Winter foraging behaviour of the Dune Lark in the Namib Desert, and the effect of prolonged drought on behaviour and population size

Uriel N. Safriel, Mitrani Centre for Desert Ecology, Jacob Blaustein Institute for Desert Research, Ben-Gurion University, Sede Boqer Campus, Israel.

Mean annual rainfall at Gobabeb, Namibia is 27,2 mm (Lancaster *et al.* 1984, *Madoqua* 14: 5–61), but the variation around this mean is very high. In 1976 and again in 1978 annual rainfall amounted to > 100 mm, but in all following years and at least until Janury 1989 annual rainfall was < 20 mm. In August 1981 three years after the last good rainy year, Cox (1983, *Ostrich* 54: 113–120) studied the foraging behaviour of Dune Larks *Mirafra erythrochlamys* inhabiting a longitudinal dune ("Mole End") 8–9 km SSE of Gobabeb. Four years later, from April 1985 to December 1986, Boyer (1988, *Ostrich* 59: 30–37) studied the breeding biology of Dune Larks at !Khomabes, a small island of hummocky dunes lying across an interdune valley between two longitudinal dunes, 5–6 km northwest of Gobabeb. Between 7 and 12 January 1989 I made some observations on Dune Larks at both these sites.

Cox (1983) found that the larks roost in clumps of *Stipagrostis sabulicola* on the upper dune slope and, after emerging, work their way downward in the morning feeding mainly on arthropods. When they reach the dune base and the interdune valley, dominated by *S. gonatostachys*, they feed nearly solely on seeds. They later move upslope, feeding again mainly on insects, and roost in *S. sabulicola* during the hot hours of midday. In the afternoon this pattern is repeated. Cox (1983) suggested that insectivory is required for balancing the birds' water budget, and that the timing of switches between periods of granivory and insectivory, and the lengths of these periods, are determined by ambient temperatures and by the birds' water requirements. Cox (1983) predicted that shifts in foraging pattern and in use of the various dune-vegetation zones, hence in the granivory : insectivory ratio, should occur between winter and summer. These shifts should be related to differences in water requirements between the two seasons, depending on ambient tempertures. It can be expected that, after seven years of prolonged drought following Cox's observations, seeds would be relatively scarce, and that the birds would take a much higher proportion of insects than observed by Cox in winter, and even higher than predicted by him for summer.

I sampled the vegetation (*S. sabulicola* was flowering, *Centropodium glaucum* was either dead or just dormant clump bases, and *S. gonatostachys* was all dead and looked as if severely clipped) in the site studied by Cox (1983) using his methods. Where granivory mostly took place, *S. gonatostachys* and *C. glaucum* clumps were 6,6 and 6,2 times fewer respectively in summer 1989 than in winter 1981, but there was no significant difference in the number of *S. sabulicola* clumps, where most insectivory occurred (Table 1). The percentage cover of clumps in the granivory zones was lower in 1989 than in 1981, though not significantly so. There was also an increase in mean clump area of all three plant species (Table 1), probably indicating that during this dry period smaller dead clumps were torn away, and smaller live plants might have died. I sampled seeds using Cox's methods (Cox 1983), and found (Table 2) that the density of seeds in the *S. gonatostachys* zone was reduced between 1981 and 1989, markedly and significantly so under the surface, at a depth reached by "cratering", a method used by larks (Willoughby 1971, *Zool. afr.* 6: 133–176) in this zone (Cox 1983; pers. obs.). The seeds sampled by Cox in 1981 had probably been produced three years earlier, and between 1981 and my sampling only a few *S. gonatostachys* produced seeds, in June 1987 (M. Seely, pers. comm.).

My 1989 summer observations on the dune ridge studied by Cox revealed a foraging pattern similar to that found in winter 1981. The birds moved downslope and upslope twice a day foraging mainly on insects, and spent time at the dune base twice a day, foraging solely on seeds and using the "cratering" technique (Willoughby 1971;

TABLE 1

DENSITY AND COVER OF GRASSES AT THREE POINTS ALONG A TRANSECT FROM INTERDUNE FLAT TO BASE OF SLIPFACE OF A LINEAR DUNE NEAR GOBABEB, NAMIBIA, IN AUGUST 1981 (COX 1983) AND IN JANUARY 1989

