Journal of Arid Environments (1980) **3**, 309–317

Colouration and diurnal activity patterns in some Namib Desert Zophosini (Coleoptera: Tenebrionidae)

R. A. Wharton*

Accepted 6 May 1980

Six diurnal zophosine Tenebrionidae are geographically sympatric on the gravel plains of the Namib Desert near Gobabeb, SWA/Namibia. Behavioural data suggest that most species are segregated both spatially and temporally. Paler species are generally more exposed during warmer seasons or times of the day. All species appear to control body temperatures during foraging periods by occasionally seeking shelter in vegetation. The importance of pale colouration in camouflage is also discussed.

Introduction

The Namib Desert of South West Africa/Namibia contains a large and varied fauna of diurnal tenebrionid species. Early studies (Gebien, 1939; Koch, 1961, 1962) focused on morphological adaptations of this group, while subsequent workers (Edney, 1971*a*, *b*; Hamilton, 1971, 1973, 1975; Hamilton *et al.*, 1976; Hamilton & Penrith, 1977; Hamilton & Seely, 1976; Henwood, 1975*a*, *b*; Holm & Edney, 1973; Louw & Hamilton, 1972; Roer, 1975, 1977; Seely & Hamilton, 1976) examined physiological and behavioural characteristics. Based partially on such studies, several authors (Hamilton, 1971, 1973; Henwood, 1975*b*; Penrith, 1977) have concluded that partitioning of microhabitats is an important characteristic of Namib Desert Tenebrionidae. Spatial and temporal separations are further examined here in a study of colouration and diurnal behaviour as evolutionary strategies in six closely-related tenebrionid species in a region of sympatry.

Materials and methods

Eighty-two species of the tentyriine tribe Zophosini are known from South West Africas Namibia (Penrith, 1977). About a dozen of these have been recorded from the gravel plain/habitat in the vicinity of Gobabeb (23° 34′ S, 15° 03′ E) (Penrith, 1977). Between November 1978 and July 1979, the following species were found in sufficient numbers to permit detailed observations: *Calosis amabilis* Deyrolle, *Occidentophosis cerea* Penrith, *Zophosis devexa* Péringuey, *Z. dorsata* Péringuey, *Z. mniszechi* Deyrolle, and *Z. moralesi* (Koch). All are small, oval, convex beetles. Body length varies from 4 to 18 mm, but most individuals used in this study were 8 ± 2 mm long. They are readily separated both from each other and from related species in this area by colour patterns and sculptural characteristics (Penrith, 1977). Voucher specimens have been deposited in the Transvaal Museum, South Africa, and the Namib Desert Research Station reference collection, Gobabeb.

The Namib Desert in the vicinity of Gobabeb can be roughly divided into three major

---

* Desert Ecological Research Unit, P.O. Box 953, Walvis Bay 9190, South West Africa/Namibia.
Present address: Department of Entomology, Texas A & M University, College Station, Texas 77843, U.S.A.

0140–1963/80/040309 + 09 $02.00/0

biotopes: sand dunes, gravel plains, and the seasonally dry Kuiseb River bed (Sandelowsky, 1977, Map 1). Much of the previous work on the Namib Desert Tenebrionidae has involved species from the dune and river habitats. For this study, species from the gravel plains were chosen for comparison. Major study sites were at Gobabeb, Mirabib (23° 28′ S, 15° 17′ E), and Hope Mine (23° 34′ S, 15° 15′ E) (Seely, 1978, Map 2). This region consists primarily of granite rubble and quartz-gravel plains with numerous dry, sandy washes and occasional inselbergs. Besler (1972) gives a more detailed geomorphological picture; and Robinson (1978) lists major vegetational components.

The vegetation of the gravel plains forms a mosaic pattern, and the amount of cover is strongly correlated with the patchy and sporadic rainfall (Seely, 1978). In general, however, there is a gradual increase from a few scattered shrubs along the coast to a moderately heavy and continuous cover of grasses and forbs 20 km E of the Mirabib site (Willoughby, 1971, fig. 2; Schulze & Schulze, 1976, plate 2).

