Environmental Correlates of Aquatic Faunal Distribution in the Namib Desert

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The very limited literature on the limnology of the Namib Desert is reviewed. The major habitat types are described: permanent systems include two relatively large lakelets, a number of freshwater springs that form shallow trickles or pools, and a series of brackish to hypersaline mineral springs on gypsous crusts; ephemeral systems include rainpools that form in endorheic basins, pools left in river-beds after they have stopped running, and the rivers themselves, which contain water for very short periods.

A checklist of the aquatic fauna is provided. Analyses of the entries in the list show that ephemeral waters are dominated by crustaceans and permanent waters by insects, especially immature forms. The number of taxa is greatest for permanent lakelets and streams and least for endorheic rainpools and gypsous springs. The number of taxa does not correlate with salinity for any of the habitat types nor with depth of water in any except the gypsous springs. The major determinant of faunal richness is isolation, the number of taxa showing strongly significant negative correlations with distance from a given pond to another of the same kind, or another of any kind, for all types except the gypsous springs.

INTRODUCTION

The characteristics of athalassic (non-marine) surface waters in any region depend primarily on the geology of their catchments and on the climate. In arid areas, by far the most significant of these two is the climate, to the extent that one might expect deserts to have no surface waters at all except for ephemeral pools that form, or rivers that run, for a brief period after rain. This is far from the truth, although the most obvious waterbodies in deserts are certainly temporary.

The Namib Desert is no exception. Climatic conditions are severe, to the extent that evaporation rates may reach 4000 mm y⁻¹ (Lancaster, Lancaster and Seely, 1984, give a mean pan evaporation rate of 3168 mm y⁻¹ for the central Namib). Rainfall is spatially erratic and highly unpredictable from year to year, while the mean annual rainfall over most of the Namib is considerably less than 100 mm y⁻¹ (Lancaster et al., 1984). Winds are high. Thus it is not surprising that, as in deserts everywhere, although surface waters do exist in the Namib, they are small, scattered, and often ephemeral.

Despite their small sizes and scattered distribution, the inland waters of the Namib are chemically very diverse, resulting in a variety of permanent or semi-permanent pools and springs with a more diverse aquatic fauna than may otherwise be expected in the region. Because the rate of evaporation exceeds rainfall, permanent waterbodies cannot form unless they are fed from underground sources. Thus all the surface waters in the Namib can be divided into ephemeral ones that form as a result of rainfall, and semi-permanent or permanent ones fed by groundwater.

This paper briefly reviews the literature pertinent to Namib limnology, documents what is known of the distribution and the physical and biotic features of the major types of surface waterbody in the Namib Desert and examines some of the determinants of species richness in the aquatic fauna. The area under discussion is limited to that from the Munutum River in the north (Fig. 1) to Lüderitz (27° N, 15° E) in the south and extends inland to about the 100 mm isohyet because, although the Namib Desert extends well into Angola, no limnological information is available on that region. Further, with the exception of ephemeral pools forming after rain at Sossusvlei and in a few small depressions near Lüderitz, there are virtually no athalassic surface waters (i.e., those not influenced by the sea) in the dune field south of the Kuiseb River.

Largely for logistic reasons, including the unpredictability of rainfall, the Namib Desert is remarkably poorly known limnologically so that the literature on the topic is very limited. A few papers provide some limnologically pertinent information on climate (Lancaster et al., 1984), historical climatology (Seely and Sandelowsky, 1974; Sandelowsky, 1983) and geology and soils (Martin, 1965; Scholz, 1972) or a combination of these topics (Logan, 1960; Goudie, 1972). Some aspects of the distribution of surface and subsurface waters are mentioned in, for example, Hellwig (1988).

Somewhat more published information is available on the chemistry of surface waters on the gravel plains of the central Namib (Kok and Grobbelaar, 1985), on gypsous crusts (Martin, 1963; Watson, 1979), on hot springs (Gevers, Hart and Martin, 1963), on waterholes in the Kuiseb River canyon (Kok and Grobbelaar, 1980), and on Kuiseb River water (Grobbelaar and Seely, 1980). Some aspects of the limnology of Sossusvlei, a large ephemeral interdune lake, are described.
by Grobbelaar (1976) and of Hosabes, a hypersaline spring, by Day and Seely (1988). A number of features of the Kuiseb River are described in the report edited by Huntley (1985) and by Stengel (1964), who also examines the Swakop River.

With the exception of several articles on frogs, including those by Channing (1976) and Jurgens (1985), it appears that nothing has been published on the biology of the Namib aquatic biota, although a number of systematic papers (see references in Table 1) deal either exclusively with, or include information on, Namib forms. The paper on the flamingoes of Etosha Pan (Berry, 1971) and that on the diatoms of thermal springs near Windhoek (Schoeman and Archibald 1988), for

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**Fig. 1**

Map of the northern and (inset) central Namib Desert showing the positions of the waterbodies referred to in the text. Each symbol may refer to more than one site.
example, contain some information on taxa that probably also occur in the Namib itself.

**MAJOR TYPES OF AQUATIC ECOSYSTEM**

In most climatic zones, surface waters are conveniently divided into standing (lentic) and running (lotic) systems. In deserts, though, a more appropriate and fundamental division is between permanent and semi-permanent, and temporary (ephemeral) waters, a division that is also reflected in the major elements of the biota. Below is a classification and brief description of the major types of aquatic habitats in the Namib. The localities of those known to the author are indicated in Fig. 1 and Table 1.

**Permanent and semi-permanent waterbodies**

Such systems are fed by groundwater springs. Their surface areas and fluctuations in depth are thus determined by the relationship between the rate of flow of spring water (they are often recharged by subsurface flow from rain that has fallen many kilometres inland), the rate of evaporation, and the occasional influx of rainwater.

Although no systems in the Namib fit the definition of a true lake (a waterbody too deep for rooted plants to grow on the bottom), at least two lakelets ( Ausis and 'The Oasis', both in the region of Môwe Bay) cover several hundreds of square metres, reach a depth of a metre or more, and appear to be permanent. They can be classified as permanent endorheic (closed-basin) lakelets (PL in Table 1).

On some geological formations, the water in smaller permanent springs remains fresh, or nearly so. On others, usually on gypsous crusts, evaporation from the surface, together with precipitation of CaCO₃, results in brackish to highly saline surface waters. Freshwater springs (FS in Table 1) are found in dry river-beds or on the open plains and vary from small trickles to standing pools up to a metre or so deep. Most are permanent. In a few places (near the mouth of the Unibi River and at Wolfswasser, for instance) enough groundwater escapes to produce very fresh, fast-running, permanent streams (St in Table 1).

The small, highly mineral springs on gypsous crusts (GS in Table 1) are common in several deserts, where they seep from faults, extend for a few tens or hundreds of metres, and then disappear. A fault-line running along much of the coast of the Namib provides a series of these springs, one of which has been described in detail by Day and Seely (1988). It appears that the groundwater supplying the springs is fresh, or nearly so, but owing to the intense solar radiation and the hygroscopic gypsous soils, the water evaporates until enough CaCO₃ precipitates for the water to become a slightly calcium-enriched NaCl brine. One of these systems in the central Namib is unique in possessing the only known athalassic species of the protozoan group Foraminifera (Brain and Adams, 1984).

**Ephemeral waters**

Ephemeral waters include rivers that run for short periods after rain has fallen high in their catchments, the pools that they leave behind as they cease to flow, and pools that form in depressions after rain.

The borders of that part of the Namib under discussion are more or less coincident with the Orange River in the south and the Cunene River in the north, the only permanent rivers in the region. Nothing has been published on the Cunene, while Cambray, Davies and Ashton (1986), Agnew (1986) and Skelton (1986) address various aspects of the limnology of the Orange River.

One of the characteristic features of the Namib north of about 22°S (roughly Walvis Bay) is a series of dry river-beds running perpendicular to the coast. They act more as canals than as rivers in the usual limnological sense, in that they carry water infrequently and do not develop a lotic biota. Their waters are allogenic (derived from elsewhere, being precipitated in the more mesic uplands and channeled towards the sea via the rivers) and in many cases little or no water actually reaches the sea, except during periods of unusually heavy rain. The more northerly rivers run to the sea almost every year, while those in the south are less predictable. Of all the rivers, the Kuiseb, which divides the dune fields of the southern Namib from the gravel plains of the north, is the best known. The upstream damming of both the Kuiseb and the Swakop Rivers, and extraction of water from below the bed of the Kuiseb (Huntley 1985), has resulted in these rivers flowing for shorter distances and for shorter periods, and consequently in less frequent and less intense flooding in recent years. Nonetheless, when flood-waters recede, pools of very fresh water are left in the river-beds (RR in Table 1). In deep canyons, these may persist for months.

Although surface flow is seasonal and ephemeral, the river-beds act as permanent courses for subsurface water. Where this water is close beneath the surface of the river-bed, the rivers form longitudinal oases supporting a variety of plants (often including large trees) and their associated fauna, while larger mammals are able to excavate waterholes in the river-beds.

After rain, water will also collect in rainpools in endorheic basins (RE in Table 1), which may be depressions in rocky outcrops or on any other sealed surfaces such as clay or salt pans. Depending on the intensity and duration of rainfall, the pools may persist for as little as a day or two, or for as long as several weeks or, exceptionally, months. Although the water in most pools remains fresh to brackish, in some it may become very saline.

**THE AQUATIC FAUNA OF THE NAMIB**

Table 1 is a preliminary list of the taxa known so far from athalassic waters of the Namib. It has been compiled from the available literature on the taxonomy and distribution of the aquatic fauna of the Namib Desert, together with records from my personal collections and hatching experiments on dried mud, and from the State Museum, Windhoek. As is frequently the case in Africa, the taxonomy of most groups is poorly known, so that many of the taxa are incompletely or tentatively identified. For this reason, the term 'species diversity' has been avoided in the following discussion, where 'richness' refers merely to the number of taxa. Further, the apparent distribution of the various taxa must reflect collecting bias, in that most samples were obtained from the central Namib and the
### Table 1

A preliminary checklist of the aquatic metazoan animals known from athalassic surface waters in the Namib. RR = rainpools in river-beds; RE = endorheic rainpools; PL = permanent lakelets; FS = permanent freshwater springs; SI = permanent streams; GS = springs on gypsoid beds. 'Sp. indet.' refers to species considered to be new by the authorities who have examined them.

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**Insecta**

- **EPHEMEROPTERA**
  - Baenidae
  - Ciccompsidae
  - Other
  - ODONATA
    - Libellulidae
    - Nannochromis sp. (nymph) 13
    - Neuphaea sp. (nymph) 13
    - Pantala flavescens (adult) 13
    - Trithemis kirbyi anders (adult) 5

- **COLEOPTERA**
  - Gomphidae
    - Paragomphus genei 13
    - Paragomphus sp. (nymph) 13
  - HEMIPTERA
    - Nottoneclisidae 13
    - Anisopidae
    - Gerridae 13
    - Limnogonidae
    - Hebridae 13
  - EVESTEIDA
    - Sigara sp. (Characidae) 13
    - Sigara sp. 13
  - TROGOPTEROGNATHUS
    - Pregnantus
  - TROPOPTEROSOMATIDA
    - Dytiscidae
    - Gyrinidae
    - Sphaeridae
    - Sigara sp. (Characidae) 13
    - Sigara sp. 13

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**Platyhelminthes**

- Polycystis dayae
- Polycystis pygmaea
- Polycystis perangusta
- Polycystis tigrina

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**Hirudinea**

- Limnesia sp. inopinatus

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**AQUATIC FAUNA IN THE NAMIB DESERT**

- **AQUATIC FAUNA IN THE NAMIB DESERT**

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**TURBELLARIA**

- *Huara poeppigii* 2
- *Hydrochilidae*

---

**NEMATODA**

- *Hydrophilidae*
- *Hydrophilidae*
- *Ephemeroptera*
- *Hydrophilidae*

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**PLATYHELMINTHES**

- *Polycystis dayae*
- *Polycystis pygmaea*
- *Polycystis perangusta*
- *Polycystis tigrina*

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**CONCHOCRACA**

- *Caenestheres cf. australis*
- *Eucyclops sp.*
- *Euleptodora cf. africana*
- *Lepidocolphlea cf. inermis*
- *Lepidocolphlea cf. rubidoni*
- *L. cf. strigiliscola*

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**ANOSTRACA**

- *Branchipodopsis cf. kaloeschis*
- *Branchipodopsis sp.*
- *Streptocara cf. dianthus*
- *Streptocara sp.*

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**CRUSTACEA**

- *Caenestheres cf. australis*
- *Eucyclops sp.*
- *Euleptodora cf. africana*
- *Lepidocolphlea cf. inermis*
- *Lepidocolphlea cf. rubidoni*
- *L. cf. strigiliscola*

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**AQUATIC FAUNA IN THE NAMIB DESERT**

- *Polycystis dayae*
- *Polycystis pygmaea*
- *Polycystis perangusta*
- *Polycystis tigrina*
Skeleton Coast. Most of the ephemeral waters have been sampled only once, so that temporal variations are entirely unknown. Despite these limitations, some points of interest arise. A second of the beetles occurring both in gypsous and ephemeral waters have been sampled only once, so that temporal variations are entirely unknown. Despite these limitations, some points of interest arise.

Calculation of the ratio of the number of taxa recorded for a particular habitat type to the number of sites in that category allows the different types to be ranked according to richness of the fauna (i.e., number of taxa per site). Although the data on which the numbers are based are far too incomplete to use for anything other than such ranking, these numbers do indicate that permanent lakes and streams are richest in taxa, followed by freshwater springs and rainpools in river-beds, with gypsous springs and endorheic rainpools supporting relatively few taxa.

Endorheic rainpools are dominated by crustaceans, especially ephippioptera and ostracods, which are able to withstand long periods of desiccation within ‘egg’ shells (which are actually cysts containing young larvae). Typically, they are uncommon in, or absent from, permanent waters and preliminary personal observations suggest that a dry resting period is obligatory before the eggs can hatch. Although this appears not to be true for the copepods or the cladocerans, these, too, generally occur in ephemeral waters and must also have a desiccation-resistant phase in their life-cycles. Sixteen of the 48 species of Crustacea are ostracods, reflecting both their species richness in the ephemeral waters of the Namib and the extensive recent systematic work on the group by Martens (1984, 1986, 1988). Further information on the crustaceans of desert waters is available in the reviews by Hartland-Rowe (1972) and Belk and Cole (1975).

The fauna of rainpools in river-beds comprises an element typical of ephemeral pools and, if the river has a distant origin, may also include lotic elements brought downstream from further inland. Thus some such pools may have a rather diverse fauna for this, and other, reasons. First, rainfall is more predictable inland, so that organisms able to withstand only seasonal desiccation can survive in river-beds because they are usually flooded annually. Second, at least some pools persist for long enough to be colonized by flying insects and propagules imported on the fur and feathers of vertebrates visiting the pools. Third, a number of the rivers have been dammed in their upper reaches; the resulting permanent lakes provide habitats for a variety of aquatic organisms that may be washed downstream in floods to join the temporary pond fauna. Even the obligatorily aquatic frog Xenopus laevis has been recorded from pools in the Kuiseb River (Channing, 1976), where fish have also been found in pools.

The insects, especially immature forms, are poorly known systematically so that the number of species must exceed the number of taxa listed. Some seem to have wide distributions, occurring in several types of waterbody. The beetles, which can generally be separated into different species or placed fairly reliably into genera even by non-coleopterists, are widespread in all types except endorheic rainpools. The only species so far found in these pools is the cosmopolitan Eretes stictus (Dytiscidae), a strong flier occasionally found even in very isolated and hypersaline gypsous springs, the fauna of which is otherwise restricted to surface-dwelling spiders and a few aquatic beetles and dipterans.

Interestingly, only one of the 31 taxa that occur in the gypsous springs is crustacean. A third of the taxa (mostly insects) appear to be restricted to this type of habitat, while somewhat less than a third co-occur in gypsous and freshwater springs. Five species of beetle occur both in gypsous and ephemeral waters, reflecting their ability to withstand either

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| Number of systems sampled | 16  | 35  | 2  | 17  | 3  | 16  |
| Number of taxa            | 48  | 51  | 10 | 43  | 21 | 31  |
| Number of taxa separable to species | 41  | 45  | 9  | 42  | 13 | 20  |
| Ratio of taxa : systems   | 3.0 | 1.5 | 5.0| 2.5 | 7.0| 1.9 |

1 Longhurst (1955)
2 Barnard (1929)
3 Barnard (1926 or 1928)
4 Ris (1921)
5 Longfield (1926)
6 Hutchinson (1929)
7 Grobbeil (1976)
8 Channing (1976)
9 Nkut (1955)
10 Omer-Cooper (1955)
11 Gillans and De Mollon (1969)
12 Identifications of taxa belonging to the State Museum, Windhoek, or to the author and tentatively identified by systematists.
13 Identifications of taxa belonging to the State Museum, Windhoek, or to the author and tentatively identified by her, often from unsatisfactory non-African sources.
desiccation or extremes of salinity (or both), and their strong flying abilities.

The faunas of the two permanent lakes are, characteristically, dominated by planktonic crustaceans with the odd species of beetle, hemipteran and chironomid.

The permanent freshwater springs are dominated by insects, particularly beetles, while crustaceans are virtually absent. The relatively low ranking of taxa per pool may be an artefact caused by the number of insect taxa identified only to family. The faunal richness in freshwater springs seems to be positively correlated with their degree of permanence, although insufficient information is available to confirm this suspicion. Certainly the number of taxa is greatest in the true streams, which are also unusual for the Namib in that their fauna is typically lotic rather than lentic.

The relative similarities of the faunal communities of the six habitat types can be simply analysed (Table 2) using Sorensen's Community Coefficient (Southwood, 1966), which expresses the number of shared species in any two habitats relative to the total combined number of species:

\[ CC = \frac{2j}{a + b} \]

where \( CC \) is Sorensen's Community Coefficient, \( j \) is the number of shared species, and \( a \) and \( b \) are the number of species in each habitat type.

There is an interesting contrast between the two ephemeral habitats: while those in river-beds share a good proportion of their species with all other habitat types (for reasons mentioned above), endorheic rainpools, which are generally isolated habitats, show a close similarity only with rainpools in river-beds. The similarity between these two types is determined largely by those crustaceans that are confined to ephemeral habitats. Of the permanent running waters, the freshwater springs share 30% of their species with both the streams and the gypsous springs.

**FACTORS DETERMINING FAUNAL RICHNESS OF THE HABITAT TYPES**

Because of their small sizes and isolated positions, and the generally perceived harshness of their physical and chemical environments, desert waters, especially temporary ones, have often been considered to be useful models for an improved understanding of distribution patterns, dispersal, isolating mechanisms, island biogeography and competition theory. The resulting hypotheses often propose that the number of taxa in desert and/or ephemeral pools will be determined by the size of the waterbody (see, for example, Weir, 1966; Pajunen and Jansson, 1968; Dehoney and LaVigne, 1984; Ebert and Balko, 1984), its isolation (e.g., Pajunen, 1986) and its chemical composition (e.g., Weir, 1986, Ranta, 1982).

These hypotheses presuppose that: either dispersal from pond to pond is limited (e.g., McLachlan, 1983a, b) or that dispersal is common (e.g., Dimetman and Margalit, 1981) and 'easy' (on the feet of birds, for instance: Maguire, 1963); that species richness will be greater in larger pools because, in the case of ephemeral waters at least, larger pools are likely to persist for longer (Ebert and Balko, 1984; Dehoney and LaVigne, 1984); and that the number of taxa will be inversely proportional to environmental 'harshness', usually some measure of a variable such as salinity (e.g., Ranta, 1982) or oxygen content of the water (e.g., Morton and Bayly, 1977).

It has generally been found that the number of taxa is most closely related to pool size, however (e.g., Weir, 1966; Dehoney and LaVigne, 1984). This is easily explained for the inhabitants of temporary pools, where size, especially depth, is proportional to longevity and therefore to the likelihood of an animal being able to complete its life-cycle. It is less easily explained for permanent systems, though, since increased size per se does not necessarily result in increased habitat diversity, the commonest explanation in island biogeographic theory for increased species diversity in 'islands' of increasing size (but see, for instance, Fryer, 1985).

Even with the rather limited data presently available to me, it is possible to make a preliminary assessment of the relationship between faunal richness (i.e., number of taxa) and salinity, size of system, and distance from other systems. The analyses described below and/or shown in Fig. 2 are based on data from all the sites indicated in Fig. 1 for which measurements of the other variables are available. Those from the Skeleton Coast were all collected in January 1983, while data from the central Namib Desert (inset in Fig. 1) have been collected by me from time to time over several years. Thus a major source of error in these analyses, especially for the ephemeral pools, lies in the fact that samples were collected after different intensities of, and at different times after, rainfall.

Linear regressions (Zar, 1984) of the number of taxa upon salinity (measured in the field with an American Optics refractometer) are not statistically significant for the data-set as a whole or for any of the habitat types individually \( (P > 0.05) \). Indeed, although a plot of the number of taxa versus salinity shows considerable scatter, the trend reflects, if anything, an increase in the number of taxa at least at intermediate salinities.

