles, and feathery seed awns of grasses, sunk in a slight depression at the base of a small plant or beside a stone (Fig. 12), so that the rim was more or less even with the surrounding ground level. The nest was invariably placed on the south to southeast side of the protecting object so as to be shaded in the early and middle afternoon. Table 4 summarises the nesting data. It appears that two- and three-egg clutches are about equally prevalent, but statistics on actual clutch size are not presented because I learned nothing about mortality in the nest, or whether the observed clutches were completed ones in every case.

Nestlings leave the nest a few days before they can fly, and totter after the adults to to be fed (Fig. 12). As soon as they can fly, they join large flocks of adults and other immatures.

FIGURE 13
Nest and eggs of the Grey-backed Finch-lark, 6 miles southeast of Hotsas, 8 April, 1966. The grass is *Stipagrostis ciliata*.

TABLE 5
SUMMARY OF NESTING DATA FOR *Eremopterix verticalis*

| *Date* | *Number of eggs or nestlings*[1] | *Nest dimensions (inside diameter × depth, cm)* | *Protective object* | *Compass direction from protective object* |
|---|---|---|---|---|
| 8 Apr. | 2 e. | — | Tuft of *Stipagrostis ciliata* | SE |
| 15 Apr. | 2 e. | 4·8 × 2·5 | Tuft of *S. ciliata* | S |
| 16 Apr. | 1 n. | 5·7 × 2·5 | Tuft of *S. ciliata* 38 cm tall | SE |
| 16 Apr. | 2 e. | 5·1 × 3·0 | Small *Zygophillum simplex* | ESE |
| 16 Apr. | 1 e. | 4·8 × 3·8 | *Cleome suffruticosa* 30·5 cm tall | SSE |
| 16 Apr. | 2 e. | 5·4 × 2·5 | Tuft of *S. ciliata* 38 cm tall | SE |
| 30 Apr. | 1 e. | 5·7 × 3·8 | Tuft of *S. obtusa* 17·8 cm tall | S |
| 5 May | 2 e. | 5·6 × 2·8 | Tuft of *S. obtusa* 25 cm tall | S |
| 7 May | 2 e. | 5·6 × 2·8 | Small *Z. simplex* 5 cm tall | S |
| 7 May | 2 e. | 5·1 × 2·8 | Tuft of *S. ciliata* 41 cm tall | SSE |
| 7 May | 2 e. | 5·3 × 3·3 | Tuft of *S. obtusa* 23 cm tall | SSE |
| 14 May | 2 e. | — | 4 tufts of *Stipagrostis* sp. 25 to 30 cm tall | N, W, S |
| 14 May | 2 e. | 5·1 × 1·9 | Tuft of *S. obtusa* 23 cm tall | S |
| 14 May | 2 e. | 5·6 × 2·5 | Tuft of *S. obtusa* 25 cm tall | S |
| 20 May | 2 e. | 5·0 × 2·5 | 2 tufts of *S. obtusa* 20 and 25 cm tall | SE |
| 25 May | 2 e. | 5·5 × 3·0 | Tuft of *S. ciliata* 41 cm tall | S |

[1] e. = eggs, n. = nestlings.

*Grey-backed Finch-lark*. The marked testicular cycle was correlated with a breeding period during the autumn months at the end of the rainy period. Nesting occurred side by side with Stark's Lark. The nest of the Grey-backed Finch-lark was practically indistinguishable from that of Stark's Lark (Fig. 13), differing mainly by a tendency to have the materials built a bit more loosely into the cup lining. The nest of the Grey-backed Finch-lark also occasionally had a surrounding apron of small pebbles which apparently had been taken from the nest excavation and placed around the nest rim. Table 5 summarises the data for the 16 nests that I observed.

Two eggs made the usual clutch. In contrast to Stark's Lark, none of the nests was beside a stone. All nests were shaded from midday through the middle of the afternoon by small plants beside them.

## MOULT AND PLUMAGES

*Large-billed Sabota Lark*. Data in Table 3 indicate that a complete moult occurred in autumn and winter months (March to September). These data do not give any information on whether or not there is a partial moult at some time during the year. All the specimens were mature birds, judging from the fact that their skulls were fully ossified. Probably the two males in early stages of complete moult (729 and 876) were at the end of a breeding cycle, judging by their enlarged testes.

*Karroo Lark*. Data are too meagre for definitive statements on moult in this species. The juvenal plumage persists for several weeks, the white edges to the feathers of the head and back gradually wearing off before the post-juvenal moult begins. It is not clear from the few specimens of immature birds in moult whether there is a partial post-juvenal moult, or whether it is complete, but I suspect the latter. Adult Karroo Larks did not show any definite partial moult. Most of the moulting adult birds were undergoing complete moult after breeding.

Macdonald collected 18 specimens of *C. a. erythrochlamys* at Tsondab Vlei, not far outside the present southern border of Game Reserve No. 3, on 5 and 6 March, 1950. One of these specimens was in juvenal plumage, and the adults were either in extremely worn plumage with enlarged but apparently regressing gonads, or were just beginning to moult (Macdonald 1953a, p. 333). My observations are consistent with these findings.

*Spike-heeled Lark*. The fragmentary data indicate that moulting may occur throughout the year, which is consistent with the evidence that reproduction may occur at any time of year. It appears likely that an individual experiences a post-nuptial body moult beginning when the gonads start to regress after a period of sexual activity, followed immediately by, or merging into, a complete moult. Young birds experience a post-juvenal body moult starting perhaps within the first two months after fledging, although it is impossible to determine precisely the time relationships in moulting from the data that I collected (Fig. 5). It is safe to say that there is little or no synchrony in either gonadal or moult cycles among individuals of the particular population sampled.

*Gray's Lark.* Individual birds in some stage of moult were collected all year long. Most specimens showed synchronised seasonal moult as diagrammed in Figure 6. A post-juvenal body moult occurred beginning a few weeks after fledging, and this merged into a complete moult during spring and early summer months at the same time that older birds were undergoing a complete moult. Breeding birds were either not moulting or were in very weak complete moult. The general picture of moult in Gray's Lark was one of definite long periods of strong moulting by most of the population, alternating with periods when moulting occurred at a low level in a small part of the population.

*Stark's Lark.* There was definite, synchronised moulting cycle in the population I studied, as diagrammed in Figure 7. In May, immediately following breeding, adults went through a heavy post-breeding moult that involved secondaries 7–10 (the tertials), lasting only about a month per individual and being so precipitous as to leave the birds with large bare patches on head, neck or breast covered only by the short pin-feathers coming in to replace the feathers that had dropped out. At the same time, beginning within a month of fledging, juveniles went through a heavy post-juvenal body moult.

