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Thermal and water relations of desert beetles

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Abstract The physical problems that living organisms have to contend with in hot deserts are primarily extremes of temperature, low humidity, shortage or absence of free water, and the environmental factors that accentuate these – such as strong winds, sand-storms, lack of shade, rocky and impenetrable soils. Climatic factors are particularly important to smaller animals such as arthropods on account of their relatively enormous surface to volume ratios. Nevertheless, beetles (especially Tenebrionidae and, to a lesser extent, Chrysomelidae) are among the most successful animals of the desert, and are often the only ones to be seen abroad during the day. Similar physical problems are experienced by insects in all terrestrial biomes, but they are much enhanced in the desert. Although climatic extremes are often avoided by burrowing habits coupled with circadian and seasonal activity rhythms, as well as reproductive phenology, several species of desert beetle are nevertheless able to withstand thermal extremes that would rapidly cause the death of most other arthropods including insects. The reactions of desert beetles to heat are largely behavioural whilst their responses to water shortage are primarily physiological. The effects of coloration are not discussed. In addition to markedly low rates of transpiration, desert beetles can also withstand a considerable reduction in the water content of their tissues. The study of desert beetles is important because it illustrates many of the solutions evolved by arthropods to the problems engendered, in an extreme form, by life in all terrestrial environments.

I would like to dedicate this review to the memory of a dear friend, Prof. Dr. E.B. Edney

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Introduction

If, as J.B.S. Haldane once remarked, the work of the Creator demonstrates ‘an inordinate fondness for beetles’, nowhere is this affection more apparent than in the hot deserts of the world. Not infrequently, the only animal to be seen during the day, if any is visible at all, will be a tenebrionid beetle – for the family Tenebrionidae contains the most conspicuous and often most abundantly represented species of Coleoptera in arid regions. In the oases of the Middle East and elsewhere, where animal dung is plentiful, scarab beetles (Scarabaeidae) are also numerous while, for those who look more closely, Carabidae are also not uncommon. Oases, however, provide not only a source of food, but also shade and protection from the climatic stresses to be experienced in the desert beyond their fringes.

Many other beetle families are represented in arid regions (Pierre 1958; Cloudsley-Thompson and Chadwick 1964). Some, less well adapted, penetrate into the desert only along river banks, wadis and into oases. For instance, the Chrysomelidae are mesophyllic insects which survive by selecting moist microhabitats and reproducing only in early spring (Ghilarov 1964; Lopatin 1999). Apterism is common among them and the tarsi are specialized for digging. Those species living under stones are flattened, whereas others that bury themselves in sand have evolved a fusiform body shape (Chen and Wang 1962). The North American species of *Timarcha* are entirely nocturnal whereas, with few exceptions, African species are day-active. The exceptions include species found in the Atlas Mountains of Morocco, which are crepuscular. In North Africa, *T. pimelioides* is sympatric with various *Pimelia* spp. Both genera are toxic and may show concordance in elytral sculpture (P. Jolivet, personal communication, 6 August 2000).

It is often claimed that, of the principal characteristics responsible for the success of insects, the power of flight is one of the most important. Yet, paradoxically, a surprisingly large proportion of beetles, including most of the larger desert species with which this review is mainly

concerned, have lost their operational metathoracic wings, and only the elytra (the modified forewings of the prothorax) remain. However, the subelytral cavity which lies beneath them and into which the abdominal spiracles open, plays an important role in desert adaptation (see below).

Deserts are notoriously dry for most of the year and have unpredictable rainfall. At least during daytime they may be extremely hot too, while in the depth of the winter's night, they can be surprisingly cold. The adaptations of desert beetles have attracted so much research that it will be possible, in a short review, merely to draw attention to some of it and to cite a selection of the more important of the relevant publications.

Avoidance of climatic extremes

The primary response of most desert beetles to excessive heat and low humidity during the day is to avoid them and come into the open mainly at night. Behavioural responses thus consist primarily of taking shelter rhythmically during the day in burrows, hiding beneath stones and rocks or tunnelling into loose sand (Cloudsley-Thompson 1961, 1964a, 1970, 1975, 1990, 1991). Even day-active species take shelter when their body temperatures (T_b) begin to reach lethal levels – although these may be surprisingly high (see below).

Morphological and behavioural adaptations

The family Tenebrionidae, as already mentioned, contains the most conspicuous of the ground-living desert beetles. One of these, *Onymacris plana*, is a large black day-active species of the Namib desert. Here adaptive speciation is particularly well marked (Seely and Griffin 1986). The fastest pedestrian insect known, with an average speed of 90 cm s^{-1} , *O. plana* runs swiftly across the hot dune sand from the shade of one plant to another without its body temperature becoming unduly elevated (Edney 1971a). Another Namib desert species, *Stenocara phalangium* (Fig. 1), behaves in a similar way. Day-active desert beetles, notably among the African Adesmiini and Zophosini (Tenebrionidae) tend to be very speedy, often having evolved extremely long legs (Crowson 1981) and large, almost contiguous hind coxae (Koch 1955). Ward and Seely (1996b) found little evidence among *Onymacris* spp. to suggest that the function of long legs is to improve the efficacy of 'stilting' (see below). Inland species nevertheless, have longer legs than do those of cooler coastal districts where shorter legs minimize the cost in energy of breakages.

Other desert beetles avoid the heat of the sun by hiding in vegetation, under stones or, like the nocturnal *Stips stali*, bury themselves deeply in the substrate (Wharton 1983). This takes place when T_b rises and may result in a significant reduction in temperature (Ward and Seely 1996a, b). *S. stali* has a flattened body and short

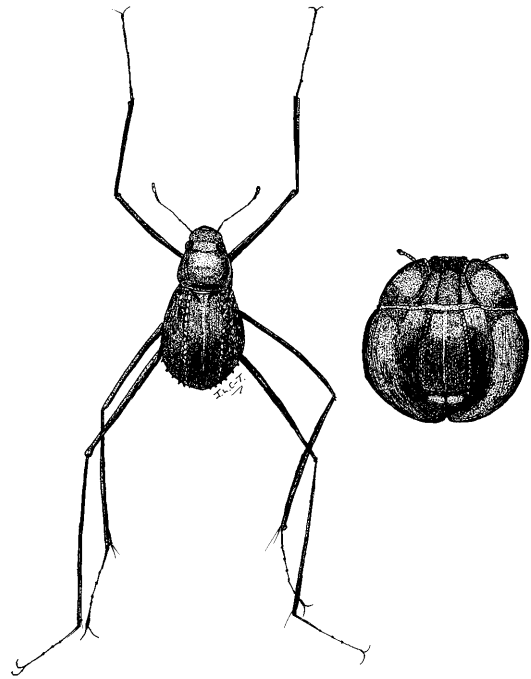


Fig. 1 *Stenocara phalangium* (left); *Stips stali* (right). From Cloudsley-Thompson (1991) redrawn after Koch (1961)

legs, well adapted for burrowing in sand (Koch 1961; Cloudsley-Thompson 1991). Nocturnal species comprise the majority of desert beetles, but why the common Saharan *Adesmia antiqua* should be day-active while the sympatric *Trachyderma hispida* and *Pimelia grandis* are nocturnal (Cloudsley-Thompson 1963) has never been satisfactorily explained. It may possibly be related to avoidance of competition.