	Density/m² (x ± SD)			Cover (% ± SD)			Mean clump area	
Grass Species	Aug 1981	Jan 1989	P	Aug 1981	Jan 1989	P	Aug 1981	Jan 1989
Centropodium glaucum	20,50 ±3,76	3,10 ±3,57	***	1,16 ±0,62	0,82 ±0,91	ns	5,67 (cm²)	20,31 (cm²)
Stipagrostis gonatostachys	0,74 ±0,53	0,12 ±0,07	*	4,02 ±2,15	2,28 ±2,15	ns	543,42 (cm²)	2 135,95 (cm²)
Stipagrostis sabulicola	0,017 ±0,145	0,010 ±0,008	ns	3,02 ±1,67	4,70 ±7,16	ns	1,524 (m²)	4,705 (m²)

t-tests for differences between years — *P<0,05; ***P<0,001; ns — not significant.

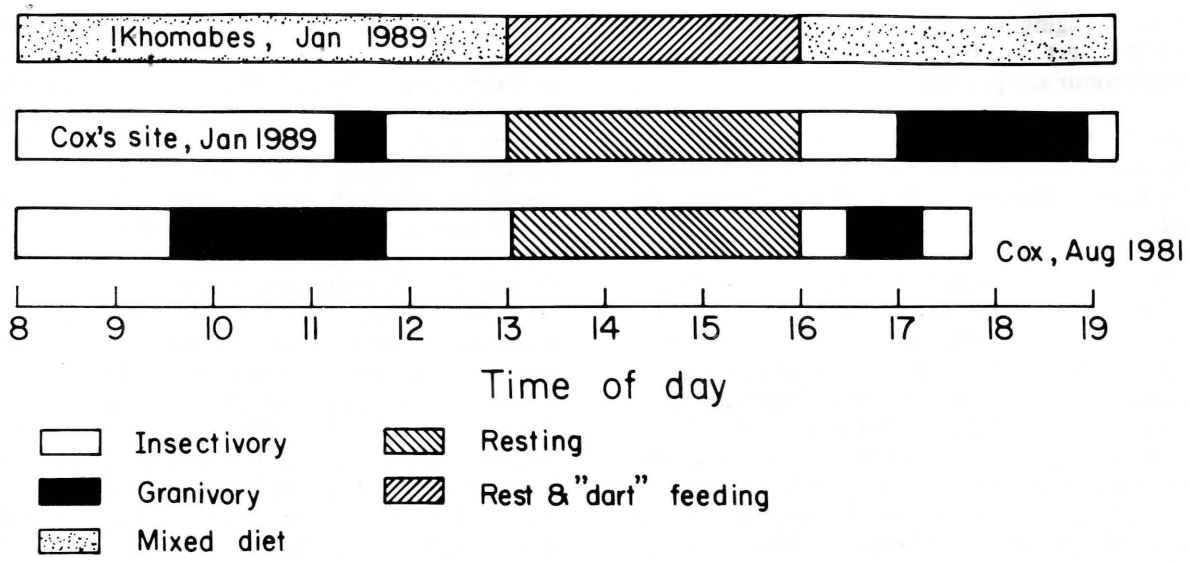

FIGURE 1

Approximate periods spent by Dune Larks on various activities near Gobabeb, Namibia ("Cox, Aug 1981" is in winter, at Cox's study site on a longitudinal dune, based on Cox (1983), Fig. 1; "Cox's site, Jan 1989" is based on my observations at Cox's site in summer).

Cox 1983). However, the major periods of granivory started later in the day in summer 1989 than in winter 1981, both before and after the midday rest (Fig. 1). Also, whereas the afternoon period of granivory was shorter than the morning one in winter 1981, it was the opposite in summer 1989. The 1989 morning period of granivory was about quarter the length of that in 1981, but this period was terminated at the same time, when the birds started their upslope movement. The 1989 afternoon period of granivory was longer than the 1981 one, probably in conformity with the late summer sunset (Fig. 1). The timing of entering and quitting the midday rest period in the upper slope's *S. sabulicola* clumps was nearly identical for both studies (Fig. 1), and seems to have no relation to absolute temperatures (Table 3). Altogether, the ratios of granivory : insectivory periods were 0,8 and 0,375 for winter 1981 and summer 1989 respectively.

