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# ECOLOGY OF DESERT ENVIRONMENTS

(A Festschrift for Prof. J.L. Cloudsley-Thompson on his 80th Birthday)

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## ANIMAL ECOPHYSIOLOGY IN THE NAMIB DESERT : COPING WITH LITTLE WATER, SCARCE FOOD AND ELEVATED TEMPERATURES

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# Animal ecophysiology in the Namib Desert: Coping with little water, scarce food and elevated temperatures

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## Abstract

In the hyperarid Namib desert, animals face water- and food-shortages coupled with heat. Some ecophysiological and physiological factors that enable animals to exist in the Namib have been examined by the Desert Research Foundation of Namibia (DRFN) and its affiliates during the past 40 years. The main findings are reviewed here. They include the physiological tolerance of desiccation and osmotic stress, non-conventional methods of acquiring free water from fog and from humid air, soil moisture and metabolic water. Further investigations concerned the reduction of water loss through cuticular, respiratory and excretory processes, the selection of tolerable microclimatic conditions, a low metabolic rate that reduces food and water requirements as well as the water losses, mechanisms of losing or avoiding heat, heat tolerance, and thermophily. These conditions and mechanisms have far-reaching consequences to the ecology. Of particular interest for future research would be investigations of the physiological mechanisms relating to an osmotically stressed inner milieu - as water is compulsory - and of thermophily - as enzymes of eukaryotes function in a rather restricted thermal range.

**Keywords:** water balance; desiccation; fog; water loss; excretion; microclimate; low metabolism; heat tolerance; thermophily; behaviour; physiology; morphology; desert resource management

## Introduction

Deserts present special conditions for life due to their inherent variability. This concerns especially a limited supply of water, essential for all organisms, often coupled to food shortage and exposure to harsh climatic conditions (Maloiy, 1972; Hadley, 1974, 1994; Edney, 1977; Louw & Seely, 1982; Dawson *et al.*, 1989; Safriel *et al.*, 1989; Louw, 1990, 1993; Seely, 1990; Cloudsley-Thompson, 1991a; Heinrich, 1993; Lovegrove, 1993; Somme, 1995; Heatwole, 1996; Bradshaw, 1997; Degen, 1997; Punzo, 2000). Various physiological mechanisms allow animals to cope with these conditions and to exist in deserts. These include physiological control of water and salts within the organism, such that osmotic phenomena do not interfere with cellular and molecular functioning (Hadley, 1994). Similarly, control of body temperature and tolerance of high temperatures ensure the physiological functioning on the cellular and molecular level.

We dedicate this paper on Namib animal ecophysiology to Prof. John Cloudsley-Thompson, who contributed to our knowledge of the Namib Desert (Cloudsley-Thompson, 1990 a,b,c, 1991 a,b). As the doyen of desert animal ecophysiology, Cloudsley-Thompson emphasised the fundamental importance for animals in tropical desert environments of coping with shortages of water and food and elevated temperatures (Cloudsley-Thompson, 1962a, b, 1964, 1965a, b, 1967a, b, 1968a, b, 1969a, b, 1970a, b, c, 1971, 1972, 1973, 1974, 1975, 1976, 1977, 1979a, b, 1982, 1983, 1984, 1986, 1987, 1988, 1990a, 1991a, 1993a, b, 1994, 1995, 1996; Carlisle & Cloudsley-Thompson, 1968; Cloudsley-Thompson & Cloudsley, 1984). Cloudsley-Thompson's thinking significantly affected the development of these fields of ecophysiological research in deserts of the world. He considered reptiles and arthropods to be pre-adapted to life in deserts (Cloudsley-Thompson, 1991). Bradshaw (1997) emphasised this by pointing out that desert ectotherms do not differ qualitatively from mesic members of their respective groups except in respect of their degree of adaptation necessary to deal with the extreme temporal and spatial variation of abiotic and biotic resources.

This paper concerns the functioning of animals in the highly variable conditions of water, food and temperature prevailing in the Namib Desert. The Namib Desert is relatively well studied, thanks largely to the Desert Research Foundation of Namibia at Gobabeb (DRFN and its predecessor, the Desert Ecological Research Unit) and its affiliates over a period spanning four decades (Henschel *et al.*, 2000a; Seely *et al.*, 2000a). A central programme connecting various studies over the past forty years has been the Long-Term Ecological Research Programme (Henschel *et al.*, 2000b; Na-LTER, 2000). Developments in the field of ecophysiology in the Namib were particularly influenced by Prof. Gideon Louw, as elucidated to some extent in this paper (e.g. Louw, Belonje & Coetzee, 1969; Louw, 1971, 1972; Louw & Hamilton, 1972; Louw & Holm, 1972; Joubert & Louw, 1976; Seely, de Vos & Louw, 1977; Dixon & Louw, 1978; Hadley & Louw, 1980; Louw & Seely, 1980; Seely & Louw, 1980; Withers, Louw & Henschel, 1980; Withers, Siegfried & Louw, 1981; Louw & Seely, 1982; Robertson, Nicolson & Louw, 1982; Louw, 1984; Louw & Seely, 1984; Nicolson, Louw & Edney, 1984; Bartholomew, Lighton & Louw, 1985; Seely, Mitchell & Louw, 1985; Louw, Nicolson & Seely, 1986; Seely & Louw, 1986; Loutit, Louw & Seely, 1987; Hofmeyr & Louw, 1987; Louw, 1990, 1993; Skinner & Louw, 1996).

In the Namib, evaporation exceeds precipitation by a factor of 200, and this desert contains excellent examples of the principles of desert ecophysiology in animals in a water-constrained environment (e.g., Willoughby, 1967; Coutchié & Crowe, 1979; Hadley & Louw, 1980; Withers *et al.*, 1980; De Villiers, 1984; McClain *et al.*, 1985; Seely & Griffin, 1986; Downs, 1989; Fielden, 1989; Nicolson, 1990; Roberts, 1991; Clarke, 1992; Naidu, 1992; Grube, 1993; Jacobson & Jacobson, 1998). Food availability tends to be coupled to highly unpredictable rainfall, and tolerance of hunger is important between these infrequent periods of plenty (e.g., Seely & Louw, 1980; Nagy *et al.*, 1993; Henschel, 1994; Lubin & Henschel, 1996; Seymour & Seely, 1996; Seymour *et al.*, 1998). This is compounded by daily hot surface conditions and extreme daily temperature fluctuations (e.g., Henwood, 1974; Hamilton, 1975; Curtis, 1985a; Marsh, 1985, 1987; Seely & Mitchell, 1987; Pietruszka, 1988; Lombard, 1989; Cloudsley-Thompson, 1990a; Lubin & Henschel, 1990; Robinson, 1990, 1993; Roberts, 1991; Ward, 1991).

In this paper we review some of the main findings of ecophysiological research conducted in the Namib. We emphasise invertebrates, particularly tenebrionid beetles that have enjoyed considerable attention (over 180 papers, e.g., Koch, 1962; Hamilton & Seely, 1976; Seely & Hamilton, 1976; Seely, 1983; Nicolson *et al.*, 1984; Cloudsley-Thompson, 1990a; Nicolson, 1990; Roberts, 1991; Ward & Seely, 1996a, 1996b). The study of tenebrionids demonstrates how studies of one key group of organisms can be used to illuminate the functioning of a particular ecosystem. Ecophysiology is emphasised, although Louw (1990) pointed out that delineation of behaviour versus physiology is primarily semantic and not really important when one is dealing with many organisms, as both ultimately alter and maintain optimal cellular function within the constraints of phylogeny. Thus, the question whether animals show specific adaptations to deserts can be answered in a general way by agreeing that an adaptation is (Louw, 1993; p.x) "any physiological or behavioural characteristic which allows an organism to survive and reproduce in a particular environment, thereby contributing to its fitness".

After describing some important abiotic characteristics of the Namib, we examine how many animals cope with water scarcity through osmoregulation, by behavioural, morphological and physiological methods of acquiring free water, and through reducing water loss. Coupled with water shortage is reduced primary production, ultimately resulting in a shortage of food over considerable lengths of time for many animals, with profound consequences to foraging behaviour and metabolism. Lastly, we explore how temperatures in this desert affect its inhabitants in terms of thermoregulation, physiological tolerance and thermophily. Besides summarising some of the current knowledge of ecophysiology in the Namib, we compare it to findings from other deserts and highlight avenues for further study.

## The Namib

The Namib Desert is a 200 km-wide coastal strip that stretches for over 2000 km from South Africa northwards across western Namibia into Angola (Fig. 1). The Benguela Current of the Atlantic Ocean forms its western boundary, and the Western Escarpment its eastern delimitation. In the Central Namib, where Gobabeb is located and most of the studies reported here were conducted, the ephemeral Kuiseb River divides the southern Great Sand Sea, comprising various types of dunes, from the vast gravel plains that are scattered with inselbergs (Seely, 1987).