At high altitudes, a combination of cold and a stony substrate leads to the development of small size and a cylindrical shape (Seely et al. 1988). This allows the tenebrionids of the Namib and Sonoran deserts to retreat from the hostile conditions above ground. Studies on tenebrionid populations frequently emphasize structural modifications such as the length and form of the legs (Pierre 1958; Medvedev 1965; Broza et al. 1983) of the elytra (Cloudsley-Thompson 1964b; Fiori 1977; Nicolson et al. 1984b; Draney 1993) and body size (Coineau et al. 1982; Thomas 1983; Doyen and Slobodchikoff 1984) as adaptations to microclimate and edaphic factors.

Burrowing and swimming in sand

The typical morphological adaptations of deserticolous Tenebrionidae were listed by Marcuzzi (1960) as follows: (1) increase in the volume of the subelytral cavity; (2) an unusually dark-coloured integument; (3) fossorial legs in both larvae and adults; (4) large body size; (5) shortening and broadening of the bodies of the larvae. In the Namib desert, which is in many ways unique, there are seven endemic genera and 17 species of Tenebrionidae that inhabit vegetationless dunes, whilst none have

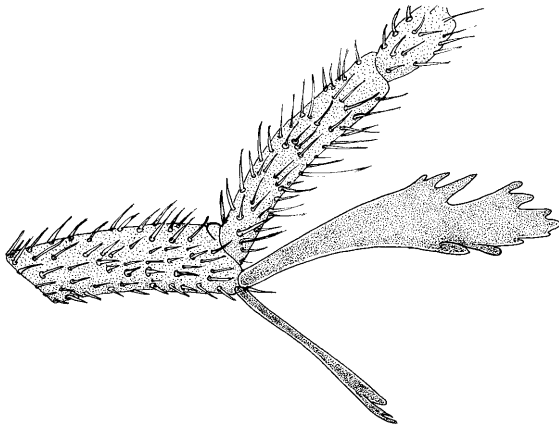


Fig. 2 Posterior leg of *Lepidochora* sp. showing apical portion of the tibia with extensions of the normally spiniform calcarea and hypertrophic development of tactile bristles. From Cloudsley-Thompson (1991) redrawn after Koch (1961)

been recorded in the Sahara, Somalia, Malagasi, Gobi or Australian deserts according to Seely (1978). This may be the reason why, as Koch (1961) noted, the ultra-psammophilous tenebrionid beetles of the Namib differ from those in Marcuzzi's (1960) list as follows:

1. Subelytral cavity varies from extremely large (e.g. *Onymacris unguicularis*) to practically non-existent (e.g. *Stips stali*); all degrees of size occur in both day-active and nocturnal forms.
2. Coloration varies from black to reddish-brown and yellow to structurally white with unpigmented elytra. [Coloration will not be discussed in the present review as its functions have already been debated in *Naturwissenschaften* (Cloudsley-Thompson 1999)].
3. Fossorial legs occur in the larvae of nearly all ground-living Tenebrionidae in steppe and forest as well as in desert. They are rare among Stizopina, in which they are a phylogenetic character, and in Zophosini. Here they are found in *Dactylocalcar caecus* which lives permanently under sand.
4. Body size is equally variable in diurnal and nocturnal Namib desert species.
5. Larvae are usually slender and elongated (Adesmiini, Zophosini etc) and only rarely shortened and dilated (e.g. *Lepidochora* spp.).

Koch (1961) also described a number of adaptive modifications of the legs of dune species. These consist of hypertrophy of the claws as well as of the bristles and spines in regions of the body which are in continuous contact with the sand. Furthermore, there are extensions of the gripping surfaces of the tarsi. In sand-swimming forms, such as *Lepidochora* spp., supplementary structures have been developed in the form of fingerlike extensions of the normally spiniform calcarea (Fig. 2), and the hind legs work together instead of alternately.

de los Santos et al. (2000) found two morphological adaptive trends in populations of the genus *Hegeter*

(Tenebrionidae) collected from different ecosystems along an altitudinal gradient on Tenerife. The first is a general increase in size, especially in abdomen volume and the length of the legs. This is mainly associated with soil-surface temperatures, while more silt in the soil has the opposite effect. The second trend is a general widening and flattening of the body and shortening of the appendages. This is related to burrowing habits and is influenced by rainfall and the ecological factors associated with it, such as plant cover and biomass, soil carbon and organic content. The adaptations of the limbs of desert Tenebrionidae have been reviewed in detail by Dajoz (1984). In general, the morphological adaptations of desert beetles are related primarily to the structure of the substrate and, consequently, only secondarily to thermal extremes and shortage of moisture.

Circadian activity

Changes in the behaviour and physiology of living organisms usually take place rhythmically. The daily activity of North American tenebrionid beetles has been described as thermally opportunistic because the insects show variable activity patterns associated with a range of air temperatures (Kramm and Kramm 1972; Kenagy and Stevenson 1982; Whicker and Tracy 1987; Cooper 1993). Daily patterns of movement, during which the insects emerge from their burrows, and of rest within, are an important feature in the lives of desert beetles. Scholtz and Caveney (1988, 1992) have described how daily biphasic behaviour in the Kalahari desert Trogidae *Omorgus casperulatus* and *O. freyi* varies in relation to climate. Feeding predominates in the morning, breeding behaviour and dispersal in the afternoon. [I noted a reversed order of behaviour in *Adesmia variolaris* on Jebel Marra, Western Sudan, in November 1964 (Cloudsley-Thompson 1967).] Emergence may often be a direct response to the physical conditions both inside the burrow and without, in which case the rhythm is said to be exogenous. In almost all examples of activity cycles that have been studied, however, there is also an endogenous component – a biological clock – and the rhythm is then said to be composite. It is obviously advantageous for an animal not only to be preadapted physiologically, but also to be ready to emerge from its burrow the moment that environmental conditions outside are optimal.