Surface area of each system was calculated from measured or estimated lengths and widths, and depth was measured in situ, both within an accuracy of about 10%. Distances shorter than about 1 km were estimated in the field and those exceeding 1 km were measured from appropriate maps. The results can be considered only to be preliminary because of the problem of incomplete identifications of the animals, resulting
in the use of various taxonomic levels in the analyses.

Regression of the number of taxa per site upon depth was not significant \((P > 0.05)\) for the data-set as a whole and for each habitat type individually. Regression upon surface area (Fig. 2a) was significant only for the gypsous springs \((n = 13, P < 0.01, y = 3.03 + 0.67 \ln x)\). Thus these data suggest that, for most habitat types in the Namib Desert at least, size (as reflected by depth and surface area) is not a primary determinant of faunal richness.

If, on the other hand, the geographical isolation of individual pools or springs has an effect on faunal richness, and if the individual elements of the fauna are at all able to select, or differentially to survive in, different types of habitat, then one can predict that the number of taxa in any pool should decrease with increasing distance apart of individual systems. Further, the regression lines for different habitat types should reflect their permanence: the faunas of permanent waters should be less influenced by distance from other systems than should the faunas of ephemeral pools. Finally, where faunal richness is greatly influenced by isolation, one might expect the relationship to be exponential.

Figure 2b illustrates the regression of the number of taxa upon the shortest distance from a given system to any other and Fig. 2c illustrates the regression of the number of taxa upon the shortest distance from a given system to another of the same type. Although no significant relationships exist in either case for the fauna of the gypsous springs, all the other habitat types show strongly significant \((P < 0.01)\) negative
correlations. The regression equations are shown in Table 3.
These results are fascinating, not least because they differ quite markedly from those of several of the authors referred to above (e.g., Dehoney and LaVigne, 1984; Ebert and Balko, 1984).

It is not clear why the richness of the fauna of the gyspous springs should be more strongly related to surface area (and therefore size) than to degree of isolation, or why these systems should be different from the others in this respect. It is possible that the habitat diversity of the larger gyspous springs is greater than that of the smaller ones; perhaps, on the other hand, the relative permanence of these systems may allow even isolated ones to accumulate species over long periods of time.

Certainly a comparison of the results for the other habitat types suggests that the richness of the fauna increases with increasing permanence and predictability, in that the curves for both types of ephemeral pool lie closer to the axes in Fig. 2c (i.e., the exponent is larger) than does the curve for the permanent springs, with that for the permanent streams lying farthest away. Finally, a comparison of the curves for the permanent springs and the rainpools in river-beds in Figs 2b and 2c suggests that the fauna of the springs is more dependent on the closeness of other springs of the same kind, while that of the rainpools responds to the closeness of any type of pool.

In conclusion, the data strongly suggest that, with the exception of the gyspous springs, the various types of aquatic habitat in the Namib Desert are strongly dependent on neighbouring systems as sources of 'new' species. This in turn suggests that extinction in individual pools plays a significant role in the determination of community structure.

ACKNOWLEDGEMENTS

I should like to thank the following systematists for identifying various components of the fauna: Dr Denton Belk (Anostraca); Prof. Jim Green (Cladocera) and Mrs Nancy Rayner (Copepoda and Cladocera); Dr Koen Martens (Ostracoda); Dr Bruce McIntosh (Culicidae); Dr S. Endrödy-Younga (some Coleoptera); Dr A. Prins (adult Ephydridae), and Belinda Day for drawing the figures. I am also most grateful to the following people for their kindness, helpfulness and hospitality in organizing or assisting in various collecting trips: Dr Mary Seely and her staff at the Desert Ecological Research Unit of Namibia, Gobabeb; Barbara Curtis, Charmanne Meyer and Shirley Bethune at the State Museum, Windhoek; Mike Griffin and Rudi Loulit of the Directorate of Nature Conservation and Recreation Resorts, Namibia. I also thank Barbara Curtis for providing some of the information included in Table 1.

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The Biology and Ecology of Namib Desert Ants

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Current knowledge of Namib Desert ant biology and ecology is reviewed. The review covers the composition of the ant fauna of the central Namib in qualitative and quantitative terms at the level of subfamily, genus and species. The dietary patterns of the ants are described and adaptations that facilitate species persistence are discussed. These adaptations include granivory and behavioural plasticity. Ecologically dominant ant species from the dune sea and gravel plains are compared in an attempt to identify those characteristics that have enabled these species to become particularly successful desert inhabitants. The reasons that the thermophilic genus *Ocymyrmex* forages during the heat of the day are considered. The reproductive biology and social structure of dominant ants such as *Messor denticornis* and *Camponotus detritus* are compared with that of relatively rare ants that have small colony sizes such as *Ocymyrmex* species and members of the *Monomorium* Salomonis-group. Marked differences occur between these two groups of ants and the adaptive value of these differences is discussed in relation to survival and reproduction in a desert environment.

INTRODUCTION

Numerically and in terms of biomass, ants represent one of the dominant animal taxa in hot deserts throughout the world (Crawford, 1981; Pisarski, 1978). Seed predation is probably the most important ecological effect that ants have on desert ecosystems (Stradling, 1978; Buckley, 1982) but they are also important in the conservation, localization and turnover of nutrients (Crawford, 1981) by virtue of their central place foraging and subterranean nesting habits.

Despite their ecological importance and biological interest, Namib ants remained unstudied until the present decade. Barbara Curtis commenced a study of the ecology of the large, conspicuous dune ant *Camponotus detritus* in 1980, and in 1981 I commenced a general study of the ecology of Namib Desert ants in which attention was focused largely on the ants of the gravel plains to the north of the dune sea. As the work on *C. detritus* is reviewed elsewhere in this volume (Curtis, 1990), the present paper focuses on my own work and that of a few other researchers who have subsequently commenced studies on the Namib ant fauna. In this review I examine overall ecological patterns and trends that characterize Namib ants and emphasize particularly interesting aspects of the biology of some of these ants.

THE ANT FAUNA OF THE NAMIB

To date 38 species of ants have been discovered in the central Namib Desert. Thirty six species are listed in Marsh (1986a) and additional taxonomic notes are given in Appendix I. The remaining two species are *Monomorium rufulum*, which occurs on the eastern edge of the dune sea, and *Iridomyrmex humilis*, the Argentine ant, which was discovered subsequently at Mirabib. As *I. humilis* is a tramp species, distributed by man’s activities, and as it has been located once only it has been disregarded in this review. Thus, 37 species of ants are currently recognized as occurring naturally in the central Namib. The central Namib has, however, not been comprehensively sampled and the species list will inevitably grow with time. Of the three major habitats in this region, the gravel plains have been the most comprehensively sampled, followed by the dune sea. The ant fauna of the Kuiseb River bed has been sampled sporadically and remains largely unknown. Ant collecting in other regions of the Namib has barely commenced.

Many of the ant species of the central Namib are new to science. Nine of the 13 *Monomorium* species were only recently described (Bolton, 1987). Furthermore, the ant fauna elsewhere in the Namib Desert is likely to be quite different. For instance, based on brief and unsystematic collecting, four species of *Ocymyrmex* new to science have been recorded in regions outside the central Namib (*O. tachys* and *O. afradu* in the Skeleton Coast Park, *O. engytachus* from the top of the Gamsberg Pass, and *O. okys* from the Naukluft Mountains).

Clearly a comprehensive survey of ants in the Namib Desert will reveal a wealth of new material and our current knowledge of the most basic issue, namely the species composition of the desert, is far from complete.

Nevertheless, sufficient is known about the composition of the ant fauna of the plains and sand sea in the central Namib Desert to make four general statements that will probably remain true even when more detailed information is available:

1) More species occur on the gravel plains (33 species) than in the dune sea (13 species) (Marsh, 1986a) despite the existence within the dune sea of extensive interdune valleys that resemble the gravel plains. A possible explanation involves the existence of large inselbergs on the gravel plains. The runoff from these inselbergs is concentrated into water courses that support perennial vegetation, and hence several species of ants that are dependent on this vegetation. In contrast, the interdune valleys lack these more productive habitats. The dunes themselves

support perennial plants but the unstable nature of the substrate probably prevents most ant species from being able to colonize the dunes. Only specially adapted ants such as *C. detritus*, which make use of the roots of these plants to provide structure to their sandy nests (Curtis, 1985a), are able to occupy the dunes. Greater species richness of ants in gravel plain habitats as opposed to sand sea habitats has also been reported for the Sahara Desert (Bernard, 1964; Delye, 1968).

2) Four of the eleven subfamilies of Formicidae occur in the Namib Desert. Twenty-eight species belong to the Myrmicinae, seven species belong to the Formicinae, one species, *Tetraponera ambigua*, belongs to the Pseudomyrmecinae (Marsh, 1986a) and an unidentified *Technomyrmex* sp. belonging to the Dolichoderinae has been collected in the Kuiseb River bed (Robertson, personal communication). The arboreal *T. ambigua* was found once only on an *Acacia* sp. tree on the eastern border of the desert (i.e., the most productive edge of the desert). Subsequent searches of other *Acacia* trees were unsuccessful and it appears that this species is a marginal occupant of the Namib. Thus, at the subfamily level, the Namib is almost identical to the Sahara, but unlike deserts in the United States of America and Australia which contain an additional two subfamilies, the Dorylinae and the Ponerinae (Briese and Mackauley, 1981; Chew, 1977; Greenslade and Hallday, 1983; Whitford, 1978). Marsh (1986a, b) suggests that the most likely reason for the exclusion of these subfamilies in the Namib and Sahara is the greater aridity of these deserts. This results in lower productivity and greater unpredictability in production, which effectively excludes trophic specialists and conversely only permits opportunistic, desert-adapted species to occupy these regions.

3) The genus *Monomorium*, comprising small to medium-sized monomorphic ants, is the dominant ant genus in the Namib. Of the 37 naturally occurring species in the Namib, 13 are *Monomorium* species, i.e., 35 % of all ant species belong to this genus. Furthermore, the majority (10 species) belong to the arid-adapted Salomonis-group (Bolton, 1987). This is the dominant group of *Monomorium* species in Africa in habitats ranging from savannah through to desert. Bolton (1986) has postulated that the dominance of this group in deserts is partly related to the occurrence of apterous and ergatoid females in it. The importance of this aspect of their reproductive biology is elaborated upon elsewhere in this paper.

4) On the gravel plains, ant species richness is strongly correlated with mean annual rainfall, an indirect indicator of productivity (Marsh 1986b). Thus, species richness increases progressively from the coast inland. A particular site on the gravel plains supports anything from six sympatric species (14 mm rain p.a.) to 23 species (87 mm rain p.a.). With three exceptions, all ant species occur at the eastern, more productive edge of the desert but penetrate the desert towards the west to different extents. One species, *Monomorium mantazenum*, is restricted to the cool, coastal fog zone and the other two species are apparently rare, having been collected at one or two sites only.

**Endemism**

It is not possible to make a reliable statement as regards the degree of endemism of the Namib ant fauna. Although many previously unknown species have been discovered in the Namib, the ant fauna of the rest of Namibia and surrounding countries, including South Africa, is largely unstudied. It is conceivable that many species occurring in the Namib also occur, and may be more abundant, in the semiarid habitats to the north, south and east of the desert. *Monomorium mantazenum* appears to be confined to the fog belt on the western edge of the Namib and it is therefore probably a Namib endemic. Similarly, *C. detritus* is confined to the sand sea and is undoubtedly a Namib endemic.

**Dietary patterns of Namib ants**

Since most ants are opportunistic foragers it is unrealistic to assign any species to a particular trophic group without some clarification. Here I have assigned a species to a trophic group if most of its diet consists of a specific food type. The diet of 27 Namib ants, from a wide variety of habitats, is sufficiently known to make some generalizations. Ten of the species are granivorous (harvester ants), ten honeydew/nectar feeders, three omnivores and three insectivores (Marsh, 1986a). One species, *Pheidole tenuinodis*, can be classified as either a granivore or a honeydew/nectar feeder depending on where it occurs, and illustrates the problems encountered when assigning a species to a trophic group.

Restricting the analysis to 12 sympatric species from the barren gravel plains on the eastern edge of the desert, is more illuminating. Seven of the species are granivorous (i.e., 58 % of the species), two are honeydew/nectar feeders, two omnivorous and one insectivorous (Marsh, 1985a). Most individuals (94,7 %) are granivorous making up 96,7 % of the total forager biomass. Harvester ants are therefore overwhelmingly the predominant trophic group in this ant assemblage. Their pre-dominance in deserts is attributed to the fact that they are primary consumers reliant upon a relatively dependable, nutritious food resource which can be stored for extensive periods (Carroll and Janzen, 1973). Within this species assemblage, the relative abundance of species ranges from rare to abundant, with two harvester species, *Messor denticornis* and *Tetramorium rufescens*, representing 90 % of the forager biomass (Marsh 1985a).

Numerically *T. rufescens* is the dominant species making up 42 % of the assemblage, whereas, in terms of biomass, *M. denticornis* is dominant, comprising 58 % of the assemblage. The above assemblage occurred on a barren gravel plain devoid of perennially green vegetation and characterized by episodic pulses of superabundant seed. In other habitats, however, other trophic groups may be dominant. For example, in the dune sea it is apparent, even without quantitative data, that the dominant ant in terms of biomass is *C. detritus*, a honeydew feeder. This habitat supports perennial grasses that support large numbers of honeydew-secreting homopterans (Curtis, 1985b). Although *Tetramorium jordani* is a numerically common granivore where grass occurs in the dunes, in terms...
of biomass, granivores are probably not very important in the dunes.

Adaptations facilitating species persistence

An important characteristic of many Namib ants that facilitates their persistence is their use of storable seeds. After episodic rainfall events, seeds are superabundant, enabling harvester ants to collect in excess of their immediate requirements, to store the surplus and later to use these seeds during periods of drought. Another important characteristic of Namib ants is their degree of opportunism and behavioural flexibility. These characteristics are particularly evident in terms of activity and diet (Marsh, 1985a, c, 1986c, 1988). Desert ants have several attributes that make behavioural plasticity advantageous if not essential. Colonies are relatively long-lived, permanently ‘rooted’ in the soil and individuals are small.

These attributes restrict exploitation of the surrounding habitat by a colony to a small area. From this habitat patch, a colony has to obtain all the resources necessary for its survival, growth and reproduction.

In an environment where food is spatially and temporally patchy, the ability to use diverse food types is clearly advantageous. Thus, although most species are classified as harvester ants, in reality they are highly opportunistic foragers taking a wide range of food types depending on availability and hunger. For example, when grass seeds are abundant, *M. denticornis* and *T. rufescens* exploit seeds exclusively but switch readily to non-seed food, especially insects, when seed availability is low (Marsh, 1986c). Shifts in diet are often accompanied by changes in foraging behaviour. For example, when seeds are abundant, *M. denticornis* uses extensive trunk trails that lead to specific patches up to 80 m away, but when seeds are rare, it switches to more localized diffuse foraging to facilitate the discovery of less spatially predictable food items such as mobile termites (Marsh, 1986c).

Epigaean desert ants also forage in a region where thermal conditions vary considerably on a diel and seasonal basis. Flexibility in the periods used for surface activity (mainly foraging) is therefore adaptive in that it enables ants to select appropriate microclimatic conditions. For example, in summer the majority of foraging excursions within a particular ant assemblage occur at night, whereas in winter, diurnalism predominates (Marsh, 1985a). Most strictly diurnal species have a unimodal pattern of activity (centred on mid-day) in winter and a bimodal pattern in summer (Marsh, 1988). Likewise, species that are nocturnal in summer become crepuscular in winter and thereby avoid thermally stressful conditions (Marsh, 1988).

In view of the foregoing discussion on opportunism and behavioural plasticity, it is conceivable that, at different localities, ants from one species could be consuming different food types and doing so at different times within the diel cycle. This is particularly likely in the central Namib where rainfall is extremely patchy (Seely, 1978), creating a mosaic of productive/unproductive habitats, and where there is a steep climatic gradient. This dynamic aspect of ant ecology is worth investigating.

Ecological dominance

Any species that can survive, grow and reproduce and thereby persist through time is by definition an evolutionary success; however, some species are much more abundant than others and could be construed as being more successful ecologically than rarer species. Investigations of these dominant species may reveal adaptations that are particularly important in a given environment.

On the eastern edge of the gravel plains there is evidence that the dominant ant species is *M. denticornis* (Marsh, 1985a), whereas in the dune sea the dominant species is *C. detritus* (Curtis, 1983). There are many characteristics that these two species share and that are generally not shared with other sympatric species. Both species are the largest ants in their respective habitats (*M. denticornis* total length 5.5–11.0 mm, *C. detritus* total length 7.0–16.0 mm); they exhibit continuous size variation; their colonies are polydomous, comprising up to four widely scattered nests; colony size is large comprising, several thousand individuals; both species derive most of their nourishment from temporally and spatially predictable food sources (Curtis, 1985b, c; personal observations). There are also some obvious differences between the two species. *Camponotus detritus* is a diurnal, highly aggressive honey-dew-feeding ant whereas *M. denticornis* is a nocturnal, unaggressive seed-harvesting species.

The ecological dominance of these species is indicative of their success as foragers. Large body size and hence long legs enables the ants to cover long distances efficiently and their foraging range is therefore large. In a desert environment where food sources are typically patchy, increasing the foraging range will increase the number of food patches encompassed by the colony. Polydomy further increases the foraging range substantially. An additional advantage that polydomy confers on these ants is that of spreading the risk of extinction (*sensu* Den Boer, 1968) and thereby minimizing the effects of catastrophic events. For example, a *M. denticornis* nest that was partially excavated by an aardvark resulted in mass emigration and resettlement of the nest occupants at a sister nest (personal observations). The presence of sister nests that remain untouched by predators means that even in the event of total destruction of one nest and its occupants, the colony remains alive. Furthermore, survivors from the destroyed nest rapidly find a place of refuge. Similarly, *C. detritus* nests become unsuitable for occupation from time to time when wind either deposits excessive sand on the nest or alternatively erodes too much sand from the nest and mass migration of adults and brood ensues (Curtis, 1983).

Large colony size is advantageous for much the same reasons advanced above with reference to catastrophe and spreading the risk. Furthermore, in a successful polydomous species each sister nest must be sufficiently large to facilitate ergonomic efficiency; a polydomous colony is therefore inevitably relatively large.

The advantages of continuous size variation are more elusive. It may ensure a more efficient division of labour in the colony (Oster and Wilson, 1978), but this aspect of social structure has not been rigorously quantified in either species. For example, it is possible that size matching between forager and food item occurs in *M. denticornis*. However, the importance of size matching remains questionable in an environment where most seeds retrieved are of one size only (Marsh, 1986c), but it could be important during prolonged droughts.
when seeds are scarce in the environment. Size matching between forager and food in the predominantly honeydew-feeding *C. detritus* is only evident on those rare occasions when large solid items are retrieved (Curtis, 1983). Therefore, it seems more likely that continuous size variation has evolved in *C. detritus* in response to the need to defend food-bearing host plants against conspecifics.

In *M. denticornis* continuous size variation may be an adaptation for trail construction. By clearing small pebbles off the trail, workers construct permanent trunk trails, leading from the nest to food patches (personal observations). These trails appear to be constructed in part as an incidental consequence of foraging activity (unsuccessful workers retrieve pebbles and thousands of foraging trips along the pathway inevitably displace loose pebbles to the side) and in part as a deliberate effort whereby workers pick up pebbles in their mandibles, deposit them off the trail and return to the trail to repeat the operation (personal observations). Large individuals may be best suited to carry these relatively heavy pebbles, whereas smaller workers would be adapted to carry seed. Work currently in progress indicates that trail-using foragers travel substantially more rapidly than non-trail users (Seely, personal communication), suggesting that the construction and use of trails enhances foraging efficiency and will be adaptive provided the costs of building the trail are more than offset by increases in food retrieval.

**Thermophilic ants**

Perhaps the most fascinating ants in the Namib are members of the strictly diurnal, insectivorous genus *Ocymyrmex* which have adopted a unique temporal niche, specializing in foraging during the heat of the day. *Ocymyrmex robustior*, for example, commences foraging activity when surface temperature approaches 30°C, has maximal activity at 52°C and only ceases activity as the temperature approaches 70°C (Marsh, 1985b, c). The ants possess a suite of morphological, physiological and behavioural features that enable them to forage during thermally stressful conditions. They have long legs, facilitating rapid locomotion and the exploitation of the steep temperature lapse profile above the desert floor, and low thermal inertia enabling them to rapidly offload excess body heat in cool thermal refuges (Marsh, 1985b). They can repeatedly tolerate high heat loads, in excess of 50°C, for short periods of time (Marsh, 1985b). They very effectively exploit the thermal mosaic, which even a barren desert floor presents to a small organism, employing thermal respite behaviour whenever heat stressed (Marsh, 1985b).

*Ocymyrmex* species are thermophilic because they usually scavenge heat- and desiccation-stressed prey, and by foraging during the heat of the day, obtain exclusive access to their prey (Marsh, 1985c). Foragers voluntarily tolerate potentially lethal heat loads on particularly hot and dry days when carrion is more abundant than usual (Marsh, 1985b, c).