*Grey-backed Finch-lark.* Figure 8 summarises observations on moulting. There was a very rapid post-breeding body moult that involved secondaries 7–10, and occasionally the central pair of rectrices. Although I obtained no immature specimens at the end of the 1966 breeding season to show it, presumably they began a post-juvenal body moult about the first part of July.

The marked sexual dimorphism in plumage colour is of interest. The female is generally brown with dark streaks, and has a black patch on the belly, whereas the mature male has a strongly contrasting black and white head pattern, black breast, and grey-brown back streaked with black. Very young males were indistinguishable from young females and did not attain any of the male plumage colouration in the post-juvenal moult. During their first complete moult, young male Grey-backed Finch-larks took on more or less of the male plumage colouration, but in few instances did they attain the full black-and-white pattern until their first post-breeding moult. Some of these young males with streaked upper breast and only the suggestions of the black and white face pattern showing on the still streaked head were observed at nests, and collected specimens had fully enlarged testes, indicating that first-year males may breed despite their immature plumage.

## FOOD

*Large-billed Sabota Lark.* The stomachs of three of the specimens were preserved. The total volume of organic matter was 0·5 ml, consisting of small seeds (mainly of *Stipagrostis* spp., *Cleome* spp., and others), 60 per cent; insects (*Hodotermes* and a few ants), 40 per cent;

and a trace of green vegetation (part of a grass stem). The stomach of the fourth individual held only small seeds.

*Karroo Lark*. The proportionate volumes of food items from 19 stomachs collected in January, February, April and June are 32 per cent seeds, 68 per cent arthropods, and traces of green vegetation. Nearly all of the seeds were from the grass *Stipagrostis sabulicola*. A larger proportion of these seeds in stomachs in June (87 per cent, compared with about 20 per cent in other months) may have resulted from increased availability of this food, since this grass produced seed in March and April. The arthropods consumed were primarily large ants that swarm in the dunes around the clumps of *S. sabulicola*. Besides ants, Karroo Larks ate small locusts, beetles, caterpillars, and possibly *Hodotermes*. They probably eat whatever insects are available.

*Spike-heeled Lark*. Throughout the year food consisted chiefly of insects—ants, *Hodotermes*, small beetles, and other arthropods such as solifugids. Seeds consumed were mainly from grasses (*Stipagrostis* spp.) and the herb *Monsonia umbellata*. The average percentages of food items for the whole year are 16 per cent seeds, 84 per cent arthropods, and traces of green vegetation.

*Gray's Lark*. Percentages of food items for monthly samples are diagrammed in Figure 6. Small seeds formed the bulk of the diet in the driest seasons, but after rainfall that resulted in plant and insect growth, insects were more prevalent in the diet. The means of the percentages for all months are 61 per cent seeds, 36 per cent arthropods, and 3 per cent green vegetation. When the total volumes of food items in the year's collection are combined, the percentages work out to 56 per cent seeds, 43 per cent arthropods, and 1 per cent green vegetation. The discrepancy between the means of the percentages of monthly samples and the percentages of the combined year's sample comes from the fact that the sample volumes varied greatly from month to month, so that a sample of small volume consisting mostly of seed, for example, contributed more strongly to the seed category when taken as a monthly sample than when added as part of the total volume of collected material. However one calculates the percentage composition of the diet, it is clear that seeds predominate.

The seeds consumed by Gray's Larks were primarily grass seed (*Stipagrostis* spp.) with substantial amounts of seeds of the herbs *Cleome* spp. and *Monsonia umbellata*, plus smaller amounts of other species. The green vegetation consisted mainly of grass, which was ingested both directly, and as the stomach contents of herbivorous insects such as locusts. The arthropods eaten were mainly insects—*Hodotermes*, ants, various small beetles, small stick insects and locusts, flies, and moths, roughly in descending order of frequency. Other arthropods included in the diet were small spiders and solifugids. Two nestlings one day old were crammed with small locust nymphs, several spiders, and a beetle larva. Two nestlings estimated to be seven to nine days old contained a large (2 cm long) locust nymph and a large fly, respectively. None of the nestlings contained seeds, and the data suggest that the young are fed exclusively on insects while in the nest.

*Stark's Lark*. The average percentages of food items are 75 per cent seed, 20 per cent arthropods, and 5 per cent green vegetation (Fig. 7). When the whole year's stomach contents were combined and volumes worked out, the percentages were 77 per cent seed, 19 per cent arthropods, and 4 per cent green vegetation. The reasons for the discrepancy are the same as those for Gray's Lark discussed above. It is clear that seeds form the bulk of the diet.

Small seeds of all kinds were consumed, but were primarily of grasses (*Stipagrostis* spp.), *Cleome* spp., and *M. umbellata*. The green vegetation consumed was mostly grass. The birds obtained this by pulling at the culm until it slipped out of the sheath, and then nibbling at the tender, juicy basal joint and discarding the rest of the stem. I saw a bird take bites out of the yellow flowers of *Tribulus* sp., a prostrate, creeping perennial herb that bloomed after rains. Arthropods in the diet were primarily ants and *Hodotermes*, with additions of small beetles, bugs, flies, and spiders and solifugids. It should be noted that a large amount of green grass had been consumed by birds collected the first week of October following rains on September 30, which had caused grass seed to germinate, and that collections in February and March also had considerable amounts of green vegetation which had grown up following rainfall in those months.

*Grey-backed Finch-lark*. Food consisted overwhelmingly of small seeds. In a series of specimens collected in January just after a rainfall, harvester termites predominated; but this was an unusual situation and very likely was owing to the sudden conspicuous emergence of winged sexual individuals, at which time all kinds of birds were feeding on the termites. The means of the monthly percentages of food items are 91 per cent seed, 8 per cent arthropods and 1 per cent green vegetation. Because some of the monthly stomach collections contained nothing but seeds, they were not preserved, so no figures based on total volume of stomach contents for the year are given.

The seeds most common in the stomachs were of grass *Stipagrostis* spp., and of the herbs *Cleome* spp. and *Monsonia umbellata*. There were lesser amounts of small, unidentified seeds. The green vegetation was chiefly grass shoots and sprouting grass seeds. Arthropods included ants, *Hodotermes*, and small beetles; and unmeasurable traces of insects, such as mouthparts and chitin fragments, were usually present in the stomachs.

