# Desert invertebrate physiological ecology: is anything special?

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*Basic physiological adaptations of desert invertebrates tend to differ quantitatively but not qualitatively from adaptations for terrestrial life in general. From a suite of physiological and behavioural capabilities open to all invertebrates, some species have evolved physiological and related behavioural adaptations which allow them to assume a central ecological role as macrodetritivores in desert systems.*

In this review I examine the question: is anything special about the physiological ecology of desert invertebrates? Superficially, this question may appear trivial, because the ubiquity of insects and arachnids in deserts[1] intuitively leads to the conclusion that these invertebrates must be particularly well adapted to arid conditions and that their adaptation must depend on their physiological capabilities.[2]

The physiology of desert invertebrates has received attention for most of this century,[3] with emphasis on adaptation to high temperatures and low water availability,[2,4] two attributes of desert environments particularly noticeable to man. Nevertheless, few studies of desert invertebrate ecophysiology are directly comparable and fewer still address related desert and non-desert forms. Most studies have been confined to adult forms of desert insects and then only to their responses to extreme surface conditions.

Unlike mammals, and especially large mammals, which can tolerate extreme desert conditions for prolonged periods by using a combination of physiological adaptations, for example oryx[5] and camels,[6] invertebrates cannot rely solely on physiological mechanisms to withstand desert extremes. Instead, invertebrates and many other desert organisms use behavioural options, such as escape or retreat from surface extremes,[7] in addition to strictly physiological adaptations (i.e. modification of intrinsic body functions). Large surface area to volume ratio alone is sufficient to deny smaller animals the predominantly physiological option.[7,8] Thus, to understand the occurrence of assemblages of invertebrates in deserts, we must look further than intrinsic body functions.

The intuitive assumption, that physiology must play an important role in providing certain invertebrates with attributes necessary to live in deserts, stems from the basic character of the environment. In deserts, abiotic factors influence fauna and flora more than biotic interactions.[9] Very special physiological adaptations would appear essential to allow small organisms to live in what is perceived to be a hostile abiotic environment. To test the assumption, I examine several key environmental factors—high temperatures, general scarcity of water and food, and unpredictability of the environment—in the context not only of physiological but also of related behavioural adaptations of desert invertebrates. For purposes of this discussion I have differentiated between physiology and behaviour, although such a distinction is clearly untenable when considering the suite of adaptations necessary for life in any environment. In my view, the physiological and behavioural adaptations exhibited by invertebrates have allowed some novel solutions to the problems of life in arid environments.

## Behavioural physiology

Few early studies of desert animals examined the relative importance of behaviour and of physiology to the organism. Authors who addressed the problem directly include Bartholomew,[10] who discussed the relationship of mammalian body size to physiological and behavioural adaptations, and Stevenson,[11] who considered the relative importance of physiology and behaviour to temperature regulation of lizards. Some recent publications have discussed desert invertebrates[1] in this regard. Although the great variety of invertebrate species makes it difficult to generalize, I have attempted to summarize the relative importance of physiological and behavioural adaptations to extremes of temperature and water, and food availability (Table 1).

When extreme conditions of temperature, energy and water availability occur together, the relative importance of physiological and behavioural adaptations depends on which environmental factor poses the greatest threat (Table 1). For example, although desert invertebrates may have higher temperature tolerances and higher selected temperatures than invertebrates living in other environments,[12,13] these physiological adjustments are inadequate to ensure survival unless they are coupled with avoidance of extremes of thermal stress. Avoidance may take the form of temporary escape from short-term extremes, e.g. a shift from unimodal to bimodal diurnal activity,[14] or longer term modification of behaviour, e.g. a shift from diurnal to noctur-

Table 1. Summary of the relative importance to an invertebrate of physiology and behaviour for maintenance of homeostasis in relation to four major desert environmental factors.

| | Importance of physiology | Importance of behaviour |
|---|---|---|
| Extreme water deficits | + + + | + |
| Extreme food shortages | + + | + + |
| Extreme high temperatures | + | + + + |
| Unpredictable rainfall events | + + + | + |

nal activity with season.[15] So, with respect to temperature, behaviour is ultimately more important to invertebrate survival than are physiological adaptations. Several authors (e.g. Casey[16]) have pointed out the importance of behaviour to temperature regulation in insects from other environments.

In contrast to the potential effects of exposure to high temperature, exposure of a desert invertebrate to extremely low humidity is not immediately lethal. Reduction of the rate of body water loss by physiological means can ensure survival for days, if not months, for at least some invertebrates.[17,18] Escape or avoidance of low environmental water vapour pressure conditions is often not possible, thus behavioural options usually are not available.

A third environmental factor frequently encountered in deserts, paucity of food, can also be accommodated physiologically, at least temporarily, by the use of food reserves[19] or behaviourally, by moving into more productive areas as locusts do.[20] Thus, with respect to the three factors under consideration, physiological adaptations which relate to maintaining water balance are probably more important to the overall biology of desert invertebrates, whereas behavioural adaptations are more important with respect to temperature regulation or energy acquisition under extreme conditions.