In addition to their thermophilic behaviour, *Ocymyrmex* species exhibit highly plastic behaviour that facilitates their survival in desert environments. The ants are normally diffuse foragers, reflecting their spatially unpredictable food resource (Marsh, 1985c), but when a particularly rewarding food patch is located (e.g., a patch of active termites or a large carcass) a large proportion of the normal forager force as well as individuals that have not previously been outside of the nest, can be recruited to exploit the resource (Marsh, 1985c, 1986d). Heat is probably the dominant component of environment in the ecology of the Namib *Ocymyrmex* species, and definitely is for the *O. robustior* population living in the dry Kuiseb River bed. Heat generates their food, regulates the speed of locomotion and hence foraging range, regulates forager activity at the colony level, regulates the behaviour of individual foragers, regulates the intensity of predation from ant-lion larvae and acts as a stochastic malignity, killing foragers that are too slow to locate thermal refuges (Marsh, 1985b, c, 1987, 1988).

**Reproductive biology and social structure**

The ultimate measure of success for individuals of any species is whether they are able to reproduce themselves and thereby perpetuate the species. Desert environments pose particular reproductive problems to ants. The important component of environment for most desert organisms is rainfall. The rarity and unpredictability of rainfall ensures that mating and colony founding conditions are similarly rare and unpredictable. The pattern of rainfall also ensures that food resources are sparse. Although detailed investigations of reproduction in Namib ants has just commenced, certain patterns are evident from the little information that is currently known.

Dominant ant species, such as *M. denticornis*, *T. rufescens* and *C. detritus*, reproduce in the standard formicid manner. Colonies produce large numbers of fertile, alate males and females which typically have nuptial swarms after rainfall events (Curtis, 1985c, personal observations). Colonies are presumably founded by inseminated females immediately after the swarming event when the earth is still moist and capable of being excavated with relative ease. The majority of swarming reproductives are usually consumed by predators (Bolton, 1986; personal observations) and it is also possible that suitable conditions for swarming and colony foundation may not occur during the lifespan of certain reproductives. Such a pattern of reproduction is expensive and can represent a huge drain on colony resources. To reproduce successfully in this manner requires a large colony that has access to a dependable food supply.

The reproductive pattern that has evolved in the genus *Ocymyrmex* and in certain species belonging to the *Monomorium* Salomonis-group stands in marked contrast to the standard formicid mode of reproduction. In these species the reproductive females are apertoral and ergatoid, and autoparasitism followed by colony fission occurs (Bolton, 1986; Marsh, 1986d). That is, worker-like reproductive females remain in the mother colony for variable lengths of time after insemination and then start a colony by recruiting nest mates from the mother colony. Bolton (1986) suggests that autoparasitism and subsequent colony fission is adaptive in environments where food is sparse as it facilitates the production of a few females with high survival potential, thereby minimizing wastage of scarce resources.

*Ocymyrmex* colonies are monogynous but produce large numbers of ergatoids; on average *O. robustior* colonies comprise 13% virgin ergatoids (maximum 40%) and *O. tumeri* colonies have a mean of 14% virgin ergatoids. Furthermore, ergatoids and alate males are produced throughout the year. Such a system would be very wasteful of resources were it not
for the fact that uninseminated ergatoids adopt roles that are indistinguishable from those of sterile workers (Forder and Marsh, 1988). The efficiency of this role flexibility is enhanced by the fact that reproductive females are indistinguishable from sterile workers in size and gross morphology. Accordingly, it appears that Ocymyrmex species have evolved a reproductive system that is highly adaptive in an energy-poor, unpredictable environment. It is hypothesized that virgin ergatoids and males are produced on a regular basis to take opportunity of any suitable mating or colony founding conditions that may occur (Marsh, 1986d). If such conditions do not occur by an as yet unknown age, the ergatoid adopts worker roles and no longer represents a drain on colony resources but contributes positively to their acquisition. This hypothesis will undoubtedly require modification as new information is obtained. For example, it remains uncertain that excavation of new nests by a relatively large worker force can only take place after rainfall events. In fact, the evidence collected to date indicates otherwise. Information on reproductive phenology is required to facilitate a deeper understanding of the evolution of the unique social structure found in Ocymyrmex species. Similar studies of the reproductive biology of species of the Monomorium Salomonis-group in the Namib, could be very rewarding.

CONCLUSION

Studies of ant ecology and biology in the Namib Desert are in their infancy. Inevitably, the pioneering research has tended to be descriptive in nature. While there remains a need for further basic descriptive work, it would be opportune to start building upon the initial foundation using a more rigorous approach that attempts to answer certain specific questions. Many questions could be addressed from further systematic collecting of ants. In the central Namib, the regions that deserve special attention are the dune sea and the Kuiseb River. Beyond this relatively well-studied area of the Namib, surveys are urgently needed in the northern and southern Namib as well as in the regions immediately to the east of the Namib. Surveys are also required in all semiarid and arid areas of southern Africa. Only once these have been carried out will we be able to see the Namib fauna in context. From such surveys it will become possible to answer fundamental questions such as: Why are the Dorylinae and Ponerinae excluded from the Namib and how close to the Namib do they occur? Why is the genus Monomorium so prevalent in the Namib? How many Namib endemics are there?

More detailed ecological studies at specific sites would be appropriate to answer questions such as: What is the relative importance of different trophic groups in the dune sea and how does this compare to that found in ants that breed in the conventional desert shrub community? What are the energetic similarities and differences in reproductive biology and social structure in these two groups of ants? What is the energetic cost of the social system in the above ants and how does this compare to that found in ants that breed in the conventional formicid manner such as Messor denticornis and Camponotus detritus?

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**Appendix I**

In several of the early papers by Marsh, many of the ant species were either not described or their taxonomy was in the process of revision at the time of going to press. Consequently, code letters were used for these species. The correct species names for *Monomorium* species are:

- B = *vatranum*
- C = *alamarum*
- D = *mictilis*
- E = *drapenum*
- F = *mantazenum*
- G = *katir*
- H = *eshare*
- I = *marshi*
- J = *nirvanum*
- K = *kitectum*

*Ocyomyrmex barbiger* = *O. robustior.*
The Biology of *Leucorchestris arenicola* (Araneae: Heteropodidae), a Burrowing Spider of the Namib Dunes

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The ecology, distribution, behaviour and life history of *Leucorchestris arenicola* Lawrence, 1962 (Araneae: Heteropodidae), a 2–5 g endemic spider of the central Namib Desert, were studied over a 20-month period. These spiders live in 33 ± 13 cm long silk-lined burrows, which are constructed in firm dune sand on dune bases and lower dune plinths. Foraging activity is inversely related to light intensity, wind speed and fog condensation. They capture prey on the surface about once a month and usually consume it in the burrow. Coleoptera form the bulk of the diet, followed by Lepidoptera and conspecific spiders. Small vertebrates are rarely eaten. Foraging activity, reproduction and development rate are seasonal, with a 4 to 5-month period of quiescence in winter. Females lay an average of 76 eggs per clutch and tend offspring for about 75 days. On average, nymphs moult every 85 days in summer and every 156 days in winter. Adulthood is reached in the 10th instar at an age of 2 years. Adult males are short-lived (1–2 months) and travel long distances (20–450 m) in pursuit of mating opportunities, while adult females are philopatric, long-lived (6–15 months) and produce up to three egg clutches in a breeding season. Territoriality and cannibalism of juveniles favour site fidelity and avoidance of neighbours at distances of about 4 m. Predation by gerbils and conspecific spiders could limit populations in a density-dependent manner. This spider appears to have a K-selected life history pattern, in which relatively constant annual food availability, variable risk of predation and climatic seasonality favour slow development, high longevity, small brood size, iteroparity and extended brood care.

**INTRODUCTION**

Desert sand dunes, such as are found in the Namib, are characterized by sparse vegetation, loose substrate, strong winds and a dry and thermally fluctuating surface climate (Robinson and Seely, 1980; Louw and Seely, 1982). Such desert climates do not favour aerial web-building spiders so that nocturnal wandering spiders predominate, which have specialized morphological and behavioural traits that enable them to burrow and hunt in and on sand (Main, 1957; Chew, 1961; Cloudsley-Thompson, 1983).

Spiders are an important but little studied component of the Namib dune fauna. Knowledge is limited to faunistic data and anecdotal descriptions of their biology (Lawrence, 1959, 1962, 1965a, b, 1966; Holm and Scholtz, 1980; Robinson and Seely, 1980; Wharton, 1980). Lawrence (1959) first noted the importance of large heteropodids in the Namib dunes and a discussion of distribution in different Namib dune habitats of some heteropodids was presented by Holm and Scholtz (1980).

One Namib heteropodid, the dancing white lady spider *Leucorchestris arenicola* Lawrence, 1962, is particularly well suited for ecological and physiological study owing to its large size, abundance, ease of handling and detectability in the field. The ability to track the movements of these spiders by their footprints on the smooth sand surface and to regularly inspect and recognize known individuals in their burrows without disturbing them provided a rare opportunity to investigate such aspects of their ecology as have seldom been recorded for desert spiders. These aspects include their spatial relationship to the environment, their foraging and reproductive behaviours and, ultimately, their long-term life history strategies.

In the present paper, I present details on the biology of *L. arenicola*, including morphology, distribution, habitat use, burrow structure, foraging behaviour and predator-prey interactions, reproduction, development, population ecology, intraspecific and intraguild relationships, and mortality. Characteristics and environmental determinants of these aspects are compared with patterns exhibited by other wandering arachnids in deserts and in more mesic zones. With these data, I re-examine the hypothesis that biotic interactions may not be as important to many desert invertebrates as physical factors (Noy-Meir, 1973). Further details relating to diet, reproduction and population ecology of *L. arenicola* are being gathered for future presentation.

**STUDY AREA AND METHODS**

**General study area**

*Leucorchestris arenicola* were studied from October 1986 to June 1988 at 26 sites within the area 23–24° S, 14–16° E of the central Namib Desert. During a general survey, 143 *L. arenicola* were collected from burrows and 108 empty burrows were excavated at 15 sites. The habitat classification of Robinson and Seely (1980) was adopted.

**Burrow and spider measurements**

At all 26 sites, tracks left by active *L. arenicola* on the smooth sand surface, which were especially visible after sunrise, facilitated the discovery of burrows. Burrows located in this way were used for density estimates in some areas on
6 m-wide line transects according to the method of Burnham, Anderson and Laake (1980).

The following measurements were made on excavated burrows (Fig. 1): slope (\(\theta\); SS) of sand surface at burrow entrance, diameter of trapdoor (mm; TD), burrow circumference estimated as twice the measured width of the collapsed burrow (mm; BC), burrow slope (\(\theta\); BS) for the first 30 cm of its length, burrow length (cm; BL) and vertical depth of burrow (cm; BD). Prey remains were collected from all burrows for identification by comparison with voucher specimens.

Spiders were captured from excavated burrows or in a specially designed trap (Henschel, in press). The age, sex and live mass (± 0.1 mg) were determined and the following measurements (± 0.1 mm) were taken: maximum width of carapace; prosoma (cephalothorax) length from the dorsal centre of the clypeus edge to the posterior end of the sternum ventrally; ventral width of opisthosoma (abdomen); dorsal length of opisthosoma; body length from clypeus to base of anal tubercle; and length of the sclerotized shaft of left femur I antero-laterally. Regression equations interrelating body dimensions were calculated and coefficients of determination obtained for their simplified formulas. For all mean values throughout this paper, ± one standard deviation is indicated.

**Intensive Study Area**

A fenced site of 0.75 ha (Visnara) was established on a flat stretch of interdune sand 1 km S of Gobabeb (23° 34' S, 15° 02' E) for an intensive study of reproduction, development and population ecology. The vegetation at Visnara consisted of a sparse covering of grasses, *Stipagrostis ciliata*, *S. gonato-stachys* and *Centrapodium glaucum*, and a cucurbit, *Acanthosicyos horridus* (Nara). On the northern side, this area was bordered by riparian vegetation: *Acacia erioloba*, *Euclea pseudebenus*, *Tamarix usneoides* and *Salvadora persica*. Meteorological conditions were monitored at the first order weather station at Gobabeb.

The herbivorous and detritivorous invertebrate fauna at Visnara comprised a diverse community of dune and riverine origin, dominated by tenebrionid, scarabid and curculionid beetles, moth larvae and adults, termites and ants. In addition to *L. arenicola*, the spider fauna consisted of a gnaphosid, *Asemesthes lineatus*; two eresids, *Seothyra* sp. and *Gandanomeno echinatus*; three salticids; one philodromid; and one dysderid. Other predators of possible significance to *L. arenicola* were geckos, *Palmatogecko rangei* and *Ptenopus* spp.; a legless lizard, *Typhlosaurus braini*; scorpions, *Opisthopthalmus flavescens* and *Parabuthus villosus*; a pompilid wasp, *Schistonyx aterrimus*; solifugids, *Metasolpuga picta*, *Prosolpuga schultzei*, *Solpugista bicolor* and *Unguiblissa cauduliger*; gerbils, *Gerbillurus paeba*, *G. tytonis* and *Desmodillus auricularis*; jackals, *Canis mesomelas*; mongooses, *Galerella sanguinea*; genets, *Genetta genetta*; owls,
**Bubo africanus** and Tyto alba; and various passerines, especially *Mirastra erythrostolmys*, Cercomela familiaris and Picronotus nigricans.

**Activity, life history and demography**

During the course of intensive observations at Visnara from October 1986 to April 1987, all burrows of *L. arenicola* in a 0.5 ha area were marked with numbered flags placed 20 cm from the burrows. Spider activity was monitored by observations at night and by following tracks in the early morning, which provided detailed records of the spiders' activities on the sand surface. Burrow occupation status was ascertained by signs of activity at entrances. Data were collected for 79 nights during which 8836 observations were made of 312 burrows.

During further intensive studies from June 1987 to June 1988 at Visnara, activity data for *L. arenicola* were recorded as above for 7241 observations of 319 burrows on 122 nights in a 0.33 ha area. Nearly all individuals were captured and later recaptured after moult (n = 309). Individuals were identified, measured, and marked using five colours of water-soluble fluorescent paint (Plaka) in various combinations. Paint was applied to the central dorsal surfaces of leg patellae, areas on the legs apparently without important sensory functions. Spiders excavated were released at the capture sites and protected in enclosures until they constructed new burrows. Trapped spiders were returned to their burrows. At approximately fortnightly intervals, optometrist's and dentist's mirrors were used to look into burrows to verify the identity and reproductive status of their occupants.

Burrows of reproducing females were examined at shorter intervals (usually < 7 days) to determine nymphal stages and their duration, litter size, development rate and duration of maternal care. After the nursery burrow was abandoned, it was excavated and all exuviae of nymphs were counted.

The minimum duration of each post-nursery instar was determined from the interval between two observed mouling events (n = 85). Half the interval between sightings was added to the minimum period to estimate the duration of instars. The total number of instars was calculated from successions of recorded nymphal stages of individuals that were first marked at a very young age or finally recaptured as subadults or adults.

**RESULTS AND DISCUSSION**

**Table 1**

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<tr>
<th>Carapace Width</th>
<th>Mass</th>
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<td>1.01 x Femur I</td>
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<tr>
<td>0.59 x Trapdoor diameter 0.93</td>
<td>0.83</td>
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<tr>
<td>0.22 x Trapdoor diameter 2.741</td>
<td>0.79</td>
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**Identification of sexes**

Live adults, subadults and some pre-subadults could be sexed in the field on the basis of epigynum and pedipalps. These individuals of known sex were used to define other sex-related attributes. Of all other external characteristics examined (eye arrangement, leg spination, pedipalp structure, tibial claws, dimensions of prosoma, opisthosoma and legs), only leg spination was found to be a useful guide to sex. A median dorsal spine on the tibia was found on most (5-8) legs of adult and subadult males. This spine was rarely found on legs of adult and subadult females and then only on a maximum of 4 legs. The presence of this feature on five or more legs thus provided a guide for sexing juvenile males older than nymph stage III (carapace width > 7 mm). The sex of younger individuals could not be determined.

**Morphology**

Desert spiders are often larger than close congeners in less arid habitats, and as a result have low surface-to-volume ratios (Remmert, 1981; Clodseley-Thompson, 1983). *Leucorchestris arenicola* is large, up to 5.0 g (X = 1.7 ± 0.9 g) and 32 mm (X = 20.9 ± 4.8 mm) body length; adult females are usually heavier than adult males (2.6 ± 0.9 g vs. 2.0 ± 0.5 g; t = 5.43, d.f. = 120; P < 0.05). Legs of males grow allometrically during the moult to adulthood, attaining a final standing leg-span of 10–14 cm (6–9 cm for adult females).

Hagstrum (1971) found that carapace width corresponded closely with instar stages of 13 spider species. As carapace width correlated with mass, he concluded that it can be used as a field guide to size and development stages of many species. In *L. arenicola*, carapace width was 2.1–14.0 mm (X = 9.4 ± 2.1 mm; n = 386). Where it could not be measured without injuring a spider, it was estimated for nymphs and adult females from the length of the sclerotized shaft of left femur I (Table 1). A simple linear relationship could not be established for adult males because of the allometry described above (R² = 0.45; n = 36).

Live mass was difficult to measure accurately in the field, but could be estimated on the basis of body length, carapace...
width, abdomen width and abdomen length (Table 1).

**Distribution and habitat**

*Leucorchestris arenicola* appears to be confined to the southern Namib dune sea and adjacent sandy areas (Fig. 2). It lives in the central, warm, foggy zone and the warm, inland zone where high daily fluctuations of temperature and humidity occur (Besler, 1972; Lancaster, Lancaster and Seely, 1984). It is rare or absent in the cold, foggy, coastal, crescentic dunes that extend approximately 20 km inland from the coast. This may be due to an unsuitable climate dominated by strong winds, or a scarcity of adequate habitat. Their distribution is limited in the east by the edge of the dunes and in the north by gravel plains abutting the Kuiseb River. The southern limit is unknown. *Leucorchestris sabulosa*, which may be synonymous with *L. arenicola*, is the southernmost *Leucorchestris* captured at 27° 30' S, 15° 45' E (Lawrence, 1966).

Relatively open stretches of firm, gently sloping dune sand with sparse vegetation were favoured by *L. arenicola*. Burrows were usually found within 1 to 10 m of plants (96 %). The abundance of *L. arenicola* decreased up dune slopes: 91.0 % were collected on dune bases and interdune sand accumulations surrounding vegetation mounds, 7.4 % on the lower plinth, 1.4 % on the upper plinth and only 0.2 % on the slipface. These proportions differed from the proportion of surface area covered by these habitats (Fig. 3), indicating selection ($\chi^2 = 73.6; d.f. = 4; P < 0.05$) and contradicting Holm and Scholtz's (1980) conclusion that the Heteropodidae ($n = 16$ individuals of three species) did not appear to have strong preferences for different dune habitats. During the present survey, other heteropodid species were found in habitat adjacent to that dominated by *L. arenicola*: *Carparachne aureoflava* and *C. alba* on the upper dune plinth, slipface and dune crest; *Orchestrella browni* and *O. longipes* on the interdune gravel plains.

**Burrow structure**

*Leucorchestris arenicola* lives in straight, silk-lined burrows dug at an angle into sand (Fig. 1; Table 2). Spiders excavate burrows by removing sand from the base of a circular depression as described by Lawrence (1965a). The leg coxae, and curled pedipalps bearing stiff interlocking setae, are used to push loose sand sideways up to the entrance. Sand is dispersed from the entrance by flinging it sideways with the brush-like tarsal scapulae. The lower end of the depression is secured by lifting and interweaving loose sand with adhesive silk from the spinnerets and pressing the sand-silk mixture into the substratum. This forms a nodule of silk and sand embedded in the surrounding sand. The burrow end is secured with 25-35 adjacent nodules in an arc of about 330° (Fig. 1). A 3-10 mm wide floor remains free of silk along which sand is pushed to the entrance. The spider lengthens the burrow by 3 to 6 mm before securing another arc of silk nodules; additional arcs may be added at any time. The entrance is closed with a reinforced curtain of silk and sand. The rim is later severed to form a thin (c. 1 mm) circular trapdoor, flush with the sand surface (Fig. 1). A moderate wind suffices to obscure signs of the burrow.
Spiders position themselves anywhere along the length of the burrow in an upside-down posture facing the side of the burrow (Fig. 1). The feet are in contact with the roof and appear to be sensitive to vibrations on the sand surface.

Trapdoor diameter and burrow circumference varied with body size and could be used to estimate the occupant’s size (Table 1). Burrows were usually constructed in firm sand of a gentle slope (Table 2). They rarely occurred on steeper slopes associated with vegetation mounds or slipfaces. Burrow slope was $28 \pm 3^\circ$ from the horizontal, slightly less than the angle of repose ($33^\circ$), the maximum slope at which dry sand can be swept upwards. If surface slopes were $> 15^\circ$, some burrows ($n = 7$) were at angles of $< 20^\circ$. Burrows with slopes of $33-40^\circ$ were sometimes ($n = 6$) built in moist sand.

*Leucorchestris arenicola* often failed to make burrows if kept in darkness in the laboratory, but burrowed when exposed to light, suggesting that light may elicit burrowing behaviour. Similar responses have been reported for other nocturnal desert arachnids (Polis, Myers and Quinlan, 1986).