## DRINKING

*Large-billed Sabota Lark*. I did not see this species drink, although it occurred in the rocky terrain around the Tinkas water holes and would thus seem to have the opportunity to do so. It probably gets most of the water it requires from the insects it eats.

*Karroo Lark*. Surface water does not exist in most of the habitat of the Karroo Lark, and dew or other condensation is rare in dunes of the Inner Namib where Karroo Larks are most abundant. I did not see this species drink at any of the watering places in the bed of the Kuiseb River adjacent to parts of its habitat, such as the fresh-water pools at Rooibank some 20 miles southeast of Walvis Bay. The Karroo Lark probably obtains all its water from its food.

*Spike-heeled Lark*. This species was never observed to drink, and since its diet consists mainly of insects, which provide a relatively good source of water, it probably never has to drink.

*Gray's Lark*. Gray's Lark does not normally drink. Although on one occasion at the Zebra Pan water installation several birds walked along the edge of the water briefly, only one of them stuck its beak into the water, which it did once. This was the only time in many hours of observation that I saw this species at water.

*Stark's Lark*. Stark's Lark was one of the two larks that gathered at watering places to drink. During dry times, August through the first half of January, Stark's Larks often came in flocks to the Gross Tinkas water hole, but rarely to the Ganab and Hotsas watering places. I also observed this species drinking at a stock-watering installation at the eastern border of Game Reserve No. 3 on the farm Onansis, and at a water hole in a wide part of the Kuiseb Canyon where the main Walvis Bay Road crosses the river. Although several hundred individuals would sometimes drink in a day at Gross Tinkas, which was the watering place most regularly frequented by Stark's Lark during August to January, it became clear early in the study that these birds represented a relatively small proportion of the population in the surrounding gravel flats. On the basis of road counts and population estimates, I concluded that something on the order of 10 per cent or less of the population within a five-mile radius of the water hole drank there per day. Later in the summer and autumn months after rains had brought up the grasses and when insects were abundant, it was unusual to see Stark's Lark at water anywhere, although it literally swarmed in grassy areas on the surrounding flats. The distribution of Stark's Lark showed no definite relationship to watering places in the Namib. It is thus evident that some individuals of this species did not normally drink every day, if at all, even in dry conditions, and that when there was green grass and abundant insects, they were independent of surface water.

*Grey-backed Finch-lark*. The Grey-backed Finch-lark drank most frequently of all the larks of the Namib. At all times of the year they could be found at watering places that were near their population concentrations. The watering place most frequently visited was Gross Tinkas. Hotsas, Ganab and Zebra Pan were visited during the breeding season when many breeding birds had collected in the fresh grass around these locations. Nevertheless, the distribution of this lark did not appear to be bound to the locations of drinking water, as I observed large flocks in the Inner Gravel Flats which appeared to be independent of drinking water. The distribution of this lark was more strongly correlated with the presence of its preferred grassy habitat than with surface water.

BEHAVIOUR

*Large-billed Sabota Lark.* I had little opportunity to observe behaviour in this species.

*Karroo Lark.* The Karroo Lark spends its life on the Sand Dunes, foraging between and around the clumps of dune grasses and seeking refuge within the bases of the grass clumps. It takes food by several methods. One method is simply to pick up food, such as ants, from the surface of the sand. Another method is to uncover buried food with the beak by rapid sideways jerking of the head so that the tip of the beak scatters the sand aside. Besides using these methods of feeding, Karroo Larks frequently hop up several centimeters, or as high as a meter, to seize insects and seeds directly from the overhanging stems of plants, but in doing so they do not perch on the stems.

One of the most marked aspects of the behaviour of the Karroo Lark, particularly with regard to water conservation, is its inactivity during the warmest time of day. The Karroo Larks forage and display actively in the morning until around 10.00 or 11.00 on a hot summer day, when the ground surface temperature approaches 50°C. Then all birds disappear into the bases of the large shady grass clumps and do not stir again until about 16.30, when the ground cools off somewhat. Then they suddenly reappear and forage and display actively until dusk. Some representative temperatures taken during a time when the birds were inactive will show how they avoid undue heat stress by remaining still in the shade: On 20 April, at 13.00 at a location in the Sand Dunes about 10 miles southeast of Gobabeb, the surface temperature of the sand on level ground was just 50°C. The air temperature in the shade 10 cm above the ground was 33°, and the air temperature in the shade of a clump of *Stipagrostis sabulicola* at the spot where a Karroo Lark had been squatting a few seconds before was also 33°. Sand surface temperatures in the sun often exceeded 50°C. It is quite evident from these figures that the bird crouching in the shade at a temperature of 33° was avoiding contact with the hot ground, and radiation from the ground and sun, and was in this way minimising its water loss to evaporative cooling.

I did not have a chance to study the advertising song and displays of this species in detail, but the following notes are included because they add to general biological information on the Karroo Lark. The advertising song, given both when flying and when perching, was fairly stereotyped and not very loud. I transcribed it into syllables as follows: *tip-tip-tip-tip-tip-zree'-trrrr*. The first five notes are incisive, staccato notes, the sixth a buzzy, high-pitched note, and last a lower-pitched trill. The entire song has a duration of two to three seconds. This song was given by birds standing on mounds of sand, perching on grass stems several feet above the ground, and when flying slowly around with slow, deep wing beats 3 to 20 m above ground. Besides the advertising song, a rapid series of mellow bubbling notes was given, usually by birds hovering about 3 m up with feet dangling. When one bird was vigorously chasing another, as if a territorial dispute were in progress, a buzzy note was repeatedly uttered.

During the breeding season I usually saw Karroo Larks in pairs, or in what appeared to be family groups of two adults and one or two juveniles. Later, when breeding had finished, I found them most often in small parties of four to eight individuals that included both adult and immature birds. Thus there is no evidence that they form large flocks as do some other species of larks.

*Spike-heeled Lark*. The Spike-heeled Lark occurs in Inner Gravel Flats with sparse grass, and I found it most frequently where there were widely-spaced, low, woody perennial shrubs up to about 60 cm tall. The birds occasionally perched on these shrubs, thus avoiding contact with the hot ground during midday; but more often they stood in the shade beneath.

I seldom encountered single Spike-heeled Larks, but usually found them in pairs and small parties of up to six individuals. The latter groups were made of birds of both sexes and all ages, even including older fledglings still being fed by adults. It thus appears that the Spike-heeled Lark is sociable except when nesting, and tends to associate in small groups rather than large flocks when not tied to a specific nest site. Nestlings leave the nest and run after the adults before they can fly.