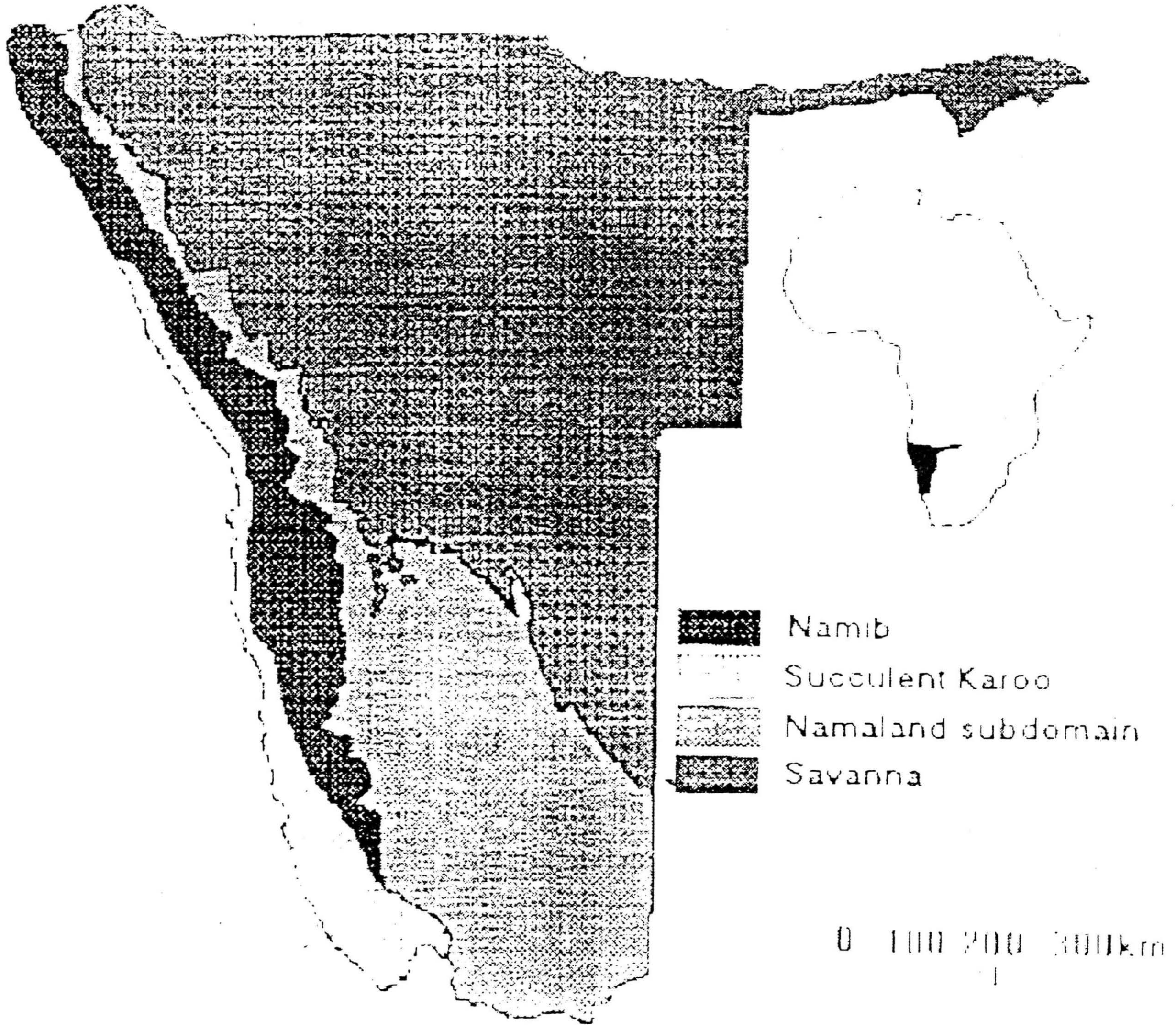

**Figure 1:** In Namibia, the Namib Desert is situated west of the Great Escarpment, which forms the western boundary of the Namaland subdomain of the Nama-Karoo Biome. The Namib Desert comprises the Namib subdomain of the Nama-Karoo (darkest shading) as well as the Succulent Karoo (lightest shading) (after Jürgens, 1991).

Important abiotic factors that affect organisms in the Namib (Robinson & Seely, 1980) include fog and rain precipitation, humidity, temperature and its daily range at the surface and at depth, substratal grain size, wind, and surface topography. Wind is important, as it affects dune morphology and the compaction, moisture and mobility of sand. The interaction of wind and sand drives the major organic resource, the detritus cycle, affecting its storage and gradual release (Crawford & Seely, 1994; Hanrahan & Kirchner, 1997), while rainfall affects its production (Seely & Louw, 1980; Southgate *et al.*, 1996) and breakdown (Jacobson & Jacobson, 1998). Because of the low vegetation cover, diurnally active animals are exposed to heat, exacerbated by the desiccating atmosphere. Heat is gained and lost very quickly by the physical environment as well as by the organisms (Roberts, 1991).

The Namib has been arid since the end of the Cretaceous Period, with the current hyper-aridity beginning during the Miocene (Ward *et al.*, 1983). This desert is situated at the lowest end of a rainfall gradient that begins at the Indian Ocean in the east and declines westwards. This decline is pronounced from east to west across the Namib, and there are years when no rain at all falls in the western Namib (Table 1). Wet years (>80 mm rainfall per annum) are rare, and occurred only two to four times in the last century, depending on location. Fog, the other source of water, occurs mainly in the western 60 km of the Namib (Table 1; Lancaster *et al.*, 1984; Henschel *et al.*, 1998). Fog ameliorates the potential aridity of the Namib adjacent to the coast (Seely *et al.*, 1998) and is more predictable than rain (Pietruszka & Seely, 1985). Fog water is, however, only temporarily available as this source of moisture disappears as soon as the fog lifts each day and the soil surface dries again (Gut, 1988; Besler & Gut, 1997).

**Table 1**. *Annual mean and range of climatic conditions across the Namib Desert. Data sources: DRFN, 2000; Meteorological Services of Namibia; Lancaster et al., 1984; Besler, 1972.*

| MEASUREMENT ZONE | Coastal Foggy Zone | Inland Foggy Zone | Middle Namib Zone | Eastern Namib Zone |
|---|---|---|---|---|
| Distance from Coast (km) | 0-20 | 20-60 | 40-90 | 70-120 |
| Rainfall, mean ± SD (mm) | 10.1 ± 16.4 | 15.4 ± 13.1 | 21.2 ± 26.0 | 41.2 ± 27.4 |
| Rainfall, range (mm) | 0-90 | 0-65 | 2-127 | 6-374 |
| Fog precipitation, mean (mm) | 80.2 | 183.6 | 30.8 | 3.8 |
| Fog precipitation, range (mm) | 49-158 | 88-271 | 8-48 | – |
| Fog day frequency, mean | 75 | 118 | 75 | 3 |
| Temperature, mean (°C) | 15.5 | 19.3 | 21.1 | 21.5 |
| Temperature, range (°C) | 5.5-36.0 | 1.7-41.9 | 1.0-44.9 | 0.9-39.4 |
| Daily temperature amplitude, mean (°C) | 5.7 | 17.2 | 17.3 | 13.9 |
| Relative humidity, mean (%) | 87 | 56 | 50 | 36 |
| Relative humidity, range (%) | 21-100 | 4-100 | 1-100 | 1-100 |
| Evaporation, total (mm) | 1328 | 1935 | 3470 | 3697 |
| Days with Berg Wind | 10-15 | 30-60 | 40-70 | 60-90 |
| Aridity Factor | 1.37 | 2.36 | 0.87 | 1.83 |

The terrain changes from north to south along the Namib Desert, but the major feature is an extreme climatic gradient across the desert from west to east. This gradient can be divided into several biophysical zones that lie parallel to the coast (Table 1; Besler, 1972; Lancaster *et al.*, 1984; Hachfeld, 1996; Henschel *et al.*, 1998): (1) coastal foggy Namib zone; (2) interior foggy zone; (3) middle zone; (4) the eastern Namib. Besides precipitation, other climatic changes from west to east across the desert are increasing average and range of temperature, decreasing humidity, increasing evaporation, and increasing number of days with warm, extremely dry easterly Berg winds in winter (Table 1). The steep climatic gradient makes the Namib an ideal place to study, as found nowhere else in such a compact form.

Seasons in the Namib are not as pronounced as in other temperate regions and are mainly characterised by desiccating, easterly Berg winds during winter, sometimes resulting in sand storms, as opposed to the dominant, humid, moderately strong westerly sea breeze and plain-mountain wind during summer (Lancaster *et al.*, 1984). Average air temperatures change little with season (Table 2), and extreme values decline by a mere 5-7 °C in winter (Fig. 2), despite substantially lower solar radiation. However, daily amplitude in air temperatures is 16-17 °C throughout the year (Table 1 & 2), and this is even more pronounced on the soil surface. There are often extremely strong temperature gradients at near-surface height above the ground and near-surface depth below the ground (Fig. 2). Surface temperatures also change with time of day and season, but daily temperature ranges are negligible at 20 cm depth and seasonal ranges are negligible at 120 cm (Fig. 2).

**Table 2.** *Climatic conditions at Gobabeb (56 km from the coast) in the Middle Namib Zone, showing annual mean, summer mean (October-March), winter mean (April-September) and total range. Data sources: DRFN 2000; Lancaster et al., 1984.*

| MEASUREMENT PERIOD | Annual | Summer | Winter | Range |
|---|---|---|---|---|
| Rainfall (mm) | 21.2 ± 26.0 | 18.2 | 9.0 | 2-127 |
| Fog (mm) | 30.8 | 14.5 | 16.3 | 8-48 |
| Air temperature (°C) | 21.1 | 23.1 | 19.2 | 1.0-44.9 |
| Daily air temperature amplitude (°C) | 17.3 | 16.4 | 17.1 | 4.0-30.0 |
| Daily maximum surface temperature (°C) | 53.6 | 59.8 | 47.5 | 41-75 |
| Humidity (%) | 50 | 55 | 44 | 1-100 |
| Daily Evaporation (mm) | 9.5 | 10.9 | 8.2 | – |
| Daily Sunshine Hours (h) | 10.4 | 11.2 | 9.5 | – |
| Daily Solar Radiation ($MJ.m^{-2}$) | 19.2 | 23.6 | 13.8 | 7.9-26.1 |
| Wind Speed (m/s) | 2.9 | 3.0 | 2.8 | 0-28 |
| Daily Wind Duration (h/day) | 17.0 | 18.3 | 15.6 | 0-24 |
| Predominant Wind Direction | – | SW & NW | SE | – |

Macro- and micro-climatic patterns of the Namib vary on spatial scales of tens of kilometres to centimetres and on time scales of decades and years, to seasons and hours. Namib animals thus have a wide variety of different conditions available to them that may affect their times and places of activity and non-activity.

