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**Ecophysiology in the Namib Desert: coping with little water, scarce food and elevated temperatures**

Mark B. Robertson<sup>2</sup>, Joh R. Henschel<sup>1</sup> & Mary K. Seely 

Desert Ecological Research Unit, Gobabeb, P.O.Box 1592, Swakopmund, Namibia

Tel: +264-61-229855; Fax: +264-61-230172; Email: [drfn@iwwn.com.na](mailto:drfn@iwwn.com.na)

## **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 Ecological Research Unit (DERU) and its affiliates during the past 35 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, humid air, soil moisture and metabolic water, 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.

<sup>1</sup> To whom correspondence should be addressed

## **Introduction**

Deserts present special conditions for life due to their inherent variability: a limited supply of water, essential for all organisms, often coupled to food shortage and exposure to harsh climatic conditions (Fig. 1) (Seely & Louw 1980; Safriel, Ayal, Kotler, Lubin, Whittaker & Pinshow 1989; Southgate, Masters & Seely 1996). Various physiological mechanisms allow animals to cope with these conditions and to exist in deserts (Dawson, Pinshow, Bartholomew, Seely, Shkolik, Shoemaker & Teeri 1989). 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.

The Namib Desert, where evaporation exceeds precipitation by a factor of 200, contains some excellent examples of the principles of desert ecophysiology. This desert is relatively well-studied, thanks to the Desert Ecological Research Unit (DERU at Gobabeb, Namibia) and its affiliates over a period covering 35 years.

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 (e.g., Seely 1972; Hamilton & Seely 1976; Nicolson, Louw & Edney 1984; Nicolson 1990; Ward & Seely 1996a, 1996b; Roberts, McClain, Seely & Mitchell 1997). After describing some important abiotic characteristics of the Namib, we examine how an animal copes with its scarce supply of water by osmoregulation, by behavioural, morphological and physiological methods of acquiring free water, and by reducing water loss. Coupled with the water shortage is reduced primary production, ultimately resulting in a shortage of food over considerable lengths of time for many animals, with 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 is a narrow coastal desert that stretches for over 2000 km from the Oliphants River in South Africa northwards to the Carunjamba River in Angola. The Benguella Current of the Atlantic Ocean forms its western boundary, and the Western Escarpment its eastern delimitation, 200 km inland. Some of the abiotic influences that affect organisms in the Namib (Robinson & Seely 1980) are specific to this desert and others are general to deserts. These include temperature (at the surface and at depth), precipitation (fog and rain), substratal grain size, wind, and surface topography. Wind is important in the dunes, as it affects dune morphology and the compaction and moisture of the sand. The interaction of wind and dune morphology drives the major organic input, the detritus cycle (Seely 1993). Low vegetation cover means diurnally active animals are exposed to heat, exacerbated by the desiccating atmosphere. Heat exchange occurs rapidly in the physical environment as well as in organisms.

The Namib has been arid since the end of the Cretaceous Period, with the current hyper-aridity beginning during the Miocene (Ward, Seely & Lancaster N. 1983). This desert is situated at the bottom end of a rainfall gradient that begins at the Indian Ocean in the east and declines westwards. Rainfall averages  $<50 \text{ mm.yr}^{-1}$  in the eastern Namib, while the western half receives no more than a few millimeters in an average year. Fog, the other source of water, declines from west to east in a gradient from 200 fog events per annum at the coast to 60 at Gobabeb, 60 km inland (Seely 1993, DERU 1997). This fog ameliorates the potential aridity of the Namib adjacent to the coast (Louw 1972, Seely 1979, Robinson & Seely 1980, Seely & Griffin 1986) and is much more predictable than rain (Pietruzska & Seely 1985).

The Namib is divided into three zones from west to east (Besler 1972): (1) cool coastal fog desert; (2) alternate fog desert, with a wide daily temperature range; (3) the desert steppe,  $>80$  km inland, with some rainfall and ephemeral grasses in most years.