Spike-heeled larks have a marked tendency to stay around rodent burrows, especially the large burrow complexes of the ground squirrel *Xerus inauris*, and the birds spend considerable time foraging in and around the burrow entrances. This may be partly because wind-blown seeds and surface-running insects tend to drop into the mouths of burrows and to collect there. At the same time the birds can take advantage of the shade and cooler ground temperatures available in the burrow entrances when foraging, which they do at all times of day, and thus reduce the need to use evaporative cooling.

Spike-heeled Larks readily go down rodent burrows when wounded, and several times I was obliged to dig birds out of these refuges. Macdonald (1953b) noticed this same escape reaction in the north-western Cape Province. It appears that the burrows of rodents serve the Spike-heeled Lark well as cool feeding spots and ready predator-escape tunnels in an otherwise nearly featureless habitat.

Besides foraging around the mouths of rodent burrows, Spike-heeled Larks also forage on the open ground. They take food items directly off the surface of the ground and also uncover buried items by digging with rapid sideways jerks of the beak, as described for the Karroo Lark. I have no definite observations on advertising song and sexual behaviour. The usual note heard was a mellow, low-pitched chatter or trill. Otherwise this species appears to be comparatively silent.

*Gray's Lark*. Gray's Lark inhabits gravel flats exclusively, with or without sparse grass; but it was encountered most frequently where there was sparse grass standing 15 to 50 cm tall with much bare gravel surface between tufts.

All year long this species associated in small parties of from three or four up to as many as 30 birds, including both sexes and old and young birds. The mean size of 121 groups totalling 396 individuals observed in January, February and March was 3·3 birds, with a range from 1 to 10. Individuals did not appear to be strongly associated in these small groups, and when foraging they spread out over wide areas covering several acres and sometimes would join other similar groups that passed by. But wherever Gray's Lark occurred, there was a marked tendency for several birds to associate together and to travel as a group. These groups wandered over large expanses and nowhere showed definite signs of staying in a circumscribed range.

In parts of the study area where Spike-heeled Larks occurred, I occasionally saw small groups of both species close together around the same rodent burrows. However, Gray's Lark tended to be scarce in areas of low scrub where the Spike-heeled Lark was most prevalent.

Like the Spike-heeled Lark, Gray's Lark has the habit of foraging in and around the mouths of rodent burrows, and no doubt avoids daytime heat to some extent this way. This species also dives down burrows when wounded. However, these habits are not so marked as in the Spike-heeled Lark, and Gray's Lark spends considerable time foraging in the open on the bare gravel surface, even at midday when temperatures are around 38°C. Between bouts of foraging during the heat of the afternoon, however, Gray's Larks stand on stones or twigs a few centimetres above the gravel surface with the folded wings held away from the sides of the body so as to expose the thinly feathered surfaces of the sides and under the wings, and face into the prevalent westerly sea breeze, thus doubtlessly facilitating the loss of body heat to the cooler air by convection.

Gray's Lark takes food principally from the surface of the ground, but it also uncovers buried items with sideways jerks of the beak as do the other lark species. It feeds on grass the way Stark's Lark does, discarding the culm after nibbling the tender, juicy basal node.

Nests of Gray's Lark were exceedingly difficult to find. The incubating or brooding adult on the nest was practically invisible because of its concealing colouration. I saw birds get off their nests and walk away foraging while I was approaching in a vehicle or on foot and still about 20 or 30 metres away, making it hard to find the nest when its location was not already marked. Nestlings leave the nest well before being capable of flight and follow the adults to be fed. When able to fly, but still being fed by adults, they join with the usual small mixed social groups.

Courtship and sexual behaviour was difficult to study because of the lack of sexually dimorphic plumage. One rather unusual trait of Gray's Lark is that the flight song—what one would ordinarily consider the full song or advertising song—is performed primarily in the dark. From early February through May, but most frequently in March and April, there would be a burst of calling and singing for about half an hour after sunset, and again for about two hours before dawn and ending before sunrise. Singing and calling of this sort were also observed in the daytime, but this vocalisation was rarely as vigorous then as at dusk and before dawn. The song was a combination of high-pitched, very sharp tinkling notes with a loud, up-slurring whistled note, and when given in flight was accompanied by a loud, reedy whirring of the wings. Two variants of the song are diagrammed in Figure 14. Although the number and order of tinkling notes varied some, the slurring whistle was invariable. When this song was given in flight, the wing whirring preceded the vocal phrase and overlapped the initial tinkling notes, as diagrammed in Figure 14. When I observed the flight song performed during the day, the bird followed an undulating flight path about seven metres above the ground (Fig. 14). In this display the only time the wings were beating was when they produced the whirring sound. In ordinary level flight the wing sound was much less audible, and it thus seems that the wing sound is produced as a definite part of the display.

Other vocalisations include a high-pitched *tseet*, given by birds disturbed by the presence

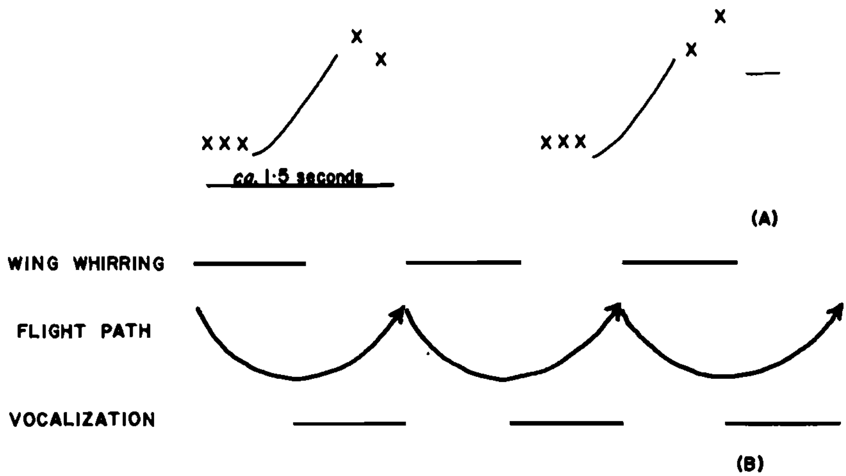


FIGURE 14
Diagrams of advertising song (A) and song flight (B) of Gray's Lark. An *x* denotes a sharp, tinkling note, and a thin line denotes a whistled note.

of man, a mellow *tew*, given in an indefinite series, and a series of three piping notes which were uttered by birds associating in groups.