The use of burrows for protection from extreme desert climates is well known for arachnids (Polis et al., 1986). In the case of *L. arenicola*, the vertical depth of the burrow end (Fig. 1), usually approximately 25 cm, provided a suitable microclimate, which differed considerably from that at the surface (Lancaster et al., 1984; Seely and Mitchell, 1987). Burrow depth did not relate to surface slope ($r = 0.06$), but was primarily a function of burrow length ($d = length \times 0.55$; $r^2 = 0.81$; $n = 210$).

Of 631 burrows monitored at Visnara, 5.3% were temporary shelters used for one day only. All others were occupied for a mean of $68 \pm 53$ days up to a maximum of 460 days. With one exception, re-use of an existing, vacant burrow by a second individual was not observed.

---

**Table 2**

Measurements of 560 *Leucorchestris arenicola* burrows from 15 sites in the central Namib Desert (Fig. 1).

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Unit</th>
<th>Mean ± S.D.</th>
<th>n</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Surface slope (SS)</td>
<td>°</td>
<td>8.7 ± 6.8</td>
<td>358</td>
<td>0–33</td>
</tr>
<tr>
<td>Burrow slope (BS)</td>
<td>°</td>
<td>28.4 ± 3.4</td>
<td>314</td>
<td>14–40</td>
</tr>
<tr>
<td>Trapdoor diameter (TD)</td>
<td>mm</td>
<td>19.6 ± 4.1</td>
<td>433</td>
<td>7–30</td>
</tr>
<tr>
<td>Burrow circumference (BC)</td>
<td>mm</td>
<td>80.8 ± 18.0</td>
<td>415</td>
<td>26–48</td>
</tr>
<tr>
<td>Burrow length (BL)</td>
<td>cm</td>
<td>33.4 ± 13.4</td>
<td>437</td>
<td>7–125</td>
</tr>
<tr>
<td>Burrow depth (BD)</td>
<td>cm</td>
<td>23.5 ± 7.0</td>
<td>216</td>
<td>4–48</td>
</tr>
</tbody>
</table>

---

**Foraging behaviour and resources**

Similar to large desert spiders elsewhere (Cloudsley-Thompson, 1983), Namib heteropodids are predominantly nocturnal. Diurnal activity in *L. arenicola* was observed in April 1987 during termite eruptions following rainfall of 14 mm. It was apparent from the behaviour of captured spiders which were released in the heat of the day, that diurnal conditions were stressful; moreover, their light colour against the reddish-brown sand rendered them conspicuous to predators. When released during the day, spiders commenced burrow construction immediately and sealed the entrance within 15 minutes when the burrow was about 10 cm long. Spiders sought plant cover when the sand was too hot for burrowing. Prey was usually not captured by day, but diurnally active prey species were sometimes caught at dusk.

Other limitations to activity appeared to be cold nights (ambient temperature $< 15 ^\circ C$), bright moonlight ($\geq 3/4$), strong wind ($> 5$ m/s) and condensing fog, which made the trapdoors clammy. Reduced activity during strong wind could be due to sand abrasion or the high noise level of moving sand particles which would mask prey and predator vibrations.

The eight eyes of *L. arenicola* are relatively small and probably are not important in locating prey. It most likely detects potential prey through the vibrations the latter makes when moving on the sand surface. Such surface vibrations are transmitted over long distances (Reichmann, personal communication) and are probably detected by sensitive mechanoreceptors (tactile hairs, trichobothria and slit sensilla; Foelix, 1982; Barth, 1982) on the legs of *L. arenicola*, which would enable it to orientate accurately towards the prey, as is the case in the Central American ctenid *Cupiennius salei* (Hergenröder and Barth, 1983).

Two methods of foraging were observed in *L. arenicola*. They generally rushed out of their burrows to intercept approaching prey at distances of up to 3 m. On occasion, spiders hunted actively on the sand surface within 3 m of their burrow. At Visnara, only 47% of the population ventured from their burrows on a given night. Of these, 75% remained within 1 m and 92% within 3 m of the burrow. Nearly all of those that travelled further were adult males apparently in search of mates, or, on rare occasions, any other spider that immigrated.

An attack on prey involved a short jump, re-orientation, seizing the victim with the front legs and pedipalps, and biting immediately. The fangs penetrated exoskeletons of tenebrionid and scarabid beetles ventrally, contrary to earlier...
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Although the fangs injected venom (observed when biting into plastic), its potency appeared to be low. For example, a Namib tenebrionid beetle which was bitten, initially became paralysed, but recovered completely three days later. A bite by Leucorchestris arenicola merely caused local irritation in a person. Another large heteropodid, Palystes natarius, has very low toxicity to larger vertebrates (Newlands and Martindale, 1981), even though it occasionally captures small vertebrates (Warren, 1923).

A distinctive record of prey capture in the form of intermingled tracks of predator and prey was left on the sand near the burrow; drag marks often led away from the capture site to the spider's burrow. Although small prey items (<0.2 g), such as termites, did not leave distinctive traces in the sand, most other prey could be identified on the basis of their tracks. Prey capture was recorded 186 times on 122 nights at Visnara during 1987 and 1988 and the estimated annual predation rate was 1670 prey captures/ha.

In summer, September to March, the average interval between prey captures for a spider was 31 nights and on average 3.2% of the spiders caught prey on a given night, with a maximum of 14% in December. In winter, the capture rate dropped to 1.5% per night and most Leucorchestris arenicola became quiescent, some even torpid, possibly in response to adverse climate as is the case in other desert spiders (Riechert and Bennett, 1980), may obviate the need for emigration during periods of temporary food scarcity (Anderson, 1974).

The soft parts of prey were chewed into tight balls, whereas harder cuticle, such as elytra or legs, often remained intact. Prey remains were stored at the base of the burrow. Analysis of 377 prey items collected from 145 burrows (Table 3) showed that the diet reflected prey availability. Approximately 80% of their prey consisted of Coleoptera, half of which were tenebrionid beetles, thus confirming previous incidental observations (Holm, 1970; Seely, 1985). The curculionid Leptostethus waltoni was the most frequently captured single species (14%). Lepidopteran larvae and adults represented 8% of the items and were also important in terms of biomass. Termites were sometimes captured and eaten on the surface, as evidenced by spider tracks leading to Hodotermes mosambicus exit mounds where chewed termite remains were seen, but their importance in the diet appeared to be relatively low.

Chewed remains of Leucorchestris arenicola were found in 21 of 214 burrows and cannibalism was confirmed by direct observations. Conspecifics formed 4% of the prey items, but could be more important in terms of biomass. Occasionally, remains of other unidentified spider species, dune scorpions (Opisthopthalmus flavescens) and solifugids (Metasolpuga picta and Prosolpuga schultzei) were found (n = 12). Some of these were bigger than their captors.

The remains of small geckos, Pamatogecko rangei, were found only three times and represented about 0.3% of the spiders' diet items (Table 3). Two of these were excavated after evidence from tracks and drag marks suggested that geckos had been captured. Based on a set of tracks, Lawrence (1959, 1962, 1965b, 1966) noted that Leucorchestris arenicola preyed on P. rangei, but did not mention observing drag marks from the attack site to the spider's burrow. This original observation has been construed as evidence that all major genera of Namib dune heteropodids frequently prey on geckos (Lamoral, 1971; McCormick and Polis, 1982; Newlands, 1987).

Although vertebrates may be minor diet items of arachnid predators that have low toxicity venom, McCormick and Polis (1982) found that their impact on certain vertebrates that are smaller than them can be substantial. The size of the Namib palmatogeckos taken by Leucorchestris arenicola could not be established, but judging by skeleton fragments they were probably lighter than the spider.

Leucorchestris arenicola must have water to survive. In the laboratory, they died within three months if kept with food but without water. Water was imbibed directly when it was offered on wet cotton wool. Possible sources of water in the field include metabolic water and free water content of prey and condensed fog or dew water, which might be obtained by drinking from drenched trapdoors in a manner similar to that observed in the laboratory with wet cotton wool.

**Reproduction and development**

Reproduction was strongly seasonal in the population studied at Visnara. Adult females were present throughout the year, forming 10 to 30% of the population. In contrast, adult males were absent in winter (May to August of 1987 and 1988). Many males moulted to adulthood in September, reached peak abundance (8–12% of the total population) in October and declined in abundance until May (<5%). The frequency of mating and the number and size of egg clutches and litters all peaked in December. No mating or egg clutches were observed from May to August.

**Table 3**

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Number of species</th>
<th>Percent items</th>
</tr>
</thead>
<tbody>
<tr>
<td>Insecta</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Coleoptera</td>
<td>30</td>
<td>48</td>
</tr>
<tr>
<td>Curculeionida</td>
<td>4</td>
<td>22</td>
</tr>
<tr>
<td>Scarabaeidae</td>
<td>3</td>
<td>8</td>
</tr>
<tr>
<td>Other</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Lepidoptera</td>
<td>&gt;1</td>
<td>8</td>
</tr>
<tr>
<td>Hymenoptera</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>Orthoptera</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>Other</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Arachnida</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Araneae</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>L. arenicola</td>
<td>&gt;2</td>
<td></td>
</tr>
<tr>
<td>Scorpionida</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>Solifugae</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Squamata</td>
<td>1</td>
<td>0.3</td>
</tr>
<tr>
<td>Reptilia</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gekkonidae</td>
<td>&gt;58</td>
<td></td>
</tr>
</tbody>
</table>

Mature Leucorchestris arenicola males frequently (on average every 4th
and abandoned the burrow.

Eggs 26.3 ± 19.6 1–74 24 75.8 ± 59.0 25–161 4
Larvae 13.0 ± 7.2 1–23 15 45.1 ± 31.5 1–95 18
Nymphs I 8.8 ± 9.2 1–35 24 8.0 ± 9.2 2–25 6
Nymphs II

* Live juveniles were difficult to count accurately until the female abandoned them at nymphal stage II.

This was probably underestimated, as the exuviae of larvae were fragile and difficult to count.

Table 4
Litter size of juvenile stages of *Leucorchestris arenicola* at Visnara determined by counting live young seen within burrows, or by counting excavated exuviae.

<table>
<thead>
<tr>
<th>Instar Development stage</th>
<th>Mean</th>
<th>Range</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nursery</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1 Egg and pre-larva</td>
<td>15 ± 3</td>
<td>9–19</td>
<td>13</td>
</tr>
<tr>
<td>2 Larva</td>
<td>13 ± 3</td>
<td>10–16</td>
<td>8</td>
</tr>
<tr>
<td>3 Nymphal stage I</td>
<td>23 ± 10</td>
<td>12–38</td>
<td>10</td>
</tr>
<tr>
<td>4 Nymphal stage II</td>
<td>33 ± 9</td>
<td>22–45</td>
<td>14</td>
</tr>
<tr>
<td>Female with nymphal stage II</td>
<td>14 ± 9</td>
<td>4–34</td>
<td>13</td>
</tr>
<tr>
<td>Female with brood</td>
<td>75 ± 19</td>
<td>59–115</td>
<td>8</td>
</tr>
<tr>
<td>Between broods</td>
<td>44 ± 21</td>
<td>14–77</td>
<td>12</td>
</tr>
</tbody>
</table>

Post-nursery

4 Nymphal stage II | 52 | 1 |
5 Nymphal stage III | 84 ± 43 | 38–128 | 4 |
6 Nymphal stage IV | 98 ± 4 | 95–101 | 2 |
7 Nymphal stage V | 95 ± 66 | 38–278 | 14 |
8 Nymphal stage VI | 114 ± 61 | 32–249 | 19 |
9 Nymphal stage VII | 118 ± 42 | 37–204 | 31 |
10 Adult male | 47 ± 29 | 17–98 | 22 |
10 Adult female | 130 ± 79 | 31–483 | 47 |

While on the nursery, adult females hunted frequently and carried prey into the burrow. This food source may have been utilized by the nymphs since the total mass of litters increased about five-fold during nymphal stages I to II, but no data are available to support this notion. Some social or periodic-social spiders exchange food by trophallaxis or indirectly via the prey (Foelix, 1982; Lubin, 1982). This has not been studied in asocial species such as *L. arenicola* that have extended brood care. Attempts in the laboratory to raise two litters of orphaned *Leucorchestris* stage I nymphs, using crushed insects as food, failed.

On one occasion, an adult male from a burrow 22 m away provided stage II nymphs with prey after the female had left the nursery. He caught a large moth, dragged it 1 m into the nursery and returned to his burrow. The nymphs were feeding on the moth upon excavation. All other observations indicated that only the female provided food to her offspring.

The reproductive cycle was estimated at about 120 days, based on observed durations of maternal care and periods between successive broods (Table 5). In one year 58 adult females produced 44 litters, or 0.76 litters/female/annum. Some females moved in from or to adjacent areas, giving rise to a slight underestimate in their reproductive rates. In one breeding season 45 % of the adult females produced no offspring, 40 % produced one litter, 10 % two and 5 % three
litters. One female produced 5 litters in two breeding seasons.

Kessler (1971) noted that the size of eggs of female wolf spiders remains constant, but egg clutch size varies as a function of food supply. In L. arenicola, it appears that both egg clutch size and the interval between clutches may vary, while some females fail to produce any clutches in a breeding season. Differences in egg sizes were not detected.

Within a month of reaching nymphal stage II, the number of spiderlings in a litter decreased to about 9 (Table 4). No dried-up carcasses of nymphs and no evidence of early dispersal or interspecific predation were found, thus suggesting that nymphs cannibalized siblings. However, cannibalism cannot account solely for the 42-fold increase in the mass of juveniles while in the nursery. Sibling cannibalism is not uncommon among communal spiderlings of non-social species (Tumbull, 1973; Polis, 1981). Resorption or consumption of eggs by a female as well as sibling cannibalism can be considered bet-hedging by desert arachnids and would enable rapid population response to favourable conditions (Polis, 1988).

At approximately 70 days and 169 g (Table 6), remaining stage II nymphs constructed a small exit next to the trapdoor of the nursery and built individual burrows close by. They moulted to nymphal stage III about 52 days later. Each subsequent moult occurred at a mean interval of 110 ± 54 days (32–278 days; n = 85). The moultling interval did not differ significantly between nymphal stages (Table 5: f < 0.94), nor with size or magnitude of size change (carapace width; r < 0.16), but varied seasonally (see below).

Between successive nymphal stages, carapace width increased by 1.1 ± 0.7 mm, body length by 2.3 ± 1.9 mm and mass by 144 ± 44 % of initial mass (n = 55; Table 6). This was similar for both sexes. Measurements taken one day before and after ecdysis from nymph stage IV to V indicated that carapace width increased by about 20 % at the expense of a 20 % decreases in abdomen length and width. For nymphs of stages III to VII, the average rate of mass gain was 7.4 ± 10.8 mg/day (n = 53). However, some spiders (28 %) lost mass between instars, although they usually increased in carapace width. Normally this occurred if they moulted without having fed. Sometimes a large decrease in mass (> 0.5 g) was caused by the loss of a limb or of haemolymph due to injury.

Adult males were no heavier than subadults (Table 6), and they did not appear to feed in the field although they sometimes accepted food in the laboratory. The size of adults, especially females, varied considerably: by a factor of two for carapace width and body length, and by a factor of eight for mass (Table 6). Their mass could increase rapidly by as much as 50 % after eating a large prey item, or drop by 15 % when they laid eggs. Similarly, adult size of some other spiders varies by a factor of two for carapace width and by a factor of 12 for mass (Jocqué, 1981; Vollrath, 1987). Because of this, it is impossible to estimate the age or nymphal stage from size for L. arenicola beyond nymphal stage III.

Pronounced seasonality in activity was evident. According to the classification of Schaefer (1977, in Foelix, 1982), L. arenicola can be classified as a eurychronous species that overwinters in various stages of development. All L. arenicola instars lasted significantly longer in winter, between April and August, than in summer, September to March (156 ± 42 vs. 85 ± 41 days; t = 8.99; df = 59; P < 0.05). In winter, the rate of prey capture dropped to less than half the summer rate (see above). Adult males were absent and females were reproductive inactive. Some spiders were in a torpid condition. It is not unusual for spiders to reduce activity and prolong development in winter (Almqvist, 1969).

Successive recaptures indicated that L. arenicola of both sexes have a total of 10 instars. No evidence was found that this may vary as it does in some other spiders (Vollrath, 1987). From pre-larva and larva, L. arenicola went through seven nymphal stages, reaching adulthood at 24 months of age. This age was calculated by adding the nursery and the post-nursery nymph II periods (70 and 52 days respectively) to two winter and three summer instar periods (156 and 94 days each respectively) to give a total of 716 days. Adults were not observed to moult. Upon reaching adulthood, males survived for only 47 ± 29 days. In contrast, adult females survived for at least 130 ± 79 days (maximum 463). Discounting mortality by predation, the life expectancy of females was 30–40 months.
Old females sometimes \((n = 4)\) displayed aberrant behaviour. Becoming very aggressive, they abandoned territories and moved burrows frequently. They eventually failed to construct proper burrows (burrow length < 5 cm), which became too hot in the day; these were abandoned in favour of shelter amongst plants. At night, these females moved into other territories, where they wounded or killed the residents if challenged. Eventually, they died of heat stress in shallow burrows, or were wounded or captured by predators.

In general, the phenology of \(L.\ arenicola\) appears to be similar to that of a Sonoran Desert wolf spider, \(Lycosa caroliensis\), which has a period of quiescence in winter and is most active and has the largest proportions of adults in mid-summer. Females of this wolf spider produce two litters per season, development is relatively slow, and sexual maturity is achieved only in the third year of life (Shook, 1978).

### Population ecology

Within a suitable habitat, densities of \(L.\ arenicola\) varied spatially and temporally. In addition to seasonal fluctuations of mature males and of reproducing females, a major factor influencing population density appeared to be predation (see below). The estimated abundances ranged from 9/ha in winter on a dune plinth at Khommabes, 5 km from Visnara, to a peak of 302/ha in summer at Visnara (Table 7); the wet biomass ranged from 15–513 g/ha.

Between June 1987 and June 1988, 58 adult females and 22 adult males were resident in 0.33 ha at Visnara. Another 12 males wandered through the area. During that year, 44 litters were produced with approximately 9 stage II nymphs entering the population from each litter (Table 4). The potential recruitment rate was thus 1188/ha/annum, or 6.8/female/annum. Assuming that emigration balanced immigration for all instars and that recruitment and development rates were similar in previous generations, the probability of post-nursery nymphs surviving to adulthood was calculated as 0.134 (egg to adult: 0.016).

Visnara had a peak of 81 burrows \((0,025/m^2)\) on 8 January 1988. These were occupied by 24 adult females (4 of which had a total of 55 nymphs), 1 adult male, 14 subadult females, 6 subadult males and 33 immature spiders, with a total mass of 111 g. The population was distributed unevenly: 52% of the burrows occurred in 24% of the area \((0,05/m^2)\) with a maximum of 0.11 burrows/m² in one patch of 0.01 ha.

Females and nymphs of other species of wandering spiders have relatively small home ranges (Turnbull, 1973). In \(L.\ arenicola\), an area described by a 1–3 m radius around a burrow was usually defended against intrusion by smaller conspecifics. The presence and size of the defended area was confirmed by releasing spiders in small enclosures close to known burrows and monitoring the response of the resident. According to Kaufmann's (1983) definition, \(L.\ arenicola\) is territorial: at a given time an individual has priority of access to resources in a fixed area within its home range. Territory boundaries were not clearly delimited by natural boundaries or marks and occupation was advertised physically.

Energy-based territoriality is widespread in desert spider families (Cloudsley-Thompson, 1983). Territorial agelenids (Agelenopsis aperta) adjust the cost of physical defence according to resource quality at a site (Riechert, 1979). Although the contest situation favours the territory owner, its intensity may serve as a cue of site quality to the intruder. More energy is required to gain or maintain territories in regions where spider densities are high than where they are low. Territory sites should thus be selected optimally (Riechert, 1979). In this respect, the uneven distribution of \(L.\ arenicola\) burrows in an area warrants further investigation.

The average nearest-neighbour distances of 997 different pairs of \(L.\ arenicola\) burrows measured in one year was \(3,90 \pm 2,10\) m. Close neighbours (< 2 m apart) remained in their relative positions for shorter periods than more distant pairs. Distant neighbours (91%) with burrows > 2 m apart remained in position for 20 ± 28 days, 14% of them for > 1 month. In contrast, closer neighbours remained in position for only 9 ± 16 days \((t = 3.01; \text{d.f.} = 159; P < 0.05)\), with only 6% lasting > 1 month, which is indicative of instability among close pairs.