Behavioural observations were made at all three sites throughout the study period. Reactions to excessive heat were recorded on several days when ground surface temperatures reached or exceeded 60 °C at the First Order Weather Station, Gobabeb. Response to moisture was recorded at Gobabeb during precipitating fogs, both on 4 May and the morning of 12 July when ground surface temperatures did not rise above 23 °C.

Field censuses, similar to those employed by Hamilton (1971) and Henwood (1975*b*) to determine numbers of beetles active above the surface, were conducted between April and June. Each census consisted of a 20–25 minute walk per hour along a predetermined route.

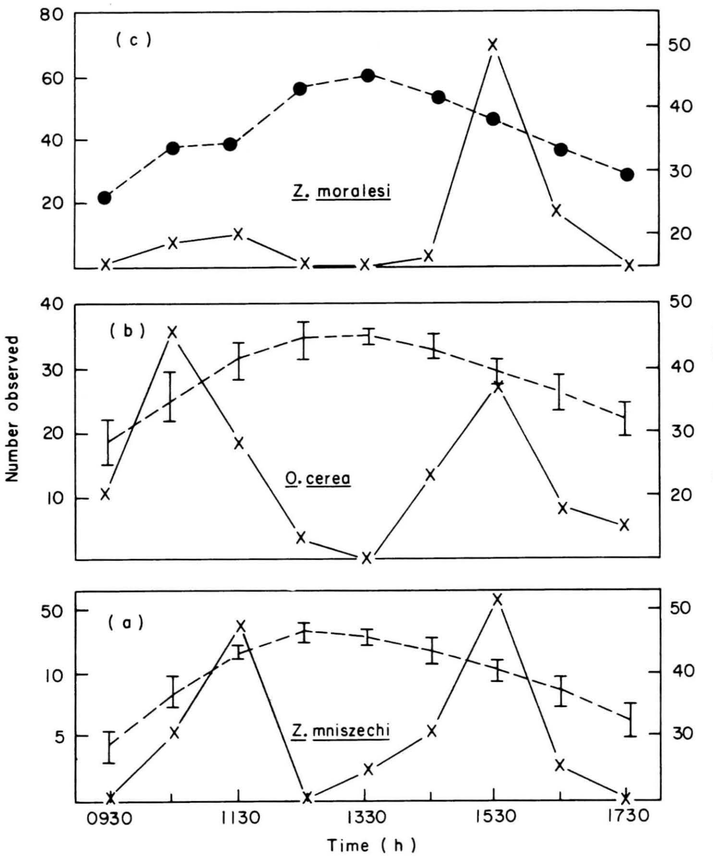

Figure 1. Activity patterns of *Zophosis mniszechi*, *Occidentophosis cerea* and *Zophosis moralesi* on warm days (temperatures indicated by dashed lines). In graphs representing more than one day, number observed is the sum from all days. (a) 2 days; (b) 3 days; (c) 1 day.