## Water

Problems of water gain, balance, reduction of water loss, tolerance of water loss, and consequent osmotic phenomena have been a focus of 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, Clarke, Seely, Mitchell, & Lighton 1991) and predators (Fielden, Perrin, & Hickman 1990) do not face the same problem, because their food is comparatively water-rich, while some flying insects can generate water through metabolic activity (Louw & Hadley 1985). 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 1979; Seely & Griffin 1986). 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 Namib 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 in press). 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).

Soil capillary water is a source of water for Namib termites, such as *Psammotermes allocerus*. They use their hypopharynx pseudergates to drink (Grube & Rudolph 1995). Free water is not available to many small arthropods 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. (Coutchie & Crowe 1979) and several thysanurans (Edney 1971; Heeg 1967a, 1967b; 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 & Coutchie 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.

#### 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  $\frac{1}{3}$  to  $\frac{1}{2}$  of the water lost to respiration in the extremely fast-running tenebrionid *Onymacris plana* ( $0.122 \text{ mg.g}^{-1}.\text{h}^{-1}$ ). This is less in the slower-moving *O. unguicularis*  $0.35 \text{ mg.g}^{-1}.\text{h}^{-1}$  (Cooper 1982), whilst in a resting *O. unguicularis*, metabolic water contributed only  $0.02 \text{ mg.g}^{-1}.\text{h}^{-1}$  (Bartholomew, Lighton & Louw

1985; Louw, Nicolson & Seely 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 et al. 1997).

Some Namib rodents produce metabolic water from dry seeds (Withers, Louw & Henschel 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 & Stark's Lark can also survive exclusively on dry food (Willoughby 1968). The abilities of all these animals relates 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 (r.h.) in order to understand water vapour flow.

During the day, water vapour flows into the retreat, even if the retreat has a higher r.h. than the outside environment. Vapour pressure differences, created by temperature differences, drive this phenomenon, where the vapour moves from the higher vapour pressure to the lower. 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). Perhaps this is used by burrowing animals as a signal to begin activity.

## 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 (Coutechie & Crowe 1979; Machin 1981) and adults (Cooper 1982; Naidu & Hattingh 1986, Naidu & Hattingh 1988; Nicolson 1980; Nicolson 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 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 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, including the Namib psammophilous scorpion *Opisthophthalmus flavescens*, have poor regulation of their haemolymph, but tolerate resulting osmotic stresses (Robertson, Nicolson & Louw 1982). 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 *et al.* 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).

#### 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, McClain & Gerneke 1984; McClain & Gerneke 1990). There is a positive correlation between incidence of wax blooms and aridity (McClain *et al.* 1984; McClain, Seely, Hadley & Gray 1985; McClain, Hanrahan & Gerneke 1986). Furthermore, beetles with blooms (e.g., *Zophosis mnischechi*) are active on the surface of sand dunes for longer periods than those without blooms (e.g., *Zophosis moralesi*) (McClain, Kok & Monard 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) and the infra-red transmittance model of Henwood

(1975b). An alternative hypothesis, namely, conservation of moisture by resisting water vapour diffusion, has, however, gained better support (Hadley & Louw 1979; Nicolson 1990). For example, cuticular water loss through elytra for the Namib tenebrionid *Onymacris plana* was found to be  $0.75 \mu\text{g}\cdot\text{cm}^{-1}\cdot\text{h}^{-1}\cdot\text{mm}^{-1}$  Hg. Nicolson, Louw & Edney (1984) noted that this is the lowest cuticular permeability ever reported for an insect and is comparable to that of desert scorpions. Blooms develop at low humidity (McClain, Praetorius, Hanrahan & Seely 1984) and possibly restrict loss of water vapour, functioning as passive diffusion barriers. This is analagous to intricate structures covering the spiracles of the tick *Ixodes ricinus* that act as barriers to passive diffusion of water vapour (Pugh, King & Fordy 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 all 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 & Wisman 1981). 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 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, Siegfried & Louw 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 metabolism 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. 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. Waste must be converted into a non-toxic form that should not be osmotically disruptive before being eliminated; there are many ways to achieve this.