Juvenile and adult sex ratio was uneven. Owing to their short natural life expectancy upon reaching adulthood (7 weeks), the number of adult males in an area was usually low. During the breeding season at Visnara, there were usually only one or two adult males to 19–32 adult females, except in early October 1987, when there was a peak of 8 adult males to 19 adult females \((1 : 2.4)\). In the course of a year, the proportion of resident males to females was 1 : 2.6 for adults \((n = 80)\) and 1 : 1.6 for nymphs V to VII \((n = 105)\). These ratios differed

### Table 7

Density of \(Leurochrestis arenicola\) burrows in the central Namib Desert dunes determined by various methods:

<table>
<thead>
<tr>
<th>Site</th>
<th>Census method</th>
<th>Census period</th>
<th>Sample days</th>
<th>Area (ha)</th>
<th>Number counted</th>
<th>Population number/ha</th>
</tr>
</thead>
<tbody>
<tr>
<td>Khommabes Dune Base</td>
<td>1</td>
<td>May 87</td>
<td>1</td>
<td>1,00</td>
<td>16</td>
<td>32</td>
</tr>
<tr>
<td>Khommabes Dune Plinth</td>
<td>1</td>
<td>May 87</td>
<td>1</td>
<td>1,56</td>
<td>7</td>
<td>9</td>
</tr>
<tr>
<td>Far East Dune</td>
<td>1</td>
<td>Nov 86</td>
<td>1</td>
<td>1,50</td>
<td>23</td>
<td>31</td>
</tr>
<tr>
<td>Noctilivaga</td>
<td>1</td>
<td>Oct 86–Jan 87</td>
<td>2</td>
<td>1,00</td>
<td>10</td>
<td>20</td>
</tr>
<tr>
<td>Visnara I</td>
<td>2</td>
<td>Oct 86–Apr 87</td>
<td>73</td>
<td>0,50</td>
<td>120 ± 34</td>
<td>239 (64–302)</td>
</tr>
<tr>
<td>Visnara II</td>
<td>3</td>
<td>Jun 87–Jun 88</td>
<td>122</td>
<td>0,33</td>
<td>59 ± 14</td>
<td>176 (75–243)</td>
</tr>
</tbody>
</table>
significantly from parity ($X^2 > 6.5; \ d.f. = 1; \ P < 0.01$), but not from each other ($X^2 = 2.8; \ d.f. = 1; \ P > 0.05$).

**Cannibalism**

Cannibalism was observed among marked individuals at Visnara on 14 occasions. Additional remains of conspecifics were found in 21 of 214 excavated burrows (see above). Although conspecifics formed a minor proportion (4 %) of the total diet of post-nursery spiders, cannibalism was an important mortality factor, contributing 19.4 % of the known causes of death.

All post-nursery cannibals, but one, were subadult or adult females larger than their victims (difference in carapace width $= 1.5 \pm 1.2 \mathrm{~mm}; \ n = 14$). Victims were captured at distances of $5.4 \pm 4.2 \mathrm{~m}$ from their own burrows by cannibals that were $1.4 \pm 1.9 \mathrm{~m}$ from their burrows. In 13 cases, smaller spiders survived the attack of larger ones by retreating into their burrows $0.2 \pm 0.4 \mathrm{~m}$ away. When interactions with close nearest-neighbours (mean distance $= 2.3 \pm 2.3 \mathrm{~m}$) were repeated, smaller individuals were prevented from foraging and relocated their burrows ($n = 13$).

Hallander (1970) described similar behaviour in two species of wolf spider, both in the field and in the laboratory. Conspecific lycosids made up 20 % of their diet. In particular, adult females caught nymphs and adult males, and spiderling siblings ate each other. These lycosids, like *L. arenicola*, countered cannibalism by having very distinctive courtship signals and by juveniles that remain concealed beyond the reach of adults.

In a review of the occurrence of intraspecific predation among animals, Polis (1981) found that generally the more cannibalistic individuals were large, female and hungry. Starvation increased the likelihood of choosing conspecifics as prey and the vulnerability of juveniles. Cannibalism increased as other resources decreased, forming a type of reserve for the rate of cannibalism was density-dependent and increased when nearest neighbours were close (Polis, 1981). This makes cannibalism a potentially sensitive regulator of population densities.

**Other causes of mortality**

Cannibalism was one of eight identified causes of death of *L. arenicola* that were observed in 72 incidents at Visnara (Fig. 4). Four old females died after exposure to adverse climate or injury. Non-feeding adult males became inactive and died after several periods of intense activity in pursuit of mating opportunities. Some spiders, unable to free their legs, died during ecdysis. This was recorded four times in the field and often in the laboratory. Once, a coleopteran larva killed and partially consumed a *L. arenicola* during ecdysis in the field.

The most important predators of *L. arenicola* were gerbils, *Gerbillurus paeba*, *G. tytonis* and *Desmodillus auricularis*, accounting for 64 % of known deaths. The density of gerbils at Visnara was determined in February 1988 by Dednam (1988) over a 1 ha area containing about 207 *L. arenicola* burrows. Using a mark-recapture technique for 8 trapping nights, the gerbil density was calculated as 66/ha, with $47 \pm 7.3 \ G. \ paeba, \ 13 \pm 5.1 \ G. \ tytonis$ and $6 \pm 1.3 \ D. \ au-

![Fig. 4](image)

**Cannibalism**

Fig. 4

Cause of death of *Leucorchestris arenicola* in 72 incidents at Visnara. Percentages are indicated.

 ricularis*. This density of gerbils was high compared with a maximum of 18.2 gerbils/ha found elsewhere in the dunes (Boyer, 1988). Namib dune gerbils are omnivores with 53–59 % of their diet, determined from stomach contents, consisting of invertebrate matter, including spiders (Boyer, 1988).

Between June 1987 and June 1988 at Visnara, 253 attacks by gerbils on spiders on the surface or in their burrow entrances were recorded. In one extreme night, 51 % of the burrows were disturbed and 18 % of the post-nursery population was killed. Attacks were concentrated during January and June when the spider population abruptly decreased by 27 % and 51 % respectively. Many attacks destroyed the burrow entrances but did not harm the spiders. Spiders were often attacked again when they were repairing the damage. Those attempting to build new burrows were sometimes captured by gerbils or by conspecifics.

Infrequently, pompilid wasps opened *L. arenicola* trapdoors and entered burrows. Usually they were evicted by the spider. Once, a wasp did not emerge from a burrow in 15 minutes and the unharmed wasp was excavated together with a live immobilized spider (wasp body length 13.6 mm; spider nymph stage III, body length 11.9 mm, mass 240 mg). This behaviour resembles the pattern of hunting, paralysis and oviposition by *Anoplius* spp. pompilid wasps on *Geolycosa* wolf spiders (Gwynne, 1979) and several other wasp-spiders pairs (Groat and Brothers, 1982). It is not known whether Namib pompilids specialize in hunting only one family of spiders, but it is likely that the finding and excavation of heteropodid burrows requires particular skills. Gess and Gess (1980) suggest that one South African pompilid species is a specialist hunter of Heteropodidae, although other species capture several other spider families as well (Gess and Gess, 1974).

In the present study, two *L. arenicola* were caught on the surface at dawn by a dune lark, *Mirafra erythrocilium*. The scorpion *Opisthopthalmus flavescens* was recorded once as predator and twice as prey, an example of cross-predation (McCormick and Polis, 1982). Similarly, a large *Palmatogecko rangei* once caught an *L. arenicola* on the surface and three...
small geckos were consumed by spiders.

Cross-predation has previously been recorded for several arachnids, when they prey on juveniles of a species, but themselves fall prey to larger individuals of the same species (McCormick and Polis, 1982). Besides the acquisition of food, the benefits of cross-predation include reductions in future risks of predation for the predator or its offspring.

*Leucorchestris arenicola* display several anti-predator behaviour patterns. Spiders at the bottom of their burrows appear to be safe from most predators. Risk-sensitive foraging, as seen by Polis (1988) for the scorpion *Paruroctonus mesaesensis*, may enable *L. arenicola* to avoid the time and region where their predators forage. The suggestion that *L. arenicola* has the capability to flee by cartwheeling (Newlands, 1987) in the manner of *Carparacne aureoflava* (Henschel, 1990) was not confirmed. In a series of trials, no *L. arenicola* of any size showed an ability to wheel on a slope.

Many spiders of sandy deserts, like *L. arenicola*, are very pale and lack distinct markings, which may render them less visible to predators at night (Cloudsley-Thompson, 1983). When approached by potential predators on the surface, *L. arenicola* scuttled for their burrows, sheltered in a nearby plant, or froze motionless if shelter was remote, as in the case of wandering males. When confronted closely, they showed overt aggression, jumping forwards, then standing threateningly with body up, some legs raised and spines erect. Approach and threat posture alternated to give the appearance of a dance (Lawrence, 1962). Upon contact with the foe, the spider vigorously embraced it with the legs and chelicerae and then tried to flee.

Aggression can account for dominance of temporal zones by one arachnid species over others in an area (Polis and McCormick, 1986a). Polis and McCormick (1986b) found no evidence of exploitation competition among sympatric desert arachnids of a guild, but suggested that intraguild predation directly influenced their behaviour, distribution and abundance. Similar circumstances may apply to *L. arenicola* in the Namib Desert.

**GENERAL DISCUSSION**

The biomass of Namib spiders appears to be at least an order of magnitude lower than that of wandering spiders in other temperate regions (Chew, 1961; Turnbull, 1973). In the present study, most of the surveyed areas were selected for their high densities of *L. arenicola*. On visits to other sparsely vegetated firm dune slopes in the central Namib that were not surveyed systematically, searches on calm mornings usually revealed the presence of *L. arenicola* burrows. The general impression was gained that within suitable habitat, *L. arenicola* densities were approximately 5–10/ha and that this species appears to be the dominant spider in terms of biomass (8–17 g/ha) although small gnaphosids, *Asemesthes* spp. (0.1 g), and an erisid, *Seothyra* sp. (0.3 g) appear to be locally more abundant (Henschel, unpublished data). Accepting Seely and Louw’s (1980) estimate of 55 g/ha biomass of all invertebrate carnivores on a dune plinth during a dry year, *L. arenicola* would constitute 15–30 % of the carnivore biomass.

The *L. arenicola* population at Vissana underwent five and three-fold density fluctuations in two successive years. Based on measurements of minimum territory size, the theoretical maximum population density is 1000 spiders/ha, a density that was actually achieved only in small patches of 0.01 ha. Variable predation pressure, which reached catastrophic proportions in some patches, produced uneven density patterns of spiders in suitable habitat with abundant prey.

It has been proposed that populations of many other desert organisms are not affected by biotic interactions, but that climate plays a fundamental role in producing aetecological effects (Noy-Meir, 1973). For example, although Namib tenebrionids have many predators, these do not appear to limit their populations, but densities probably depend on environmental conditions (Seely, 1985). In contrast, *L. arenicola* and many other desert arachnids appear to be affected to a large degree by biotic interactions, especially intra- and inter-specific predation (Polis and McCormick, 1986b).

Several common tenebrionid beetles, prey species of *L. arenicola*, foraged on detritus and reproduced throughout the year (Seely, 1983, 1989). Soil temperatures at a depth of 20–30 cm, where *L. arenicola* reside, fluctuate little on a daily basis, but vary seasonally, dropping from approximately 30 °C in summer to approximately 20 °C in winter (Lancaster et al., 1984). Cooler soil temperatures during winter may decrease the metabolic rate of *L. arenicola*, suppressing activity and eliciting torpor in some cases. Climate, rather than prey availability, could thus explain seasonal patterns in the foraging behaviour, reproduction and development rate of this chthonic nocturnal spider.

Wandering spiders that live in burrows are generally longer-lived in deserts (Cloudsley-Thompson, 1983) than similar spiders in more mesic regions (Foelix, 1982). In a few known cases, the longevity of large araneomorph spiders was found to be more than two years in deserts, whereas elsewhere such spiders usually have annual life-cycles. This may be related to food availability, which appears to be less predictable on a daily basis in a desert than it is in wetter and tropical regions.

Unpredictable environmental extremes may affect food availability and offspring survival of many desert invertebrates (Louw and Seely, 1982). Under such circumstances, a pattern of bet-hedging (Murphy, 1968) is often adopted, indicated by the long life of females, iteroparity and small broods as seen in many Namib tenebrionids (Seely, 1983). *Leucorchestris arenicola* is iteroparous and produces relatively small egg clutches compared with semelparous spiders, for example many orb-weavers (Foelix, 1982). Although reproductive effort of *L. arenicola* females in the form of brood care is high (62 % of reproductive cycle) in contrast to some other Namib invertebrates (Seely, 1983), the reproduction of *L. arenicola* is consistent with a pattern of bet-hedging. This may enable a rapid population response in the form of increased survival of offspring if conditions should suddenly improve, such as after rare events of rainfall (Seely and Louw, 1980).

It is concluded that the phenology of *L. arenicola* closely fits a K-selected life history strategy (Pianka, 1970). On an annual basis, this spider has a fairly predictable supply of food, but its foraging activity and spatial organization are influenced by the risk of predation, whereas its metabolism and development...
rate appear to be subject to climatic seasonality. Under these conditions, L. arenicola grows and develops slowly, has a high longevity, produces relatively small clutches of eggs, is iteroparous and has an extended period of brood care.

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Behaviour and Ecophysiology of the Namib Dune Ant, *Camponotus detritus* (Hymenoptera: Formicidae)

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*Camponotus detritus* is a large formicine ant which occurs in the Kuiseb River and dunes of the central Namib Desert. Aspects of its biology, ecophysiology and behaviour are discussed in relation to the dune ecosystem, and possible areas of future research are considered. It is a diurnal species, avoiding the most stressful periods of the day by returning to the nest or staying in the shade of the vegetation. For and ant, it has a high resistance to temperature and desiccation. It is the major consumer of honeydew, limited chiefly by intraspecific competition for food and the availability of honeydew.

INTRODUCTION

*Camponotus detritus* Emery is a large and conspicuous formicine ant occurring in the central Namib Desert, where it is confined to the sand dunes south of the Kuiseb River and to the dry river-bed (Curtis, 1985a). Morphologically and behaviourally *C. detritus* is very similar to *Camponotus fulvopilosus* De Geer, which occurs in the arid and savannah areas of southern Africa. The latter species is present on the gravel plains of the central Namib Desert and the dunes of the Skeleton Coast, but is not sympatric with *C. detritus*.

Apart from a few passing mentions (Robinson and Cunningham, 1978; Seely, 1978; Holm and Scholtz, 1980), no study had been made of *C. detritus* before 1980. In 1980 I started a two-year study of the natural history and general ecology of this species. I examined its physiological tolerances and compared them with data on other ant species. I also determined the effect of an environmental gradient across the dune-field on the distribution and abundance of workers.

This paper provides a synthesis of my published findings and other information on *C. detritus*. The ant is discussed in relation to the dune ecosystem as a whole and future research possibilities are considered.

BIOLOGY

The genus *Camponotus* has a worldwide distribution with over 1500 species and almost as many variations in behaviour and ecology (Wilson, 1971). In southern Africa alone there are more than 70 species (Prins, 1978), of which four have been recorded in the Namib Desert (Marsh, 1986).

Like many *Camponotus* species, *C. detritus* workers are polymorphic, with a continuous, nonisometric size distribution from 7–16 mm. This polymorphism results in a certain amount of task specialization, but behavioural flexibility is retained. For example, although the majority of foraging is performed by minor workers, majors assist in retrieving food items too large for the minors (Curtis, 1985a).

Colonies comprise from one to four nests that are excavated among the roots of the perennial dune vegetation (Curtis, 1985b). Nests consist of a series of tunnels and chambers extending to a maximum depth of about 0.4 m, often lined with detritus. The comparatively simple nest construction enables the ants to exploit a fairly wide range of nesting sites as well as allowing them to excavate new nests with relative ease, either when old nests become too small or when environmental factors such as the encroachment of a dune or strong winds destroy the nest (Curtis, 1985b). Multi-nest colonies may have disadvantages since workers appear to spend considerable time and energy walking between nests. Nevertheless, should one nest be destroyed suddenly, the entire colony is not lost, and workers can rapidly transport surviving brood and other colony members to an established nest. *C. detritus* colonies generally only have one queen (or occasionally a few queens) in one of the nests and brood is transported by the workers to other nests. This seems a hazardous task for a diurnal desert species exposed to desiccating external conditions and predators. For example, Murray and Schramm (1987) observed the lizard, *Meroles cuneirostris*, robbing *C. detritus* 'carrying objects in their jaws', some of which may have been brood. However, queenless nests containing brood occur in both *C. maculatus* and *C. werthi* (Skafie, 1961), suggesting that this phenomenon is not unusual for the genus.

One factor contributing to the success of *C. detritus* appears to be its ability to reproduce all year round as a result of fairly high temperatures throughout the year, combined with a constant food supply. Although brood is present throughout the year, there is a great variability in the ratio of brood to workers and number of callows in different nests (Curtis, 1985a). The highest numbers of pupae were found in summer.

Alate reproductives were present in the nests throughout most of the year with a maximum in December (summer) (Curtis, 1985a). Since one nuptial flight was actually witnessed, it could not be established exactly what factors trigger the flight. Rainfall is presumably important, since that flight occurred after 3 mm of rain. However, not all rainfall...
events trigger nuptial flights. Rainfall in the Namib is unpredictable and may not occur for extended periods, particularly in the west (along the coast). What, then, happens to the alates which are present in the nest if there is no nuptial flight? Alates may often be seen just outside the nest entrance, especially after a light rain. On one occasion a worker was seen laying a pheromone trail, followed by several alate females. On a few other occasions alate males and females were observed with their heads in Trianthema hereroensis flowers, collecting pollen. Dealate females were also seen collecting honeydew with the workers. Although dealate females acting as workers have been recorded for other advanced genera such as Formicoxenus (see Buschinger, 1987), this behaviour is unusual among ants with a definite queen caste, as is foraging by alates.

Opportunism and flexibility are characteristics of many of the larger, longer-lived species inhabiting areas where environmental conditions are variable and unpredictable and productivity is low (Louw and Seely, 1982). An ant colony, regarded as a whole, is large and long-lived. Most ant species are omnivorous opportunists, combining predation and scavenging with collection of plant foods (Carroll and Janzen, 1973; Stradling, 1978). This is largely true of C. detritus. Although the majority of its diet at all times of the year consists of the honeydew excretions of scale insects and aphids, it is opportunistic in its honeydew collection, tending any homopteran. The succulent, Trianthema hereroensis, is infested with the mealy bug, Eriococcus sp., which is always tended by numerous C. detritus workers. Aclerda namibensis is another important species for the ants and infests grass of the species Stipa groenlandica, S. lutescens, S. cf. namaquensis and Cladoraphis spinosa. A third species, Membranaria sp., occurs quite frequently on S. cf. namaquensis and less frequently on S. lutescens. This was not utilized very often by C. detritus. Unidentified aphids on Acanthosicyos horridus and leaf hoppers on Acacia spp. were tended by ants living nearby but were not widespread.

C. detritus is also opportunistic in its scavenging behaviour, taking dead and defenceless animals and consuming pollen and nectar when this is available. It rapidly exploits new and transient food sources. For example, when an experiment was being carried out in the dunes on the decomposition of an oryx carcase by maggots, C. detritus workers collected the maggots as they moved across the sand and transported them back to the nest (Curtis, 1985c).

The suggestion that C. detritus is a detritivore (Holm and Scholtz, 1980) is not supported by evidence from stomach content analyses (Curtis, 1985c). The workers use detritus extensively for nest construction, however (Curtis, 1985b), and may often be seen carrying it back to the nest.

Unlike various other Camponotus species (Prins, 1978; Wilson, 1971), C. detritus maintains no food stores in the nest, nor does it have a replete caste. Only 10% of 200 workers dissected contained fat deposits (Curtis, 1985c). This suggests that all food returned to the nest is consumed immediately and that availability of food for most of the year, at least, is sufficient to meet the colonies’ needs.

A puzzling phenomenon is the ants’ attraction to nitrogenous compounds such as bird and lizard faeces and mammalian urine. Of the 346 identifiable objects which were transported back to nests, 22% were bird and lizard faeces (Curtis, 1985c). These may have been used as building material, but unlike gravel and detritus, which were used for external as well as internal nest construction, the faeces were only found inside the nests, often in piles at the end of tunnels. Workers were also seen breaking sand hardened by oryx urine into small pieces and carrying them to the nest (Curtis, 1983). Again, these may simply be used for nest construction.

Rat and bat droppings have been found in the nests of Cataglyphis halophila and were thought by Bernard (1960) to be utilized as a food source. The rumen of cattle contain bacteria which can synthesize amino acids from urea (Schmidt-Nielsen, 1975) and it is known that various Camponotus species possess intracellular bacteria in their guts (Hecht, 1924; Lilienstern, 1932; Kolb, 1959). Thus the possibility exists that C. detritus also has amino acid-synthesizing bacteria.

Availability of honeydew appears to be the critical factor that limits the number and distribution of ant colonies. This was shown when distribution and abundance of workers was correlated with various biotic and abiotic factors across an environmental gradient (Curtis and Seely, 1987). As with other Camponotus species (Wilson, 1971; Hölldobler and Lumsden, 1980), workers are aggressive and highly territorial, maintaining discrete foraging territories. In this way the number of colonies which can become established is limited. The dependence of ant colonies on their honeydew food source has been demonstrated at a site in the dunes near Gobabeb. In October 1980 all nests and plants hosting scale insects were mapped in an area of 9.4 ha. At that time there was a total of 14 nests and 30 scale-hosting plants. Gradually the plants began to die off and along with them the scale insects and nests, until, in January 1984, there were only nine plants and 4 nests. By the end of 1987 not a single scale insect or nest remained (Curtis, personal observation).