In areas of sand dunes, species of beetles tend to replace one another throughout the day and night. For example, Holm and Edney (1973) found that, during summer in the Namib desert, *Onymacris laeviceps* was most active at 0700–0800 hours and again 1800–2000 hours while *O. plana* was active at 0900–1200 hours and 1600–1800 hours. Both species were bimodal, but the modes occurred at different times. *Lepidochora argentogrisea*, on the other hand, emerges briefly at dusk when the temperature drops (Kühnelt 1969; Louw and Hamilton 1972). Buxton (1923) commented upon the diurnal and seasonal appearance of desert beetles and showed that

many large Tenebrionidae, such as *Adesmia* spp. which are conspicuous in North Africa and the Middle East at all times of day in March and April, seek shelter under stones and in the shade of bushes in May and June. Bodenheimer (1934) likewise found that the time of maximum activity of desert beetles varies with season. Erbeling (1983) showed that *Thermophilum* (= *Anthia*) *sexmaculatum* (Carabidae) is able to survive in the northern Sahara by modification of its diel activity patterns. Similar observations have been made by a number of other authors (reviewed in Cloudsley-Thompson and Constantinou 1985).

The presence of endogenous clocks has been demonstrated experimentally in several species of desert beetles. By means of a mechanical aktograph, the North African *Thermophilum venator* was found to be nocturnal while, of Tenebrionidae, *Akis spinosa* was mostly day-active, *Trachyderma* (= *Ocnera*) *hispidata* showed a peak of activity at dusk, *Blaps requieni* was even more crepuscular and *B. mucronata* almost entirely nocturnal (Cloudsley-Thompson 1956). Similar experiments have demonstrated that *T. hispidata* and *Pimelia grandis* are strictly nocturnal in Sudan whereas *Adesmia antiqua* is diurnal. The first two of these were found to be photonegative at all temperatures, while the photopositive response of *A. antiqua* was more marked at higher ambient temperatures. All species responded to near-lethal temperatures by digging into the sand (Cloudsley-Thompson 1963). Using more sophisticated technology, Constantinou (1983) demonstrated circadian rhythmicity in *Blaps wiedemanni* from Kuwait, while Constantinou and Cloudsley-Thompson (1980, 1982) investigated the physiological basis of the rhythm in *Adesmia cancellata* from Kuwait and in *Trachyderma hispidata* from Sudan, respectively. They also found that *Erodius octocostatus* (Tenebrionidae) from Kuwait is crepuscular, although its rhythm is physiologically more akin to that of a nocturnal than that of a day-active animal (Cloudsley-Thompson and Constantinou 1985).

Thermophilum duodecimguttatum, also from Kuwait, is primarily nocturnal but, when high temperatures coincide with the light phase of an experimental light-dark cycle, activity takes place mainly during the second half of the light period (Constantinou and Cloudsley-Thompson 1985). The related *T. sexmaculatum* has been described both as nocturnal and as diurnal by various authors cited by Erbeling and Paarmann (1985). Raymond (1950), Fiori (1968) and others have attempted to correlate the pattern of diel activity with temperature or season. The contradictory data in the literature can, however, best be explained in terms of a seasonally changing pattern of daily day-to-day changes in activity patterns, correlated with responses to short-term variations in temperature, radiant energy and wind velocity. The northern subspecies, *T.s. submaculatum* adapts to seasonal climatic changes by becoming either nocturnal or day-active, while the south Saharan *T.s. marginatum* remains strictly nocturnal throughout the year (Erbeling and Paarmann 1985).

In all seasons of the year, *Eleodes armata* of the Mojave desert has a higher daily rate of energy than the sympatric *Cryptoglossa verrucosa*. *E. armata*, however, can exploit a wider range of thermal regimes and is thought to have evolved in northern regions, whereas *C. verrucosa* is considered to be endemic to deserts (Cooper 1993). A field study in the Kara-Kum desert of Turkmenistan of the circadian rhythm of *Trigonoscelis gigas* by Zotov et al. (1996) showed that the rhythm is controlled by a mechanism of 'gates': the tenebrionids are active only from 0600 to 1000 hours and from 1600 to 2000 hours, regardless of weather and season, although the beetles may skip some gates and remain under the sand when the weather is exceptionally unfavourable. An additional complication has been introduced through the discovery by Costa et al. (1987) that the endemic tenebrionid *Pachyphaleria capensis* of the southwestern coast of Africa responds to solar radiation not only by skototaxis but also by non-chronometrical solar orientation. On overcast or foggy days, this response tends to occur in a north-south direction.

Seasonal rhythms and life cycles

Seasonal influences on the circadian activity rhythms of desert beetles have been outlined in the previous paragraphs. (Brun 1975) analysed those of *Pimelia bipunctata* in the sand dunes of the Carmargue. Other seasonal cycles by which the more extreme environmental conditions are avoided, include varying behavioural responses. For instance, as noted above, Buxton (1923) remarked that some tenebrionid beetles, which are active in bright sunshine in Israel during the spring, shun the light during the summer months and become crepuscular in habit. Not only is their activity cycle changed but also their response to light. Comparable results have been obtained from the Namib desert by Holm and Edney (1973), in Tunisia by Heatwole and Harrington (1989), by Hinds and Rickard (1973) in arid south-central Washington, and in the North American desert by Smith and Whitford (1976), Thomas (1979), Marshall (1985), Marino (1986) and Whicker and Tracy (1987) among others. Aldryhim et al. (1992) noted that in Saudi Arabia the numbers of tenebrionids trapped in winter and mid-summer were low, reaching a peak in June; and that earlier rainfall had a positive effect on their abundance. Seasonal changes in darkling beetle communities have also been studied in Israel by Krasnov and Ayal (1995) who found not only that *Erodius edomitus* was a temporal specialist but that most species exhibited 7-10 month cycles of activity with one or two peaks of abundance. Paarmann (1979) suggested that a reduced number of larval instars is an adaptation of *Thermophilum sexmaculatum* to its arid environment, while Erbeling and Paarmann (1986) concluded that the essential adaptation of *T.s. submaculatum* to the climatic conditions of the northern Sahara is caused by the development of a seasonal rhythm of gonad maturation. Seasonal rhythms of activity and behav-

four are generally less important in the ecology of desert beetles and other insects than are seasonal reproductive cycles and seasonal quiescence or diapause (Cloudsley-Thompson 1970; Erbeling and Paarmann 1985).