## Water

Problems of water gain, balance, reduction of water loss, tolerance of water loss, and consequent osmotic phenomena have been a focus of much study in desert arthropods (Seely, 1989). Desiccation may be tolerated physiologically or avoided behaviourally. Methods of acquisition of free water are especially important for the detritivores such as tenebrionid beetles and thysanurans that predominate in this desert, because water is required to process desiccated detritus. Herbivores (Nagy *et al.*, 1991) and predators (Fielden *et al.*, 1990) do not face the same problem, because

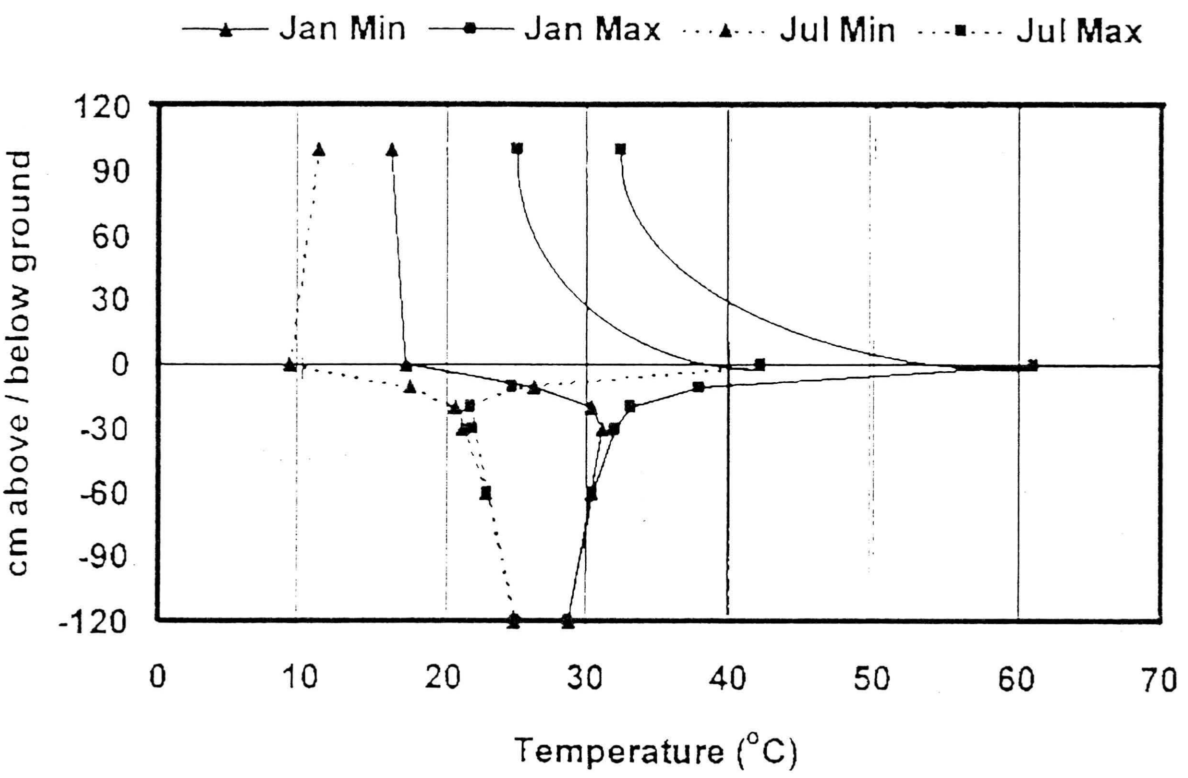

**Figure 2.** Mean daily range of temperatures at various levels above or below the ground during the hottest (January) and coldest (July) months. Derived from Lancaster *et al.* (1984).

their food is comparatively water-rich, while some flying insects can generate water through metabolic activity (Louw & Hadley, 1985). Different water problems exist, however, for herbivores and predators respectively. Herbivores' food sources often contain high levels of potassium, resulting in alterations of osmotic relations within the 'milieu interieur' of the herbivore. Predators frequently consume prey with greater electrolyte concentrations than the predator's own body fluids, resulting in a water deficit in terms of the ultimate ability of the animal to excrete these ions (Bradshaw, 1997). These osmotic consequences of consumption must also be dealt with rapidly for most organisms to survive.

Two methods exist for desert organisms to counter the effects of water loss. Either they reduce the water loss or they develop a tolerance to the osmotic stresses that develop as waste accumulates and water is lost.

### *Acquiring Free Water*

Fog is a predictable source of water near the Namib coast (Pietruzska & Seely, 1985). Many animals have evolved novel mechanisms for accessing this water (Louw, 1972; Seely, 1979; Seely & Griffin, 1986). For example, the endemic tenebrionids, *Onymacris unguicularis* and *O.bicolor*, fog-bask on dune slopes, allowing fog to condense on their bodies and trickle down towards their mouths (Hamilton & Seely, 1976; Seely & Griffin, 1986) (Fig. 3). Similarly, the sidewinder adder, *Bitis peringueyi*, drinks fog water that condenses on its cold body (Louw, 1972; Robinson & Hughes, 1978). The tenebrionid *Lepidochora discoidalis* constructs a trench in sand that enhances condensation of fog water, enabling the beetle to drink it from the sand surface (Seely & Hamilton, 1976). The scorpion *Parabuthus villosus* imbibes fog water that has condensed on grass stems (Polis & Seely, 1990), as do several tenebrionids. Spiders drink water from fog-drenched trap-doors (Henschel, 1997). Fog water that condenses on soil is above field capacity, which facilitates drinking (Louw, 1993; Seely, 1979). One drink by fog imbibers is equivalent to 12-14% (maximum 42%) of their original body weight (Seely, 1979). Acquisition of water from fog plays an important role for the Namib food web (Fig. 4).