Courtship and pairing appear to take place within the small groups, since I observed adults feeding other adults (presumably males feeding females) and mounting of one bird by another several times within groups of four or five birds in April and May. At the same time territoriality was not markedly expressed, and the impression these observations gave me was that birds paired while still moving about with a group, left the group to establish a nest, and then rejoined a group as soon as the fledglings could fly.

*Stark's Lark*. When foraging, the Stark's Lark creeps along holding its body close to the ground and pecking at the surface of the ground or occasionally using the sideways jerking of the beak to uncover buried food items. When a bird finds a seed or other food item it usually raises its head and squats down while nibbling and swallowing the object. It thus gives the impression of being somewhat lethargic. The observer may walk within three or four metres of several birds without being aware of them until they suddenly rise and fly a short distance making soft chirping sounds. Stark's Lark showed a tendency to fly towards vehicles and hover above or land beside them, as if inspecting them out of curiosity.

I nearly always encountered Stark's Lark in flocks of four or five to several hundred individuals. These flocks were continually wandering around from one grassy area to another so that I did not always encounter them at the same places from week to week; and after rainfall they had a marked tendency to collect where green grass was growing, where they sometimes congregated by the thousands in an area of a few square miles. Their habitat preference was Inner Gravel Flats with grass standing 25 to about 51 cm tall and separated by plenty of bare ground (Fig. 11).

I first heard singing on 6 December, and thereafter song became more frequent, reaching a high level from February through April and then declining. The song, a long series of soft churring chirps and whistles, is given on the ground or in the air. I transcribed an example of this song into the following syllables to try to record the character of it: "*chur-chirr-cheer-chor-cheer-reel'o*." In performing the flight song display, the bird typically rises steadily from the ground nearly vertically, singing continuously until reaching a height of 50 to 200 m, where it hovers against the wind, or circles slowly if there is no wind so that it remains above the same spot on the ground, and sings continuously for several minutes; and then it closes its wings and dives vertically to the ground where it may often indulge in a brief aerial chase of another Stark's Lark that has been on the ground. Sometimes birds sing while flying distances of several metres a few feet above ground with feet dangling and wings fluttering slowly. Birds singing on the ground often accompany the song with crest raising. A male displaying to a female on the ground sings continuously and faces toward the female with body horizontal, crest raised, and head bobbing slowly up and down.

During the month or so prior to actual breeding, thousands of Stark's Larks gathered in areas where green grass was growing and displayed and sang; but there was a great deal of milling around and moving from place to place during this time, and actual nesting did not begin until the grasses had begun to mature and set seed. Then suddenly nests appeared and the singing and milling around that had been prevalent only a week before was much reduced. Meanwhile in adjacent areas where the grasses had not yet begun to mature, Stark's Lark continued to fly about and sing conspicuously. The densest populations of this species that I found in these grassy areas I estimated at two to five birds per acre.

Nesting, once begun, proceeded rapidly, with non-flying young leaving the nests in a month and then joining post-breeding flocks of adults and juveniles shortly after they could fly.

During the hottest times of day, Stark's Larks usually avoided the heat by crouching in the shade of stones, overhanging rocks, or, most frequently, of vegetation. Occasionally birds would perch atop low shrubs or rocks and stand facing into a breeze with the folded wings held away from the sides so as to expose the thinly-feathered sides of the thorax and axillae. In two such instances, I measured a ground surface temperature above 50°C (off the scale of my thermometer) and air temperatures at a height of 61 cm of 36° and 33°C., respectively.

*Grey-backed Finch-lark*. In general behaviour the Grey-backed Finch-lark resembles Stark's Lark in many ways. It forages in the same manner as Stark's Lark, rests in the shade of small plants, and occurs in large flocks like Stark's Lark. It differs mainly in not perching on bushes or rocks, but staying constantly on the ground when not flying. It is much harder to approach than is Stark's Lark, and although it was actually more numerous than the latter in some areas, it was much more difficult to collect.

Like Stark's Lark, the Grey-backed Finch-lark wandered in flocks from place to place prior to breeding, accumulating in great numbers where green grass was growing, and nesting when these grasses reached heights of 20 to 50 cm and began to mature. In fact, the Grey-backed Finch-lark wandered much more freely than Stark's Lark before and during the breeding season in late summer and autumn, and it was at this time that flocks turned up in the Inner Sand Dunes and far out toward the coast on the Outer Gravel Flats.

The flight song display is less conspicuous than that of Stark's Lark because the flight is not usually so high — only 15 to 30 m high — and the song is weaker and less sustained. In flight the displaying bird circles about slowly in undulating flight rather than hovering over one spot; and the song notes are sharp and tinkling rather than churring and chirping as in Stark's Lark. This song flight typically ends in a vertical dive to the ground. I estimated population densities of from two to five birds per acre in the best breeding areas.

## DISCUSSION

### REPRODUCTION AND MOULT

It is possible to draw some conclusions about how the reproductive and moult cycles of larks in the Namib Desert are adaptive to the environment. The five lark species that are most abundant in the central Namib show two general patterns of response to the environment with respect to reproduction and moulting. On the one hand Gray's Lark, the Spike-heeled Lark, and the Karroo Lark are sedentary species that remain constantly in the Namib, and do not wander far. These species include a large proportion of insects and other arthropods in their diets — more than 40 per cent in Gray's Lark, and more than 60 per cent in the other two species. In them, with the possible exception of the Karroo Lark for which data are lacking, gonadal activity and moulting are not strictly synchronised throughout their respective populations. Thus Spike-heeled and Gray's Larks with enlarged testes or undergoing some stage of moult were collected at all times of year.

On the other hand Stark's Lark and the Grey-backed Finch-lark are very mobile, moving from region to region in large flocks and gathering temporarily in places with favourable conditions for feeding and breeding. These birds consume primarily seeds – more than 75 per cent in Stark's Lark and more than 90 per cent in the Grey-backed Finch-lark. They show a high degree of synchrony of gonadal development and moulting within their respective populations.

Reproduction in all these species occurred during or at the end of the summer-autumn rainy period of the Inner Namib, and thus was timed to correspond with periods when insect food was at a peak of abundance, owing to the new grass that came up following the rains. However, in the primarily insectivorous Spike-heeled Lark there was evidence that reproduction took place at other times of year as well; and in Gray's Lark, the fact that there was no clear-cut synchrony of moulting and testicular development in the whole population suggests that reproduction probably can take place at other times of year, given favourable environmental circumstances such as abundant insect food and green grass. The data for the Grey-backed Finch-lark and Stark's Lark give no suggestion at all that they bred, or were capable of breeding, at any time except during the summer and autumn rainy season. Therefore, I suggest that the following relationships exist between these species and their environments:

The Spike-heeled Lark, specialising in a diet of small insects, is restricted to areas in the Namib with a relatively rich and perennial arthropod fauna. Some segment of the population is capable of reproducing at any time that local rainfall produces or maintains favourable conditions for raising young. Such rainfall may occur at any time in the Namib, but is most likely to occur in summer and autumn at the latitude of Game Reserve No. 3.