In hot, dry deserts the developmental stages of beetles and other arthropods usually appear at the time of the rains, when the weather is cooler and there is abundant food. For example, adult *Adesmia bicarinata* begin to appear in small numbers in Egypt during late October. Throughout the hot season, the life cycle is continued by the larval and pupal instars (Hafez and Makky 1959). At other times they are frequently dormant – either in a state of facultative quiescence, parapause (obligatory dormancy) or in eudiapause. In the case of the latter, which again is facultative, induction is engendered by one factor and terminated by another, whereas in paradipause both induction and termination are genetically determined and triggered by drastic alterations in the level of a single environmental factor (Thiele 1977). This probably applies not only to Carabidae but to all families of desert beetles. For instance *Timarcha*, a steppe and savanna chrysomelid genus, has also adapted progressively to zones of high temperature, thanks to complicated diapauses (Jolivet 1967). According to Tombes (1965), aestivation has been recorded in 37 insect species, representing five major orders, most of which occur in arid or semi-arid regions. Indeed, diapause is primarily an adaptation to drought, rather than to high temperature. According to de Wilde (1962), experiments show that high temperatures tend to avert diapause in ‘long-day’ insects although they may promote it in ‘short-day’ insects. The adaptive significance of the biochronosystem is obvious, especially in desert regions, but its physiological basis is less clearly understood. That subject is not strictly relevant to the present article and, moreover, has been reviewed by Cloudsley-Thompson (1969), Applin et al. (1987), and others.

Thermal relations

Heat may be gained or lost by conduction, convection and radiation. In the case of surface-living desert beetles, heat exchange by conduction can largely be ignored because only very small areas of the tarsi are normally in contact with the substratum. Not surprisingly, however, as already mentioned, the claws, bristles and spines that are in continuous contact with the sand tend to be hypertrophied (Koch 1961). In contrast, heat exchange by convection is very important (Clarke 1967; Turner and Lombard 1990). Radiant heat, too, can increase body temperature far above that of the surroundings and may affect different parts of the body to varying extents. Most studies of tenebrionid populations have focused on the adaptive and behavioural characters associated with thermoregulation (Holm and Edney 1973; Henwood 1975; McClain et al. 1985; Røskaft et al. 1986; de los Santos et al. 2000). For instance, Parmenter et al. (1989) found that different species of *Eleodes* in Wyoming show ther-

mal preferences and tolerance of high temperatures that are related to the thermal regimes in the microclimates they inhabit. Doubtless thermal adaptations involve stress responses as well as the evolution of heat-resistant proteins.

Thermoregulation by shuttling

The maintenance of an optimum T_b by day-active ectotherms is often achieved by shuttling between open areas exposed to sunshine and shaded places. Dreisig (1985) has presented a time budget mathematical model of thermoregulatory sun-basking, based upon physical laws of heating and cooling, and on the assumption that upper and lower limits for T_b exist. In general, one basking episode is sufficient to restore T_b if the lower equilibrium or operative environmental temperature of an animal increases to the optimum in the same or a shorter time than the T_b decreases from the upper limit of activity to the lower equilibrium temperature. This is most probable when the change of equilibrium temperature is quicker, the animal larger, and the equilibrium temperature higher at the onset of foraging after basking. The model requires that the animals react not only to specific temperature levels, but also possess receptors that are sensitive to rates of change. This is only possible in the case of small animals whose T_b alters rapidly. The model is supported by observations of basking and shuttling between sunshine and shade by the tiger beetle, *Cicindela hybrida* (Dreisig 1980). Shuttling is also frequently resorted to by Tenebrionidae: in the Namib desert, for example species of *Onymacris*, *Sternocara*, *Physostena* and so on (Edney 1971a; Hamilton 1973; Roer 1975; Cloudsley-Thompson 1991) – while *Eleodes* spp. do the same in the North American deserts (Kramm and Kramm 1972). The microclimatic conditions under which beetles are active have been measured by Cloudsley-Thompson (1956, 1962a), Hadley (1970), Ahearn (1971), Hamilton (1971), Kramm and Kramm (1972), Holm and Edney (1973), Henwood (1975) and others (reviewed in Cloudsley-Thompson 1991).

Positional reactions to heat

Not only do desert beetles avoid excessive heat and cold by seasonal and circadian rhythms and by shuttling, but they also respond by immediate behavioural actions as well as by various physiological adaptations. For example, many day-active desert Tenebrionidae have been shown to respond to heat by ‘stilting’ – that is, elevating the body as high as possible above the hot substrate. Hamilton (1971, 1975) described this in *Cardiosis hybrida*, which is active in the Namib desert at ambient temperatures above 40°C, Henwood (1975) in *Onymacris plana* and *Stenocara phalangium*, Broza et al. (1983) considered it to be significant in the evolution of longer legs among *Trachyderma* spp. Stilting may permit

an extension of the period of activity by preventing the T_b from rising too quickly. When conditions become intolerable, however, tenebrionid and other beetles frequently burrow in the sand (Holm and Edney 1973). Ward and Seely (1996a) considered shifts in microhabitats to be far more important than postural adjustments for controlling T_b . Stilting does not occur in *O. ruga-tipennis* (Ward and Seely 1996b), which selects the warmest habitats (Roberts et al. 1991), but is found in *O. bicolor*, a short-legged coastal species. Dreisig (1980) observed stilting in the tiger beetle, *Cicindela hybrida*, over a number of years in Danish sand dunes during May. In addition, Namib desert tenebrionids move from directly insolated dune faces into shade, or to faces on which the angle of insolation is lower (Hamilton 1971; Henwood 1975). Insect thermoregulation has been reviewed by various authors cited in Heinrich (1981).

Thermal preferences

Although it is generally agreed that the T_b of desert tenebrionid beetles is controlled behaviourally, comparatively few recordings have been made of actual T_b in the field. Edney (1971a), however, measured them with indwelling thermocouples in both dead and tethered specimens, and Hadley (1970) in beetles inside enclosures. Seely et al. (1988) passed the thermocouple extensions through the eye of a fishing rod so that the beetles could move unhindered. Other workers have obtained single measurements from free-ranging individuals captured in the field (El Rayah 1970a; Edney 1971a; Kramm and Kramm 1972; Hamilton 1973, 1975; Henwood 1975; Hamilton Slobodchikoff 1983; Nicolson et al. 1984a; Abushama and Al-Salameen 1989; Cloudsley-Thompson 1990). The results of these various studies indicate a range of maximum tolerated temperatures between 43°C and 53°C for beetles from a variety of deserts and over varying periods of time. Not all Tenebrionidae of arid regions show high temperature preferences, however. Kenagy and Stevenson (1982) found that in the *Artemisia* steppe of eastern Washington, eight species of day-active tenebrionids showed preferences 10–15°C lower than those of most other terrestrial insects. They suggested that a low range of preferred T_b had evolved that extends activity into earlier and later times of the year when food supplies are better.

