

# FORAGING BEHAVIOUR OF THE DUNE LARK

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## SUMMARY

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Foraging behaviour of the Dune Lark *Mirafra erythrochlamys* was studied in a dune environment at the Namib Research Institute, Gobabeb, South West Africa/Namibia in August 1981. Birds foraged for a total of 7 h per day in morning and afternoon periods separated by 3 h of inactivity during the warm midday. The birds exploited a distinctive series of vegetational belts dominated by three grasses. About two-thirds of total foraging time was spent in zones of dead and dormant grasses where seeds were sought by excavating small craters in the sand with the bill. Samples taken in the field, and simulations of bill-cratering behaviour in the laboratory, showed that this behaviour displaced seed-poor surface sand and exposed deeper, seed-rich layers. Birds formed small flocks when foraging for seeds in these zones. The remaining third of foraging time was spent in zones with large, live grass clumps, where insects were sought. Insect foraging was concentrated at the start and end of each activity period, but was most intense just before the midday period of inactivity when temperatures approached 30°C. Rough calculations of energy and water balance suggest that the larks are unable to maintain water balance under the observed conditions on seed food alone, and that this balance is achieved by feeding on insects. It is predicted that relative seed and insect foraging effort varies with temperature and season, as also suggested by limited published data on stomach contents in summer and winter.

## INTRODUCTION

The Dune Lark *Mirafra (Certhilauda) erythrochlamys*, formerly considered a red subspecies of a species including the Karoo Lark *M. (C.) albescens* and the Red Lark *M. (C.) burra* is a resident of sandy desert and sandveld from the Namib Desert near Walvis Bay, South West Africa/Namibia, south to the Orange River. Of nine species of larks that occur in the central Namib Desert, this is the only one that is completely restricted to sand dunes and the colour of its dorsal plumage closely matches that of the dune sand (Willoughby 1969, 1971).

Male Dune Larks weigh about 29,4 g (26,3-33,1 g; n = 8) and females about 26,8 g (24,8-28,9 g; n = 10) (Willoughby 1971). Nesting evidently occurs in spring. Analysis of stomach contents indicates that the birds are omnivorous, feeding on seed and various insects, primarily ants, but including locusts, beetles, caterpillars and perhaps termites; stomachs examined in June contained 87% seeds, while those in January, February and April contained only 20% seeds, suggesting that a seasonal shift in diet occurs (Willoughby 1971). The species has not been observed to drink.

In August 1981 I initiated studies of the Dune Lark at the Namib Research Institute at Gobabeb, South West Africa/Namibia, to determine how these larks exploit the various habitats and foods available in the dune environment, and how these foraging patterns contribute to maintenance of water and energy balance at different seasons.

In this paper I present the results of studies of winter foraging behaviour, and examine the question of how seasonal shifts in foraging can contribute to maintenance of a positive water and energy balance.

## STUDY SITE

Most of the Namib dune system consists of linear dunes, oriented NNE to SSW, separated by interdunal flats up to 3 km wide (Robinson & Seely 1980). Associated with the dune ridges are four distinctive habitats, which constitute the foraging areas for larks: interdune (trough), dune base, plinth (lower slope), and slipface (see Holm & Scholtz 1980, Fig. 4, for a description of this gradient). The sandy interdunal flats typically lack perennial plants, but develop dense stands of the ephemeral grass *Stipagrostis gonatostachys* after rains that deliver over 20 mm in a short period (Holm & Scholtz 1980). This grass grows in small clumps and reaches a height of 20-30 cm. The dune base is occupied by larger perennial grasses (and a few other plants), especially *Asthenatherum glaucum*, *Stipagrostis lutescens*, and *Eragrostis spinosa*. These grasses are taller and form clumps up to several decimetres in diameter, but become dormant during dry periods (see Robinson & Seely 1980, Plate 1, for an illustration of this habitat). The plinth region is dominated by large clumps of *Stipagrostis sabulicola*, which create semi-stabilized sandy hummocks up to 1-2 m high and several

metres across. This grass is in leaf and physiologically active year-round because of its ability to absorb fog moisture from the surface sand by means of an extensive, shallow lateral root system (Louw & Seely 1980; see this reference also for an illustration of this habitat). The slipface upward to the dune crest is typically devoid of vegetation.