Gray's Lark eats a large proportion of seeds, and is widely distributed over the Namib Platform, but must have abundant insects to feed its young. Some segment of the population is ready to breed at any time local rainfall produces the right environmental conditions, but since this was most prevalent in summer and autumn during the time of this study, the majority of birds showed approximately the same moulting and reproductive timing.

The Karroo Lark probably has the same moulting and reproductive relationship to the environment as Gray's Lark, although data to make a good case either way are lacking.

The Grey-backed Finch-lark and Stark's Lark specialise in a diet of seeds, but must have insects to raise their young. At the same time they are highly mobile and travel long distances in large flocks in search (so to speak) of favourable feeding and nesting conditions, and move into the Namib from the semi-arid highlands to the east when these favourable conditions occur. Therefore, they are strongly influenced by the marked annual dry and rainy cycle of the central interior of South West Africa. They nest when grass growth is sufficient to provide nesting material and shelter from the sun, when insect food is abundant for the nestlings, and when seed becomes abundant for fledglings and adults.

## MOULTING AND PLUMAGE

Thus far I have treated moulting and reproduction together, because in most birds the time of moulting is closely associated with the sexual cycle. Because moulting — the replacement of feathers — takes energy, its timing is sensitive to natural selection (Amadon 1966), and it is appropriate to ask how the moulting and plumages of the larks in the Namib are adaptive to their environment.

The moulting patterns of larks are not well known, but Vaurie (1951) distinguished three main patterns of moult among Asiatic representatives of the Alaudidae. One is a single complete annual moult occurring as post-breeding or post-juvenal moult, the first winter bird being indistinguishable from the adult. This pattern occurs in most of the larks that Vaurie studied. A second pattern involves a single annual moult, but with only a partial post-juvenal moult in which the body feathers are changed. The third pattern consists of a complete post-breeding and post-juvenal moult together with a more or less restricted pre-breeding body moult.

Some of the larks in the Namib present still other moulting schemes. The Large-billed Sabota Lark possibly has one complete moult a year, without a partial moult, but data are meagre. The Karroo Lark also appears to have a single complete moult a year—a post-breeding and post-juvenal moult. The Spike-heeled Lark seems to have a post-breeding and post-juvenal body moult that merges into a complete moult. Gray's Lark definitely shows a rapid post-breeding and post-juvenal body moult that is followed by a prolonged complete moult. Both the Grey-backed Finch-lark and Stark's Lark have intense post-breeding and post-juvenal body moults followed after an interval by a prolonged complete moult.

It is evident that the rapid post-breeding and post-juvenal body moults that occur in Gray's Lark, Stark's Lark, and the Grey-backed Finch-lark are timed to occur when food in the form of insects and seeds is still abundant at the end of the breeding period. The subsequent prolonged complete moult during the dry period is sustained mainly by the seeds produced in the previous rainy period. It is hard to assess the adaptive significance of having two changes of body plumage, especially when there is no seasonal colour variation in any of these birds. It may be that two body moults are not adaptive in these species, but that this moulting pattern has been inherited from ancestral species in which it did at one time have some adaptive function, and the descendants have been unable to eliminate or suppress the post-breeding body moult without associated mal-adaptive side-effects. In this case they have done the next best thing in advancing and accelerating one body moult so that it comes within a time of plenty. Or on the other hand, the extra body moult may be adaptive; and a possible way that it could be so is in replacing excessively worn and faded body plumage that results from the constant exposure to wind, sand, and intense sunshine in the desert. It is a fact that even with the two changes of body plumage a year, feathers in these larks become quite ragged and faded, and I am inclined to favour this second alternative.

## ENVIRONMENTAL STIMULI FOR BREEDING

The breeding of the larks in the Namib clearly coincided with the seasonal rainfall that brought an abundance of succulent foods. This is true generally of birds in arid and semi-arid regions of Africa (Moreau 1950) and Australia (Immelmann 1963). A pertinent question is what specific environmental factors stimulate the birds to commence breeding. The data provide no answer, but they do suggest some possibilities.

It has been shown that in north temperate regions, lengthening daily photoperiods in the spring stimulate gonadal recrudescence, northward migration, and breeding in numerous species; and the literature on photoperiodism in birds is extensive (for a recent review, see Lofts and Murton 1968). However, in equatorial regions where photoperiod varies little during the year, and in arid and semi-arid regions where rainfall and favourable breeding conditions occur irregularly, photoperiod has little influence in timing events in the normal reproductive cycles of birds. Instead, responses to various environmental stimuli connected with the circumstances favourable to breeding as well as endogenous rhythms have been postulated as timing mechanisms for breeding (Marshall 1960; Immelmann 1963). In the case of the larks of the central Namib, photoperiod is probably not important as a timing factor, and some other exogenous factors or endogenous factors or both are responsible for the timing of the breeding cycle.

In the Spike-heeled Lark, which shows what appears to be a tendency to breed any time that environmental circumstances are favourable, the stimulus might be falling rain itself. Immelmann (1963) observed birds in the arid interior of Australia in which the falling rain appeared to trigger latent breeding tendencies so that the birds were well along with breeding even before the increased food supply and nesting material resulting from the subsequent plant growth had appeared. Marshall and Disney, in experiments with *Quelea quelea* in East Africa, found that watering the cages with sprinklers apparently had the effect of accelerating the reproductive cycle (Marshall and Disney 1957; Marshall 1961, p. 323). I think it likely that green grass and an abundance of insect food are also important stimuli for breeding in the Spike-heeled Lark.

These same factors may be at work in the timing of reproduction in Gray's Lark. The one nesting that had occurred before the grasses resulting from rainfall had grown enough to provide nest-building material (Fig. 10) may have been stimulated partly by the rain itself. The fact that rainfall on 30 September which caused some growth of grass did not result in any detected breeding activity in this species suggests that an endogenous physiological process may have been at work in the bulk of the population which made most individuals unresponsive to the environmental stimuli at that early date when the majority of birds were undergoing the complete moult.