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, Louw & Retief 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, Campbell & Jarvis 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 1992). Insects have rectal pads that are involved in absorption of water, before excreting urate salts. In beetles, the rectal pads form a cryptonephridial complex (Nicolson 1990). Work done on Namib tenebrionid larvae, *Onymacris plana* and *O. marginipennis*, has shown that this cryptonephridial complex 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 (Seymour & Seely 1996).

Reduced metabolic rate, is, however, not normally an option open to mammals. Exceptions include the Namib Golden Mole *Eremitalpa granti namibensis*, which has a much lower metabolic rate than is expected for a small mammal (Fielden 1989; Seymour & Seely 1996). This is, however, not unique, as the Naked Mole Rat can be regarded as a poikilotherm (Buffenstein & Yahav 1991; Louw 1993). These are probably adaptations to the 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, Seely & Buffenstein 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 the arachnids. These animals, especially scorpions, have very low metabolic rates compared to most other arthropods. Calculations of the metabolic rates of huntsman and eresid spiders in the Namib (Henschel 1994; Lubin & Henschel 1996) 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), scorpions (Brownell 1977, 1984; Brownell & Farley 1979), tenebrionids (Hanrahan & Kirchner 1994), and possibly some vertebrates (pers.obs.).

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 scorpions *Parabuthus villosus* and *Opisthophthalmus flavescens* have incredibly low oxygen consumption. Their heart-beat rate varies from 4-5 beat.min<sup>-1</sup> at rest, to 178 and 152 beats.min<sup>-1</sup>, respectively, at rare times of high activity (Bridges, le Roux & van Aardt 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, Belonje & Coetzee 1969; Withers, Siegfried & Louw 1981). Vertebrates, small & large, often seek suitable microclimates or create these to become tolerable. Some examples of the former from the Namib are sand-diving by the

ultrasammophilous 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, 1990b). 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 1 in Appendix 1).

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; Mitchell, Seely, Roberts, Pietruzka, McClain, Griffin & Yeaton 1987b), under rocks (Lamoral 1979; Huey, Peterson, Arnold & Porter 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 no daily variation, whereas the daily variation at the surface can be over 60 °C (Robinson & Seely 1980; Seely & Mitchell 1987; Seely, Roberts & Mitchell 1988; Seely 1989) (Fig. 2). Animals that penetrate the substratum can choose from its range of temperatures.

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, Bartholomew & Seely 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; McClain *et al.* 1984; Curtis 1985b; Marsh 1985; Ward & Seely 1996a, 1996b).

## 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; Marsh 1985, 1987; Lubin & Henschel 1990; Cerda, Retana, & Cros 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, Retana & Cros 1997).

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. Table 2 in Appendix 1 indicates the range of CTM's of a variety of arthropods that have been studied. 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.

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, 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; see Appendix 1). The dune ant *Camponotus detritus* (Curtis 1985b, 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 1985b).

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. 3; 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, Henschel & Lubin 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).

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-lions 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, 1996b), 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, Seely, Ward, Mitchell & Campbell 1991), higher in the Namib than in other deserts. Their C<sub>TM</sub>'s range from 47 to 52 °C (Hamilton 1973, 1975; Roberts *et al.* 1991). 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 plama* (Roberts, McClain, Seely & Mitchell 1996a). Male *O. plama*, that spend longer periods on the hot surface than the females (Enders *pers. comm.*), are more thermally labile, heating up and cooling down at 6 °C.min<sup>-1</sup> as compared to females at 4 °C.min<sup>-1</sup> (Roberts *et al.* 1997). 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 cm.s<sup>-1</sup>, some even achieving 115 cm.s<sup>-1</sup> (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, Roberts & Mitchell 1988). Many of the predictions were, however, not confirmed by further investigations (Pietruzska 1988; Ward 1991; Turner & Lombard 1993).

## **Conclusion**

Deserts are fascinating environments for study of many aspects of biology, they provide a vivid window into how life flourishes in these 'harsh' environments. The Namib is a show-case for the characteristics that animals need to exist in conditions of water- and extreme food-shortages, coupled with high temperatures. This desert provides an ideal laboratory for the study of biological interactions and abiotic factors; especially in the dune-seas. These dune-seas, which are in National Parks, can be used to illustrate how ecosystems respond to abiotic factors in the near-

absence of anthropogenic factors, compared to other similar ecosystems where anthropogenic influences prevail. This may enable one to recognise which ecosystems are affected by climatic changes and which by management factors, ultimately allowing one to identify those management factors that are contributing to desertification (Zeidler *pers.comm.*).