The site of the present observations was the eastern slope of a dune ridge about 2 km southwest of the Namib Research Institute and 0,5-1,5 km south of the Kuseb River channel. The vegetation of this slope was dominated almost exclusively by the grasses *S. gonatostachys* (SG), *A. glaucum* (AG), and *S. sabulicola* (SS); the first two of these were dead and dormant respectively, and had been grazed to their bases by various ungulates. The occurrence and overlap of these species from interdune to upper plinth defined five zones within which foraging by larks was recorded: 1. SG alone, 2 SG and AG, 3. AG alone, 4. AG and SS, 5. SS alone.

#### METHODS

To define this vegetation gradient quantitatively, a transect from the interdunal flats to the base of the slipface was analyzed at a point considered to be representative. In each of the five zones the numbers and diameters of grass clumps were recorded in 10 quadrats (five for Zone 3) at fixed intervals along a line perpendicular to the transect at the midpoint of the zone. Quadrat size varied with species: SG = 1 m<sup>2</sup>, AG = 25 m<sup>2</sup>, SS = 100 m<sup>2</sup>. In zones with two species, quadrats for the smaller species were nested in one corner of those for the larger. The width of the zone was measured, and the elevational change of the zone from lower to upper edge estimated.

Lark foraging behaviour was observed in these five vegetation zones from 4-10 August 1981. Observations were scheduled to cover the entire diurnal activity cycle. When I first arrived at the study area, I walked up and down the dune slope, crossing all zones, until one or more birds were found. These birds were followed, observed closely with binoculars, and the number of individual foraging minutes in each zone recorded at 5-min intervals. I did not approach foraging birds closer than about 25 m. When I stood quietly, foraging birds sometimes passed within 10 m, but showed no evidence of alarm or avoidance. Between one and five individuals were under simultaneous observation. Observations were continued until a predetermined stopping time, or until the birds disappeared. Air (1,5 m height) and sand surface temperatures were recorded at 15-min intervals. Specific feeding

behaviour and movement patterns were also recorded as far as possible.

The Dune Lark exhibits a specific feeding behaviour adapted to a sandy substrate. In this behaviour, which may be termed bill-cratering, the bill is inserted into the sand surface and the head flipped rapidly from side to side, so that a conical depression about 3-4 cm wide and 2-3 cm deep is made. In the process, sand is scattered as far as 25 cm to either side. This action, noted by Willoughby (1971) and others, was the nearly exclusive foraging pattern used in Zone 1.

To determine the significance of this behaviour in seed location, I took three sets of sand samples in a typical Zone-1 location and designed experiments to test the alternative hypotheses that increased availability of seed due to bill-cratering was the result of (a) a concentrating effect of sand agitation, which accumulated seeds in the crater while displacing sand ("Concentration Hypothesis") to a distance, or (b) the simple uncovering of seed-rich deeper sand by removal of seed-poor surface sand ("Exposure Hypothesis"). Sand was collected in a small (15,5 cc) plastic scoop. Four aggregate samples, each comprising 25 scoops, were taken in each of three ways: (a) of surface sand (0-10 mm depth), (b) of sand from a 0-42 mm depth profile, and (c) of sand forming the walls and bottom of simulated bill craters (about 2 cm deep) formed by manually vibrating a pencil tip back and forth in the sand surface. All samples were taken at points adjacent to dead clump bases of SG where bill cratering was most frequently practised by larks. The aggregate samples were weighed and the contained seeds separated by flotation. After drying, seeds were separated from flotation debris and counted under a dissecting microscope.

To investigate further the effect of the bill-cratering action, a simple lark-bill simulator was constructed and a set of experiments conducted in the laboratory at San Diego State University. The device consisted of a modified 6-10 V electromagnetic doorbell unit with a length of 3,5-mm diameter wire soldered to the striking arm of the doorbell to create an arm 33 cm long. When activated, the tip of this arm vibrated in an arc about 2,5 cm in length. The tip, filed to a point 1 mm wide, represented the lark bill. When inserted into the sand and activated, this element excavated a small crater similar to that produced in the field by the Dune Lark.