In the case of holometabolous insects, immature and adult forms differ in their behavioural repertoires and physiological capabilities. The less mobile immature forms are usually less able to adjust behaviourally to adverse conditions and are compelled to tolerate these conditions, rather than to escape or retreat. Hence physiological adaptations tend to be relatively more important to immature forms than they are to adults. This difference implies an ontogenetic shift, as the organism develops, from reliance on physiological adaptations to greater reliance on behaviour. The conditions immature forms tolerate, however, are often those which adults seek as a retreat, and are thus relatively benign.[21] Varying adaptations to aridity by different life stages of holometabolous insects may thus provide illuminating examples for considering the question of what is special about the physiology of desert invertebrates.

Differing life-history patterns also result in varying suites of physiological and behavioural adaptations to desert environments. Those species whose adult and immature forms are active throughout the year should provide the best examples of extreme desert adaptation. For such species, environmental conditions above ground may be tolerated or avoided temporarily during extremes.[7] Other species have life histories entrained to season, thus ensuring that surface-active stages avoid annual extremes. Activity may be synchronized with longer term environmental events also. For example, surface-active adults may emerge only after episodic rainfall attended by high productivity and persistently available moisture.

Related behaviours thus appear to be an integral part of the physiological adaptations of desert invertebrates. Nevertheless, are there any intrinsic physiological adaptations that may be termed special?

## Water relations of desert invertebrates

Because of their basic structure, which includes a cuticle that retards water loss, desert insects are pre-adapted to aridity. This structure is shared, however, by insects resident in all environments.[2] In all terrestrial insects, water proofing is provided by a superficial cuticular layer of high lipid content;[22] in desert forms, this layer may be particularly well developed.[23]

Differences of scale, rather than fundamental function, are also evident elsewhere. For example, invertebrates inhabiting arid areas often have reduced rates of water loss but do not necessarily tolerate a body water content any lower than that of animals living in more mesic environments.[2] Although water loss rates have been measured for many desert species, regrettably few studies have directly compared different species under identical conditions.

Low water loss rates are neither exclusive to, nor do they necessarily occur in, desert organisms. *Tenebrio molitor*, a tenebrionid living in the arid, but not desertic, environment of grain stores, has a water loss rate equivalent to that of desert species.[24] Comparing Namib tenebrionids with *Trigonopus* sp. from a more mesic region, Edney[25] found that the mesic species lost water at least five times more rapidly than the desert species. The mesic rate, however, was almost the same as that measured for *Eleodes armata*,[26] a North American desert tenebrionid, but slightly lower than the range for five species of grassland *Eleodes*.[27]

Desiccation resistance appears also to vary among desert organisms. Although conditions of measurement are critical for such determinations, and comparisons between studies unsatisfactory, at least some desert invertebrates can survive weeks or months without water. Wharton[24] states that most mesic insects are not able to tolerate five days of desiccation, suggesting that, although variable, desiccation tolerance of desert species is an order of magnitude greater than that of more mesic insects. The production of metabolic water may play an important role in resistance to desiccation. Two studies of adult desert tenebrionid beetles suggest that about one third of their water requirement is provided by metabolic water.[28,29] About 10% of the water loss of desert locusts is replaced metabolically.[30] Studies with desert tenebrionid larvae indicated that only about 1.65% of their total weight loss, measured over one day, was replaced by metabolic water.[31] In contrast, meal worm, *Tenebrio molitor*, and flour moth, *Ephestia kuhniella*, larvae,[24,32] inhabiting non-desertic but arid environments, gain more than 90%, and perhaps all, of their total water requirements from metabolic water. From the scant evidence available, it would appear that metabolic water is important in the water balance of some desert invertebrates, and some non-desert invertebrates too.

Rates of water uptake, when free water is available, are high in some desert tenebrionid species. For example, *Onymacris unguicularis* may take up 50% of its total water content in a single fog of a few hours' duration.[33] Invertebrates living in ephemeral pools, in arid and mesic areas, may take up water equally rapidly.[34]

Water uptake from vapour has been observed in tenebrionid larvae and fishmoths from varied environments. Desert thysanurans, *Ctenolepisma* sp., and the fire brat, *Thermobia domestica*, appear to take up water from atmospheres with exceptionally low relative humidity.[2,24] Tenebrionid larvae from the desert, *O. plana* and *O. marginipennis*,[31] and *T. molitor* from grain stores,[24] require somewhat higher humidity levels before water vapour can be taken up directly.