**ECOPHYSIOLOGY**

It has been suggested that ants are not physiologically well-adapted to arid environments, but that they use behavioural means of escaping the extreme climatic conditions (Delye, 1968; Schumacher and Whitford, 1974; Kay, 1978). Laboratory studies of preferred temperatures show that, compared with ant species from mesic areas, and with various species from the Sahara and New Mexico, C. detritus has a rather high preferred temperature of 31 °C (Curtis, 1985a). This is only exceeded by various Cataglyphis species from the Sahara (Delye, 1968) and possibly Ocymerx spp. (Marsh, 1988). The laboratory-determined critical thermal limits for C. detritus are CTmin of 4.6 °C and CTmax of 53.8 °C (Curtis, 1985d), which give it a very wide range of temperatures over which activity can take place. The CTmax is comparable with that of various Pogonomyrmex species from North America (Whitford and Ettershank, 1975), but higher than that for other desert species, both in North America and the Namib (Schumacher and Whitford, 1974a; Kay and Whitford, 1978; Marsh, 1988). Thus, compared with other ants, C. detritus is rather well adapted physiologically to withstand the high temperatures of the desert. It cannot tolerate the extremely high temperatures tolerated by other desert arthropods (Cloudsley-Thompson,
Although high by comparison with other desert arthropods, *C. detritus* has a low rate of water loss for an ant (Curtis, 1983). In addition, it is able to tolerate high losses of tissue water, up to 60% of initial body weight. This, combined with its predominantly liquid diet, allows it to be present on the vegetation throughout the most desiccating periods of the day.

**BEHAVIOUR**

*Camponotus detritus* can be regarded as a diurnal ant. Although workers may be present on scale-infested plants throughout the night, there is no transit activity (movement between nests or between the nest and the foraging grounds) at night (Curtis, 1985e). Briese and Macauley (1980) divided the determinants of activity into those that are stimulatory-inhibitory and those that are regulatory. Light can be regarded as a former determinant of transit activity for *C. detritus*, but has no effect on the collection of honeydew (Curtis, 1985e). Temperature is a regulatory factor, determining the intensity of transit activity, which is bimodal in summer, with a total cessation during the hottest part of the day. Workers avoid excessively high temperatures by remaining either in the nest or on plants, where air temperatures seldom exceed about 45°C. In summer, transit activity starts with first light and ceases when surface temperatures reach about 56°C. Owing to the steep thermal gradient above the sand during the heat of the day, and to the relatively long legs of the workers, temperatures to which the ants’ bodies are exposed are about 10°C less than surface temperatures. Thus their activity range is well within their physiological limits. Peak activity occurs when air temperatures at ant level are 25–38°C. In winter, transit activity only begins when surface temperatures are 10°C and continues throughout the day until just before sunset.

Since *C. detritus* is the dominant ant species in the southern dunes, it is able to utilize the full thermal range available to it, unlike ant species of the North American deserts, where interspecific competition has led to temporal partitioning of food resources (Bernstein, 1974; Schumacher and Whitford, 1974; Whitford and Ettershank, 1975; Chew, 1977; Davidson, 1977). Nor is the activity of *C. detritus* restricted by seasonality in food production, as occurs among seed-harvesting species (Briese and Macauley, 1980; Whitford, Depree and Johnson, 1980; Whitford, Depree, Hamilton and Ettershank, 1981).

Trophallaxis is particularly adaptive in an arid environment where the rate of desiccation is high. One individual can obtain liquid from another without having access to the source of moisture. This was observed frequently among *C. detritus*. Furthermore, groups of ants had lower rates of desiccation than solitary individuals (Curtis, 1983). These two factors appeared to increase the survival time of *C. detritus* workers at extreme temperatures and humidities.

**CAMPONOTUS DETRITUS AND THE ENVIRONMENTAL GRADIENT**

Despite the narrowness of the Namib Desert dune-field (approximately 130 km), there is a distinct climatic gradient from the coast inland (Besler, 1972; Curtis and Seely, 1987). This has an effect on the species diversity and abundance of plants (Robinson, 1976) as well as on the abundance and distribution of various arthropod species (personal observation). When the density of *C. detritus* nests and the abundance of individual ants were examined at six different sites across the dune-field, it was found that although there was great variability in the number of workers per nest (standard errors of up to 2700 around a mean of 5076), the largest nests occurred in the Gobabeb area (56 km inland) (Curtis and Seely, 1987). This corresponded with the size of the mounds which accumulate around the plants. However, the greatest nest density and the overall abundance of workers per hectare was at Noctivaga, midway across the dune-field. This corresponded with the apparent abundance of scale insects.

Ant density was not significantly correlated with any environmental factor, but did show a similar trend to mean annual temperature and mean temperature amplitude. Near the coast, nests were small and had little brood. The lower temperatures may have affected brood production and therefore ant density. Activity and honeydew production may also be affected by lower temperatures.

**CAMPONOTUS DETRITUS AS PART OF THE DUNE ECOSYSTEM**

Being a member of the dune base and plinth communities described by Robinson and Seely (1980), *C. detritus* occupies a unique position as the major exploiter of honeydew. From the coast to about midway across the dune-field, *C. detritus* is the only honeydew-collecting species of ant found on the dune plinth. In the eastern dune-field, where productivity and habitat heterogeneity are greater, and other ant species are present, *C. detritus* shows the same behaviour as at Gobabeb. Its chief potential diurnal competitor, *Crematogaster* sp., appears to avoid competition by predominantly tending the gall-forming scale insect, *Membranaria* sp., on *Stipagrostis namaquensis*, which *C. detritus* only rarely tended. The nocturnal species, *Camponotus maculatus* and *C. mystaceus*, are honeydew feeders (Skafie, 1961) but were never seen collecting honeydew. Thus, as the dominant species in the honeydew-feeding guild, *C. detritus* appears to be relatively free from the effects of direct interspecific competition.

It is not possible to determine the exact contribution of *C. detritus* to the total biomass of the dune fauna since no data on other animals are available. The study by Seely, De Vos and Louw (1977) of the satellite fauna of *Trianthema hereroensis* showed that these ants contributed about 11% of the biomass while the biomass of the honeydew-producing coccids represented 46%. Seely and Louw (1980) also showed that biomass varies considerably from dry to wet periods. They found that total faunal biomass (dry weight) at Gobabeb increased from 100 to 600 g ha⁻¹ while that on the dune slopes, where *C. detritus* occurs, increased from 80 to 900 g ha⁻¹. Biomass of *C. detritus* measured at Gobabeb during 1981 was 96 g ha⁻¹ (Curtis, 1983). As 1981 may be regarded as a fairly dry period, the contribution of *C. detritus* to the total dune fauna is therefore likely to be fairly high.

*Camponotus detritus* does not appear to have many major predators. It is probably avoided by vertebrates because of the unpalatable formic acid which it secretes. The dune lark, *Mirafra erythrochlamys*, takes the occasional worker
(Willoughby, 1971; personal observation) and Ludwig's bustard, *Neotis ludwigi*, will dig open a nest to get at the brood (personal observation). Both species of dune lizard, *Meroles cuneirostris* and *Aporosaura anchietae*, prey on *C. detritus* (Louw and Holm, 1972; Robinson and Cunningham, 1978; Murray and Schramm, 1987; R. Pietruszka, personal communication). However, none of these predators seems to take the ants in large numbers.

On only one occasion did I find indirect evidence of mammalian predation. A nest had been opened and was surrounded by small canine footprints of either the Cape fox, *Vulpes chama*, or the bat-eared fox, *Otocyon megalotis*. The predator did not appear to have done much damage to the nest. Near the river, baboons tear open nests to eat the brood and workers (M. K. Seely, personal communication).

Invertebrate predators in the form of spiders and solifuges probably account for most of the predation on *C. detritus*, although this aspect has not been quantified. The ant-mimicking spider, *Cosmophobia* sp., which closely resembles *C. detritus* in colouration, was seen on two occasions with a dead ant in its jaws, but was never observed to capture the ants (Curtis, 1988). The buckspoor spider, *Seothyra* sp., is a sand-dwelling species which constructs a web on the sand surface. *C. detritus* workers, and other arthropods, which walk across the web become entangled in the silk and can be bitten by the spider. This has been observed on numerous occasions (J. Henschel, personal communication). *Asaseastes* sp. is a tiny, extremely fast moving spider with sandy colouration. It has been seen to rush up and run a thread of silk around an ant before moving in to kill it (J. Henschel, personal communication). *Eberlanzia flav*a, a small solifuge, can be seen climbing up and down grass stalks at night and on two occasions they were observed catching and consuming *C. detritus* (J. Henschel, personal communication).

**CONCLUSION**

Although ants in general may not be as well-adapted physiologically to arid environments as many other desert arthropods, for an ant, *C. detritus* shows a comparatively strong resistance to high temperatures and desiccation, and behaviourally avoids the most stressful periods of the day. It exhibits social behaviour common to formicines, much of which pre-adapts it to life in a harsh environment, for example its ability to share food and moisture with nestmates by trophallaxis. The simple nest construction, using the roots of perennial vegetation to provide the structure, enables it to exploit the unstable substrate of the dunes. Multi-nest colonies allow for rapid movement of ants and brood to other nests if one of the nests becomes uninhabitable.

With few competitors and predators to limit its distribution and activity periods, *C. detritus* has become a very successful species, forming a dominant part of the dune fauna and utilizing a food resource not utilized by other animals—honeydew. Although its opportunistic use of various other food sources allows it to supplement its diet, the most limiting factor to *C. detritus* is probably the availability of honeydew and intraspecific competition for food, as shown at the study site near Gobabeb. It thus plays an important role in the dune ecosystem as secondary consumer.

There are still many unanswered questions about the biology of *C. detritus*, which may profitably be pursued in the future. This ant is a very suitable species for research for various reasons. Nests are easy to excavate. The workers are large and conspicuous, which makes behavioural studies possible without interfering in the ants' activities. They inhabit a relatively simple, open environment.

More detailed studies on the reproductive biology of this species are needed. The following questions could profitably be addressed: What is the rate of egg production and how is this influenced by biotic and abiotic factors? What is the rate of development of the brood? How does brood transport from one nest to another affect the survival of the brood? What factors determine whether a nest has one or more queens and how are new queens recruited? What factors trigger nuptial flights and what happens to alates if there is no nuptial flight? An interesting field for future research would be to consider the possibility of dealate females acting either as a fat storage depot or as foragers when nuptial flights do not occur.

A study of the composition of the honeydew and the amount assimilated by a colony would be beneficial. This could be linked to a search for any evidence of amino acid-synthesizing bacteria in the guts of *C. detritus*, or some other reasons for the transporting of faeces to the nest by the workers. The association between these ants and the honeydew-producing homopterans appears to be very close, but more detailed studies are needed to establish the exact extent of this association, and the extent to which colonies are regulated by intraspecific competition for food. Further studies on the interactions of this species with others would help to elucidate the position of this species in the dune ecosystem.

**ACKNOWLEDGEMENTS**

This research was carried out while I was a post-graduate student stationed at Gobabeb. I thank the C.S.I.R. and the Transvaal Museum for financial and logistic support; the Directorate of Nature Conservation and Recreational Resorts for permission to work in the Namib-Naukluft Park and Prof. G. N. Louw and Dr M. K. Seely for supervision of the project. I should also like to thank Bob Pietruszka, Johannes Henschel and Mary Seely of DERU for their observations on these ants; Eryn Griffin, John Burke, Mary Seely and Alan Marsh for their comments on the manuscript and the Department of National Education (Namibia) for permission to publish.

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Scale-related Habitat Use by *Physadesmia globosa* (Coleoptera: Tenebrionidae) in a Riparian Desert Environment

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Scale-related use of habitat by the tenebrionid beetle, *Physadesmia globosa*, was studied beneath tree canopies on the Kuiseb River's floodplain in the Namib Desert. Beetle activity and relative density were estimated using pitfall traps installed in soil-litter subcanopy substrates, which provide the insects with shelter and food. Considerable variability in both large-scale (ca. 0.5 km) use of subcanopy space among different trees, and in intermediate-scale (1-5 m) use of quadrants under the same trees, was recorded between late August and mid-November, suggesting that quality of substrate influences habitat use.

We tested beetle responses to substrate quality at two scales. At the intermediate scale we placed different substrates in circles around traps in field arenas beneath canopies. No preferences were noted for 'good' or 'poor' litter from selected trees, or for *Acacia erioloba* leaf and flower litter, *Salvadora persica* leaf litter, or bare soil. However, in a separate experiment, crops of *P. globosa* confined for 48 h beneath acacias contained significantly more flowers than leaves, despite the obvious abundance of leaves. Therefore, we placed beetles in small laboratory arenas containing leaf litter on which flowers were positioned 0.5, 2.5, and 5.0 cm apart. Flowers were again chosen significantly over leaves. We conclude that nutritional components of the substrate are meaningful to *P. globosa* only as they are encountered, while non-nutritional compounds determine habitat use at larger scales.

INTRODUCTION

Terrestrial detritivores frequently inhabit substrates that provide both food and shelter. Therefore, the relative value of each of these resources to a detritivore should influence its spatial use of a given amount of substrate. Two possibilities exist. The detritivore may respond to cues emanating from both resources. Alternatively, space use may be based on information from only one resource. How a mobile detritivore responds to food and shelter may also be scale-related. Morris (1987) points to the need to study habitat preference at different scales. Versions of this approach have been used for some time to study insects that first search for a habitat in which certain resources may be present, and then, in a more restricted space, locate a specific resource. Behaviour of this sort occurs in some herbivorous species seeking oviposition sites (e.g., Chew, 1977; Rauscher, 1979), and is common in parasitoids (Vinson, 1976). We are unaware of reports dealing specifically with scale-associated habitat use by detritivores. In this paper we investigate the use of a mixed soil-litter habitat by the tenebrionid beetle *Physadesmia globosa* (Haag). This diurnal species is endemic to dry riparian woodlands in the Namib Desert, where it is locally abundant in litter and loose soil beneath canopies of acacia trees. We ask here whether its use of substrate depends on responses to the same resources at different spatial scales.

METHODS

Study Area

Study sites were located in riparian woodland on the north bank of the normally dry bed of the Kuiseb River 1 km from Gobabeb, in the central Namib Desert. The Kuiseb at this point separates the extensive dune fields to the south and west from the gravel plain to the north and east. The woodland is irregular in width, but seldom exceeds 0.5 km. Theron, Van Rooyen and Van Rooyen (1980), Giess (1962), and Seely, Buskirk, Hamilton and Dixon (1980/81) describe its vegetation, which includes the following major woody species: *Acacia albida* Del., *A. erioloba* E. Meyer, and *Salvadora persica* L. We intensively studied habitats provided by the canopies of eight large acacia trees (five *Acacia erioloba*, three *A. albida* and three *S. persica* trees. Other special studies were conducted using other *A. erioloba* trees and are described in the text. Figure 1 is a map of the woodland showing locations of all study trees in relation to each other and to the river bed and gravel plain.

Three of the *A. erioloba* trees (designated AeN, AeE and AeW after their relative compass-direction locations) were adjacent to smaller trees of *S. persica* having the correspond-
Fig. 1
Map of trees in the Kuiseb study area. Most large species are either Acacia albida or A. erioloba. Many smaller trees, especially at the upper right, are Salvadora persica. The three S. persica associated with A. erioloba as study pairs are shown in black. Tree symbols are indicated in the text.

ing directional designations: SpN, SpE and SpW. The two other A. erioloba (FAeE and FAeW) were not associated with S. persica, and had been enclosed for about five years by a fence to prevent access by domestic stock. Likewise, the three A. albida habitats were not studied in association with other vegetation. The tree termed AaS grew in the river bed but shaded its bank, whereas AaE and AaW were in the main woodland strip. We monitored habitat temperatures by placing maximum-minimum thermometers – one per tree – upright against the south-facing (shaded) trunk bases of AeE, AeN, and AeW.

Depth, compressibility and organic content of the relatively loose litter and soils were measured, in early September, beneath the canopies of AeN and AeE. We chose these trees because although they were close to each other, early in the study the populations within their subcanopy habitats differed markedly in apparent density (see below). Depth of loose material was measured by pushing the blunt end of a pencil into the litter. Relative compressibility (in kg m\(^{-2}\)) was measured with a Farnell pocket penetrometer, fitted with a circular plate of brass, that was pushed into the litter until the plate had sunk to a distance equal to its thickness. Proportions of organic and inorganic materials were determined by inserting a metal cylinder, 7.2 cm in diameter, to a depth of 6 cm (approximately the minimum depth recorded by pencil pushing). Cylinder contents were weighed, then poured through a Tyler Standard Screen (0.991 mm mesh size). The residue (considered organic matter only) was then weighed again.

An average of five readings of both depth and compressibility was taken from representative locations at each of the following sites in each directional quadrant of the two subcanopy habitats: 1) one-third of the distance from the trunk to the canopy edge (a single location), and 2) two-thirds of the distance from the trunk to the canopy edge (two locations). Proportions of organic in relation to inorganic matter were recorded from single measurements at each of these locations.

Numbers of fallen flowers on the surface litter of the same two trees were recorded on 10 September (shortly after peak flowering) and 23 November (just before the next flowering period) by photographing – at the locations described above – units of relatively undisturbed surface confined within a 23 x 25.5 cm metal rectangle. Flowers enclosed in the rectangle were counted later from projected slides.

Use of the substrate habitat
Pitfall traps were established periodically beneath the canopies of all regular study trees. Traps were made of hemispher-
ical metal bowls, 17 cm in diameter and 10 cm deep. In population studies, unless otherwise indicated, four traps, each representing one of the four cardinal directions, were each situated halfway between the canopy edge and the trunk of an acacia, and about 0.5 m inside the canopy edge of an S. persica. Special uses of pitfall traps for other purposes are discussed below.

Traps were used in population studies during the following intervals: 26–29 August, 27–30 September, and 14–17 November, 1985. During each interval, pitfall captures were recorded in daylight within two hours of dawn or dusk. All captured specimens were released at the canopy edge (acacias) or several metres beyond in the case of S. persica. Trapped beetles were colour-marked with a fine brush and poster paint, according to a code indicating the particular tree, trap and date. Densities of active P. globosa were estimated for each of the six main study trees by the Schnabel mark-recapture method, a variant of the Lincoln Index, which takes into account observations made on a series of occasions (Overton, 1971).

We documented the potential for inter-tree movements of P. globosa by designating trapped beetles as 1) ‘residents’ when they bore only colour marks assigned to the tree where they were trapped, 2) ‘transients’ when their marks were from that tree and at least one other, and 3) ‘immigrants’ when they were either unmarked or only bore marks with colours assigned to other trees. Trapped ‘immigrants’ were marked, and then became ‘transients’ or ‘residents’ if they were trapped again.

**Substrate choice**

We tested potential substrate choice using 1) an arena, and 2) habitat manipulations beneath trees. The arena tests compared choice of litter from presumably ‘good’ and ‘poor’ sites. The former was adjacent to the east trap at AeE, where an average (± SE) of 12.5 (± 2.4) P. globosa was trapped over the previous two sampling periods, while the latter was next to the west trap at AeN, where an average of only 4.6 (± 0.6) beetles was trapped simultaneously. The arena consisted of six pre-constructed sheet metal enclosures, each 1 x 2 m in length and about 30 cm in height. The enclosures were partly shaded by overhanging branches. Preparation of the arena consisted of sift ing out most of the accumulated litter, then adding about 2 cm of clean river sand.

Single pitfall traps were inserted 30 cm from the ends of each enclosure. Around each trap – in a circle 30 cm in diameter – we spread experimental litter to a depth of ca. 5 cm. Circles of ‘good’ and ‘poor’ litter were arranged at opposite ends of an enclosure, and alternated at the same end of a row with circles of the opposite litter type, so that six circles of each type were always at the east or west ends of enclosures. Cardboard cut to trap dimensions was used to prevent beetle entry when traps were not in use, and to shade traps during collection periods.

Ten beetles, collected from beneath acacias ca. 7 km downstream, were placed in each enclosure 24 h before traps were uncovered for testing. During subsequent tests, which ran for three days each, beetles in traps were counted and removed to the centre of the arena twice a day. Traps were kept covered when P. globosa was inactive (late afternoon to mid-morning). In sequential choice tests involving each enclosure, we first used 10 males, then 10 females, then five beetles of either sex. Results are expressed as adjusted G values from contingency tests.

Habitat manipulations beneath trees were performed in mid-October following completion of the arena tests. Here we tested whether certain obvious litter components might influence the choice of habitat when free-roaming beetles were presented with four substrate options within the subcanopy habitat. We selected three previously unused A. erioloba trees, each having a subcanopy habitat with a deep layer of mainly leaf litter, within which we initially installed three sets of four pitfall traps, each set arranged in a 1 m² area. The trap sets were roughly equidistant from each other and situated about halfway between the canopy edge and main tree trunk. For the first three days after trap installation we recorded the number of P. globosa found in each trap by late afternoon. Beetles were then released at least 3 m distant. In the early morning of the fourth day, we removed litter from within a circle 1 m in diameter around each trap in every set. Sets were then treated so that, for each one, four new conditions existed following litter removal: 1) replacement by newly fallen flowers from another A. erioloba tree, 2) replacement by leaf litter from beneath an S. persica tree, 3) replacement by the original substrate, and 4) nothing added so that nearby bare soil remained. Trapping and recording then proceeded for another three days.