Experiments employed 200 seeds of lawn bluegrass *Poa pratensis* (3 300 seeds/g) which were easily distinguished from seeds of native dune plants already present in the sand (taken from the Algodones Dunes, Imperial County, California). In each

TABLE 1

DENSITY AND COVER OF GRASSES ALONG A TRANSECT FROM INTERDUNAL FLAT TO BASE OF SLIPFACE OF A LINEAR DUNE NEAR GOBABEB, SOUTH WEST AFRICA/NAMIBIA, AUGUST 1981.

Zone		1	2	3	4	5
Height above interdune (m)		0	0-1	1-3	3-6	6-20
Zone width (m)		50+	12,6	30	45	270
Density/m <sup>2</sup> ( $\bar{x} \pm SD$ )	SG	20,50 $\pm 3,76$	4,70 $\pm 1,98$			
	AG		0,16 $\pm 0,33$	0,74 $\pm 0,53$	0,05 $\pm 0,26$	
	SS				0,024 $\pm 0,126$	0,017 $\pm 0,145$
Cover (% $\pm SD$ )	SG	1,16 $\pm 0,82$	1,29 $\pm 1,00$			
	AG		0,86 $\pm 0,93$	4,02 $\pm 2,15$	1,20 $\pm 1,44$	
	SS				3,67 $\pm 1,79$	3,02 $\pm 1,67$
Mean clump area	SG (cm <sup>2</sup> )	5,67	27,51			
	AG (cm <sup>2</sup> )		540,25	543,42	2309,42	
	SS (m <sup>2</sup> )				1,542	1,765

\*Dead clump bases

\*\*Dormant clump bases

test, 200 g of sand was placed in a metal container 8,4 cm in diameter. This container had a hole 1,5 cm across in its bottom; the hole was covered by a paper disc before the sand was introduced. After simulated cratering, the sand in the central, cratered part of the container was confined by inserting a plastic cylinder and the paper bottom pierced to permit this sand to drain into a collecting dish. The samples so collected were weighed, and the number of seeds present determined by sorting.

A set of 20 control samples was analyzed; for these the 200 seeds were mixed with 200 g of sand, placed in the metal container, and sampled by inserting the plastic cylinder and removing sand without simulated cratering. A second set of 20 samples, designed to test the Concentration Hypo-

thesis, was prepared in the same way, but subjected to a 1-mm bill-cratering simulation (centre of container). In this simulation, the sample container was raised by hand so that the vibrating "bill" dipped into the sand surface. The container was moved back and forth, perpendicular to the axis of vibration, over a 1-cm distance, and kept in contact with the vibrating tip by gradually raising it as the crater was formed. The duration of this experimental action exceeded that typically spent by birds engaged in bill cratering.

## RESULTS

Along the transect from Zone 1 (edge of interdunal flats) to Zone 5 (upper plinth) the vegetation