Another remarkable difference between Cox's observations and mine is in the number of birds. Cox (1983) mentioned foraging groups of 2–6 birds. I saw only two individuals, nearly always close to each other, in spite of meticulous searches over the whole dune slope and base along 1 km of dune length comprising Cox's study site. It thus seems that the population has declined to at least a third of its size in winter 1981. The remaining birds maintained the pattern of regular alternation between insectivory and granivory, but with a higher proportion of insectivory relative to winter 1981.

At !Khomabes the transverse dune seems to retain more water than a longitudinal dune (Boyer 1988). *S. sabulicola* is commoner than on the longitudinal dune, and *Trianthema hereroensis* (Aizoaceae) abounds. This succulent plant has tiny juicy leaves which taste agreeable to humans. It was flowering and producing seeds at the time of my observations, and its foliage attracted a lot of insects. Here the larks did not show a pattern of regular alternation between granivory and insectivory. Rather they fed mostly around and within clumps of *T. hereroensis* on seeds and insects. They were also observed picking at leaves or

TABLE 2
MEAN NUMBER OF SEEDS (± SD) PER 500 G SAND IN FOUR COMPOSITE SAMPLES TAKEN BY TWO PROCEDURES ADJACENT TO DEAD CLUMP BASES OF *Stipagrostis gonatostachys* ON INTERDUNE FLATS AT THE EDGE OF A DUNE BASE NEAR GOBABEB, NAMIBIA

Month	Surface to 10 mm depth	Surface to 42 mm depth
August 1981	4,62 ± 4,77	34,15 ± 12,00*
January 1989	0,38 ± 0,75	1,50 ± 1,00

* The only significantly different mean, at $P < 0,05$ (*t*-test for small samples with unequal variances).

TABLE 3
TEMPERATURES (°C) ON ENTERING MIDDAY INACTIVITY PERIOD, AND ON EMERGING FOR RENEWED FORAGING (AIR TEMPERATURES TAKEN AT 1,5 M HEIGHT FROM GROUND, SAND TEMPERATURES TAKEN IN WINTER 1981 ABOUT 5 MM BELOW SAND SURFACE WITH A GLASS-BULB THERMOMETER, AND IN SUMMER 1989 AT THE UPPER 1 MM OF SAND SURFACE, WITH A THERMOCOUPLE)

Phase of inactivity	Winter 1981		Summer 1989	
	Air	Sand	Air	Sand
Entering	29,4	44,4	28,6	54,7
Emerging	30,0	40,0	27,5	54,9

buds, and possibly eating them. Thus, of 105 *T. hereroensis* that I inspected just when the activity of the larks ceased before sunset, only four did not have larks' footprints around them. Even clumps as small as 10 cm in diameter were intensively searched, as evidenced by footprints.

The larks foraged also on the sand between plants, apparently feeding mostly on insects, and "cratering" was hardly observed. Feeding on the open sand between vegetation clumps was here much commoner than in Cox's site. There the larks mostly pecked around clumps of *S. sabulicola* and *C. glaucum*, while working their way up and downslope, whereas at !Khomabes they pecked a lot in the open. Also at Cox's site I saw larks fly only once, whereas at !Khomabes covering distance by low flight rather than by running was much commoner. Even during the midday break, the birds of !Khomabes ventured at times from their *S. sabulicola* roosting sites to the nearby sand patch or adjacent *T. hereroensis* clump, feeding rapidly before retreating to the *S. sabulicola* shelter.

Boyer (1988) observed at least six pairs in this area in 1985–86, and also noted breeding in January. During my visit there was no evidence of breeding activity, and there were no more than six birds altogether. Thus, this population, though larger than the one at Cox's site, was probably reduced by about half between 1986 and 1989. I observed two of the birds ringed by Boyer at !Khomabes; thus at least some of the birds remained in their breeding areas and were at least two years old.

It is remarkable that the midday break pattern persists in both summer and winter. I measured ambient temperatures of 20,8–34,8 °C at 8 cm above surface during the midday break, and sand surface temperatures in the shade of *S. sabulicola* ranged 30,6–42,3 °C. At the same time the exposed sand between *S. sabulicola* hummocks was 52–62 °C. Thus, the sand in *S. sabulicola* shade was 15,1–21 °C cooler than exposed sand when the birds roosted there. While roosting they frequently changed position within the clump, and also perched on dead twigs, where the air was slightly cooler than the shaded sand. Apparently, these roosts provide shelter from intense radiation and from contact with very hot sand (Willoughby 1971), and possibly function also as lookout points, a safety measure against avian predators.