**Food choice: subcanopy enclosure tests**

We studied food choice in P. globosa using two approaches. One involved determining crop contents from beetles allowed to feed only at pitfall trap sites beneath particular acacias. This was first done in early September, when freshly fallen A. erioloba flowers were plentiful in the leaf litter, and later in mid-November, when those flowers had undergone some physical disintegration. We caged specimens for 24 h with one of the following available items: 1) dry, fallen green or brown leaves of both Acacia species, 2) freshly fallen A. erioloba flowers and fallen A. albida flowers several weeks old, 3) local green and brown Euclea pseudebenus E. Meyer ex A. D. C. leaves, and 4) dry leaves of S. persica.

Next, we stocked subcanopy enclosures for 48 h with beetles, seven to an enclosure, obtained the day before from ca. 7 km downriver. Enclosures of about 1.5 m² aperture were made of corrugated sheet metal strips driven into the ground adjacent to trap sites beneath AeN, AeE, and AeS. In September, we added beetles without regard to sex ratios; in November, each enclosure received four males and three females. Beetles were removed and frozen in mid-afternoon, 48–54 h after stocking; thus they had ample time to feed. Crop contents from each beetle were removed by dissection and dispersed in 2 ml water in a shallow circular container 30 mm in diameter. Examination by one of us (S.A.H.) using a dissecting microscope at ×200 magnification involved estimating proportions of flowers, leaves, insect parts, and mineral matter in three fields chosen at random. Each field was divided into four equal quadrants. The proportion of each food type in a quadrant was estimated at a percentage of all material visible, and all 12 percentages of each food type were averaged for each crop.

**Food choice: laboratory tests**

To examine preferences between acacia flowers and
leaves, we tested, in two experiments, the degree to which flower selection is independent of flower availability. One experiment involved consumption of fresh A. erioloba flowers (picked from trees in early December, since few had fallen at the time), while the other involved 'dry' flowers that had been in A. erioloba litter for at least two months. For both tests, we took leaf litter (with foreign elements removed) from beneath AeW. Plastic boxes, 15 x 30 cm in area and 10 cm in height, served as choice chambers. Leaf litter was sprinkled to a depth of 3 cm in each box, and individual flowers were placed on the litter surface at the following distances from each other: 0.5 cm (high concentration), 2.5 cm (medium concentration), and 5.0 cm (low concentration). Four boxes were prepared for each flower concentration.

One series of boxes contained no beetles and was used for controls. We added beetles collected downriver the same day to each box of the other series. One series contained 10 females per box. Beetles were allowed to feed for 48 h, then frozen before crop examination, which was done as described in the previous section. Meanwhile, proportions of flowers to leaves in the control feeding boxes were determined by first grinding the entire contents of each box in a coffee grinder until particle sizes of fragments resembled those found in crops. Subsamples were then examined microscopically in the same way as the crop contents.

RESULTS

Characteristics of substrate habitat

Temperatures taken within 10 cm of the soil-litter surface were recorded during a 3-month period (20 August – 28 November) and compared by F-test for differences in variance. In no case were differences significant at P = 0.05.

Litter and soil characteristics from beneath AeN and AeE are contrasted in Table 1. Mean values of litter depth, litter compressibility, soil-litter mass, and organic matter per cent were analysed using a simple t-test. Only organic matter per cent was significantly different (greater in AeE) between trees (t = 3.873, 14 d.f., P < 0.005).

Mean subcanopy flower densities (per m² SE), in September and November, respectively, were for AeN: 65.1 ± 10.9 and 50.8 ± 9.9, and for AeE: 77.2 ± 5.1 and 36.5 ± 5.1. Fallen flowers following 2.5 months of exposure, were noticeably reduced in size.

Use of the substrate habitat

Estimated densities of P. globosa remained relatively stable under all trees combined between late August and late September (Table 2). Summed means (± SE) for those periods were 284 ± 38 and 309 ± 92, respectively. During that period one tree (AeW) tended to have much greater populations, whereas another (AaS) had lower populations. Six weeks later populations beneath all but AaS and AaW had declined considerably (summed mean ± SE = 124 ± 45). Mean (± SE) recapture percentages (Table 3) averaged 30.6 ± 5.2 (August), 29.0 ± 3.5 (September), and 29.2 ± 4.8 (November), regardless of apparent density fluctuations.

Relative densities and activity of P. globosa beneath each tree for any sampling period are reflected by the total number of captures. Table 3 gives total capture results from each

<table>
<thead>
<tr>
<th>Tree</th>
<th>26–29 August</th>
<th>27–30 September</th>
<th>14–17 November</th>
</tr>
</thead>
<tbody>
<tr>
<td>X</td>
<td>95 % CI</td>
<td>X</td>
<td>95 % CI</td>
</tr>
<tr>
<td>AeE</td>
<td>307</td>
<td>170–461</td>
<td>206</td>
</tr>
<tr>
<td>AeW</td>
<td>410</td>
<td>308–518</td>
<td>756</td>
</tr>
<tr>
<td>AaN</td>
<td>314</td>
<td>244–387</td>
<td>200</td>
</tr>
<tr>
<td>AaS</td>
<td>144</td>
<td>95–198</td>
<td>229</td>
</tr>
<tr>
<td>AaW</td>
<td>320</td>
<td>201–451</td>
<td>155</td>
</tr>
</tbody>
</table>
sampling period for each tree. Changes in the tree-specific values (Table 3) agree with the November population decline (Table 2). In addition, they reveal a dramatic November decline beneath S. persica, and show that while densities/activity also diminished beneath most of the main acacia trees, they increased under fenced trees (especially the isolated FAEW). Since only three specimens from beneath the fenced trees had been marked as captures elsewhere, the increase must have been due to a relatively localized, nondispersing pool.

Percentages of beetles in the ‘resident’, ‘transient’, and ‘immigrant’ categories for each sampling period (Table 4) show that about one-fifth to nearly one-half of the beetles trapped under acacias were residents, whereas about one-half to over three-fourths were immigrants. (Of the immigrants, 0–34 % beneath acacias and 13–68 % beneath S. persica were marked.) Transients were sometimes nonexistent and never exceeded 23 % of the captures. Percentages of beetles in each category varied over time. For example, P. globosa exhibited a high degree of ‘residence’ beneath AeE in August and September, but showed a consistently weaker tendency to ‘reside’ beneath the nearby AeN during all three sampling periods.

Patterns of movement and habitat were less obvious for beetles beneath S. persica. Especially large changes in proportions between sampling periods characterized SpE.

Net exchanges among the three Acacia-Salvadora pairs showed that within any one sampling period generally fewer than 10 recaptured beetles travelled from one tree to another. Exceptions included exchanges during September in which AeW gave up 22 to and gained 27 from SpW, while AeE gave up 23 to and gained 7 from AeN.

Substrate choice
In the arena test, males chose AeE litter at a significant level ($G = 11.93, P < 0.05$) only once in six trials. To eliminate the possible bias of male following behaviour, we then ran six choice tests on individual males. The resulting G value was not significant at $P=0.05$, hence there is little reason to believe that P. globosa is able to distinguish between litter from sub-

### Table 3

<table>
<thead>
<tr>
<th>Tree</th>
<th>26–29 August</th>
<th>27–30 September</th>
<th>14–17 November</th>
</tr>
</thead>
<tbody>
<tr>
<td>AeN</td>
<td>128 (18.9)</td>
<td>136 (29.9)</td>
<td>66 (38.8)</td>
</tr>
<tr>
<td>AeE</td>
<td>305 (53.0)</td>
<td>170 (24.0)</td>
<td>41 (23.4)</td>
</tr>
<tr>
<td>AeW</td>
<td>280 (24.7)</td>
<td>346 (20.6)</td>
<td>20 (31.3)</td>
</tr>
<tr>
<td>AaN</td>
<td>278 (35.2)</td>
<td>206 (45.5)</td>
<td>32 (45.5)</td>
</tr>
<tr>
<td>AaS</td>
<td>119 (31.6)</td>
<td>106 (26.4)</td>
<td>19 (23.1)</td>
</tr>
<tr>
<td>AaW</td>
<td>160 (20.2)</td>
<td>105 (28.4)</td>
<td>55 (13.3)</td>
</tr>
<tr>
<td>FAEW</td>
<td>208</td>
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<td>236</td>
</tr>
<tr>
<td>FAEW</td>
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<tr>
<td>SpN</td>
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</tr>
<tr>
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</tr>
<tr>
<td>SpW</td>
<td>105</td>
<td>114</td>
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</tbody>
</table>

*Calculated as the number of individuals marked one or more times from that sampling period divided by the number of originally marked and released individuals from the same period $\times 100$. Note: values include beetles caught more than once.

### Table 4

<table>
<thead>
<tr>
<th>Tree</th>
<th>Marked residents</th>
<th>Marked transients</th>
<th>Immigrants*</th>
</tr>
</thead>
<tbody>
<tr>
<td>AeN</td>
<td>19</td>
<td>18</td>
<td>24</td>
</tr>
<tr>
<td>AeE</td>
<td>46</td>
<td>45</td>
<td>12</td>
</tr>
<tr>
<td>AeW</td>
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<td>21</td>
<td>25</td>
</tr>
<tr>
<td>AaN</td>
<td>32</td>
<td>46</td>
<td>28</td>
</tr>
<tr>
<td>AaS</td>
<td>29</td>
<td>28</td>
<td>21</td>
</tr>
<tr>
<td>AaW</td>
<td>28</td>
<td>30</td>
<td>16</td>
</tr>
<tr>
<td>SpN</td>
<td>3</td>
<td>5</td>
<td>11</td>
</tr>
<tr>
<td>SpE</td>
<td>0</td>
<td>34</td>
<td>23</td>
</tr>
<tr>
<td>SpW</td>
<td>10</td>
<td>15</td>
<td>25</td>
</tr>
</tbody>
</table>

*These may have included unmarked ‘residents’.

### Food choice: subcanopy enclosure tests
Crop dissections from beetles allowed to feed initially on tree-derived litter components indicated ready ingestion of only acacia flowers and leaves (Table 5).

More complete results were obtained when average percentages of all litter components eaten by P. globosa in habitat 139
Among means of flower
ence in proportions of fresh or dry flowers at any level of flower
concentration. As a whole, these tests show that flowers,
irrespective of freshness and concentration, are preferred over
leaves and eaten at relatively constant rates when available.

**DISCUSSION**

In the soil-litter substrate inhabited by adults of *Physadesmia globosa*, the distinction between food and shelter is not readily apparent, because the accumulation of dead leaves and flowers is used for both. To learn whether the beetle’s choice of location in this medium is directed mainly toward one or the other (or both) of the two resources, we used a combination of methods involving observation and manipulation. It soon became clear that subcanopy habitats in the Kuiseb riparian community have markedly variable thermal characteristics and states of litter quality. Thus, while the regional climate is relatively aseasonal (Pietruszka and Seely, 1985), diel habitat temperatures exhibit wide ranges, and interspecific litter accumulations as well as intraspecific substrate organic masses vary appreciably beneath acacia trees.

Against this backdrop, we determined that subcanopy-specific relative densities and activity of *P. globosa* may be relatively stable for at least a month, and that, regardless of density level, nearly 50 % of a subcanopy population may exhibit ‘habitat fidelity’ during that period. Moreover, while densities and activity beneath some trees sometimes decline significantly, those beneath other trees may simultaneously increase. A picture thus emerges of an extensive local population of *P. globosa* that roams intermittently among subcanopy habitats, and that does not necessarily follow potential resource gradients.

On the other hand, *P. globosa* movements within a single

---

**Table 5**

Seasonal and within-species comparison of *Physadesmia globosa* crop contents from individuals confined to subcanopy enclosures for 48 h.

<table>
<thead>
<tr>
<th>Tree &amp; period</th>
<th>n</th>
<th>Males</th>
<th>Females</th>
<th>Flowers (X ± SE)</th>
<th>Leaves (X ± SE)</th>
<th>Insect parts (X ± SE)</th>
<th>Mica &amp; sand (X ± SE)</th>
<th>Number with empty crops**</th>
</tr>
</thead>
<tbody>
<tr>
<td>AeE</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>September</td>
<td>16</td>
<td>12</td>
<td>4.7 ± 3.7b</td>
<td>18.7 ± 3.4a</td>
<td>1.8 ± 0.6</td>
<td>1.5 ± 0.9a</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>November</td>
<td>16</td>
<td>12</td>
<td>96.1 ± 1.1a</td>
<td>12.2 ± 0.6a</td>
<td>1.2 ± 0.5a</td>
<td>1.3 ± 0.5a</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>AeN</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>September</td>
<td>13</td>
<td>6</td>
<td>96.1 ± 3.7b</td>
<td>13.3 ± 3.6b</td>
<td>0.9 ± 0.5b</td>
<td>0.04 ± 0.04b</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>November</td>
<td>16</td>
<td>9</td>
<td>95.6 ± 1.6ab</td>
<td>2.6 ± 0.7a</td>
<td>1.2 ± 0.7a</td>
<td>1.3 ± 0.5a</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>AeS</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>September</td>
<td>16</td>
<td>0</td>
<td>50.3 ± 7.1c</td>
<td>44.3 ± 6.0b</td>
<td>3.5 ± 2.3ab</td>
<td>2.1 ± 0.8b</td>
<td>9</td>
<td></td>
</tr>
<tr>
<td>November</td>
<td>15</td>
<td>11</td>
<td>91.5 ± 1.7c</td>
<td>2.3 ± 0.6c</td>
<td>0.5 ± 0.4a</td>
<td>6.9 ± 2.2ac</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>AeS</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>September</td>
<td>9</td>
<td>2</td>
<td>73.3 ± 8.1c</td>
<td>18.7 ± 7.7a</td>
<td>6.7 ± 2.5a</td>
<td>1.1 ± 0.7ab</td>
<td>17</td>
<td></td>
</tr>
<tr>
<td>November</td>
<td>13</td>
<td>9</td>
<td>92.7 ± 2.1ab</td>
<td>0.0 ± 0.6a</td>
<td>1.7 ± 0.8c</td>
<td>5.7 ± 2.8c</td>
<td>4</td>
<td></td>
</tr>
</tbody>
</table>

*Differences in proportions, if significant at P = 0.05, are indicated by different letters (a, b, c) in each column for each season, and by P-value or NS between seasons (Kruskal-Wallis H-test).

**Not counted in calculations. All with empty crops were male, except for two females from AaS in November.*
subcanopy area can also be relatively consistent for up to 3 months. Thus, some pitfall traps under certain study trees regularly caught significantly more beetles than did other traps under the same trees. Litter quality was probably not involved, because both the arena tests and the habitat manipulation tests gave no indication that either quality or specific food type determines the temporary location of a beetle beneath a tree. Rather, some combination of factors, independent of the nutritional quality of the litter, seems to affect beetle location.

Temperature, and the hygroscopic capacity of litter (Tschinkel, 1972) as a function of its organic content (Table 1), are candidates for further study.

Food quality, however, is important to *P. globosa* at a much finer spatial scale. Our subcanopy enclosure tests show that despite low flower : leaf ratios in the soil-litter substrate, beetles consistently ate more flowers than leaves. These findings were reinforced by results of laboratory choice tests, in which flowers, regardless of their concentrations, were again selected over more abundant leaves. Since the earlier field manipulation tests, in which flowers were placed around one fourth of the pitfall traps, had no effect on trap capture, we conclude that choice of a nutritional resource (in this case flowers over leaves) operates at a spatial scale quite removed from that involving choice of a non-nutritional resource (such as litter when it serves only as shelter). In effect, the two resources categories are decoupled, because food is detected and selected at a much finer level of resolution than is substrate not being used as food.

Such a scale-related dichotomy of choice has to our knowledge, not been demonstrated for other terrestrial macro-detritivores, although patterns of species-specific feeding (Calkins and Kirk, 1973; Rogers, Woodley, Sheldon and Uresk, 1978) and habitat use (Doyen and Tschinkel, 1974; Holm and Schultz, 1980; Thomas, 1983; Sheldon and Rogers, 1984; Faragalla and Adam, 1985) have been documented for tenebrionids.

The scale-related behaviour of *P. globosa* may be explained partly in the context of its gut-symbiont relationship. Crawford (1988) has argued that an avoidance of thermal stress, combined with selection of thermally optimal habitat conditions, should maximize gut symbiont activity and, therefore, the detritivore's nutritional state. If this view is correct, then as long as high-value food, such as flowers, is available at levels exceeding some critical threshold, non-nutritional factors, such as microclimate, should be largely responsible for where a beetle spends most of its time in a subcanopy habitat. Whether this explanation can explain dispersion patterns of other mobile detritivores remains to be examined.

### ACKNOWLEDGEMENTS

We thank the following colleagues for critical reviews of drafts of this manuscript: Richard Bradley, James Brown, Manuel Mollies, Robert Pietruszka, Ken Schoenly, Eric Tolsen and Marlene Zuk. Consultation with Robert Pietruszka during and after completion of the field study was especially valuable. We appreciate the field assistance of Deborah Kelso and Janet Rasmussen, the figure illustration of Carol Pietruszka, and manuscript typing by Linda Malan, Ruth Mecklenburg, Diane Thomas and Irene Farmer. We gratefully acknowledge the Foundation for Research Development of the C.S.I.R. for research funds and a visiting fellowship (C.S.C.), and the Directorate of Nature Conservation and Recreation Resorts, Namibia, for facilities and permission to work in the Namib-Naukluft Park.

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**Table 6**

Results of food choice trials by *Physadesmia globosa* offered fresh or dry *Acacia erioloba* flowers at different proportions, and leaves.

<table>
<thead>
<tr>
<th>Relative proportions &amp; conditions of flowers</th>
<th>Per cent flowers in controls n</th>
<th>Per cent flowers in crop contents ($\bar{x} \pm SE$)*</th>
</tr>
</thead>
<tbody>
<tr>
<td>High</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fresh</td>
<td>58.3 ± 2.5 (10)</td>
<td>96.8 ± 2.5 (6) 96.2 ± 1.8 (8) 94.6 ± 2.1 (8)</td>
</tr>
<tr>
<td>Dry</td>
<td>50.4 ± 3.8 (10)</td>
<td>89.3 ± 5.5 (8) 100.0 ± 0.0 (2) 100 (1)</td>
</tr>
<tr>
<td>Medium</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fresh</td>
<td>42.2 ± 2.1 (10)</td>
<td>91.4 ± 5.6 (8) 90.6 ± 6.8 (8) 89.0 ± 11.0 (5)</td>
</tr>
<tr>
<td>Dry</td>
<td>26.0 ± 3.4 (10)</td>
<td>99.0 ± 0.2 (6) 89.6 ± 4.5 (4) 99.8 ± 0.2 (5)</td>
</tr>
<tr>
<td>Low</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fresh</td>
<td>11.8 ± 1.2 (10)</td>
<td>96.2 ± 2.4 (8) 87.6 ± 6.5 (7) 96.0 ± 2.4 (4)</td>
</tr>
<tr>
<td>Dry</td>
<td>12.8 ± 1.4 (10)</td>
<td>86.7 ± 6.3 (7) 56.3 ± 22.7 (5) 97.2 ± 2.1 (4)</td>
</tr>
</tbody>
</table>

*Beetles with empty crops were not included in calculations, which showed significant differences between controls and crop contents (ANOVA, $P < 0.05$) in all but one case. See text for details.
REFERENCES


Food and Habitat Use by Three Tenebrionid Beetles (Coleoptera) in a Riparian Desert Environment

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²Desert Ecological Research Unit of Namibia, P. O. Box 1592, Swakopmund, 9000 Namibia

Use of food and habitat by three species of diurnal adesmine tenebrionid beetles was assessed by crop analyses and pit trapping. Physadesmia globosa (Haag), Onymacris rugatipennis rugatipennis (Haag) and Stenocara gracilipes Solier were chosen for this study as they are the three most common conspicuous macrodetrivores living in the riparian woodland of the usually dry Kuiseb River in the central Namib Desert. The types of food consumed overlapped extensively among species and months of the year, whereas the overlap of habitat use among species and months was less.

INTRODUCTION

Desert environments generally have abundant detritus with relatively slow or variable rates of decomposition (Crawford and Goez, 1982). As decomposition by bacteria and fungi is limited by the pervading aridity, macrodetrivores are relatively important to nutrient and energy cycling (Crawford and Taylor, 1984). Endogenous enzymes (Marcuzzi and Lafisca, 1977) and symbiotic gut fauna (Crawford and Taylor, 1984) enable macrodetrivores to use detritus effectively.

One group of purported macrodetrivores, tenebrionid beetles, are a numerically important component of the biota of the Namib Desert (Koch, 1962). Within the riparian woodland of the Kuiseb River, three species of adesmine tenebrionid beetles are among the most common and conspicuous components of the diurnal epigeaic fauna (Wharton and Seely, 1982): Stenocara gracilipes Solier, Physadesmia globosa (Haag) (Penrith, 1978) and Onymacris rugatipennis rugatipennis (Haag) (Penrith, 1975).