Stark's Lark and the Grey-backed Finch-lark may be influenced in timing of breeding by both endogenous factors and by exogenous factors. Birds of both species captured in August and November, 1965, kept to the same moult schedules as wild birds through June, 1966, and several of the captive Stark's Larks sang vigorously in their cages at the time wild birds were breeding, although all of them were kept in individual cages inside a building. In the wild, however, actual nesting did not occur until the grasses reached maturity and began to flower, at which time insects were at a peak of abundance, and nesting material in the form of dry grass stems and feathery seed awns became available. Experiments are needed to clarify the role of such environmental factors as stimuli for breeding; and Stark's Lark and the Grey-backed Finch-lark might make good subjects owing to the ease with which they can be maintained in captivity (Willoughby 1968).

## BEHAVIOURAL ADAPTATIONS TO DESERT CONDITIONS

One of the first things a bird can do to ameliorate the effects of its environment is to find shelter. In the Namib, where water is at a premium, it is advantageous for a bird to avoid excessive heat transfer from the environment to its body so that the expenditure of water by evaporation to eliminate the excess body heat is kept to a minimum. The birds do this by keeping in the shade of bushes, grass tufts, stones, and mouths of rodent burrows during the hottest times. In addition to using these tactics, Gray's Lark and Stark's Lark avoid contact with the hot ground by standing above it on stones or bits of woody vegetation, and although they are still exposed to the intense sunshine, the relatively cool sea breeze that regularly blows across the Namib and seldom has a temperature above 38°C doubtlessly carries away a good part of their excess body heat by convection as they stand facing into the air flow with wings held away from the sides of the body. Trost (1968) has observed that horned larks, *Eremophila alpestris*, in the Mojave Desert of California rarely alight on hot ground but perch in the wind on top of creosote bushes, or stay in the shade beneath the bushes.

The larks build their nests on the surface of the ground, usually next to some protective object such as a stone or tuft of grass so that the nest and its contents receive shade during the hottest time of day, from about noon to 16.00 hr.

In the Spike-heeled, Gray's, and Stark's Larks, and probably also in the Grey-backed Finch-lark, nestlings leave the nest before they can fly, and run after the adults to be fed. This habit may have the function of dispersing the young away from the nest as soon as possible to reduce their vulnerability to predation by such animals as snakes, mongooses and jackals.

## SEXUAL SIZE DIMORPHISM

The significance of the sexual dimorphism in body size observed in some of the larks in the Namib is an intriguing question. Most species of birds do show some difference in size between the sexes, and either male or female may be larger (Amadon 1959). Among the larks in the central Namib, the male is the larger sex when there is clear sexual size dimorphism. The most interesting aspect of this dimorphism is that it is expressed to different degrees among the different species, and seems to be correlated with food habits. Thus the Spike-heeled Lark, the most insectivorous one, shows a marked dimorphism, with males averaging 24 per cent heavier than females; and Gray's Lark, feeding on nearly equal proportions of seeds and insects, shows a less marked size dimorphism, with males averaging 12 per cent heavier; and Stark's Lark and the Grey-backed Finch-lark, specialising in a diet of small seeds, show no size dimorphism. These weight differences are reflected generally in linear measurements, but there is no striking difference between the sexes in proportionate size of structures such as beak and feet. I have omitted the Karroo Lark from consideration here because of the lack of data, but the small sample I have indicates a moderate degree of size dimorphism, as in Gray's Lark.

The question of the ecological significance of sexual size dimorphism has been discussed recently for various groups of birds by several investigators (Rand 1952; Amadon 1959; Cade 1960; Selander 1966; Storer 1966); and the biological functions of sexual dimorphism in size are no doubt nearly as diverse as the species and families in which it occurs. In the larks of the Namib, the fact that this dimorphism seems to be correlated with food habits certainly suggests the hypothesis that it is connected in some way with differential utilisation of feeding niches. The hypothesis is that the sexual dimorphism in the insectivorous larks reduces intra-specific competition for food because the larger males tend to take larger insects, which results in an effective widening of the size range of prey items that can be exploited by the whole population. The ones that are granivorous, on the other hand, and eat uniformly small seeds such as those of the grasses of the genus *Stipagrostis*, are not affected by sexual differences in body size in regards the size range of food items made available to them.

Unfortunately, the biology of the larks of arid regions is too little known yet to show whether or not this relationship between food habits and size dimorphism holds generally. I do have another bit of evidence from the Spike-heeled Lark of the Namib that tends to support the hypothesis that the two sexes exploit different feeding sub-niches. When I processed the specimens, I made brief notes on the kinds of insects that predominated in the stomachs. In 16 stomachs from males, 13 (81%) included remains of beetles (mostly small tenebrionids about five to ten mm long). Ants, harvester termites, or small orthopterans predominated in the three other stomachs. In the stomachs of 12 females, however, only three (25%) contained beetle remains, and the rest held ants or harvester termites or both. This suggests that the males take a greater proportion of small, hard beetles, and females take a greater proportion of ants and soft-bodied termites. I saw no difference between males and females of the less dimorphic Gray's Lark with respect to the kinds and sizes of insects taken by them.

## WATER REQUIREMENTS OF NAMIB LARKS

The fact that none of the species of larks that live in the central Namib depends on drinking water indicates that the birds must have efficient physiological mechanisms for conserving body water, which permit them to subsist on the preformed and metabolic water from their food. This is most remarkable in those species that subsist primarily on seeds, Stark's Lark and the Grey-backed Finch-lark, because air-dried seeds contain only about ten per cent water. A study of the water metabolism of these two species in the laboratory (Willoughby 1968) has shown that they have such low evaporative, urinary and faecal water losses that under moderate conditions of humidity and ambient temperature they can maintain water balance when consuming nothing but air-dried millet seed. In the wild, an occasional insect, bit of succulent vegetation, or an infrequent visit to a watering place would provide enough water to compensate for increased losses during hot, dry weather.

Those species, such as Gray's Lark, that include a large proportion of insects in their diet, are in a more favourable position to maintain water balance in the desert, owing to the increased amount of free water in the food. The ability of the larks of the Namib to live without drinking, whatever the physiological and behavioural mechanisms permitting it may be, is one of the prime factors for the success with which these species occupy an extremely dry and barren habitat.

## SUCCESS OF ALAUDIDAE IN DESERTS

There appears to be no other passerine family that equals the Alaudidae in successful desert occupancy, as regards the numbers of species filling a variety of desert niches. It is tempting to speculate upon the basis for the adaptive success of the larks in the desert environment.