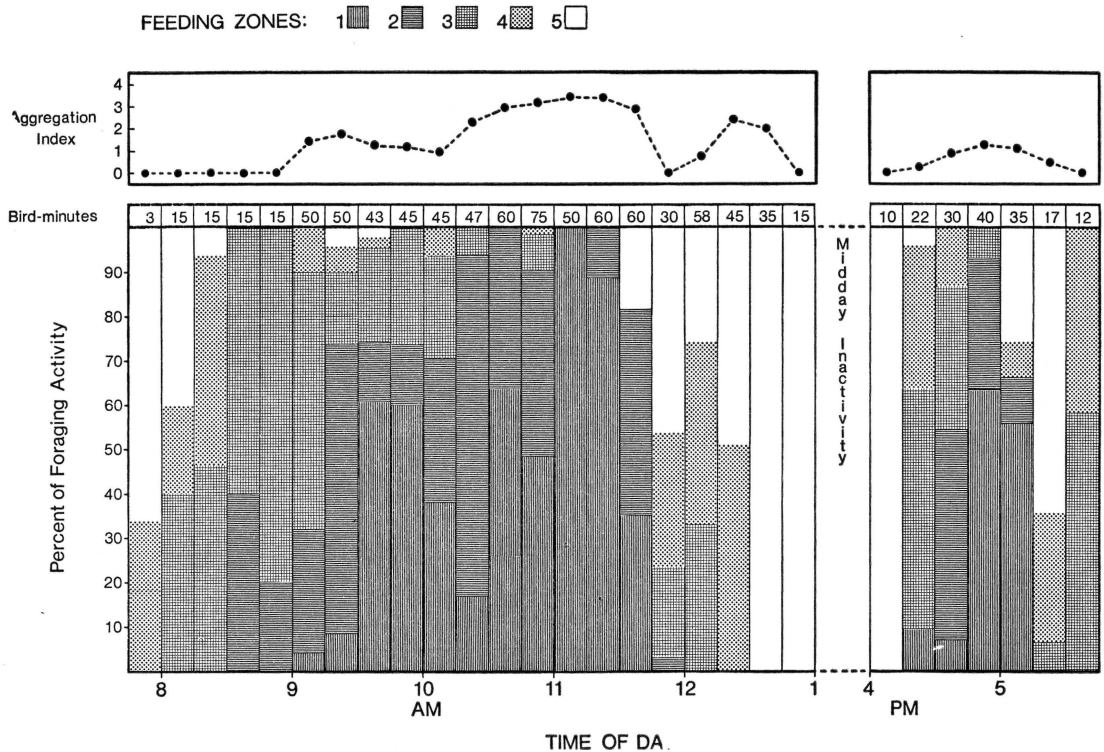


FIGURE 1

Percentage of foraging time by Dune Larks in vegetation zones from the edge of interdunal flats (Zone 1) to the upper dune plinth (Zone 5) at Gobabeb, South West Africa, in early August 1981, in relation to time of day. Also included is the aggregation index (0 = solitary; maximum value = size of group foraging in the same zone at the same time) for foraging birds.

changes from a relatively uniform and continuous cover of small grasses to a patchy cover of large grass clumps separated by wide areas of bare sand. Numerous small clumps of SG, all dead and grazed to pincushion-like basal remnants, were present on the interdunal flat and the thin apron of sand at the dune margin. Larger, but much less numerous, clumps of AG, dormant and browsed to near their base, formed a relatively narrow band along the lowest part of the dune plinth. Clumps of SS, between 1 and 2 m<sup>2</sup> in average area, dominated a belt over 300 m wide from near the dune base to the foot of the slipface. Plant cover increased from just over 1% at the edge of the interdunal flats to just under 5% in Zone 4 (Table 1). This coverage would, of course, be modified considerably after rainy periods when SG and AG become active. At the time of the study, however, the only living foliage was that of SS, and this was confined to Zones 4 and 5.

The larks evidently roosted in large clumps of SS. The observed time of emergence (7 August) was 07h55-08h00, some 20 min after local sunrise. Immediately after emerging, the birds foraged intensively in Zones 4 and 5, and then gradually worked their way downslope (Fig. 1). By 09h30 their foraging was confined largely to Zones 1 and 2. At about 11h40 they began to move back upslope, but continued to forage in the higher zones until, at 13h00, they re-entered clumps of SS for the midday period of inactivity. This period of inactivity lasted until 16h00 when they emerged again and repeated the morning pattern of downslope and upslope movement, but in a quite condensed fashion. Larks disappeared from their foraging areas by sudden flights at 17h35-17h40 (6 August), although sunset on these slopes did not occur until 18h36.

The midday period of inactivity began when the air temperature reached 29.4°C and the sand surface

TABLE 2

FORAGING EFFORT BY DUNE LARKS IN VEGETATION ZONES FROM INTERDUNE MARGIN (ZONE 1) TO UPPER DUNE PLINTH (ZONE 5) NEAR GOBABEB, SOUTH WEST AFRICA/NAMIBIA, AUGUST 1981.

Calculation	Zone*				
	1	2	3	4	5
Bird-minutes: Observed	331	240	168	104	154
Percent	33,2	14,1	16,8	10,4	15,5
Mean of percentage for 15-min summary periods	23,4	18,7	21,2	13,3	23,2
Percentage per 10-m zone width**	4,68	14,84	7,07	2,96	0,86

\*See Table 1 for descriptive information.

\*\*Mean of percentages for 15-min periods divided by width of zone in 10-m units.

temperature was 44,4°C. Emergence in the afternoon occurred when the air temperature was 30,0°C and sand surface temperature had dropped to 40,0°C.