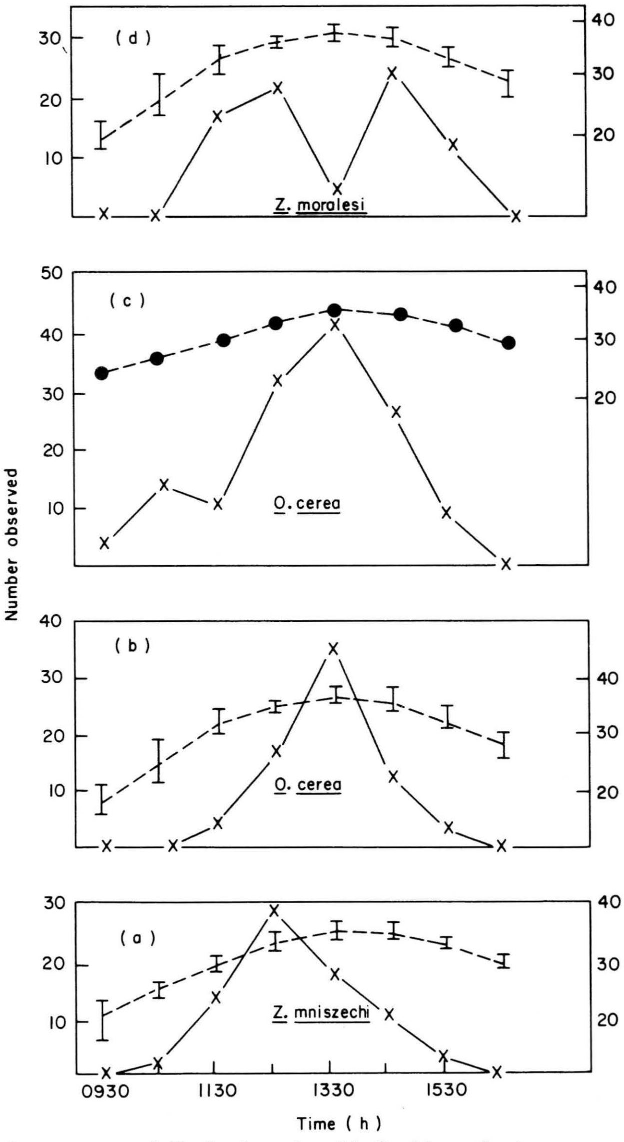

Figure 2. Activity patterns of *Zophosis mniszechi*, *Occidentophosis cerea* and *Zophosis moralesi* on cooler days (temperatures indicated by dashed lines). Two graphs given for *O. cerea* to illustrate variation. In graphs representing more than one day, 'Number observed' is the sum from all days. (a) 2 days; (b) 3 days; (c) 1 day; (d) 3 days.

All beetles within a 2 m radius of the observer were included. Censuses commenced with the beginning of above-ground activity, and terminated after nearly all beetle activity had ceased. All Zophosini not readily identifiable during a census were captured for subsequent determination. Temperatures of the ground surface–air interface were recorded before and after each walk with a YSI rapid-response telethermometer, model 44TD, using fine thermistor probes (Hamilton, 1971). Finer probes were used to measure body temperatures of *Calosis* (Hamilton, 1975); and to record temperatures of the ground surface–air interface during the same experiment. Census data were plotted as time-activity graphs (Figs 1 and 2). Where temperature regimes and activity patterns from several censuses were identical, results were included in a single graph.

Jackal (*Canis mesomelas*) and bustard (*Neotis ludwigii*) droppings were examined when encountered in the field, and the presence of various tenebrionid species was recorded. Gut contents of the following lizard species were also analyzed (sample sizes in parentheses): *Mabuya occidentalis* (20), *Mabuya variegata* (21) and *Meroles suborbitalis* (9).

Results

Major distribution patterns approximated those given by Penrith (1977). The Hope Mine region (600 m elevation) was a critical area, and the only study site where all six species were sympatric (Table 1). During this study period, it formed the approximate eastern boundary for *C. amabilis*, the western boundary for *Z. mniszechi*, and the northern boundary for *Z. moralesi*.

All six species fed in the field on arthropod or vertebrate remains, and a variety of seeds and plant debris. The results of gut analyses for *Z. mniszechi* and *O. cerea* are shown in Table 2. Similarity in foraging patterns is reflected in the similarity of the diet of these two species. The large percentage of anthers is due to the large number of grasses coming into production after moderately heavy rains one month before the sampling date. Insect parts in both species consisted primarily of *Hodotermes mossambicus*.

Zophosis devexa was often observed in the open or at the base of vegetation. However, foraging actually occurred primarily inside grass clumps and detritus pads. This microhabitat was exploited only occasionally by *Z. moralesi*, and very little or not at all by the other four species. *Zophosis moralesi* foraged mainly in sparsely vegetated areas, even during peak activity periods. *Calosis amabilis* foraged in non-vegetated portions of the gravel plains, usually several meters from the nearest plant. Because of the general increase in cover from the coast inland, the eastern distribution of *C. amabilis* may be limited as much by cover as by any other factor. *Zophosis dorsata* was also found most commonly in open, non-vegetated areas, but with fewer than 50 observations, it is not possible to confirm that this is the preferred habitat. Both *Z. mniszechi* and *O. cerea* preferred more heavily vegetated areas—particularly small washes. They were only rarely observed in completely non-vegetated areas (9·8 per cent of observations during censuses for *O. cerea*). *O. cerea* was also frequently encountered foraging in the vicinity of ant dumps.