Tolerance of thermal extremes

Behavioural responses frequently result in desert beetles maintaining body temperatures close to the optimum for long periods. For instance Hadley (1970) found that during the course of one day in the Sonoran desert of Arizona, *Eleodes* beetles maintained a T_b of 42°C while that of the air was 32°C and the substrate was 42°C. Assuming a value of 63% for surface reflectivity, he calculated the following heat balance in $\text{cal cm}^{-2} \text{min}^{-1}$: radiation

0.141 + metabolism 0.003 + conduction (?) = convection 0.134 + evaporation 0.008.

Despite avoidance behaviour, however, desert beetles may also experience wider extremes of temperature than do comparable species in temperate regions or in the humid tropics, and have been found to be able to withstand them (Pierre 1958; Cloudsley-Thompson 1962b, 1970, 1975, 1991; Délye 1969; Edney 1971a, 1974). Hafez and Makky (1959) found *Adesmia bicarinata* to be capable of withstanding slowly rising soil temperatures up to 53°C, while Punzo and Muchmore (1978) noted that, in *Tenebrio molitor*, there is a progressive increase in the mean survival time of older larvae exposed to 42°C at different relative humidities. Preconditioning also leads to enhanced resistance to heat in desert species (Cloudsley-Thompson 1970).

Voluntarily high T_b have often been recorded in summer-active diurnal species (Edney 1971a; Zachariassen 1977; Seely and Mitchell 1987). Seely et al. (1988) found that the T_b of diurnal Namib dune tenebrionids, which are active on sandy substrates throughout the year, range between 30°C and 39°C. They concluded that two factors have led to high T_b : the lack of seasons in the Namib and the presence of a readily available thermal refuge. In general, such beetles maintain a higher T_b than those recorded for other insects (Roberts et al. 1991).

The upper lethal temperatures of desert beetles have been measured by a number of authors. For instance, lethal temperatures (LT_{50}) for exposures of 24 h below 10% relative humidity (RH) have been found to be as high as 45°C in *Pimelia grandis* (Cloudsley-Thompson 1962b) and, at 5% RH, 46°C in *Adesmia antiqua* (El Rayah 1970a). [*A. antiqua* is day-active while *T. hispida* and *P. grandis* are nocturnal (Cloudsley-Thompson 1963).] The figure for *Eleodes* spp. from Albuquerque was 39.5–40°C, and from Las Cruces it was 41°C (Cloudsley-Thompson and Crawford 1970).

Tolerance of cold

In many deserts cold is a limiting factor, and both freezing resistance and supercooling have been demonstrated in some desert insects (Cloudsley-Thompson 1975, Hadley 1979a). A mean supercooling point of –11.8°C has been obtained for the North American *Eleodes* spp. (Cloudsley-Thompson and Crawford 1970), of –10.4°C in *Trachyderma hispida* and of –7.4°C in *Adesmia antiqua* (Cloudsley-Thompson 1973). For some desert animals the ability to supercool may provide protection against freezing but, for others, the capacity to do so is greater than that necessary for survival in a particular region, and may therefore be a taxonomic rather than an adaptive feature (Cloudsley-Thompson 1973).

The mechanism of heat death

Although a considerable amount of research has been carried out on the lethal temperature of arthropods the

physiological causes of heat death often remain obscure. In some cases death may be due to lack of oxygen at high T_b ; in others, the coagulation of cell proteins. In *Trachyderma hispida*, exposure to near-lethal temperature for 24 h results in a marked decrease in the pH of the haemolymph (Cloudsley-Thompson 1962b). Similar results were obtained by Ahearn (1970a) with the North American tenebrionid *Centrioptera muricata* in which both uric and lactic acid increased in the blood of beetles exposed to lethal temperatures, while the osmotic pressure also increased. In addition, there was a decrease in sodium and an increase in potassium. The similarity between the ionic ratio curve and the LD_{100} curve suggests a correlation between the two factors. More recently Abushama and Al-Salameen (1991) compared the effects of thermal stress on pH, sodium and potassium concentrations of *Adesmia cancellata* and *T. hispida*. Haemolymph osmotic pressures were consistently lower in the day-active *A. cancellata* than in the nocturnal *T. hispida*, while blood pH decreased, especially in the former, at temperatures above 50°C. At the same time, concentrations of Na^+ and K^+ ions increased at higher temperatures. These observations support the initial hypothesis that the ultimate cause of heat death in desert Tenebrionidae is failure of the excretory system to remove metabolic wastes that are produced at accelerated rates when T_b rises (Cloudsley-Thompson 1962b; Ahearn 1970a).

Water relations

The water relations of terrestrial arthropods have attracted the interest of entomologists since the pioneer experiments of Gunn (1933), Wigglesworth (1933), Ramsay (1935) and Pryor (1940) drew attention to the cuticle as a major avenue for water loss in insects, and opened up a field of investigation which has been active ever since. This important subject was reviewed by Edney (1977) in his classic text *Water balance in land arthropods*. Publication of that work engendered an explosive growth in the literature of arthropod water relations, summarized in the equally important but quite dissimilar volume by Hadley (1994) *Water relations of terrestrial arthropods*.

Behavioural regulation of water loss

As already mentioned, the water relations of insects are almost entirely under physiological control and, apart from avoidance of climatic extremes (discussed above), there are few ways in which water loss can be reduced by behavioural means. Their surface to volume ratio is so great that water cannot be expended for thermoregulation except from the thoraxes of highly active flying insects such as grasshoppers and honeybees. Although *Adesmia antiqua* is diurnal (Cloudsley-Thompson 1963) and shows a preference for a higher body temperature than the nocturnal *Pimelia grandis* (El Rayah 1970a), both species are hygro-negative unless desiccated, when

they become hygro-positive (El Rayah 1970b). It is highly probable that similar responses are present in other species of desert beetles, but they do not appear to have been investigated in great detail. Rates of water loss from different species of *Eleodes* in Wyoming, however, are not correlated with the microclimates inhabited as their thermal preferences are. Presumably microhabitat use is independent of the physiological capabilities of water conservation (Parmenter et al. 1989). Slobodchikoff (1983) tested the temperature preferences of nine tenebrionid species in laboratory gradient experiments, and measured water loss in eight of these. At their mean preferred temperatures, water loss was the same in all species, whether they came from the Lower Sonoran desert of Arizona, from pinon pine woodland or ponderosa pine forest. In times of drought, the Kalahari tenebrionid *Parastizops armaticeps* inhabits especially deep burrows in which both temperature and evaporative water loss are reduced (Rasa 1995).