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 ). These 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, and competitors. Organisms have evolved in these environments to use the predictable occurrences (detritus, fog, thermal refugia) in order to deal with the extreme and unpredictable features of this particular desert. Namib tenebrionids display the most pronounced, often unique, specialisations for existence in the Namib.

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; 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);
- ◆ occupy optimal or tolerable microclimatic conditions, including efficient use of gradients in vapour pressure and temperature above and below the ground surface;

- ◆ low metabolic rate reduces 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 allowing avoidance of 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 1983; heteropodid spiders, Henschel 1990), the absence of a proper off-season (Curtis 1985a), aseasonal and iteroparous reproduction (Seely 1983 ; Robinson 1990), and bet-hedging (Seely 1983, Philippi & Seger 1989). 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 increase in resources presented by a pulsed productivity by episodic events. 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 'too much heat' are normal (Bradshaw 1988; Seely 1993).

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## APPENDIX I

**Table 1.** Mechanisms of heat regulation in Namib mammals and birds

Mechanism	Namib example vertebrate	Source
adaptive hyperthermia	Oryx	Taylor 1969
orientation	Oryx	Taylor 1969
Thin pelage to assist cooling	Springbok	Hofmeyr & Louw 1987
	Springbok	Hofmeyr & Louw 1987
	Ostrich	Louw et al. 1969
	..	Louw 1981
heat reflectance	..	Withers 1983
	Springbok	Hofmeyr & Louw 1987
thermal shield	Ravens	Louw 1993
Counter-current systems		Mitchell et al. 1987a* <sup>1</sup>
1. carotid rete	Ungulates	Louw 1993
2. ophthalmic rete	Helmeted Guinea Fowl	Crowe & Withers 1979
	Ostrich	Withers et al. 1981
gular fluttering	Double-Banded Sandgrouse	Hinsley 1992
panting & sweating (cranial radiators)	Humans	Louw 1993
	..	Falk 1993
	..	Baker 1993