Table 1. *Distribution, foraging patterns, and dorsal colouration of six zophosine Tenebrionidae from the Namib Desert*

	Calosis amabilis	*Occidentophosis cerea*	*Zophosis devexa*	*Zophosis dorsata*	*Zophosis mniszechi*	*Zophosis moralesi*
Distribution						
Mirabib		+ + +	+ + +	+	+ + +	
Hope Mine	+	+ + +	+ + +	+	+ + +	+
Gobabeb Plains	+ + +	+ + +	+ + +	+		+ +
Gobabeb Dunes						+ + +
Foraging						
In open, away from vegetation	+ + +	+	+	+ +	+	+ + +
In open, near vegetation		+ + +	+ +	+	+ + +	+
In grass clumps and detritus pads			+ + +			+
Colouration						
Naked, black			+			+
Naked, mottled	+					
White waxy layer		+				
White pulverulent layer				+		
Pink pulverulent layer					+	

Table 2. *Gut contents of* Occidentophosis cerea *and* Zophosis mniszechi *(n = 30) (Collected July 1979)*

Food item	*O. cerea*	*Z. mniszechi*
	(Percent of sample containing food item)	
Insect parts	73	87
Anthers	77	83
Fecal pellets in crop	17	0

There was extensive activity on all soil types; and differences in substrate preferences could not be discerned, with the possible exception of *O. cerea*. While *O. cerea* was found in equal numbers with *Z. mniszechi* and *Z. devexa* in sand and gravel soils, it was also found in large numbers around small quartz and granite koppies. *Occidentophosis cerea* is thus probably slightly more lithophilic than the other species. Since burrowing behaviour was not investigated, a more adequate analysis of substrate preferences is not possible.

Due to insufficient numbers of *C. amabilis* and *Z. dorsata* during censuses, and the difficulty of accurately censusing *Z. devexa* foraging in vegetation, these three species were omitted from time-activity graphs (Figs 1 and 2). Activity periods for all species were generally correlated with ground surface temperatures and less so with dorsal colour patterns. As Table 3 shows, however, all species were active over a wide range of temperatures.

Zophosis devexa and *Z. moralesi* are black, without a pale waxy or pulverulent layer dorsally. While *Z. devexa* spends much of its time in the shade of grass clumps or detritus pads, *Z. moralesi* is more exposed, and exhibits a bimodal pattern, even on relatively cool days (Figs 1 and 2). Holm & Edney (1973) noted that activity of dune-dwelling populations is concentrated in the afternoon. For gravel plains populations, this appears to be true only for very hot days (Fig. 1). *Zophosis mniszechi* is partially covered by a pink, pulverulent layer dorsally. *Occidentophosis cerea* has a similar pattern, but it is formed by a waxy secretion, giving the beetle a pale blue to whitish appearance. Both species exhibit bimodal activity patterns on hot days and unimodal patterns on cool days (Figs 1 and 2). Major activity peaks for these two species occurred at surface temperatures between 33 and 43 °C—somewhat similar to results obtained for *Z. moralesi* (Figs 1 and 2). Variation in activity patterns is illustrated for *O. cerea* in Fig. 2. *Zophosis dorsata* is completely covered by a white pulverulent layer dorsally. This species was active at mid-day in non-vegetated areas when ground surface temperatures reached or exceeded 50 °C during the summer, but was also found on several days in June and July when temperatures did not rise above 40 °C. The elytral surface of *C. amabilis* is partially depigmented—producing a variable white, brown and red pattern (Penrith, 1977). Observations in January suggest that this species is normally active at mid-day, and at ground surface temperatures between 45 and 50 °C. During the late fall and early winter, this species is also active at mid-day, but in lower numbers (as indicated