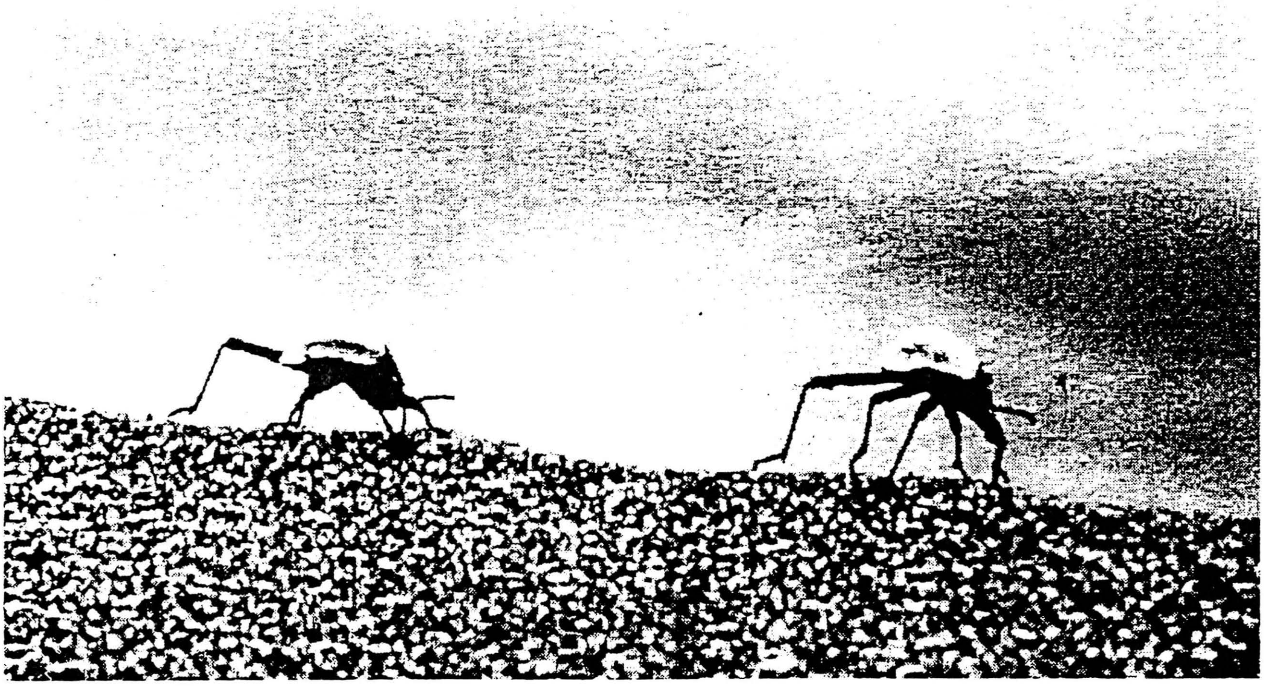

**Figure 3.** *Onymacris bicolor* beetles fog-basking on a dune crest. Photo M.K.Seely.

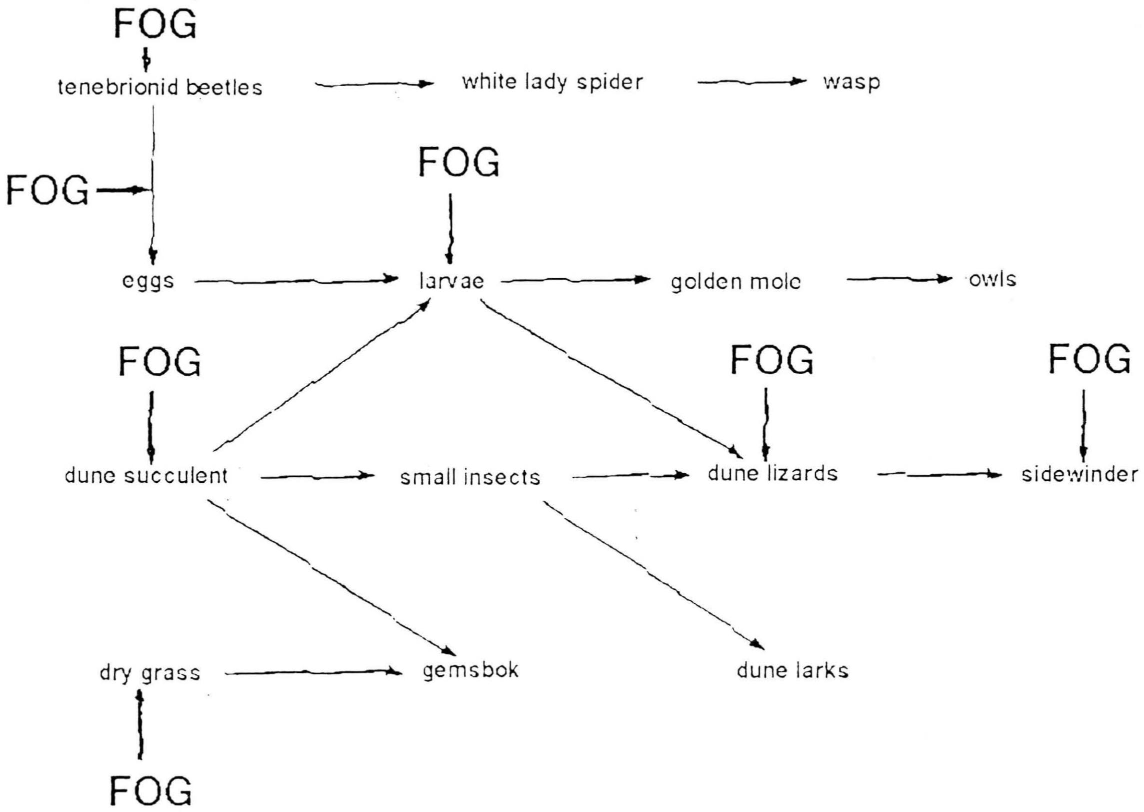

**Figure 4.** The role of fog as water source in the Namib dune food-web (adapted from Seely, 1987).

Soil capillary water is a source of water for Namib termites, such as *Psammotermes allocerus*. They use their hypopharyngeal pseudergates to drink (Grube & Rudolph, 1995). Free water is not available to many microarthropods because of problems of scale and water tension, which can result in drowning.

The ability to absorb water vapour from unsaturated air has been recorded for larvae of Namib tenebrionids *Onymacris* spp. (Coutchié & Crowe, 1979) and several thysanurans (Edney, 1971; Heeg, 1967a, b; Noble-Nesbitt, 1975). The thysanuran *Ctenolepisma longicaudata* is able to absorb water from air at a relative humidity as low as 60%. The mechanism appears to depend on ion pumps that create an osmotic gradient sufficient to draw water vapour from unsaturated air (Noble-Nesbitt, 1975; Machin, O'Donnell & Coutchié, 1982; Machin, 1983). Some tenebrionid larvae, such as *Onymacris plana*, have a very low threshold for water vapour absorption that might depend on KCl supersaturation (Machin & O'Donnell, 1991). Tenebrionid larvae use a specialised structure, the cryptonephridial complex, in the rectal cavity to absorb water vapour (Machin & O'Donnell, 1991). In Thysanura, the structures involved are also located in the rectal cavity.

### *Reduction of Water Loss*

Animals lose water by the excretion of nitrogenous waste and by evaporative losses from respiration or cutaneous/integumentary losses. Water reduction by these routes involves dealing with basic processes leading to these water losses, namely, reducing excretion and tolerating osmoregulatory consequences of waste accumulation, and reducing respiratory and integumentary evaporation.

Tenebrionids are capable of surviving extensive dehydration, as studies on larvae (Coutchié & Crowe, 1979; Machin, 1981) and adults (Cooper, 1982; Naidu & Hattingh, 1986, 1988; Nicolson, 1980, 1990) have shown. Dehydrated tenebrionids use haemolymph as a reservoir for regulating tissue water levels. The mechanism involves reversible sequestration of ions in the fat body (Nicolson, 1980). *Onymacris marginipennis* is a good example. Its haemolymph volume can decline by 60%, yet tissue water volume remains constant and its osmolality rises by only 14% (Nicolson, 1980). Use of a diuretic hormone by the Namib tenebrionid *Onymacris plana* appears to be puzzling, but it appears to facilitate haemolymph regulation, by facilitating the excretion of metabolic wastes from the haemolymph. Water used in this process is recovered from fluid secreted by the Malpighian tubules, before waste is expelled from the body (Nicolson & Hanrahan, 1985; Nicolson, 1991, 1992).

Hadley (1994) has pointed out that for arthropods with tracheal systems, functioning of the metabolising cells is maintained for as long as possible if haemolymph is used as a water reservoir. This is especially advantageous for desert fauna with restricted access to available water. By contrast, those arthropods that use their haemolymph for respiratory purposes are at a disadvantage because they have a reduced ability to use their haemolymph as a reservoir to maintain tissue water.

Most scorpions have poor regulation of their haemolymph, but tolerate resulting osmotic stresses. An exception to this general rule is provided by the Namib thick-tailed scorpion *Parabuthus villosus*, which has a good capacity to regulate its haemolymph (Robertson, Nicolson & Louw, 1982).

Reptiles normally need to regulate their body fluids to ensure physiological functioning. However, desert reptiles seem to tolerate hypernatraemia, i.e. excessive levels of sodium in their blood. When the osmotically active potassium ion is considered, the situation is different. Excess potassium increases cell excitability and impedes its proper functioning (Rankin & Davenport, 1981). This problem is solved by extra-renal excretion via powerful salt glands, which preferentially excrete potassium ions. These glands are particularly efficient in desert species, such as the Namib chameleon *Chamaeleo namaquensis* (Louw, 1993). Reptiles and birds can also stop water being lost through water absorption by the cloacal-colonic complex (Bradshaw, 1997).

### *Metabolic water*

Nicolson (1990) pointed out unusual aspects of the physiology of Namib tenebrionids compared to most arthropods. They generally have lower water content possibly due to a heavier integument and, sometimes, extensive fat reserves. Metabolic water can make a substantial contribution to their water economy (Nicolson, 1990), e.g., replacing approximately $^1/_3$ to $^1/_2$ of the water lost to respiration in the extremely fast-running tenebrionid *Onymacris plana* (up to 4.12 $mg.g^{-1}.h^{-1}$). This is less in the slower-moving *O.unguicularis* 0.35 $mg.g^{-1}.h^{-1}$ (Cooper, 1982), whilst in a resting *O.unguicularis*, metabolic water contributed only 0.02$mg.g^{-1}.h^{-1}$

(Bartholomew *et al.*, 1985; Louw *et al.*, 1986). This range in water production shows the substantial advantages of intense locomotory activity in situations where water loss, gain and thermoregulation are at a premium (Roberts, 1991).

Some Namib rodents produce metabolic water from dry seeds (Withers *et al.*, 1980). This remarkable ability enables them to survive in environments such as deserts where there may be severe limitations on available water. In the Namib, advective fog is an important source of moisture for many animals. Coupled with their ability to produce highly concentrated urine through highly modified kidney structures (Downs & Perrin, 1991), these adaptations allow rodents to survive in arid environments. The ability to survive on dry food is not, however, exclusive to small mammals, amongst endotherms; the grey-backed finch-lark and Stark's lark can also survive exclusively on dry food (Willoughby, 1967). The abilities of all these animals relate to restricting water loss to the absolute minimum physiologically possible.

### *Vapour Pressure Relations*

Burrows and psammophily provide microclimatic retreats for many animals during the day when surface temperature is high and humidity low (Seely & Mitchell, 1987). This may contribute to reducing water loss. Edney (1971, 1974, 1977) pointed out the considerable advantages of using vapour pressure rather than relative humidity in order to understand water vapour flow. During the day, water vapour flows into the retreat, even if the retreat has a higher relative humidity than the outside environment. Vapour pressure differences, created by temperature

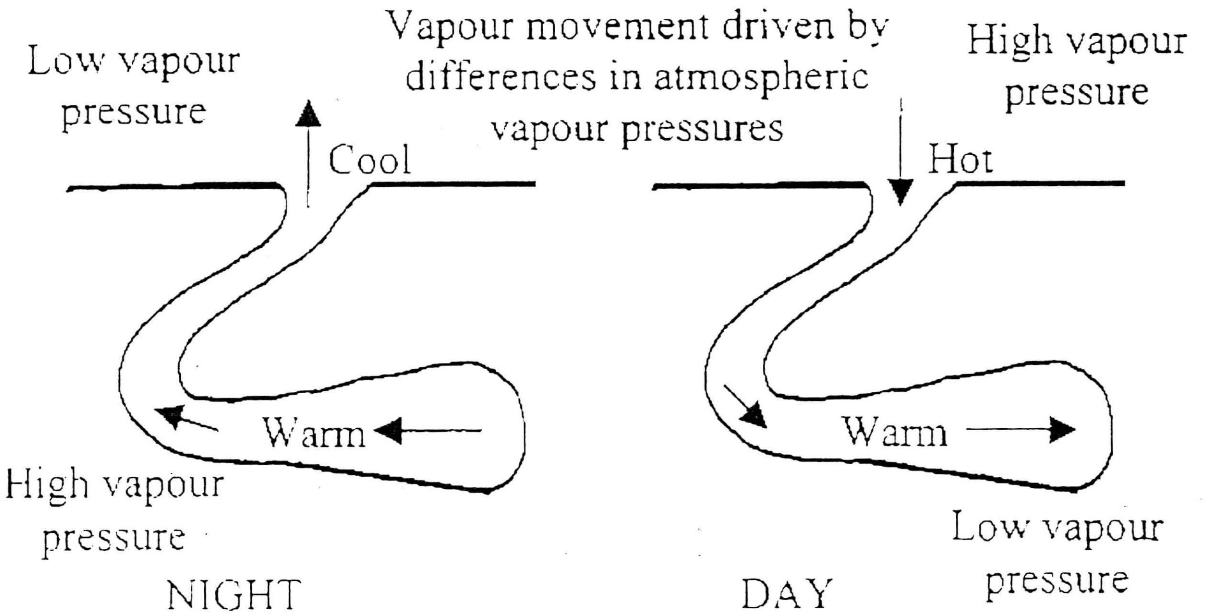

**Figure 5.** Illustration of how vapour pressure differences are generated between the bottom of a burrow and its entrance due to the temperature differences between the surface and the ground. The switch in vapour flow is caused by the diel changes in temperatures at different levels.

differences, drive this phenomenon, where the vapour moves from the higher vapour pressure to the lower (Fig. 5). Animals in burrows or within the near-surface sand layer are in a non-desiccating environment during the heat of the day. At night when surface temperatures drop, the vapour pressure gradient reverses and water vapour leaves the retreat (Louw, 1993) (Fig. 5). Perhaps this is used by burrowing animals as a signal to begin activity.