The subelytral cavity

Fusion of the elytra to form an air space above the abdomen is found especially in desert Tenebrionidae (Dizer 1955; Cloudsley-Thompson 1964b, 1975; Fiori 1972/73; Lawrence and Newton 1982; Dajoz 1984; Draney 1993), Chrysomelidae and some other families (Corset 1931; Fiori 1972/73; Jolivet 1994, 1997). Although the suggestion that, regardless of its size, the primary function of a subelytral cavity is to reduce respiratory water loss (Cloudsley-Thompson 1964b; Ahearn and Hadley 1969; Ahearn 1970b; Edney 1971a), Hadley (1972) pointed out that if the cavity is filled with air it must inevitably retard heat flow from the elytra to the abdomen. Earlier, Bolwig (1957) had found somewhat higher temperatures in the subelytral space of black *Onymacris multistriata* than in the white *O. bicolor*.

Tanner and Packham (1965) noted that Tenebrionidae in southwestern USA are most plentiful at the beginning of the rainy season, which supports the hypothesis that the subelytral cavity may allow the abdomen to expand for the storage of water, food and eggs (Fiori 1977) and, according to Slobodchikoff and Wiseman (1981) who appear to have overlooked Fiori's paper, enables advantage to be taken of ephemeral sources of water such as rain drops, fog and dew. The latter author showed a correlation between the depth of the cavity and the amount of water loss endured. Ahearn (1970b) presented evidence that the airflow within a beetle's tracheal system is unidirectional. The thoracic spiracles only take in air, which is exhausted within the body and slows evaporation even more. The functions of the subelytral cavity have been discussed at length by Fiori (1977), Draney (1993) and Jolivet (1997) and will therefore not be considered further here.

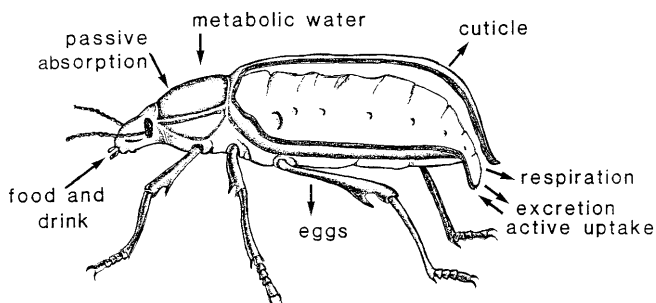


Fig. 3 Avenues of water gain and loss in a tenebrionid. *Silhouette* showing the subelytral cavity. After Ahearn (1970b)

Cuticular transpiration

The main avenues of water loss from insects are through transpiration and excretion (Ahearn 1969, 1970b) (Fig. 3). Transpiration through the cuticles of desert beetles is generally much reduced by the highly efficient epicuticular wax layer with its high critical point. Various species of desert beetles can be arranged according to their rates of water loss in dry air in a series that to some extent corresponds to their distribution and times of activity in the field (Cloudsley-Thompson 1956, 1975; Edney 1971b, 1974, 1977; Hadley 1978, 1994). Evaporative water loss has usually been measured gravimetrically. During slow dehydration, however, the loss in weight of dry matter may be considered from *Onymacris plana* in relation to that of water (Nicolson 1980). Nicolson et al. (1984b) therefore developed an alternative technique, using tritiated water, and applied it to the same species. Water loss through the elytra was $0.75 \mu\text{g cm}^{-2} \text{ mm Hg}^{-1}$. This is almost the lowest cuticular permeability ever reported for an insect (Nicolson 1990). Although most of the data in the literature are expressed in these units, the method has not been without its critics (Hadley 1994). It does, however, permit comparisons between genera and species if the test conditions are clearly stated, as shown by the often cited tables published by Edney (1977) and Hadley (1994).

In the deserts of the southwestern USA, the relatively large and conspicuous tenebrionids *Eleodes armata* and *Cryptoglossa verrucosa* occur sympatrically (Ahearn 1971; Thomas 1979), but several differences have been recorded in their morphological and physiological adaptations to the arid environment. *E. armata* is heavier and loses water at a higher rate than does *C. verrucosa* (Ahearn 1970b; Cooper 1983, 1985). *C. verrucosa*, however, mainly consumes arthropod material whereas *E. armata* feeds on plants (Cooper 1985). The mass specific oxygen consumption rate of *E. armata* at 35°C is higher than that of *C. verrucosa*, and it has been suggested that the latter species may therefore be better able to withstand conditions of drought (Cooper 1993).

Several groups of beetles from arid environments have reduced their cuticular transpiration to such an extent that respiratory water loss (see below) has become the major component (Zachariassen 1996). Thus

Zachariassen et al. (1987a) found that the rates of evaporative water loss were a function of the metabolic rate in carabid and tenebrionid beetles from dry habitats. Although the values of equally large species differed considerably, when plotted as a function of oxygen consumption in a double logarithmic plot, the rates of water loss of all species fell on the same straight line. The slope of this was close to 1.0, implying that rates of water loss and oxygen consumption were proportional, as would be expected if water loss is predominantly respiratory. Further evidence of this was obtained by Zachariassen and Maloiy (1989), who found very little change in water loss when dry habitat tenebrionids and carabids were covered with impermeable vaseline. These authors concluded that in dry habitat beetles of the families Carabidae, Curculionidae and Tenebrionidae, spiracular water loss constitutes the major component of transpiration. Zachariassen et al. (1987a) found dry habitat tenebrionids and curculionids to lose water at lower rates than dry habitat carabids, elaterids and cerambycids in East Africa. Zachariassen (1991) found that independent variation of atmospheric humidity around different parts of the body had a strong effect on water loss only where the spiracles open on the pronotum and subelytral space.