When the birds first emerged from grass clumps in morning or late afternoon, they foraged solitarily. After they began to move downslope they began to give churring calls, and to come together in groups of 2-6 individuals. The recorded data permitted an aggregation index, AI, to be calculated for the foraging birds by the equation:

$$AI = \frac{\Sigma (A - 5) + (B)}{5 (B - 1)}$$

Where:  $A$  = Bird-minutes for a specific zone during a given 5-min observation period  
 $B$  =  $(\Sigma A)/5$

This index reflects the number of birds in a foraging group and their tendency to feed together in the same zone. The index value ranges from 0, for solitary foragers, to maximum values equal to the number of individuals in a group. The observed values of this index (Fig. 1) showed that flocks did not form in the morning until birds had moved to the lower dune slopes, and that they were most strongly developed for birds foraging in Zones 1 and 2. Some degree of aggregation was maintained, however, as the birds worked their way upslope at midday. Aggregations were less strongly developed during the afternoon foraging period.

Larks spent an appreciable fraction of their foraging time in each of the five vegetational zones (Table 2). The percentage of time spent in each zone,

calculated from total bird-minutes of observation, however, is biased toward the zones in which birds foraged in small flocks (Zones 1 and 2 especially), since the existence of such groups permitted more birds to be observed at the same time. Averages of the zonal foraging percentages for 15-min summary periods (Fig. 1) therefore give a better indication of zonal use by the population as a whole (Table 2). Considered in relation to zone width, foraging was most intense in Zones 1-3, in spite of the absence of living plants. In these areas, feeding was probably concentrated almost entirely on seeds. Some 63,3% of total foraging time was spent in these zones.

Zones 4 and 5 were exploited most heavily at the beginning and end of each activity period. The period of most intense exploitation of these zones, however, was between 11h45 and 13h00 just before the midday period of inactivity, when 88,8% of foraging activity was concentrated there. The feeding behaviour employed in these zones indicated that most feeding involved insect foods.

Feeding behaviour differed markedly from zone to zone. In Zones 1 and 2, from 10h25 to 11h45, small groups of larks foraging in very sedentary fashion almost entirely by bill-cratering, concentrating their efforts at the edges of small clumps of SG. Cratering was performed as a series of rapid billing bouts separated by intervals of feeding pecks. Typically, 4-15 billing bouts in quick succession alternated with a series of 3-10 feeding pecks. After several (2-9) such sequences, an individual moved to a new location, leaving a well-formed bill-crater. By slowly working their way along the dune edge, foraging birds daily covered a large fraction of the Zone 1 area adjacent to the dune. At 16h00 on 4 August, for example, 34% of 50 1-m<sup>2</sup> random plots in this zone bore fresh lark tracks, and 26% contained fresh bill craters.

In Zone 3, dominated by AG, birds were less sedentary. They moved actively from clump to clump, but spent much time bill-cratering in and near the dormant clump bases of this grass. Foraging birds visited most clumps of this grass daily. At 15h45 on 4 August, 49 of 50 clumps in an area of Zone 3 had been recently visited.

In Zones 4 and 5, foraging activity centred on the large mounded clumps of SS, and bill-cratering was rarely observed. Larks moved rapidly from clump to clump, usually (46 of 53 cases) by running. As noted by Willoughby (1971), they frequently flew up to pick insects from grass leaves. By 15h30 on 4 August, 45 of 50 clumps of SS in one area of Zone 5 had been visited by larks, as evidenced by the presence of fresh tracks. The rarity of bill-cratering and the use of specific insect-feeding behaviour suggests that the main foods sought in this zone are insects.

Sand samples taken for seed analysis in Zone 1 showed that seed density was lowest in the surface 10 mm, higher by more than seven-fold ( $P < 0,001$ ) in the samples extending to a depth of 42 mm, and highest in the samples taken from the walls of artificial bill craters (Table 3). Although there was

TABLE 3

NUMBER OF SEEDS PER 500 g SAND IN COMPOSITE SAMPLES TAKEN BY THREE PROCEDURES. ALL SAMPLES WERE TAKEN ADJACENT TO DEAD CLUMP BASES OF *Stipagrostis gonatostachys* ON INTERDUNAL FLATS AT THE EDGE OF A DUNE BASE NEAR GOBABEB, SOUTH WEST AFRICA/NAMIBIA, AUGUST, 1981.