### *Evaporative water loss*

Since the cuticle is the major route for water loss in arthropods, many species have various forms of integumentary water-proofing (Hadley, 1994). Epicuticular waxes are the major protection against desiccation in all insects. Important in hot deserts is the occurrence of a threshold temperature, beyond which permeability of cuticle drastically increases (Hadley, 1994). This emphasises the importance of effective thermoregulation from a water conservation perspective.

Many tenebrionids and several other taxa (e.g., curculionids) in the Namib have morphologically intricate wax blooms that are secreted by dermal glands (Hanrahan *et al.*, 1984; McClain & Gernecke, 1990). There is a positive correlation between incidence of wax blooms and aridity (McClain *et al.*, 1984, 1985, 1986). Furthermore, beetles with blooms (e.g., *Zophosis mniszechi*) are active on the surface of sand dunes for longer periods than those without blooms (e.g., *Zophosis moralesi*) (McClain *et al.*, 1991). Blooms reflect a large proportion of the visible light spectrum. Two hypotheses on the function of the blooms concern their role for thermoregulation (e.g., light reflectance) and for improved water-proofing. The thermoregulatory viewpoint led to the maxithermy hypothesis of Hamilton (1973). An alternative hypothesis, namely, conservation of moisture by resisting water vapour diffusion, has, however, gained better support (Hadley & Louw, 1980; Nicolson, 1990). For example, cuticular water loss through elytra for the Namib tenebrionid *Onymacris plana* was found to be 0.75 $\mu g.cm^{-1}.h^{-1}.mm^{-1}$ Hg. Nicolson *et al.* (1984) noted that this is the lowest cuticular permeability reported for an insect and is comparable to that of desert scorpions. Blooms develop at low humidity (McClain *et al.*, 1984) and possibly restrict loss of water vapour, functioning as passive diffusion barriers. This is analogous to intricate structures covering the spiracles of the tick *Ixodes ricinus* that act as barriers to passive diffusion of water vapour (Pugh *et al.*, 1988).

The next most crucial route for loss of water for arthropods, is the respiratory route. Spiracular control is a widespread method of saving water by arthropods with trachea. This can be enhanced with structural modifications. Insects, including tenebrionids, may also conserve water by using the discontinuous ventilation cycle (DVC) (Bartholomew *et al.*, 1985; Lighton, 1993; Louw *et al.*, 1986). Tenebrionids have a sub-elytral cavity into which the spiracles open. Various functions have been suggested for this space: thermal buffering, space for water storage and reduction of water loss (Ahearn, 1970; Cloudsley-Thompson, 1975; Slobodchikoff & Wiseman, 1981) (Fig. 6). Nicolson (1990) suggested that the anatomy implies that the main function of this space is to minimise water loss.

For large vertebrates, endothermy poses problems in relation to evaporative water loss. Respiration involves exchange of gases over a very large surface area of

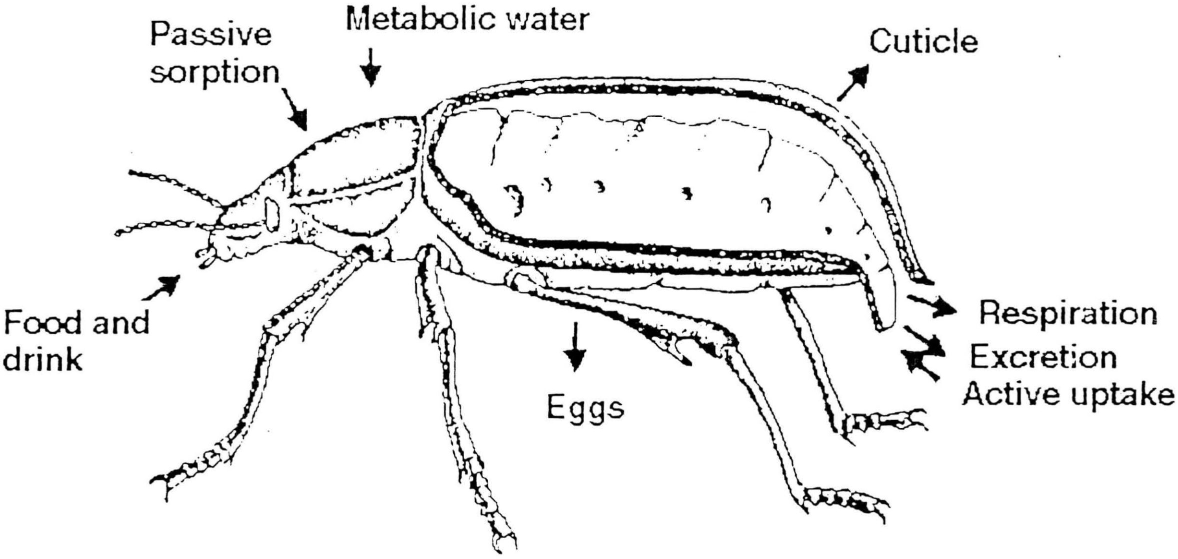

**Figure 6.** Factors that affect water gain and loss of a tenebrionid beetle (redrawn after Ahearn, 1970).

the lungs. This can result in considerable water loss as water-saturated air is exchanged. Some vertebrates such as the ostrich have, however, solved this problem and exhale air that is only 70% saturated (Withers *et al.*, 1981).

Finally, when food is metabolised and the internal milieu perturbed enough to cause osmotic stress coupled with formation of toxic compounds, then resultant waste products of catabolism must be eliminated. The mechanism by which waste is eliminated is crucial in a water-limited environment such as a desert.

### *Excretory systems and products*

Evolution has provided organisms with a plethora of physiological and anatomical mechanisms for disposing of nitrogenous wastes (Schmidt-Nielsen, 1988). Excretory systems have been modified in many ways depending on the environments in which organisms exist. Aquatic organisms use highly soluble toxic ammonia for N waste disposal. Many terrestrial organisms use non-toxic urea, which requires water to be expelled. In desert organisms there is a premium on reducing water loss while at the same time maintaining solute balance. In terrestrial environments, the excretion of toxic soluble ammonia is not an option, while use of urea is too wasteful. Waste must be converted into a non-toxic form that should not be osmotically disruptive, preferably non-soluble, before being eliminated; there are many ways to achieve this (Table 3).

**Table 3.** *Excretory systems and products*

| animal | concentrating organ | concentrated excretory compound |
|---|---|---|
| amphibians | bladder | urea |
| reptiles | salt glands | urate salts |
| cricetid rodents | kidney | allantoin |
| oryx | kidney | urine |
| birds | intestine | urate |
| tenebrionids | rectal complex | urate |
| arachnids | Malpighian tubules | guanine, xanthine |

Some desert amphibians have modified the basic physiological mechanisms of their order. Water conservation measures, however, tend not to depend on modified excretory biochemistry except for urea formation, and storage and absorption of water from the bladder (Shoemaker, 1988). Without Loops of Henle, frogs cannot produce urine that is at a higher concentration than plasma. Certain frogs, like *Chiromantis xerampelina*, have become uricotelic (Louw, 1993), and can accumulate urea in their tissues. The physiology of the Namib amphibians is, however, unknown. Their survival appears to primarily relate to burrowing, the ability to remain quiescent for long periods (Channing, 1976), and ceasing to produce urine when water-restricted (Dawson *et al.*, 1989).

Physiological mechanisms used by desert reptiles appear to be common to all reptiles, i.e. they are pre-adaptations or exaptations, rather than adaptations (Bradshaw, 1988). Modifications of the excretory system seem to depend on the degree of aridity. In xeric habitats, reptiles produce urate salts that bypass the bladder (Schmidt-Nielsen, 1988). Dry pellets are excreted after water and salt have been re-absorbed (Bradshaw, 1986, Schmidt-Nielsen, 1988; Louw, 1993); excess potassium is excreted via salt glands (see above) (Rankin & Davenport, 1981). Thus, minimal water is lost during excretion. When water is abundant, however, desert reptiles can produce urea and avoid the metabolic cost of uric acid synthesis (Schmidt-Nielsen, 1988).

The Loops of Henle allow mammalian and avian kidneys to produce hyperosmotic concentrated urine (Louw *et al.*, 1972; Downs & Perrin, 1991). Cricetid rodents, which are primarily ureotelic, produce the insoluble protein, allantoin, within their urine, thereby markedly reducing the amount of water required for excretion (Buffenstein *et al.*, 1985; Downs & Perrin, 1991). Large mammals have a similar capacity to produce concentrated urine, although not quite to the same degree as desert rodents (Hofmeyr & Louw, 1987; Louw, 1993). Birds are less capable of concentrating their excreta, but they can resorb water from various parts of their lower intestine before they excrete highly concentrated urate salts (Louw, 1993).