Table 3. *Ground surface temperatures (°C) during which Zophosini were active*

Species	Range	mean ± s.d.	Number of individuals	Number of censuses present*
Zophosis dorsata	33·5–50·0	41·9 ± 4·1	18	6
Calosis amabilis	33·5–50·5	38·5 ± 3·6	35	8
Occidentophosis cerea	24·0–50·0	36·6 ± 5·0	391	11
Zophosis mniszechi	26·0–50·0	36·3 ± 5·0	118	5
Zophosis moralesi	26·0–42·5	36·0 ± 2·9	217	6
Zophosis devexa	23·5–47·5	34·5 ± 4·0	182	9

* Usually nine hourly walks per census.

by census data for fall months, Table 3). Colour patterns of the six zophosines are summarized in Table 1.

The different seasonal temperature regimes to which *C. amabilis* and *Z. dorsata* are subjected at mid-day imply considerable acclimation ability in these species. Acclimation capabilities in the other four Zophosini are less obvious because they more readily thermoregulate behaviourly, either by seeking the shade of vegetation, or by altering activity patterns from unimodal on cooler days to bimodal on warmer days.

Activity responses during days when soil temperatures exceeded 60 °C varied according to the rate of rise in temperature. On days with relatively cool, early morning fogs, all species actively foraged most of the morning. As temperatures rapidly rose after 1100 h, beetles climbed the low vegetation (mostly dead stems and branches of *Stipagrostis ciliata* and *Zygophyllum simplex*). While climbing the plants, and for a short time thereafter, individuals of all species were quite wary, dropping to the ground and rapidly running away if approached. When examined after 2 hours up in the vegetation, the black species (*Z. moralesi* and *Z. devexa*) were extremely lethargic, and were easily collected by hand off the branches. *Zophosis dorsata*, *Z. mniszechi*, *C. amabilis*, and *O. cerea*, however, usually dropped off the stems upon approach. Nevertheless, few fled, and most climbed back onto the vegetation shortly after dropping off.

Calosis usually rested on the plants with head down, and posterior end (the most pale portion of the body) facing the sun. A similar response was noted by Henwood (1975*b*) for the black and white *Cauricara phalangium*. As other species were more uniformly coloured, their posture was not recorded.

On hot days when ground surface temperatures climbed at a more uniform rate throughout the morning, there was very little activity. *Calosis* was the only species found in appreciable numbers. As on days with early morning fogs, *Calosis* climbed into vegetation at mid-day, but only after soil temperatures exceeded 50 °C (see Table 4 for temperature gradients above the surface). At soil temperatures between 50 and 66 °C, most individuals remained in the vegetation, dropping to the ground and running off only when closely approached. A few *Calosis* foraged between 50 and 56 °C, and their body temperatures were compared with a sample taken from the stems at the same time. Body temperatures of beetles on the ground were $40{\cdot}8 \pm 1{\cdot}9$ °C, while those of beetles up in vegetation were $37{\cdot}8 \pm 1{\cdot}1$ °C ($n = 11$, $t = 4{\cdot}9$, $P < 0{\cdot}01$). In order to maintain lower body temperatures, foraging at such high surface temperatures is of necessity very brief.

A census conducted on 4 May showed that *Z. moralesi*, *Z. devexa*, and *C. amabilis* can be active at temperatures as low as 16–17 °C. Activity at such low temperatures was observed only during precipitating fogs, when droplets of moisture collected on the surface of vegetation. This response was most noticeable in *Z. moralesi*, weak in *Z. devexa*, and observed only rarely in *C. amabilis*. Foraging was not observed at these low temperatures. All individuals were very lethargic, and apparently incapable of running. While it is probable that they were obtaining moisture from the accumulated droplets (Broza, 1979; Seely, 1979), this was not actually observed.

Discussion

Namib Desert gravel plains Zophosini exhibit several behavioural and morphological adaptations which can be interpreted as mechanisms either for avoiding interspecific interactions or for reducing the hazards of heat stress and predation.