Composite sample number	Surface to 10 mm depth	Surface to 42 mm depth	Walls of artificial bill craters to 30 mm depth
1	2,45	38,87	44,48
2	2,54	30,40	48,26
3	1,75	47,72	37,01
4	11,76	19,60	47,08
Mean	4,62 <sup>a</sup>	34,15 <sup>b</sup>	44,21 <sup>b</sup>

<sup>a,b</sup> Samples with same letter not significantly different; samples with different letters significantly different at  $P < 0,0001$ .

no significant difference between seed densities in the 42-mm and bill-crater samples, the higher mean value in the latter raised the question of whether bill-cratering simply acted to remove seed-poor surface sand, or acted additionally, in some way, to concentrate seeds. Results of the laboratory tests with the lark-bill simulator showed that bill-cratering

had no significant concentrating effect. The mean density of seeds per 10 g of sand for control (un-cratered) samples was  $5,40 \pm 1,60$  SE ( $n = 20$ ) and for cratered samples with seeds mixed throughout the 200-g test sample was  $5,12 \pm 1,55$  SE ( $P > 0,05$ ). For test samples structured with 50 g of seedless sand on the surface of 150 g containing the same total number of seeds as the control samples, the mean seed density after cratering was  $7,52 \pm 2,09$  SE, a value significantly greater than that for the control ( $t = 3,60$ ;  $P < 0,01$ ). Bill-cratering thus seems to function simply to remove seed-poor surface sand.

## DISCUSSION

Use of the dune vegetation gradient by Dune Larks involves the exploitation of different basic foods in habitats of markedly different structure and patchiness. Insect foods were sought primarily in Zones 4 and 5, where the vegetation was very patchy ("coarse-grained") and dominated by the hummock-forming grass *S. sabulicola*. Seeds were sought principally in Zones 1 and 2, which had a more homogeneous ("fine-grained") vegetation. Foraging for insects in Zones 4 and 5 was also carried out largely by solitary birds that moved rapidly from clump to clump. Seed foraging, by contrast, was conducted in a more sedentary fashion by birds in small but distinct groups.

These results suggest that insect foraging strategy is defined by optimal foraging considerations. MacArthur & Pianka (1966) argued that when food resources are strongly patchy, the influence of competition should be to restrict the use of patch types by animals to those types in which hunting time is minimal. In such situations, competing animals should be restricted to different patches or patch types. Dune Larks, for which competition is intraspecific, accomplished this by solitary foraging in non-overlapping sets of grass clumps. In addition, the short foraging time in each clump suggests that the insects exploited are conspicuous, but limited in quantity, so that those available in a given clump can be depleted quickly (by an individual, or its competitor). Pyke *et al.* (1977) note that in such a resource situation, optimal foraging theory predicts a short "giving-up" time and frequent movement to new patches.

In the more open, homogeneous environment of Zones 1 and 2, seed-foraging activities evidently do not lead to detrimental competitive depletion of food resources. The rate of depletion of seed supply in the sand is slow, and it is therefore profitable to forage longer in a given area. In this habitat, therefore, beneficial aspects of aggregation, such as more efficient predator-detection, favour group foraging.

TABLE 4

HYPOTHETICAL ENERGY AND WATER BUDGET FOR THE DUNE LARK IN THE DUNE ENVIRONMENT NEAR GOBABEB, SOUTH WEST AFRICA/NAMIBIA DURING AUGUST.

Measurement	Male	Female
Body Mass (g)	29	27
Calculated Metabolic Rate (kJ/day)	81,035	78,006
Calculated Evaporation Loss (g/day)	3,663	3,421
Seed Food Contribution		
Net Assimilated Energy (kJ/g ingested)	14,334	
Net Water Obtained (g/g ingested)	0,465	
Insect Food Contribution		
Net Assimilated Energy (kJ/g ingested)	7,298	
Net Water Obtained (g/g ingested)	0,782	
Required Diet		
Seeds (g/day)	4,688 (71,2%)	4,610 (73,8%)
Insects (g/day)	1,897 (28,8%)	1,633 (26,2%)

The daily pattern of movement by foraging birds among the different vegetation zones may be the critical factor in the maintenance of balanced energy and water budgets of the Dune Lark. Foraging for insects, which are high in free water content, occurs at the beginning and end of each major activity period. The most intensive period of insect-feeding, however, precedes the midday inactivity period, which is probably the period of greatest desiccation stress because of high temperature. In general, insect-feeding at the start and end of periods of activity may provide a mechanism of "fine-tuning" the water budget.