\* a review of counter-current systems

<sup>1</sup> Mitchell, Laburn, Nijland, Zurovsky & Mitchell 1987a

**Table 2.** Critical thermal maximums of studied arthropods

Species	CTMax.	Location	Source	Animal
<i>Stegodyphus lineatus</i>	39.0*	Negev	Henschel, Ward & Lubin 1992	Spider
<i>Pheidole pallidula</i>	40.0	Spain	Cerda, Retana & Cros 1997	Ant
<i>Plagiolepis pygmaea</i>	40.0	Spain	Cerda, Retana & Cros 1997	Ant
<i>Tetramorium semilaeve</i>	40.0	Spain	Cerda, Retana & Cros 1997	Ant
<i>Tapinoma nigerrinum</i>	42.0	Spain	Cerda, Retana & Cros 1997	Ant
<i>Onymacris laeviceps</i>	42.5	Namib	Hamilton 1975	Tenebrionid
<i>Onymacris langi</i>	42.9	Namib	Hamilton 1975	Tenebrionid
<i>Pheidole tenuiodis</i>	42.9	Namib	Marsh 1987	Ant
<i>Onymacris candidipennis</i>	43.6	Namib	Hamilton 1975	Tenebrionid
<i>Onymacris brincki</i>	43.8	Namib	Hamilton 1975	Tenebrionid
<i>Messor bouvieri</i>	44.0	Spain	Cerda, Retana & Cros 1997	Ant
<i>Messor capitatus</i>	44.0	Spain	Cerda, Retana & Cros 1997	Ant
<i>Aphaenogaster senilis</i>	46.0	Spain	Cerda, Retana & Cros 1997	Ant
<i>Camponotus sylvaticus</i>	46.0	Spain	Cerda, Retana & Cros 1997	Ant
<i>Onymacris marginipennis</i>	46.0	Namib	Roberts et al. 1991	Tenebrionid
<i>Monomorium viator</i>	46.7	Namib	Marsh 1987	Ant
<i>Tetramorium rufescens</i>	46.9	Namib	Marsh 1987	Ant
<i>Onymacris bicolor</i>	47.0	Namib	Roberts et al. 1991	Tenebrionid
<i>Messor denticornis</i>	47.5	Namib	Marsh 1987	Ant
<i>Tetramorium sericeiventre</i>	47.9	Namib	Marsh 1987	Ant
<i>Camponotus cruentatus</i>	48.0	Spain	Cerda, Retana & Cros 1997	Ant
<i>Camponotus foreli</i>	48.0	Spain	Cerda, Retana & Cros 1997	Ant
<i>Onymacris unguicularis</i>	48.0	Namib	Roberts et al. 1991	Tenebrionid
<i>Trachymyrmex s. neomexicanus</i>	48.4	Chihuahuan	Schumacher & Whitford 1974*	Ant
<i>Monomorium alamarum</i>	49.0	Namib	Marsh 1987	Ant
<i>Monomorium vatranum</i>	49.0	Namib	Marsh 1987	Ant
<i>Onymacris rugatipennis</i>	49.0	Namib	Roberts et al. 1991	Tenebrionid
<i>Pogonomyrmex desertorum</i>	49.0	Chihuahuan	Whitford & Ettershank 1975*	Ant
<i>Formica peripilosa</i>	49.0	Chihuahuan	Schumacher & Whitford 1974*	Ant
<i>Pogonomyrmex rugosus</i>	49.0	Chihuahuan	Whitford & Ettershank 1975*	Ant
<i>Seothyra henscheli</i>	49.0	Namib	Lubin & Henschel 1990	Spider
<i>Cataglyphis cursor</i>	50.0	Spain	Cerda, Retana & Cros 1997	Ant
<i>Physadesmia globosa</i>	50.0	Namib	Roberts et al. 1991	Tenebrionid
<i>Onymacris plana</i>	51.0	Namib	Roberts et al. 1991	Tenebrionid
<i>Myrmecocystus romainei</i>	51.5	Chihuahuan	Kay & Whitford 1978*	Ant
<i>Ocymyrmex barbiger</i>	51.4	Namib	Marsh 1985	Ant
<i>Ocymyrmex robustior</i>	51.5	Namib	Marsh 1987	Ant
<i>Myrmecocystus depilis</i>	52.9	Chihuahuan	Kay & Whitford 1978*	Ant
<i>Myrmecocystus mimicus</i>	53.3	Chihuahuan	Kay & Whitford 1978*	Ant
<i>Cueta trivirgata</i>	53.4	Namib	Marsh 1987	Ant-Lion
<i>Camponotus detritus</i>	53.8	Namib	Curtis 1985	Ant
<i>Pogonomyrmex californicus</i>	53.8	Chihuahuan	Curtis 1985	Ant
<i>Cataglyphis bombycina</i>	55.0	Sahara	Wehner, Marsh & Wehner 1992	Ant

\*compiled from references provided by Marsh (1985)

### Figure Captions

**Figure 1** Interrelationships of abiotic elements with Namib desert organisms. From Seely (1983), by copyright permission of the Desert Ecological Research Unit of Namibia.

**Figure 2** Range of temperature (bounded by minimum recorded temperatures on the left and the maximum recorded temperatures on the right) and humidity conditions found above (to 500mm) and below (to 500mm) the surface (as indicated as 0mm) of a desert sand dune. Activities of adult tenebrionid beetles in the two locations are listed. From Seely (1989), by copyright permission of the Desert Ecological Research Unit of Namibia.

**Figure 3** Capture web and burrow of the spider *Seothyra*, on a Namib Dune. The spider remains below its lethal temperature by retreating to the bottom of the burrow, and making rapid forays when its prey is trapped in the web, which is on the hot sand surface. From Henschel & Lubin (1990), by copyright permission of the Desert Ecological Research Unit of Namibia.

ABIOTIC ELEMENTS

ADAPTATIONS

BEHAVIOURAL

PHYSIOLOGICAL