Table 4. *Temperatures at 1400 h, 14 January 1979, measured with YSI telethermometer, model 44TD*

Ground surface–air interface	55·8°C
3 mm above ground surface	50·4°C
56 mm above ground on stem of dead bush	41·0°C

Differences in activity patterns between black and pale Zophosini studied here are similar to the findings of Hamilton (1973, 1975) and Henwood (1975*b*) on other tenebrionid species, and suggest that pale colouration may permit longer activity during the warmer parts of the day and/or in more extreme environments. Thus on hot days the black *Z. devexa* is found most frequently in cooler, vegetated clumps. The black *Z. moralesi* forages in the open, but concentrates its activity in late afternoons. The pale *Z. mniszechi* and *O. cerea* forage for longer periods in the morning and afternoon, while the pale *Z. dorsata* and *C. amabilis* are more active at mid-day. The shift in activity on cooler days more towards mid-day in *Z. moralesi*, *Z. mniszechi*, and *O. cerea* emphasizes both the hazards of heat stress on hot days, and the importance of maintaining high body temperatures rather than fixed activity cycles.

Hamilton (1973, 1975) has interpreted differences in activity patterns of black and pale tenebrionids as due to different strategies for achieving maxithermy. But differences in colouration are also correlated with different strategies for avoiding competition and predation. On the gravel plains of the Namib Desert, tenebrionid food resources (in the form of dead arthropods, seeds, and plant debris) are widely scattered, necessitating foraging over wide areas. Due to the hazards of heat stress, and the consequent need to spend more time in thermoregulatory activities such as climbing, foraging time for diurnal species may be a limiting factor—particularly during summer months. The gravel plains Zophosini forage at different times and in different microhabitats; and their behaviour can be interpreted as different mechanisms for optimizing foraging success. By foraging in vegetation and detritus pads, *Z. devexa* is spatially separated from other species. By foraging later in the afternoon, *Z. moralesi* not only achieves temporal separation from most other species, but also benefits from the re-distribution of food by the fairly consistent afternoon winds. *Calosis* and *Z. dorsata* are usually separated both spatially and temporally from *Z. mniszechi* and *O. cerea.* Although their ranges overlap in the vicinity of Gobabeb, *Z. dorsata* is more easterly-distributed than *C. amabilis*. In regions of sympatry, major differences between *Z. mniszechi* and *O. cerea* were not observed during this study. Food resources may have been sufficiently abundant to support the two species at this time; and slight differences in diet and lithophily in *O. cerea* may be more important at times when rainfall is at or below normal levels, and resources are scarcer.

A wide variety of mammals, birds, and reptiles feeds on tenebrionid beetles (Bothma, 1966*a*, *b*, 1971; Smithers, 1971; Viljoen & Davis, 1973; Willoughby, 1971). In the Namib Desert plains, nearly all of these mammals and many of the reptiles are nocturnal or crepuscular, rarely appearing in late afternoons or early mornings. Diurnal activity, an apomorphic character state in the Tenebrionidae, is thus of benefit to zophosines in avoiding many potential predators. The relative abundance of the black species, *Z. moralesi* and *Z. devexa*, in the diet of certain Namib Desert predators not only indicates the importance of concentrating activity more towards the middle of the day when vertebrates are less active, but also suggests the value of camouflage for certain species.

In the study sites, soil characteristics were such that pale colours were cryptic and dark colours were not (see also Edney, 1971*a*; Hamilton, 1973; Cloudsley-Thompson, 1976). The four pale Zophosini were rarely observed in scats or among gut contents, whereas the two black species were commonly encountered. The black *Z. devexa* is partially protected by its preference for foraging in more sheltered habitats. *Zophosis moralesi*, foraging in more open areas, is not. Personal observations suggest that the latter is heavily preyed upon by jackals, bustards and lizards, but only on those occasions when major activity peaks coincide with foraging activities of these vertebrates. *Zophosis devexa* was less important in the diet of these predators in the same areas. Although the black species are subject to greater predation, the compensatory advantages of retaining the ancestral colour pattern were not detected during this investigation.

All species are capable of running rapidly and evasively when closely pursued. *Zophosis devexa*, *Z. moralesi*, and *O. cerea* immediately run for cover when disturbed. When there was no immediate sanctuary, *Z. mniszechi*, *Z. dorsata*, and *C. amabilis* usually (> 50 per cent of observations) ran for a short distance, then stopped suddenly. Unless closely approached, they remained motionless for at least 5 minutes. Cryptic colouration undoubtedly serves to protect them in such cases.