At !Khomabes the birds continued foraging also during their midday break. They spotted a prey item either on the open sand or in an adjacent *T. hereroensis* clump, moved their head as if inspecting the sky for predators, then darted forward, picked up the prey, and escaped fast to the *S. sabulicola* retreat. They usually did not stay at one spot in the hummock for more than 10 min, and darted for prey once every 4 min on the average. By the end of the midday break trails of the larks leading off as far as 5 m away and back to *S. sabulicola* hummocks were very conspicuous on the sand. Each had a tiny depression resulting from a peck, at the turning point. The temperature of the sand on which they ran was then up to 62 °C. At both Cox's site and !Khomabes the larks communicated vocally and preened while in the midday shelter, whereas during other times they were hardly seen preening.

While foraging and walking over the sand at !Khomabes or running upslope or downslope on the longitudinal dune, the birds ran fast with head extended forward. I obtained the lengths of paces by measuring distances between successive footprints. Mean pace lengths in a trail (about 15 paces in each of seven different trails) ranged from 9,1–18,0 cm. The longest paces in trails were 14, 18 and 19 cm, when sand temperatures were 38 °C, 47 °C and 55 °C respectively. While foraging, birds usually ran in a straight line. A running bird often stopped and seemed to inspect the ground or also the sky briefly. After a few seconds it either resumed running, maintaining its course, or darted and pecked the surface, always at right angles to its course. Following a peck it resumed runnng almost immediately, nearly invariably in a new course. When the wind was not blowing hard, complete foraging courses, including pace lengths, halts, pecks and course diversions could be reconstructed by observing the tracks on the sand. For example, I followed six foraging trails that included 1 463 paces, and found that on the average birds stopped and/or pecked every 9–15 running paces.

The birds behaved fearlessly with respect to man, but from their head movements it seemed that they inspected the sky frequently. Indeed, in spite of their colour, they were quite conspicuous while running on the dune. On the other hand, when "cratering" in the dune base and being then more stationary than when feeding on insects, they were more cryptic. The contrast between their dark upperparts and the paler lower parts matched the contrast between the sand and the shining pebbles and yellowish-bright dead stems of *S. gonatostachys* clumps.

Whereas Cox observed relatively large foraging groups, at neither site did I see more than two birds foraging together. When feeding at Cox's site in the dune base, the two birds were never more than 1 m apart, and often as close to each other as 10 cm. I noticed aggression only once, when the two birds were very close indeed.

I rarely saw exactly what food items the birds were taking, but with a use of a ×20 telescope I detected that seeds of *T. hereroensis* were taken from the flowers. Also the birds often perched on tops of *T. hereroensis*, causing the ripe seeds to be ejected and fall to the ground. The birds then dropped to the sand surface, and extracted the seeds, often making brief "cratering" movements. I saw a bird eating a *Camponotus detritus* ant only twice, in the afternoon (16h15 and 17h25), whereas in two cases during the morning (10h20 and 11h40) foraging birds passed very close to these conspicuous ants, but ignored them. In one case an ant seemed to cling to a foraging bird, which made a lot of running manoeuvres, rubbing its flanks against the sand.

To conclude, the structure of the plant community at the Dune Lark's habitat determines its

foraging pattern, which varies according to variation in plant composition. Differences in ambient temperatures between summer and winter modify foraging patterns and probably also the resulting diet composition. It is predicted that in habitat patches where plants remain rich, like !Khomabes, foraging patterns may remain similar the year round. By 1989 a prolonged drought seems to have caused a density-dependent population reduction, through a gradual decline in seed and insect availability. Examination of stomach contents are now necessary for verifying Cox's and my foraging observations.

I wish to thank the Department of Agriculture and Nature Conservation of the Administration of South West Africa/Namibia for permission to work in the Namib–Naukluft Park and for use of the facilities of the Namib Research Institute, and to Dr M. K. Seely for providing me with all required facilities of the Desert Ecology Research Unit at Gobabeb, for showing me Cox's research site, and for providing useful information. G. W. Cox and G. L. Maclean provided useful comments. Special thanks are due to the Sydney Press Foundation for supporting this research. This is publication no. 94 of the Mitrani Centre for Desert Ecology.