Although laboratory data on the water budget of the Dune Lark are not available, calculations based on allometric relationships involving metabolism and evaporative water loss suggest that the Dune Lark is unable, under the August conditions observed, to maintain an adequate water intake on a diet exclusively of seeds. The metabolism of male and female larks was estimated from allometric equations and other values for standard metabolism (Aschoff & Pohl 1970), heat-transfer coefficient and body and lower critical temperature (Calder & King 1974), upper critical temperature (Kendeigh & Blem 1974), and ratios of metabolism under free activity to standard metabolism (Walsberg 1980). Evaporative water loss was estimated from allometric relationships given by Crawford & Lasiewski (1968) and Dawson (1982). Calculations were for hourly

periods with temperatures corresponding to those measured in the field and ranging between 8,6 and 30,0°C. The estimated daily metabolism of these birds (free of extra metabolic demands of reproduction at this season) is 78-81 kJ/day and their daily evaporative water loss 3,4 to 3,7 g (Table 4). The estimate of daily metabolism of these larks is close to the values of 77-80 kJ/day predicted by the allometric equation of Walsberg (1980) for birds which do not forage in flight.

Energy and water budgets were balanced by feeding on both seeds and insects. Seed foods were estimated to contain 80% carbohydrate, 10% protein, 9% free water, and 1% ash. Insect food composition was estimated to be 61,6% free water, 19,4% protein, 12,4% fat, 5,6% carbohydrate and 1% ash, based on an average of values for various insects of the type taken by larks (Taylor 1975). Food energy and water content were based on values given by Bartholomew (1977) and faecal/urinary losses were based on estimates for desert larks by Willoughby (1968). To balance both energy and water budgets, Dune Larks were predicted to need a diet with 26,2 to 28,8% insects. This approximate intake appears reasonable in view of the fact that about 36,7% of foraging time was spent in Zones 4 and 5 where insects were the principal food sought. It also agrees generally with Willoughby's (1971) observation that in June, earlier in the winter, insects made up the lesser percent (13%) of stomach

contents. The energy gain per unit foraging time thus appears greatest for seed foraging. Insect and seed foraging efforts thus appear to be divided so as to balance both budgets in the most efficient manner.

During August, mean maximum temperatures average 27,4°C at Gobabeb, and rise above 35°C only on 1-2 days (Seely & Stuart 1976). Thus, at this season larks probably encounter temperatures above their upper critical limit only for short periods and infrequently. From November to April, however, mean maximum temperatures exceed 30°C, peaking at 33,3°C in March, when temperatures over 35°C occur nearly 10 days/month (Seely & Stuart 1976). At these times larks must experience severe desiccation stress. It appears likely that this stress must be countered by a major shift in foraging pattern, and by increased representation of insect food in the diet.

If it is true that foraging efforts in Zones 4 and 5 are directed toward obtaining insect food, and that this component of the diet is essential to balancing the body water budget, several predictions can be made. First, within a season, shifts of foraging intensity in various zones should occur, reflecting the changing water intake needs of cool and warm periods of a few days duration. Secondly, major shifts in foraging pattern and use of the various zones should occur between winter and summer, as suggested also by the stomach-analysis data of Willoughby (1971) indicating that in February and April as much as 80% of the diet may consist of insects. Thirdly, at different distances from the coast, foraging patterns at the same season should show differences related to the major trend of increase in mean temperature inland (Seely 1978). This may in fact set a limit to the inland edge of the range of the Dune Lark.

Thus, it is hypothesized that the foraging strategy of the Dune Lark is to maximize the rate of caloric intake within the constraint of maintenance of a balanced body water budget, and it is this constraint which determines the relative need for seed and insect foods, and the relative effort expended in the foraging microhabitats that supply these respective foods.

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