As a group the larks have specialised in living on open ground in dry situations. Within the broad limits of this specialisation, however, they have remained unspecialised (except for individual species) with respect to food and feeding, moulting, reproduction, and behaviour. It is difficult to discern any features unique among the Alaudidae other than the morphological feature that gives the family its coherence, namely that the back of the tarsus is rounded and scutellated instead of keeled and encased in an undivided sheath (Stresemann 1934, p. 850). These traits of the Alaudidae suggest that this family has probably experienced a long history of occupancy of arid and semi-arid environments, and has experienced adaptive radiation to exploit various feeding, habitat, and climatic niches in these regions. Winterbottom (1962) concluded that despite conflicting taxonomic evidence for the antiquity of the Alaudidae, the fact that the family is rather coherent tends to support the notion of its antiquity; but the indistinctness of many of the supposed genera of larks and the high ratios of species per genus and subspecies per species suggest recent radiation.

It may be that the basis for the success of the larks in arid regions is their ability to tolerate rapidly and severely changing environmental conditions associated with seasonal drought and irregular rainfall by virtue of their lack of rigid specialisation in food, reproductive habits, moulting and plumage, seasonal migration and social behaviour. A recent study by Trost (1968) of physiological responses of several North American populations of the Horned Lark, *Eremophila alpestris*, to stressful environmental conditions indicates that this one species shows considerable physiological variability between different populations, and is physiologically tolerant of wide ranges in environmental temperature, barometric pressure, humidity, and availability of water. This tends to indicate that the Alaudidae have remained physiologically adaptable to changing conditions also. It appears, therefore, that the retention of evolutionary plasticity may be adaptive to life in an open arid environment.

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## SUMMARY

The central Namib Desert is very barren, with extremely low precipitation. A study of six indigenous species of larks, family Alaudidae, gives a basic understanding of the ways by which these birds are adapted to their environment. Table 6 summarises the major findings on the biology of the larks of the central Namib.

Reproduction in all species coincided with the end of the summer-autumn rainy period of the eastern part of the Namib, and came at a time when insects, maturing grass seed, and nest-building materials were most abundant.

Although two seed-eating species, *Spizocorys starki* and *Eremopterix verticalis*, sometimes came to watering places by the hundreds to drink, these birds represented only a small proportion of the population in the region, and none of the lark species showed dependence on sources of drinking water.

*Ammomanes grayi*, *S. starki* and *E. verticalis* have a rapid post-breeding body moult followed later by a prolonged complete moult. The post-breeding body moult of these species occurred when insect food and grass seed were still abundant following breeding. It is suggested that the change of body plumage twice a year might help to counteract the attrition and fading of the plumage owing to constant exposure to wind, sand, and sun in the Namib.

The larks in the Namib minimise heat influx from the environment and thus minimise their need to evaporate body water for cooling by squatting in the shade of stones, rocks, tufts of grass and bushes during the heat of midday. *Certhilauda albofasciata* and *A. grayi* also forage in the mouths of rodent burrows, and thus avoid the hot surface of the surrounding ground. *A. grayi* and *S. starki* frequently perch above the surface of the ground on stones or shrubs and face into the relatively cool sea breeze with the folded wings held away from the sides of the body, thus avoiding contact with the hot ground and facilitating loss of body heat by convection.

The fact that the species that are most insectivorous show the greatest difference in size between the sexes (males are larger) while granivorous species show no sexual size dimorphism supports the hypothesis that the size dimorphism functions to reduce intra-specific competition for food by widening the range of size or type of prey items that the species can exploit.

It is suggested that the basis for the adaptive success of the Alaudidae in desert environments is the absence of rigid specialisation in food, reproductive habits, moulting and plumage, behaviour and physiology, making the larks better able to cope with rapidly and severely changing environmental conditions associated with drought and irregular rainfall.

TABLE 6

SUMMARY OF BIOLOGY AND WATER RELATIONS OF LARKS IN THE CENTRAL NAMIB DESERT, 1965 AND 1966

| *Species* | *Occurrence*[1] *(habitats and movements)* | *Food* | *Timing of reproduction* | *Moulting* | *Drinking habits* | *Primary sources of water* |
|---|---|---|---|---|---|---|
| Large-billed Sabota Lark *Mirafra naevia* | Uncommon, in open bush on eastern edge of Namib | Small seeds and insects about equal proportions | Probably during or at end of summer-autumn rainy period | Complete post-breeding moult; no data on partial moult | Does not drink | Metabolic water and insects |
| Karroo Lark *Certhilauda albescens* | Common, sedentary, on dunes with tall perennial grasses | 32% grass seed, 68% insects | October to May, coinciding with rainy period | Complete post-breeding moult; no definite data on partial moult | Does not drink | Metabolic water and insects |
| Spike-heeled Lark *Certhilauda albofasciata* | Common, sedentary, on grassy Inner Gravel Flats with very sparse scrub | 16% seeds, 84% insects | Breeding occurred at all times of year | Moult occurred all year; individuals have post-breeding body moult that merges with complete moult | Does not drink | Metabolic water and insects |
| Gray's Lark *Ammomanes grayi* | Common, restricted to Namib, primarily on grassy Inner Gravel Flats | 56% small seeds, 43% insects, 1% green vegetation | Late summer and autumn, coinciding with rainy period, but without a definite seasonal gonadal cycle | Occurred all year, most individuals in loose synchrony, post-breeding body moult followed by complete moult | Does not drink | Metabolic water and insects |
| Stark's Lark *Spizocorys starki* | Common, at times very abundant, wandering, on grassy Inner Gravel Flats | 77% small seeds, 19% insects, 4% green vegetation | Late summer and autumn, at end of rainy period, with a marked seasonal gonadal cycle | Synchronised seasonal moult with rapid post-breeding body moult followed by a more prolonged complete moult | May drink in numbers during dry weather when water is available, but not dependent on drinking water | Mainly metabolic water; insects and green vegetation seasonally |
| Grey-backed Finch-lark *Eremopterix verticalis* | Common, at times very abundant, wandering, on grassy Inner Gravel Flats | 91% small seeds, 8% insects, 1% green vegetation | Late summer and autumn, at end of rainy period, with marked seasonal gonadal cycle | Synchronised seasonal moult with rapid post-breeding body moult followed by a more prolonged complete moult | May drink in numbers whenever water is available, but not dependent on drinking water | Mainly metabolic water, perhaps occasionally drinking water |

[1] "uncommon" = species observed on fewer than ⅔ of visits to suitable habitat.
"common" = species observed on more than ⅔ of visits to suitable habitat.

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