In *Z. dorsata*, the colour pattern varies with the soil. The white pulverulent layer is apparently somewhat adhesive. While individuals in the study area were white, resembling the quartz-gravel background, specimens collected north of the Swakop River were pink due to adhesion of sand or clay particles to the white pulverulent layer beneath. They, too, resembled their background.

Different strategies for reducing predation and regulating body temperatures have resulted in decreased competition due to spatial and temporal separation in six sympatric species of zophosine Tenebrionidae. Similar patterns are likely to be found in most sympatric groups of Zophosini. These findings emphasize the complexity of pale colouration and diurnal activity patterns as evolutionary strategies, and studies which stress only the rôle of heat relationships or any other single factor should be interpreted with this in mind.

I am indebted to V. Gray and especially S. Falconer for assistance during censuses, and other phases of data gathering and compiling. This work could not have been accomplished without the guidance of M. L. Penrith in the identification of zophosine Tenebrionidae. Many people kindly provided useful information, suggested improvements, and helped formulate ideas through discussions. Of these, I am particularly grateful to P. Cooper, B. Heinrich and an anonymous reviewer; and to C. Clinning, J. Doyen, S. Endrödy-Younga, S. Falconer, W. Haacke, M. Seely, R. Smithers and J. Ward. My wife, Anne Louise, freely took time from her busy schedule to type copies of the manuscript. I acknowledge the Division of Nature Conservation and Tourism, SWA/Namibia Administration, for the use of facilities and permission to work in the Namib-Naukluft Park; and the CSIR and the Transvaal Museum of South Africa for assistance.

References

Besler, H. (1972). Klimaverhältnisse und klimageomorphologische Zonierung der zentralen Namib (Südwestafrika). *Stuttgarter geographischer Studien*, **83**: 1–209.

Bothma, J. duP. (1966*a*). Food of the silver fox *Vulpes chama*. *Zoologica Africana*, **2**: 205–210.

Bothma, J. duP. (1966*b*). Notes on the stomach contents of certain Carnivora (Mammalia) from the Kalahari Gemsbok Park. *Koedoe*, **9**: 37–39.

Bothma, J. duP. (1971). Reports from the Mammal Research Unit: 2. Food habits of some Carnivora (Mammalia) from southern Africa. *Annals of the Transvaal Museum*, **27**: 15–26.

Broza, M. (1979). Dew, fog and hygroscopic food as a source of water for desert arthropods. *Journal of Arid Environments*, **2**: 43–49.

Cloudsley-Thompson, J. L. (1976). Adaptive functions of the colours of desert animals. *Comparative Physiology and Ecology*, **1**: 109–120.

Edney, E. B. (1971*a*). The body temperature of tenebrionid beetles in the Namib Desert of southern Africa. *Journal of Experimental Biology*, **55**: 253–272.

Edney, E. B. (1971*b*). Some aspects of water balance in tenebrionid beetles and a thysanuran from the Namib Desert of southern Africa. *Physiological Zoölogy*, **44**: 61–76.

Gebien, H. (1939). Körperbau und Lebensweise der Wüstentenebrioniden. *VII International Kongress Entomologie Berlin*, **1**: 118–132.

Hamilton, W. J. III (1971). Competition and thermoregulatory behavior of the Namib Desert tenebrionid beetle genus *Cardiosis*. *Ecology*, **52**: 810–822.

Hamilton, W. J. III (1973). *Life's Color Code*. New York: McGraw-Hill. 238 pp.

Hamilton, W. J. III (1975). Coloration and its thermal consequences for diurnal insects. In Hadley, N. (Ed.) *Environmental Physiology of Desert Organisms*, pp. 67–89. Stroudsburg, Pennsylvania: Dowden, Hutchinson & Ross. 283 pp.

Hamilton, W. J. III, Buskirk, R. E. & Buskirk, W. H. (1976). Social organization of the Namib Desert tenebrionid beetle *Onymacris rugatipennis*. *Canadian Entomologist*, **108**: 305–316.