Cuticular impermeability is conferred by lipids (Hadley 1981, 1985). Hadley and Louw (1980) attempted to relate the quantity and chemistry of the epicuticular lipids of *Onymacris plana* and *Lepidochora discoidalis*, whilst Lockley (1982) examined the interrelationships between lipid chemistry and taxonomic diversity among Tenebrionidae. Hadley (1978, 1982) provided a comprehensive summary of the lipid-hydrocarbon body weight ratios, hydrocarbon composition and the cuticular permeability of North American tenebrionid beetles

Wax blooms

Surface wax deposits occur in many desert arthropods, and multicoloured wax blooms are found in certain desert Tenebrionidae. For example the Sonoran desert *Cryptoglossa verrucosa* exhibits colour phases that range from light blue to jet black when exposed to low and high humidities, respectively (Hadley 1979b). The same effect has been described in other desert species and has been reviewed by Hadley (1985). McClain et al. (1984) found that rates of water loss from *Cauricara phalangi-um* in the Namib desert were significantly lower from individuals collected in May, when a full bloom was present, than from others taken in August when little or no wax bloom was present. They concluded that wax blooms contribute to the protection of these day-active beetles against high temperatures and radiant heat loads. Wax blooms occur in more than 50% of Adesmiini and Zophosini in the Namib. The percentage increases from the coastal fog region to the hot dry desert inland (McClain et al. 1985). McClain et al. (1991) also pointed out that the reflective wax blooms increase day-time activity in black beetles. This subject is discussed in detail by Hadley (1994).

Respiratory water loss

Respiratory water loss is reduced in the majority of desert Tenebrionidae and Chrysomelidae because the abdominal spiracles open into the subelytral cavity. Furthermore, as in other animals, water loss is reduced by cyclical breathing or discontinuous ventilation (DV) (Bartholomew et al. 1985; Louw et al. 1986; Hadley 1994). In insects, the spiracles are kept closed for most of the time but, as oxygen is consumed, carbon dioxide accumulates in the haemolymph where it is held in solution mainly in the form of bicarbonate. Eventually the spiracles open slightly, allowing some oxygen to enter but little carbon dioxide to escape. Finally the spiracles open widely and carbon dioxide is released in a burst. DV has been measured in ten species of Namib beetles – these were motionless adults. A scaling effect was evident but discrepancies were common. It was assumed that the phenomenon is an adaptation to the scarce and patchy availability of energy and water (Lighton 1991) but, of course, it may cost energy (Lighton 1988).

Whereas Ahearn (1970b) reported that thoracic spiracular water loss from the North American *Eleodes armata* represents 15.3% of total respiratory water loss, Cooper (1993) obtained a figure of 47%. Water loss data on this species are, however, complicated by the fact that 50% of the total loss occurs through the discharge of defensive secretions. Very different results were obtained by Zachariassen (1991) with *Phrynocolus petrosus*, a tenebrionid from dry savanna in East Africa. This author estimated that 70% of total transpiration takes place through the prenotal spiracles. His estimates for subelytral water loss were approximately one third of the values recorded from *Onymacris plana* by Nicolson et al. (1984b) and from *E. armata* by Ahearn (1970b) and Cooper (1983) (see discussion in Hadley 1994).

Excretory water loss

An important adaptation of desert beetles is their exceptional capacity to eliminate nitrogenous end-products and excess electrolytes with minimal water loss (Hadley 1994). This is partly due to the cryptonephric complex through which moisture is extracted by the malpighian tubules from the faeces of the beetles that possess it. In the case of *Onymacris unguicularis* and *O. plana*, only 11–14% of total water loss occurs with the faeces (Nicolson 1980; Cooper 1982). It is therefore surprising to find that the malpighian tubules of *O. plana* are stimulated dramatically by a diuretic hormone. The only conceivable occasion on which this might be required is after drinking excess fog moisture (see below) (Nicolson and Hanrahan 1986). This topic has been subjected to detailed discussion by Nicolson (1990).

Tolerance of desiccation

Insects that live in deserts may spend long periods without access to free water. At the end of the dry season or between widely separated thunderstorms they may become increasingly dehydrated (Zachariassen 1996). Tolerance of water loss among insects may vary between 17% and 89% (Arlian and Veselica 1979). For instance, *Trachyderma philistina* can lose up to 35% or more of its body weight without ill effects (Broza et al. 1976). As Hadley (1994) has pointed out, beetles tend to exhibit some of the highest tolerance levels of all insects, and the water content of their bodies varies between about 47% and 81% body weight. There is an inverse correlation between the percentage of water and of body fat.

Water uptake

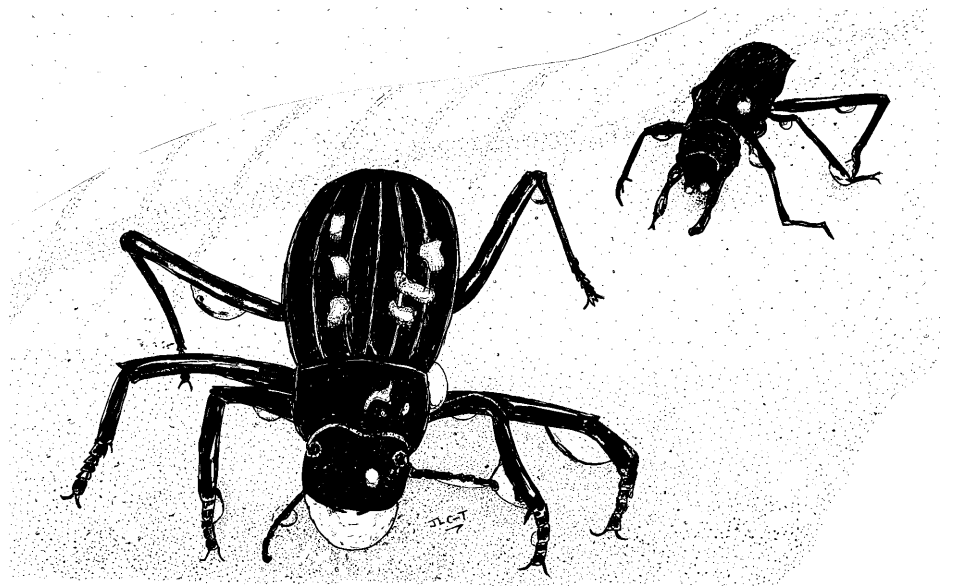
In most desert regions, free-standing water is seldom available and moisture can only be obtained with the food or from dry vegetation that has absorbed it hygroscopically. Chrysomelidae ingest preformed water from the juices of the plants on which they feed and Carabidae from the blood of their prey. Tenebrionidae, however, are mainly scavengers and extract hygroscopic moisture from dry vegetable matter (see below). Trogidae feed after rain (Scholtz and Caveney 1988). When the humidity is high, there may also be some passive absorption through the cuticle (Fig. 3).