Morphological structures and physiological mechanisms of desert invertebrates can effectively produce concentrated waste products and can recover large proportions of water from waste before it is voided (Ahearn & Hadley, 1976; Nicolson, 1991). Insects have rectal pads that are involved in absorption of water, before excreting urate salts. In beetles, the rectal pads form a cryptonephridial complex. Work done on Namib tenebrionid larvae, *Onymacris plana* and *O. marginipennis*, has shown that this structure can be extremely efficient for water recovery. This is a function of the considerably larger area of the rectal complex in *Onymacris* spp. as compared to the non-desert species *Tenebrio molitor* (Machin & O'Donnell, 1991). Desert arachnids do not appear to have special excretory mechanisms compared to their mesic counterparts, but they do extract more water before voiding waste products, mainly insoluble guanine, xanthine and uric acid. Malpighian tubules are largely responsible for concentrating the wastes, and in scorpions, the enlarged ileum of the gut greatly enhances this function (Foelix, 1982; Hadley, 1990, 1994).

## Food

Biomass production in the Namib is the lowest reported for any terrestrial ecosystem (Seely & Louw, 1980). Low metabolic rate compensates for the erratic and unpredictable nature of available food resources, a feature that is common to other deserts. Reduced metabolic activity simultaneously solves many problems besides requiring less food, such as reducing the amount of water needed to eliminate nitrogenous end-products of metabolic processes (Fielden *et al.*, 1990), and reducing oxygen consumption so that a psammophilous existence is permitted, even by mammals.

The Namib Golden Mole *Eremitalpa granti namibensis* has a much lower metabolic rate than is expected for a small mammal (Fielden *et al.*, 1990; Seymour & Seely, 1996). This is, however, not unique, as the Naked Mole Rat can be regarded as a poikilotherm (Buffenstein & Yahav, 1991, in Louw, 1993). These are probably adaptations to the unpredictably fluctuating levels of food, coupled with the energetic cost of foraging and any advantages relating to water conservation accruing from the low metabolic rate are merely fortuitous by-products.

Some diurnal poikilotherms have even lower metabolic rates than would be expected in a hot environment, such as the Namib. The Namib Day Gecko *Rhoptropus afer* has a very low standard metabolic rate, similar to the nocturnal xantusiid lizards (Peterson, 1990), a condition that was confirmed for the field metabolic rate (Nagy *et al.*, 1993). Food shortage was given as the likely reason for these low metabolic rates. Water conservation could also be important. Lizards with low metabolic rates may obtain all of their water from their prey without needing to drink free water (Nagy & Peterson, 1987).

The advantages of low metabolic rates have been exploited to the full by arachnids. These animals, especially scorpions, have very low metabolic rates compared to most other arthropods. Calculations of the metabolic rates of sparassid, eresid and zodariid spiders in the Namib (Henschel, 1994; Lubin & Henschel, 1996; Rössl & Henschel, 1999) show that they are considerably lower than those of spiders elsewhere, including those from other desert areas, nearly a magnitude less than for lycosid spiders from Europe. Lubin & Henschel (1996) concluded that most individuals in a population of *Seothyra henscheli* (Eresidae) die of starvation; ironically, these spiders increase their foraging effort with increasing state of hunger in order to maximise their chances of capturing the scarce prey.

Sand assists some animals in relation to food. Some desert animals have the ability to sense acoustic vibrations that are transmitted by sand, such as Rayleigh waves, to detect prey or the availability of detritus. This is seen in spiders (Henschel, 1990, 1997), scorpions (Brownell, 1977, 1984; Brownell & Farley, 1979), tenebrionids (Hanrahan & Kirchner, 1994), and vertebrates (Narins *et al.*, 1997).

Scorpions are supreme in the world of low metabolic rates (Polis, 1990), which makes them very well-adapted to cope with food and water shortages. The Namib scorpion *Parabuthus villosus* has incredibly low oxygen consumption and a heart-beat rate of only 4-5 beats.min$^{-1}$ when resting, increasing up to 178 beats.min$^{-1}$ at rare times of high activity (Bridges *et al.*, 1997; Robertson *et al.*, 1982).

## Heat

### *The thermal refuge*

Animals use the different microclimates that exist within desert environments to their advantage to ensure that their thermal tolerances are not exceeded. Size plays an important role. Small animals, with high surface-area-to-volume ratios, can benefit thermally by using the thermal mosaic to gain, lose or avoid heat. Diurnal arthropods tend to use behavioural mechanisms to cool (Robertson *et al.*, 1982), with less need for water-costly evaporative cooling.

Different constraints affect larger vertebrates with their higher thermal inertia. Because of their lower surface-area-to-volume ratio they cannot gain heat as quickly but they also do not lose it as quickly. They often depend on evaporative cooling, coupled to water recycling mechanisms that can be quite efficient (e.g., ostrich; Louw *et al.*, 1969; Withers *et al.*, 1981). Vertebrates, small and large, often seek or create suitable microclimates. Some examples of the former from the Namib are sand-diving by the ultrapsammophilous lizard *Meroles anchietae* (Louw & Holm, 1972), and inactivity under shady trees by baboons of the Kuiseb canyon during times of heat and water stress (Brain, 1990a, b). An example of a vertebrate changing its microclimate is the Sociable Weaver, *Philetarius socius*, whose large communal nests remain cool (Williams & du Plessis, 1996).

Heat cannot always be avoided, e.g., when escaping from predators, or pursuing prey. Physiological mechanisms are then essential for losing this heat efficiently, while minimising water loss. This is especially important for homeothermic endotherms, such as birds and mammals, that use various mechanisms (Table 4).

Compared to the large vertebrates, it is relatively easy for small vertebrates and arthropods to avoid excessive heat. They can find thermal respite in sand (Seely, 1983; Seely & Mitchell, 1987), under rocks (Lamoral, 1979; Huey *et al.*, 1989), under plants (Marsh, 1990) or in plant canopies (Ward & Seely, 1996b). Edney (1971, 1974, 1977) pointed out the advantages of burrows and psammophily when daily temperature ranges are large at the surface. During the hot hours, there is a steep thermal gradient in the upper layers of the substratum, so that at 12 cm depth the temperature is approximately 35°C compared to 70°C at the surface (Seely & Mitchell, 1987; Lubin & Henschel, 1990). At a depth of 20 cm and beyond, the temperature only changes on a seasonal basis with little daily variation, whereas the daily variation at the surface can be over 60°C (Robinson & Seely, 1980; Seely & Mitchell, 1987; Seely *et al.*, 1988; Seely, 1989) (Fig. 2). Animals that penetrate the substratum can choose from its range of temperatures.

**Table 4.** *Mechanisms of heat regulation in Namib mammals and birds*

| Mechanism | example from Namib | Source |
|---|---|---|
| adaptive hyperthermia | oryx | Taylor, 1969 |
| orientation | oryx | Taylor, 1969 |
| | springbok | Hofmeyr & Louw, 1987 |
| thin pelage to assist cooling | springbok | Hofmeyr & Louw, 1987 |
| | ostrich | Louw *et al.*, 1969 |
| | ostrich | Louw, 1981 |
| | ostrich | Withers, 1983 |
| heat reflectance | springbok | Hofmeyr & Louw, 1987 |
| thermal shield | ravens | Louw, 1993 |
| counter-current systems | ravens | Mitchell *et al.*, 1987 |
| carotid rete (Rete mirabilis) | ungulates | Louw, 1993 |
| ophthalmic rete | helmeted guinea fowl | Crowe & Withers, 1979 |
| | ostrich | Withers *et al.*, 1981 |
| gular fluttering | double-banded sandgrouse | Hinsley, 1992 |
| panting & sweating | humans | Louw, 1993 |
| cranial radiators | humans | Falk, 1993 |
| | humans | Baker, 1993 |

Likewise, the layer of air above the substratum offers a thermal gradient. On a hot day, the air temperature declines by 9-10 °C in the first cm above the surface (Nicolson *et al.*, 1984; Seely, 1989; Seely, 1991) (Fig. 2). Stilting or climbing onto projections offers an obvious thermal advantage in terms of convection for arthropods that lift themselves off the hot surface (Hamilton, 1973; Henwood, 1975a, b; McClain *et al.*, 1984; Curtis, 1985a; Marsh, 1985; Ward & Seely, 1996a, b) (Fig. 7).

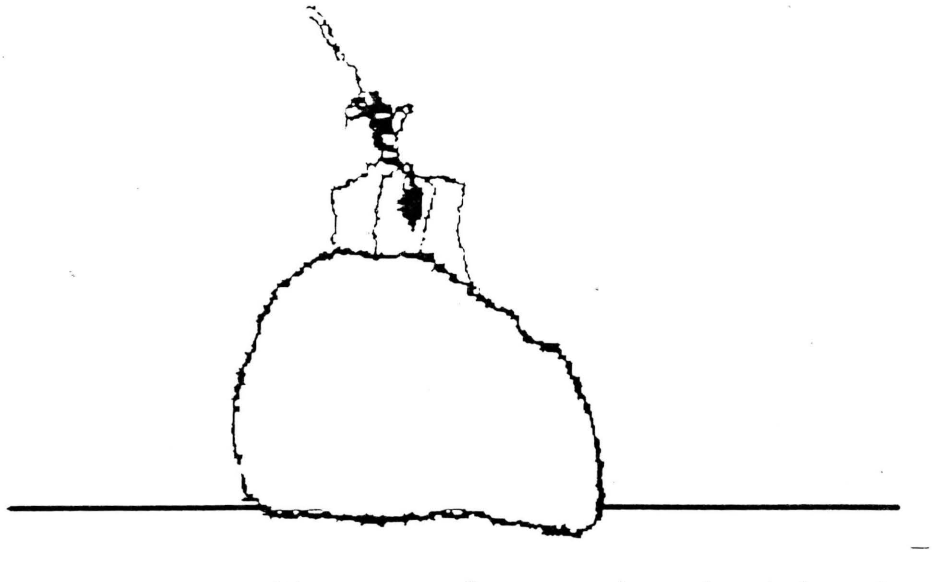

**Figure 7.** *Ocymyrmex* ant respiting on top of a stone where the air is cooler than on the surrounding ground. Drawn from a photograph by Marsh in Louw (1993).