Hamilton, W. J. III & Penrith, M.-L. (1977). Description of an individual possible hybrid tenebrionid beetle and the habitat preference of the parental species. *Canadian Entomologist*, **109**: 701–710.

Hamilton, W. J. III & Seely, M. K. (1976). Fog basking by the Namib Desert beetle, *Onymacris unguicularis*. *Nature*, **262**: 284–285.

Henwood, K. (1975*a*). Infrared transmittance as an alternative thermal strategy in the desert beetle *Onymacris plana*. *Science*, **189**: 993–994.

Henwood, K. (1975*b*). A field-tested thermoregulation model for two diurnal Namib Desert tenebrionid beetles. *Ecology*, **56**: 1329–1342.

Holm, E. & Edney, E. B. (1973). Daily activity of Namib Desert arthropods in relation to climate. *Ecology*, **54**: 45–56.

Koch, C. (1961). Some aspects of abundant life in the vegetationless sand of the Namib Desert dunes. *Journal of the South West African Scientific Society*, **15**: 8–34.

Koch, C. (1962). The Tenebrionidae of southern Africa, XXXI. Comprehensive notes on the tenebrionid fauna of the Namib Desert. *Annals of the Transvaal Museum*, **24**: 61–106.

Louw, G. N. & Hamilton, W. J. III (1972). Physiological and behavioural ecology of the ultrapsammophilous Namib Desert tenebrionid *Lepidochora argentogrisea*. *Madoqua*, **1**: 87–95.

Penrith, M.-L. (1977). The Zophosini (Coleoptera: Tenebrionidae) of western southern Africa. *Cimbebasia Memoir*, **3**: 1–291.

Robinson, E. R. (1978). Phytogeography of the Namib Desert of South West Africa (Namibia) and its significance to discussions of the age and uniqueness of this desert. In van Zinderen-Bakker, E. M. & Coetzee, J. A. (Eds). *Palaeoecology of Africa*, **10**: 67–74.

Roer, H. (1975). Zur Lebensweise des Namibwüstenkäfers *Onymacris plana* Péringuey (Col., Tenebrionidae, Adesmiini) unter besonderer Berucksichtigung seines Migrationsverhaltens. *Bonner zoologische Beitrage*, **26**: 239–256.

Roer, H. (1977). Areas and adaptations of the Namib Desert beetle (*Onymacris rugatipennis*) (Haag, 1875) (Col.: Tenebrionidae, Adesmiini) to the Kuiseb River bed in South West Africa. *Zoologische Jahrbücher. Abteilung für Systematik Ökologie und Geographie der Tiere*, **104**: 560–576.

Sandelowsky, B. H. (1977). Mirabib—an archaeological study in the Namib. *Madoqua*, **10**: 221–283.

Schulze, E.-D. & Schulze, I. (1976). Distribution and control of photosynthetic pathways in plants growing in the Namib Desert, with special regard to *Welwitschia mirabilis* Hook. fil. *Madoqua*, **9**: 5–13.

Seely, M. K. (1978). Standing crop as an index of precipitation in the central Namib grassland. *Madoqua*, **11**: 61–68.

Seely, M. K. (1979). Irregular fog as a water source for desert dune beetles. *Oecologia* (*Berlin*), **42**: 213–227.

Seely, M. K. & Hamilton, W. J. III (1976). Fog catchment sand trenches constructed by tenebrionid beetles, *Lepidochora*, from the Namib Desert. *Science*, **193**: 484–486.

Smithers, R. H. N. (1971). *Mammals of Botswana*. Salisbury: Trustees of the National Museums of Rhodesia. 340 pp.

Viljoen, S. & Davis, D. H. S. (1973). Notes on stomach contents analyses of various carnivores in southern Africa (Mammalia: Carnivora). *Annals of the Transvaal Museum*, **28**: 353–363.

Willoughby, E. J. (1971). Biology of larks (Aves: Alaudidae) in the central Namib Desert. *Zoologica Africana*, **6**: 133–176.