Fog basking and hygroscopic plant debris

In cool, coastal deserts, where fog appears at irregular intervals throughout the year, there is seldom appreciable rainfall. Fog and mist, however, are an extremely important alternative source of moisture for animals of various kinds (Louw 1972; Seely 1978). Opportunist drinking of droplets of moisture from fog that has condensed on the body is an important source of water uptake for desert beetles. Fog basking was first observed in *Onymacris unguicularis* in the Namib by Hamilton and Seely (1976). Normally day-active beetles of this species remain buried in the sand of dune slip faces at night. When fog comes, they emerge, climb to the crest and adopt a characteristic head-down stance (Fig. 4) facing into the mist-laden wind while water trickles down the body into the mouth.

Seely (1979) pointed out that Adesmiini, Eurychorini and Zophosini have all evolved specific behaviour patterns for drinking water condensed on vegetation, the dorsum of the body, or in sand. *Onymacris laeviceps* provides an example of the first pattern, *O. unguicularis* of the second and *Lepidochora discoidalis* of the third. *Lepidochora* spp. dig trenches into which water, which they drink, flows from the sand above (Seely and Hamilton 1976). *Zophosis moralisi* drinks directly from the sand, as does *Physadesmia globosa*. The posture that

Fig. 4 Fog basking by *Onymacris unguicularis* (Tenebrionidae). From Cloudsley-Thompson (1991)



the latter species adopts is similar to the fog basking stance of *O. unguicularis* and may provide an explanation of the evolution of the adaptive behaviour of the latter (Cloudsley-Thompson 1990). The responses of various species not only differ from one another, but are correlated with the water balances of individual beetles, the characteristics of the fogs, and the weather that occurred between them (Seely et al. 1983).

Utilization of fog has also been observed in Israel by Broza (1979). Here *Carabus impressus* harvests dew drops from the leaves of *Atriplex leucoclada* bushes as does *Coccinella septempunctata*, whilst the nocturnal tenebrionids *Blaps sulcata*, *Pimelia dera* and *Trachyderma philistina* have frequently been recorded taking water from damp hygroscopic plant material. The utilization of hygroscopic plant detritus as a source of moisture by desert arthropods has frequently been recorded, and was first recognized by Buxton (1922, 1923). In addition, the active absorption of atmospheric water vapour through the rectum has long been known to occur in *Tenebrio molitor* larvae and has also been demonstrated to a lesser extent in larval but not in adult *Onymacris marginipennis* (Coutchié and Machin 1984) (see discussion in Hadley 1994). Metabolic water is also produced (Bartholomew et al. 1985), although the increased respiration necessary to form this not only prevents a net gain from resulting (Edney 1977) but, as the work of Zachariassen and his colleagues cited above shows, may actually enhance total water loss. In *Phrynoscolus petrosus*, metabolism of fat produces less than 15% of the water lost in dry air at about 20°C, and cannot compensate for transpiration unless the atmosphere is nearly saturated (Zachariassen et al. 1987b).

Water balance and osmoregulation

Although the blood in the haemocoel and the fluids in the gut or malpighian tubules may often be isoosmotic,

the concentrations of ions and other solutes vary considerably (Crawford 1981). Thus, as the haemolymph volume changes with the degree of desiccation in the larvae of *Onymacris marginipennis*, concentrations of various ions, free amino acids and trehalose remain relatively constant (Coutchié and Crowe 1979). As we have seen, this balance is upset at lethal temperatures although the insects are not necessarily desiccated. Even species such as *Stips stali* (Naidu and Hattingh 1988a) and *Physadesmia globosa*, whose haemolymph osmoregularity increases over 200 mosmol kg⁻¹ during the initial stages of dehydration, closely regulate their osmotic pressure thereafter (Naidu and Hattingh 1988b).

As explained above, reduced metabolism results in lower respiratory water loss (Zachariassen 1996), although it may also result in unusual extracellular ionic composition. It appears that the reduced respiration of desert tenebrionids has developed at the expense of the ability of the beetles to maintain high extracellular sodium concentrations and thus probably high-energy gradients of sodium (Zachariassen et al. 1987a). No osmoregulation takes place in *Phrynoscolus petrosus* if less than 10% body water has been lost. Beyond this, the concentration of free amino acids in the haemolymph is regulated, but not that of sodium and potassium ions (Zachariassen et al. 1987b). The efficient reabsorption of water from the urine facilitates the reabsorption of solutes by passive diffusion back to the haemolymph across the epithelium. This allows desert Tenebrionidae to withdraw all free amino acids from the urine despite the high concentrations present in the fluid of the malpighian tubules (see discussion in Zachariassen 1996). Hadley (1994) outlined the physiological and biochemical mechanisms responsible for the conversion of potassium carbonate to potassium urate and thence to insoluble uric acid. He also explained how the secretion rates of malpighian tubules vary regionally and with the state of hydration of the insect. Edney (1977) reviewed earlier work on the physiology of insect excretion.

Like tenebrionids, desert Carabidae show low cuticular permeability, but they do not display reduced metabolic rates, low extracellular sodium concentrations or high extracellular concentrations of free amino acids. Moreover, they may produce less concentrated urine and lose more water through respiration, but they obtain much more moisture with their food; their prey contains 60–70% water (Zachariassen et al. 1987a; Zachariassen and Maloju 1989).

Discussion and summary

The key to the survival of Tenebrionidae and other beetles in hot, dry environments consists in avoiding climatic extremes as far as possible, by a combination of seeking refuge from the most adverse conditions, morphological adaptations, behaviour and specialized physiology (Cloudsley-Thompson 1988). Whereas thermal reactions are primarily behavioural, adaptational responses to aridity are mostly physiological. Exploitation of desert habitats involves a vast complex of adaptive compromises between one set of factors and another. Desert beetles avoid desiccating environments in various ways, tolerate transient fluctuations in the ionic composition of their haemolymph, restrict water loss through a combination of physical adaptations and physiological processes, and utilize moisture obtained opportunistically from a variety of sources.

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Note added in proof The following book was published after this review had been completed:

Prakash I (ed) (2001) *Ecology of desert environments* (A Festschrift for Prof. J.L. Cloudsley-Thompson on his 80th birthday). Scientific Publishers (India), Jodhpur

Of its 28 chapters the following are especially relevant to the present review:

Abushama FT (2001) Temperature relations of desert beetles, pp 263–289

Henschel JR, Robertson MR, Seely MK (2001) Animal ecophysiology in the Namib desert: coping with little water, scarce food and elevated temperatures, pp 423–457

Robinson MD, Clayton DA (2001) Thermal ecology and seasonal activity patterns of *Erodius sauditus*, an Arabian dune beetle (Tenebrionidae Erodiinae), pp 281–291