### *Thermophily*

The physiological ability of reptiles (Bradshaw, 1988) and insects (Curtis & Seely, 1987; Seely *et al.*, 1988) to withstand elevated body temperatures, heat tolerance and thermophily, can be regarded as pre-adaptations or exaptations (Gould & Vrba, 1982; Bradshaw, 1988) to desert habitats (Seely, 1989). A diverse range of desert species are thermophiles, functioning at near-lethal temperatures, and exploiting niches not available to the less heat-tolerant species (Hamilton, 1973; Henwood, 1975a, b; Marsh, 1985, 1987; Lubin & Henschel, 1990; Cerda *et al.*, 1997). Thermophiles are inclined to be very skilled users of the thermal mosaic. They often feed upon other animals that succumb to the heat. Thermophily allows populations of sub-dominant species to expand into thermal niches that the dominant species cannot tolerate (Cerda *et al.*, 1997).

**Table 5.** *Critical Thermal Maxima (CTMax) of arthropods from the Namib Desert compared to other deserts.*

| Species | CTMax | Location | Source | Animal |
|---|---|---|---|---|
| *Stegodyphus lineatus* | 39.0 | Negev | Henschel *et al.*, 1992 | Spider |
| *Pheidole pallidula* | 40.0 | Spain | Cerda *et al.*, 1997 | Ant |
| *Plagiolepis pygmaea* | 40.0 | Spain | Cerda *et al.*, 1997 | Ant |
| *Tetramorium semilaeve* | 40.0 | Spain | Cerda *et al.*, 1997 | Ant |
| *Tapinoma nigerrimum* | 42.0 | Spain | Cerda *et al.*, 1997 | Ant |
| *Onymacris laeviceps* | 42.5 | Namib | Hamilton, 1975 | Tenebrionid |
| *Onymacris langi* | 42.9 | Namib | Hamilton, 1975 | Tenebrionid |
| *Pheidole tenuiodis* | 42.9 | Namib | Marsh, 1987 | And |
| *Aphonophelma* sp. | 43.0 | USA | Seymour & Vinegar, 1973, in Cloudsley-Thompson, 1975 | Spider |
| *Onymacris candidipennis* | 43.6 | Namib | Hamilton, 1975 | Tenebrionid |
| *Onymacris brincki* | 43.8 | Namib | Hamilton, 1975 | Tenebrionid |
| *Messor bouvieri* | 44.0 | Spain | Cerda *et al.*, 1997 | Ant |
| *Messor capitatus* | 44.0 | Spain | Cerda *et al.*, 1997 | Ant |
| *Aphaenogaster senilis* | 46.0 | Spain | Cerda *et al.*, 1997 | Ant |
| *Camponotus sylvaticus* | 46.0 | Spain | Cerda *et al.*, 1997 | Ant |
| *Onymacris marginipennis* | 46.0 | Namib | Roberts *et al.*, 1991 | Tenebrionid |
| *Monomorium viator* | 46.7 | Namib | Marsh, 1987 | Ant |
| *Tetramorium rufescens* | 46.9 | Namib | Marsh, 1987 | Ant |
| *Onymacris bicolor* | 47.0 | Namib | Roberts et al., 1991 | Tenebrionid |
| *Messor denticornis* | 47.5 | Namib | Marsh, 1987 | Ant |
| *Tetramorium sericeiventre* | 47.9 | Namib | Marsh, 1987 | Ant |
| *Camponotus cruentatus* | 48.0 | Spain | Cerda et al., 1997 | Ant |
| *Camponotus foreli* | 48.0 | Spain | Cerda *et al.*, 1997 | Ant |
| *Onymacris unguicularis* | 48.0 | Namib | Roberts *et al.*, 1991 | Tenebrionid |

| | | | | |
|---|---|---|---|---|
| *Trachyrmyrmex s. neomexicanus* | 48.4 | Chihuahua | Schumacher & Whitford, 1974 | Ant |
| *Monomorium alamarum* | 49.0 | Namib | Marsh, 1987 | Ant |
| *Monomorium vatranum* | 49.0 | Namib | Marsh, 1987 | Ant |
| *Onymacris rugatipennis* | 49.0 | Namib | Roberts *et al.*, 1991 | Tenebrionid |
| *Pogonomyrmex desertorum* | 49.0 | Chihuahua | Whitford & Ettershank, 1975 | Ant |
| *Formica peripilosa* | 49.0 | Chihuahua | Schumacher & Whitford, 1974 | Ant |
| *Pogonomyrmex rugosus* | 49.0 | Chihuahua | Whitford & Ettershank, 1975 | Ant |
| *Seothyra henscheli* | 49.0 | Namib | Lubin & Henschel, 1990 | Spider |
| *Cataglyphis cursor* | 49.0 | Spain | Cerda *et al.*, 1997 | Ant |
| *Physadesmia globosa* | 50.0 | Namib | Roberts *et al.*, 1991 | Tenebrionid |
| *Onymacris plana* | 50.0 | Namib | Roberts *et al.*, 1991 | Tenebrionid |
| *Myrmecocystus romainei* | 51.5 | Chihuahua | Kay & Whitford, 1978 | Ant |
| *Ocymyrmex barbiger* | 51.4 | Namib | Marsh, 1985 | Ant |
| *Ocymyrmex robustior* | 51.5 | Namib | Marsh, 1987 | Ant |
| *Myrmecocystus depilis* | 52.9 | Chihuahua | Kay & Whitford, 1978 | Ant |
| *Myrmecocystus mimicus* | 53.3 | Chihuahua | Kay & Whitford, 1978 | Ant |
| *Cueta trivirgata* | 53.4 | Namib | Marsh, 1987 | Ant-Lion |
| *Camponotus detritus* | 53.8 | Namib | Curtis, 1985 | Ant |
| *Pogonomyrmex californicus* | 53.8 | Chihuahua | Curtis, 1985 | Ant |
| *Cataglyphis bombycina* | 55.0 | Sahara | Wehner *et al.*, 1992 | Ant |

Certain pre-requisites are, however, necessary for a thermophilous existence. The animal needs extremely accurate thermal sensory information due to the lethal consequences of exceeding the critical thermal maximum (CTM), which is the threshold temperature at which they begin to show thermal stress. In some thermophiles, CTM is very close to the lethal temperature. CTM's of Namib arthropods are compared with those of other deserts in Table 5. Thermophiles must have iso-enzymes that function optimally at temperatures far beyond the optimum temperature at which most organisms' enzymes function effectively. If proteins are damaged, then the cells need to repair them to restore cellular function. This often involves the use of heat-shock proteins (Polla *et al.*, 1998).

Many animals in the Namib, cursorial and sedentary, have adopted a thermophilous existence, indicating its advantages. A few examples are given.

**Ants** – *Ocymyrmex barbiger* usually forages at the hottest time of day, when surface sand temperatures are up to 70°C. These temperatures are well above the temperatures at which metabolic proteins are denatured. Marsh (1985) showed that the rate of temperature exchange of *Ocymyrmex barbiger* with its surroundings was such that by the use of thermal refuges (Fig. 7), it could easily cope with extreme heat. Seldom did the body temperature of *Ocymyrmex* get anywhere near its CTM of 51.5°C, allowing it to be active during the heat of the day. This enabled *Ocymyrmex* to feed on arthropods that succumbed to the heat. Eight other Namib ants had similarly high CTM's irrespective of their activity periods (Marsh, 1988; Table 5). The dune ant

*Camponotus detritus* (Curtis, 1985a, 1990; Curtis & Seely, 1987) has an extremely high CTM that increases from 52.8 to 53.8°C as the relative humidity decreases from 100 to 55%. There was no difference between different caste members (Curtis, 1985a).

**Spiders** – The spoor spider *Seothyra henscheli* of the Namib, has the highest CTM yet recorded for a spider, 49°C (Lubin & Henschel, 1990). This spider builds its web in sand, constructing a 15-20 cm deep burrow below a horizontal capture web on the surface (Fig. 8; Lubin & Henschel, 1990). The web has lobes, which are edged with structurally sticky cribellate silk (Opell, 1993) with which thermophilic ants are captured. *Seothyra* continues to capture prey even when the web reaches 70°C, far beyond its CTM. The spider accomplishes this by shuttling between the hot surface web and the cooler depths of its burrow (Turner *et al.*, 1993). In the shortest burrow of 5.7 cm, the temperature can reach 45.1 ± 2.4°C, but most burrows are deeper than 12 cm, where the temperature does not exceed 35°C so that the spider can choose from a 15-35°C range of temperatures (Lubin & Henschel, 1990). The precise shuttling pattern of the spider keeps it just below CTM, implying accurate sensory information, probably originating from the tarsal organ (Anton & Tichy, 1994; Ehn & Tichy, 1994).