Distinctive activity patterns with temporal and spatial differences have been documented for the more common species of tenebrionid beetles living in the lower Kuiseb River and adjacent gravel plains (Wharton and Seely, 1982). Despite the apparent importance of food in determining the density and the habitats used by these species, little work has been directed toward examining the types of food consumed. Holm and Scholtz (1980) stated that 'virtually all desert animals are euripagous opportunists' whereas Wharton and Seely (1982) described desert tenebrionids as 'opportunistic omnivores' and stated that 'most of the adesmines ... were observed to feed on animal remains and faeces while foraging for plant material'. A number of authors have observed the three species under consideration, as well as other tenebrionids, foraging near or under particular riverine plant species and have assumed that the beetles were feeding on locally derived detritus (Holm and Edney, 1973; Penrith, 1975; Hamilton, Buskirk and Buskirk, 1976; Hamilton and Penrith, 1977; Roer, 1977; Penrith, 1979; Wharton and Seely, 1982).

This paper investigates the diet of the three most common tenebrionid species in the Kuiseb riverine environment by: 1) examining crop contents to directly determine what food was eaten, a method not often used by workers in this field; 2) using pit-fall traps to establish any possible relationships between selected food and habitat in this environment.

MATERIALS AND METHODS

The study area was located in the Kuiseb River course near the Namib Research Institute (23° 34' S, 15° 03' E). Cladophora spinosa (L.) S. M. Phillips is the dominant grass of the river-bed. The perennial woody vegetation of the flood plain is dominated by Acacia albida Del. and A. erioloba E. Meyer (Seely, Buskirk, Hamilton and Dixon, 1981). Because of the lack of pronounced seasonal change in climate and water availability, trees and grasses growing in the river course produce leaves, flowers and fruit throughout most of the year, contributing substantially to surface litter. This plant material, together with other organic debris, constitutes the detritus that accumulates in the environment.

To examine food consumed by the three tenebrionid species, ten individuals of each species were collected by hand in the field in September and December 1983 and March and June 1984. Beetles were immediately placed on ice in the field and crops were removed within three hours. Crops were fixed in Pample's fluid and stored in 70 % alcohol.

Reference slides were made by dissecting fresh and dry plant material from species likely to be present in detritus. Samples were processed in a Waring blender and mounted in Hertwig and Hoyer's solution (Bear and Hansen, 1966).

To analyse the food consumed, crops were severed at the base of the oesophagus and at the cardiac valve. Total crop contents were washed into 5 ml of water and spread evenly in a Petri dish (53 mm diameter) containing a grid of 2 x 2 mm units. Presence or absence of animal material, plant material,
FOOD & HABITAT USE BY TENEBRIONIDS

sand or unidentifiable fragments were recorded for 100 2 x 2 mm units across 5 rows of the grid.

To determine relative availability of the four major crop components in detritus found under three major plant species, three samples of surface detritus (0-5 mm) from beneath each plant species were spread in a thin layer in a Petri dish and the percentage occurrence in four quadrats was estimated (Crawford, Hanrahan and Seely, this volume).

To examine habitat use by the three tenebrionid species, twenty pit traps (150 mm diameter, 240 mm deep) were set out: five placed in a region dominated by A. albida, ten placed in areas dominated by A. erioloba (5 north and 5 south of the river course); five placed near clumps of C. spinosa where Nicotiana glauca R. Graham also occurred. Trap distribution was in proportion to the occurrence of vegetation types. Traps were emptied at two or three day intervals, the identity and numbers of beetles noted, and the beetles released.

Statistical analyses followed procedures outlined in Sokal and Rohlf (1981) and Siegel (1956). A symmetrical overlap index (Pianka, 1973), which ranges from 0 (no overlap) to 1 (complete overlap), was used to evaluate overlap of food and habitat use within and between species.

RESULTS

Detritus samples taken from beneath individual plants were found to be derived predominantly from plants in that immediate vicinity and did not consist of a random admixture of detritus from all plant species growing in the riverine habitat. All plant material in the detritus had wind-blown dust and sand adhering to its surface. Proportions of flowers, leaves, sand and unknown material were estimated from samples taken beneath Acacia albida, Acacia erioloba and Cladoraphis spinosa (Fig. 1). Small animals and animal fragments, mainly insect material, represented such a small proportion of the surface detritus that they were not represented in Fig. 1, although closer inspection revealed small insects associated with Acacia flowers.

Plant material identified in beetle crops consisted of flowers of A. albida, A. erioloba and C. spinosa, and leaves of Acacia species. Anthers and stamens of the flowers were most commonly eaten and leaf material was rarely consumed. The animal material in beetle crops consisted almost exclusively of insect fragments, mainly unrecognizable except as parts of insect cuticle. Ant and dipteran and lepidopteran larvae remains were occasionally identifiable to order. The few whole insects consumed were probably inadvertently eaten because of their association with flower matter. Sand was also found in the crops, but it is not known if it was consumed inadvertently or is involved in digestion. All three tenebrionid species had mixed diets containing all food items listed. In three of the four

Fig. 3

For comparison with the food analyses, the percentage occurrence of the beetles within each habitat type has been depicted for September, December, March and June (Fig. 4).
and symmetrical overlap indices calculated. When habitat use between species was compared for the four months, mean overlap values (Table 1) indicated greater variation between species in habitat use than in food type consumed. When habitats occupied by a single species were compared on a monthly basis, the mean overlap values (Table 2) indicated that P. globosa and O. rugatipennis were trapped fairly consistently in the same sites; S. gracilipes showed slightly greater variability in its use of habitat.

Inspection of Figs 1 and 4 shows that there may be a positive relationship between relative amount of time spent near C. spinosa, as indicated by pit-fall trap captures, and amount of insect material consumed. The Spearman’s rank correlation coefficient was, however, not significant, falling between 0.10 > P > 0.05.

DISCUSSION

Analyses of crop contents of the three Kuiseb species show that these tenebrionid beetles are definitely detritivores, as has been suggested previously by a number of authors. They are not, however, indiscriminate omnivores as they consistently selected specific food types from detritus irrespective of species of plant under which the detritus occurred. Leaves are the major food type available in detritus (Fig. 1), whereas flowers were more commonly eaten. Insects, particularly dry cuticular fragments, represent less than 1 % of detritus whereas they formed a conspicuous part of the crop contents (Fig. 2). Those materials consumed appeared to be the more nutrient-rich components of the detritus.

Although the Kuiseb tenebrionids were found to be entirely detritivores, characteristics of their diet do not differ widely from those of the more herbivorous tenebrionids of North American deserts and grasslands. Based on field observations, dissection of digestive tracts and literature citations, Rust (1986) found four detritivores and one herbivore among the tenebrionids of a sand dune insect community in the Great Basin. Staminate conifer cones represented an average of 51 % of the diet of six beetle species in Arizona, as determined by feeding observations (Doyen and Tschinkel, 1974). The remainder of the diet consisted of living or dry vegetation. Fifty-two plant species were ingested as living, dead or litter material by 13 beetle species in a community in western Washington, although flower material was not particularly mentioned (Rogers, Woodley, Sheldon and Uresk, 1978). In the latter study, arthropod remains ranged from < 1 % to 19 % of the contents of the digestive tract of the various species. In the latter two studies, there was a high degree of overlap in diets among species examined, similar to that found in the Kuiseb detritivores.

Our results from the Kuiseb agree with previous descriptions of food and habitat use derived from a number of shorter term studies in the same area (Hamilton and Penrith, 1977; Penrith, 1979; Wharton and Seely, 1982). Although previous authors did not always differentiate between habitat and food use, they generally provided anecdotal observations of selected foraging areas (e.g., Penrith, 1975; Hamilton et al., 1976; Hamilton and Penrith, 1977; Roer, 1977; Wharton and Seely, 1982). Our analyses expand on these observations and provide direct evidence as to the types of food eaten.

The above results do not provide any evidence for exclusive habitat use by any of the three species of tenebrionid beetles investigated. They also leave unanswered the further question as to whether beetles occur randomly within their environment according to microhabitat or according to differences in availability or relative attractiveness of particular food types. Crawford et al. (this volume) provide a detailed evaluation of the question with respect to Physadesmia globosa.

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We wish to thank G. L. Prinsloo of the National Collection of Insects, Pretoria, for identification of insect fragments from beetle crops. C. S. Crawford, A. C. Marsh and R. D. Pietruszka commented on a draft of this manuscript and R. D. Pietruszka provided statistical advice. For financial assistance we thank the Foundation for Research Development of the C.S.I.R., the University of the Witwatersrand and the Transvaal Museum. The Directorate of Nature Conservation and Recreation Resorts, Namibia, provided facilities and permission for work in the Namib-Naukluft Park.

<table>
<thead>
<tr>
<th>Table 1</th>
<th>Mean monthly overlap values (± SE) between species for food and habitat during four months at different seasons.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Food</td>
<td>Habitat</td>
</tr>
<tr>
<td>P. globosa × O. rugatipennis</td>
<td>0.92 ± 0.04</td>
</tr>
<tr>
<td>P. globosa × S. gracilipes</td>
<td>0.90 ± 0.04</td>
</tr>
<tr>
<td>O. rugatipennis × S. gracilipes</td>
<td>0.90 ± 0.06</td>
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</table>

<table>
<thead>
<tr>
<th>Table 2</th>
<th>Mean monthly overlap values (± SE) within a species for food and habitat during four months at different seasons.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Food</td>
<td>Habitat</td>
</tr>
<tr>
<td>P. globosa</td>
<td>0.91 ± 0.02</td>
</tr>
<tr>
<td>O. rugatipennis</td>
<td>0.85 ± 0.05</td>
</tr>
<tr>
<td>S. gracilipes</td>
<td>0.72 ± 0.10</td>
</tr>
</tbody>
</table>
REFERENCES


The Microenvironment Associated with *Welwitschia mirabilis* in the Namib Desert

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*Welwitschia mirabilis* (Hooker fil.) creates an island of relatively moderate thermal and moisture regimes below its large leaves. In the environmentally stressful habitat in which the plant occurs, soil temperatures may be 40 °C lower below the plant than in nearby unshaded areas, and the plant thereby provides critical shelter to many desert organisms.

INTRODUCTION

Plants modify the environment in which they grow by creating shade and shelter and by accumulating wind-blown debris, silt and sand in addition to the litter they themselves produce. Although the shade and litter associated with desert plants is usually far less than that of plants in temperate and tropical forests and grasslands, even a little shade and organic matter, particularly if concentrated around shrubs, may be of significance locally in a hot desert environment (Noy-Meir, 1979/80).

*Welwitschia mirabilis* (Hooker fil.) is a long-lived gymnosperm which occurs in discrete localities (Kers, 1967; Rodin, 1953) in the Namib Desert. This plant has long straplike leaves (0.5 to 1.0 m broad and 1.0 to 2.0 m long) which create an effective umbrella of shade below the plant. *Welwitschia mirabilis* often occurs in environmentally stressful areas where other plant cover is sparse. Despite the possible importance of the climate-modulating effect of *W. mirabilis* to animals, this aspect has not received any direct attention. Schulze, Eller, Thomas, Willert and Brinckmann (1980) have examined the thermal relationships of *W. mirabilis* and state that these plants modify air and soil temperatures considerably. Their study, involving *W. mirabilis* in a grassland and a cool coastal region of the Namib, recorded that air and soil temperatures below the leaves were equal to, or slightly lower than, ambient air temperature despite high temperatures on the insolated soil surface. Furthermore, the leaves themselves were only 4–6 °C above air temperature. This was thought to be due to the high reflectivity of the leaf (Schulze et al., 1980). The central layer of the cuticle contains crystals of calcium oxalate that may play an important role in reflecting radiant energy (Bornman, 1972) as may the fibre bundles that run parallel to the leaf axis (Eller, Willert, Brinckmann and Baasch, 1983).

The present study examines the extent to which *W. mirabilis* plants modify their local thermal and moisture environment in the central Namib Desert at a site about 70 km inland from the coast. At this site the insolated soil surface temperatures regularly exceed 70 °C and *W. mirabilis* represents the most abundant perennial vegetation. A moderate thermal climate below the plants could represent a critical refuge that enables animals to survive in this environment.

METHODS

Study site

All work was carried out at 'Welwitschia Wash' (15° 36’ E; 23° 37’ S), 20 km east of the Namib Research Institute. The wash is barren and *W. mirabilis* plants form the main constituent of the vegetation, the only other perennial vegetation of importance being *Adenolobus pechuelii*, *Orthanthera albida* and *Sutera maxill*, which provide little in the way of canopy cover. During the day, owing to direct radiation, re-radiation of heat from the steep rocky sides of the wash as well as lack of air movement in the wash, insolated soil surface temperatures may be extremely high, temperatures of 78 °C having been recorded during the study.

Soil Moisture

Samples for analysis of soil moisture were collected at 15h00 on three occasions (Table I). Soil samples were taken at a depth of 50 mm:

a) On the southern side but close to the stem of *W. mirabilis* plants.

b) In an exposed area, one to two metres south of the plant’s leaf tips.

Soil moisture was determined gravimetrically by drying a pre-weighed soil sample in an oven at 70 °C for a minimum of four days.

Temperature measurements

Temperatures associated with *W. mirabilis* plants were measured using copper constantan thermocouples and a digital...
thetemperature (Bailey Instruments, Model BAT-12). Thermocouples were 30 gauge and had tips embedded in epoxy. Readings were taken at approximately hourly intervals for 24 to 48 hours on three occasions in 1982. On each occasion, soil surface temperatures were also measured at an exposed site close to the *W. mirabilis* plants. Air temperature in the shade was measured at a height of 1 m with a mercury thermometer.

1) From 17h30 on 25 January 1982 to 17h30 on 26 January 1982 the following temperatures were measured: soil surface temperature below *W. mirabilis* leaves where the ground was covered with a 20–30 mm layer of litter; 40 mm below the soil surface in an exposed area; 40 mm below the soil surface under *W. mirabilis* leaves, where the soil was covered with a 20–30 mm layer of litter.

2) From 12h00 on 19 April 1982 to 14h00 on 20 April 1982 the following temperatures were measured: soil surface temperature below *W. mirabilis* leaves, ground not covered by litter; surface temperature below *W. mirabilis* leaves, ground covered by 20–30 mm layer of litter; under a 40–50 mm layer of litter in the stem depression.

3) From 19h00 on 21 February 1982 to 18h00 on 23 February 1982 the following temperatures were measured on the east and west sides of the plant: soil surface temperature below leaf tips of plant; soil surface temperature about 30 mm from the stem of the plant and under a 20–30 mm layer of litter.

**RESULTS**

**Soil moisture**

The percentage soil moisture at a depth of 50 mm (Table 1) was significantly higher below *W. mirabilis* plants than at nearby exposed areas (*P* < 0.001 for 10 February 1983 and 13 August 1983 and *P* < 0.01 for 7 April 1983). The percentage soil moisture was not higher on days during which fog was experienced in the mornings (10 February and 7 April) than on a fogless day (13 August).

**Temperature measurements**

On 26 January 1982 surface temperatures at the exposed site reached 78 °C while surface temperatures below the plant's leaf reached a maximum of just over 40 °C (Fig. 1). Temperatures at the exposed site were greater than 40 °C for approximately 10 of the 24 hours monitored (Fig. 2).

Temperatures at a depth of 40 mm below the soil surface at the exposed site reached a maximum of just over 60 °C while at 40 mm depth below the plant, temperatures peaked at 36.6 °C and the range in temperature over 24 hours was 6.5 °C compared with a range of 36 °C at a depth of 40 mm at the exposed site.

On 20 April 1982, surface temperatures reached a maximum of 54 °C at the exposed site and 31.4 °C under *W. mirabilis* leaves on shaded, litter-free soil; soil surface beneath a 20–30 mm deep layer of litter; and in stem depression under a 40–50 mm deep layer of litter.

![Fig. 1](image-url)

Transverse section through *Welwitschia mirabilis*, showing maximum temperatures recorded on 1) 20 April 1982 and 2) 26 January 1982 in the following positions: a: 1 m above the soil; b: insolated soil surface; c: 40 mm below insolated soil surface; d: below leaves on shaded, litter-free soil; e: soil surface beneath a 20–30 mm deep layer of litter; f: 40 mm below soil surface that was covered with a 20–30 mm deep layer of litter; and g: in stem depression under a 40–50 mm deep layer of litter.

![Fig. 2](image-url)

**Table 1**

Mean (X) and standard deviation (S.D.) of the percentage soil moisture in soil samples from below leaves of *W. mirabilis* and exposed sites nearby; *n* represents the number of samples taken.

<table>
<thead>
<tr>
<th>Date</th>
<th><em>n</em></th>
<th>Percentage soil moisture below plant X ± S.D.</th>
<th>Percentage soil moisture at exposed site X ± S.D.</th>
</tr>
</thead>
<tbody>
<tr>
<td>10 February 1983</td>
<td>9</td>
<td>0.41 ± 0.08</td>
<td>0.17 ± 0.03</td>
</tr>
<tr>
<td>7 April 1983</td>
<td>10</td>
<td>0.37 ± 0.08</td>
<td>0.26 ± 0.06</td>
</tr>
<tr>
<td>13 August 1983</td>
<td>20</td>
<td>0.43 ± 0.12</td>
<td>0.25 ± 0.07</td>
</tr>
</tbody>
</table>
leaves (but not covered with litter), while temperatures under *W. mirabilis* leaves, where the ground was covered with litter, reached 28 °C. The maximum temperature under litter in the stem of the plant was 34 °C (Fig. 1). Whereas the range of temperatures was 18.5 °C for bare soil surfaces below the leaves and under the stem litter, the range was 10 °C below litter under the leaves (Fig. 3).

On 20 February 1982, exposed surface temperatures reached a maximum of 67 °C (Fig. 4). At any one time temperatures on the east and west side of the plant varied considerably, both at the leaf tips and close to the stem in constant shade.

Temperatures on the east side peaked earlier, the maxima were lower than those on the west side, and exhibited a smaller range. Even the frayed leaf tips moderated ground temperatures considerably. At 14h00 the difference in temperature between the soil surface below leaf tips and exposed soil surfaces was approximately 10 °C (both east and west sides); however, at 16h00 the temperature below leaf tips on the west side was virtually the same as the exposed soil surface, while the temperature on the east side below leaf tips was 15 °C lower.

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**Fig. 2**
Temperatures recorded during 25 and 26 January 1982: a: on exposed soil; b: at 40 mm depth below exposed soil; c: below *W. mirabilis* leaves – on the soil surface; and d: at 40 mm depth. Soil was covered by 20–30 mm litter for (c) and (d).

**Fig. 3**
Temperatures recorded during 19 and 20 April 1982: a: on exposed soil; b: under 40–50 mm litter in *W. mirabilis* stem depression; c: below *W. mirabilis* leaves – on bare ground; and d: soil surface under 20–30 mm litter.
DISCUSSION

*Welwitschia mirabilis* creates a microclimate below its leaves in which temperature and moisture regimes are considerably more moderate than those prevailing in the harsh environment in which it lives. Thus when the temperature of exposed soil was over 70 °C, soil temperatures below *W. mirabilis* plants barely reached 40 °C. Even soil temperatures below frayed leaf tips were substantially lower (up to 15 °C) than at exposed sites under certain conditions. Furthermore, temperatures varied considerably depending on the point of measurement relative to the plant. Since leaves tend to become frayed at the tips, temperatures were generally higher with increasing distance from the stem. Thermal regimes at easterly and westerly positions under the plant displayed considerable differences and the amount of litter collected within the stem depression and at the base of the stem moderated temperatures. There is therefore a mosaic of temperatures within the microhabitats associated with *W. mirabilis* at any one time.

Microhabitats associated with desert plants often provide favourable conditions for arthropod activity (Charley and West, 1977; Sartos, DePree and Whitford, 1978) and for refuge and feeding of other animals (Cloudsley-Thompson, 1962; Larmuth, 1979; Seely, De Vos and Louw, 1977). The microhabitats below *W. mirabilis* attract numerous animals, including birds, snakes, small mammals, lizards, chameleons, scorpions, spiders and a variety of insects (Bornman, 1971). Marsh (1987) has also established that a relatively rich microarthropod community flourishes in the soil mound below this species. Many of the large animals do not live permanently below *W. mirabilis* nor do they utilize the plant as a food resource. Their occasional presence below the plant is probably largely due to the thermal refuge that the plant provides. Furthermore, it is likely that the humidity beneath the plants is greater than elsewhere because of transpiratory water loss and this may also enhance the attractiveness of the microenvironment for animals. The presence of a permanent diverse microarthropod fauna below the plants and their scarcity elsewhere in this habitat (Marsh, 1987), is largely because of a relatively rich food resource base in the form of litter but their ability to persist there can also be attributed to the more favourable microclimate created by the plant.

Fig. 4
Temperatures recorded during 21, 22 and 23 February 1982: a: on exposed soil; b: soil surface under western leaf tips; c: soil surface under eastern leaf tips; d: soil surface west of stem; and e: east of stem. (d) and (e) were under 20–30 mm litter.
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