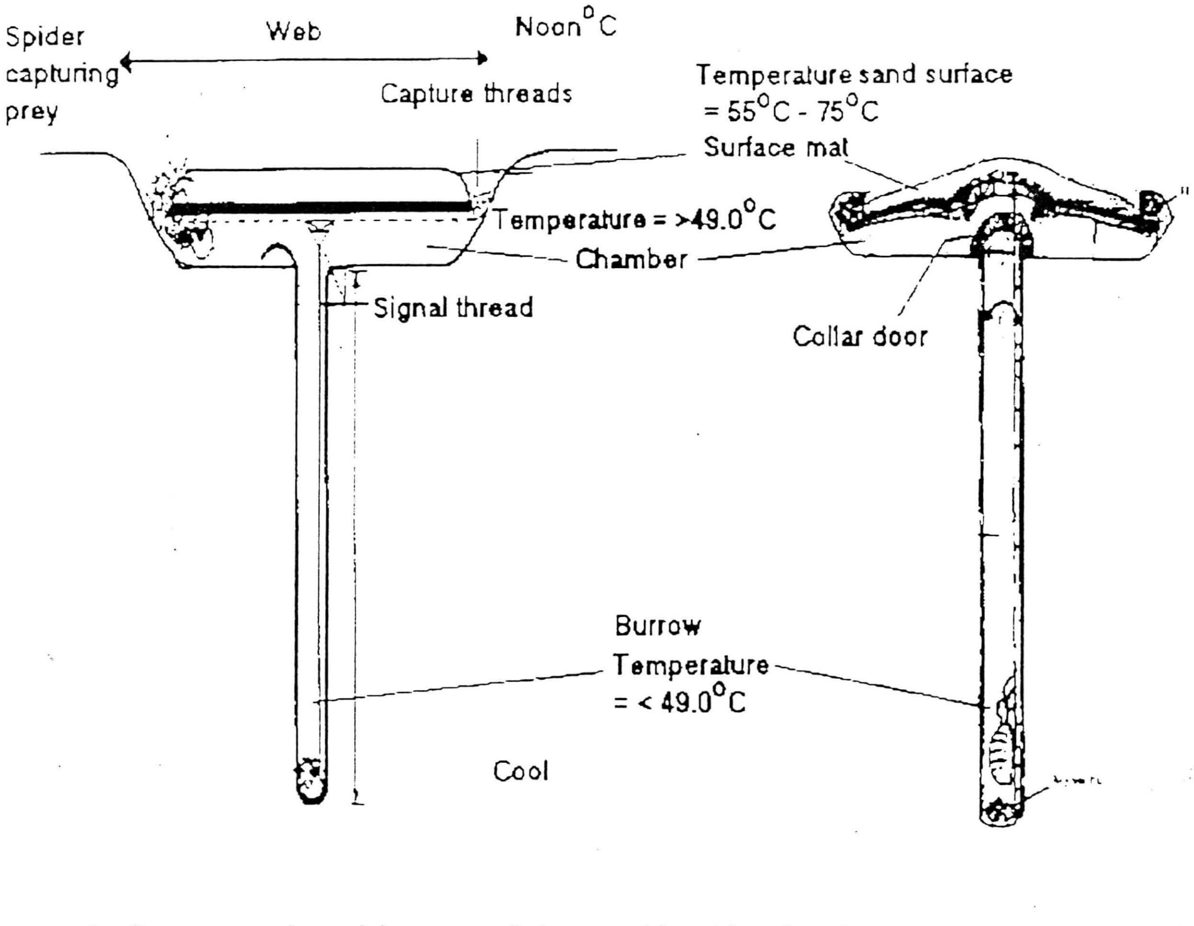

**Figure 8.** Capture web and burrow of the eresid spider *Seothyra* on a Namib dune. The spider remains below its lethal temperature by retreating to the bottom of the burrow (right), and making rapid forays when prey is trapped in the web on the hot sand surface (left). Adapted from Lubin & Henschel (1990) and Henschel & Lubin (1992).

**Ant-lions** – The neuropteran predator, *Cueta trivirgata*, has an extremely high CTM of 53.4°C. It constructs a shallow pit in sand, and uses this to capture thermophilous ants such as *Ocymyrmex barbiger*. In the heat of the day, one side of the pit is some 10°C cooler than the other, and the ant-lion orientates itself within the pit according to the shade, allowing it to forage whenever its prey is active (Marsh, 1987).

**Tenebrionid beetles** – Despite mechanisms to cool down (Ward & Seely, 1996a, b), the diverse range of apterous tenebrionid beetles endemic to the Namib are highly heat-tolerant with unusually high body temperatures (Nicolson *et al.*, 1984; Seely *et al.*, 1988; Roberts *et al.*, 1991), higher in the Namib than in other deserts. Their CTM's range from 47 to 52°C (Hamilton, 1973, 1975; Roberts *et al.*, 1991) (Table 5). The specific physiological and cellular mechanisms beg study.

The thermoregulatory techniques include some novel ways of using convection to lose heat, such as running to cool down by *Onymacris plana* (Roberts, 1991). Male *O.plana*, that spend longer periods on the hot surface than the females (Enders *et al.*, 1998; Polis *et al.*, 1998), are more thermally labile, heating up and cooling down at 6°C. $\text{min}^{-1}$ as compared to females at $4°\text{C.min}^{-1}$ (Roberts, 1991). Perhaps the extraordinary wide elytra of the males increase their surface area to dissipate heat when they increase wind convection by sprinting at the fastest speeds known for insects, 90 $\text{cm.s}^{-1}$, some even achieving 115 $\text{cm.s}^{-1}$ (Nicolson *et al.*, 1984). Furthermore, running generates metabolic water (Nicolson, 1990).

Various hypotheses have been proposed to explain the high temperatures of Namib tenebrionids (e.g., maxithermy: Hamilton, 1973; passive tolerance of diurnal conditions : Seely *et al.*, 1988). Many of the predictions were, however, not confirmed by further investigations (Pietruzska, 1988; Ward, 1991).

## Conclusion

Deserts are important environments to study so as to understand the effect of highly variable and often harsh conditions on biotic systems. This understanding is becoming increasingly important in view of possible large-scale environmental changes. The Namib is a show-case for the characteristics that animals need to exist in conditions of water- and food-shortages, coupled with high temperatures. This desert provides an ideal laboratory for the study of biological interactions and abiotic factors, especially in the dunes. A large proportion of the Namib is located in protected parks and it can be used to illustrate how an ecosystem responds to abiotic factors in the near-absence of anthropogenic factors, compared to other similar ecosystems where anthropogenic influences prevail (Seely *et al.* 2000). This may enable one to recognise which ecosystem characteristics are affected by climatic changes and which by management factors, ultimately allowing one to identify those management factors that are contributing to desertification (Zeidler, 1999).

Many of the characteristics that facilitate an organisms' existence in deserts are multi-functional and inter-linked (Safriel *et al.*, 1989). For example, in tenebrionids, adaptations to cope with food limitations and heat are focused around primary considerations of water-balance (Seely, 1983). Inter-linked factors of physiology, morphology and behaviour allow desert organisms to cope successfully with an environment characterised by high variability of many parameters. This variability is composed of spatial and temporal heterogeneity; often extreme unpredictability (occurrence and magnitude) of food (plant production), water, predators, competitors and mates. Organisms have evolved in these environments to use the predictable features (detritus, fog, thermal refugia) in order to deal with the extreme and unpredictable features of this desert. Namib tenebrionids serve as good examples of specialisation for existence in these particular desert conditions.

### Key features include

- physiological capability to tolerate desiccation (e.g., using the haemolymph as an osmotic buffer, tolerating osmotic stress and waste accumulation);
- ability to acquire free water from fog, humid air and soil capillary water and production of metabolic water;
- reducing water losses by modifying cuticular, respiratory and excretory processes (e.g., respectively : waxy blooms, controlled exhalation, water recovery before producing insoluble, dry or highly concentrated excreta);
- occupation of optimal or tolerable microclimatic conditions in a seemingly harsh environment, including efficient use of gradients in vapour pressure and temperature above and below the ground surface;
- lowering of metabolic rate so as to reduce the food and water requirements as well as the water losses (via respiration, cutaneous/integumentary and excretory routes);
- numerous mechanisms increasing the rate of heat exchange or avoiding heat gain;
- physiological and morphological mechanisms that increase heat tolerance and thermophily, the latter making the best use of the heat to gain resources, or to reduce predation and competition.

The physiological and ecophysiological conditions and mechanisms of Namib animals have far-reaching consequences to their ecology, such as habitat selection, relationship to resources, reproduction, population dynamics, and community ecology (Seely, 1991). For instance, endurance of the desert's resource shortages, underlies the tendency for many desert animals towards K-selected life history strategies (tenebrionids, Seely, 1982; sparassid spiders, Henschel, 1990), the absence of a proper off-season (Curtis, 1985b), aseasonal and iteroparous reproduction (Seely, 1983; Robinson, 1990), and bet-hedging (Seely, 1983). On the other hand, different features allow animals to exploit the unpredictable, short periods of plenty. For instance, some species (these tend to be r-selected) show a massive response towards rain, if it occurs, increasing their populations dramatically (Seely & Louw, 1980).

Recent advances in ecology have exposed a number of areas where more knowledge of the physiology of desert animals is required. These include the extraordinarily rapid responses of populations, and associated physiological mechanisms, to the rapid increase in resources presented by pulsed productivity caused by episodic rainfalls. Furthermore, for several features described in this paper, it would be important for research to progress beyond ecophysiology to the physiological and biochemical processes involved. Thermophily in a desiccating environment is an important example.

The Namib is not hostile to many of its inhabitants. By contrast, some do exceedingly well, particularly those whose ecophysiology adapts them to desert conditions where 'lack of water' and 'extreme heat' are normal (Bradshaw, 1988; Seely, 1993). Such changes in preception, based on improved understanding and awareness of the functioning of the desert and its inhabitants, ultimately facilitate the ability of environmental managers at all levels to manage deserts on a sustainable basis (Seely *et al.*, 2000b).

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