Osmoregulatory ability could also be a special attribute of desert invertebrates. Over 12 days of desiccation, haemolymph osmolarity of adult *Onymacris plana* showed only 7% of the expected increase in concentration, although haemolymph volume decreased by 66%, and tissue water content remained constant at 54%.[28] Other Namib[17] and North American desert[35] tenebrionids osmoregulate equally well. However, at least some desert scorpions do not osmoregulate at all and one desert millipede does so only partially.[35] Thus, although regulating the osmolarity of haemolymph would seem advantageous, some desert invertebrates do not appear to include this capability in their repertoire of adaptations.

In summary, some but not all desert invertebrates show a greater degree of physiological adaptation to aridity than most non-desert forms. Though quantitatively superior, those adaptations related to water relations appear not to differ qualitatively from those of invertebrates inhabiting other environments. Instead, they simply represent organisms located near the extreme in a continuum of adaptations to terrestrial life.[2]

## Temperature relations

Table 1 suggests that physiological adaptations are less effective than behavioural adaptations in ensuring invertebrate survival under extreme temperature conditions in a desert. Nevertheless, higher than usual body temperatures are selected and tolerated by some desert tenebrionid beetles. Cloudsley-Thompson[4] and El Rayah[12] found that at least some Saharan Desert tenebrionids have a relatively high temperature tolerance (body temperature >50°C). Recent measurements suggest that temperatures selected by Namib tenebrionid beetles in laboratory and field are high (35 – 40°C),[36] although several degrees lower than maxima originally measured for these species.[13] Moreover, these unusually high selected or tolerated temperatures are still well below those to which most surface-active desert invertebrates would be subjected if they remained fully exposed to surface conditions (Fig. 1). Thus, whereas high selected and tolerated temperatures may be adaptive in that they allow longer periods of surface activity towards the middle of the day, they do not obviate the need to retreat from sunlit areas to avoid thermal death. Very few organisms, e.g. snails in the Negev,[18] remain constantly exposed on the desert surface throughout the year.

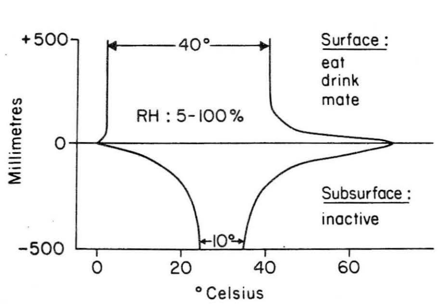


Fig. 1. Range of temperature (bounded by minimum recorded temperatures on the left and maximum recorded temperatures on the right) and humidity conditions found above (to 500 mm) and below (to 500 mm) the surface (indicated as 0 mm) of a desert sand dune. Activities of adult tenebrionid beetles in the two locations are listed.

Temperature tolerances or preferences may be interlinked with physiological adaptations related to water balance. Species that select lower body temperatures, or that are active in cooler parts of the day, are also those less resistant to desiccation.[37,38] These observations, together with parallels between higher temperature preferences and desiccation resistance in some African diurnal tenebrionids[4,12,13] when compared with North American species,[15,38] indicate an important evolutionary component of physiological adaptations to desert environments. North American desert tenebrionids, with lower temperature preferences and higher rates of water loss, apparently shift between diurnal and nocturnal foraging activity as seasonal temperatures vary (but see ref. 27 for grassland tenebrionids). In contrast, those diurnal African tenebrionids with higher temperature preferences and lower water loss rates may vary their diurnal foraging from unimodal to bimodal activity periods but rarely if ever forage nocturnally. Again, although it appears that some desert species select or tolerate higher body temperatures than non-desert invertebrates, available data indicate only quantitative differences.

Behavioural adaptations of desert invertebrates are particularly important in temperature relations involving use of the available microclimatic mosaic.[39] Even on a seemingly featureless sand dune, a thermal refuge is always present a few centimetres below the surface (Fig. 1) for organisms able to exploit the subsurface environment.[21] Indeed, it has been proposed that the availability of an immediate thermal refuge has contributed to the relatively high temperature preferences of some desert beetles.[36] The combination of invertebrates with high temperature preferences coinciding with a sandy substrate providing an immediate thermal refuge may be a special desert situation restricted to a limited set of environments.

The microclimatic mosaic, although a refuge from high temperatures, is not necessarily a refuge from aridity. The amount of water vapour in air may be greater outside than inside a desert cave in summer, even though relative humidity is greater inside.[40] A similarly counter-intuitive situation occurs in Namib sand dunes, where vapour pressure differences between tenebrionid beetles and their surroundings may be greater when the beetle is below surface than when it is above, except for a few hours each day.[21] Yet these beetles spend more than half of their time below surface. Although the environment may be more arid below surface, potentially lethal temperature extremes do not occur and air movement is greatly restricted. It is mainly above the surface, where food and mates are to be located, that lethal combinations of environmental extremes are encountered.

Opportunistic use of microhabitat refuges may be especially effective in deserts because of the unpredictability of the environment. In more predictable environments natural selection would favour environmental tracking which could be of a physiological nature. To illustrate the basis for such a view, the thermal characteristics of three different environments are depicted in Fig. 2. The relatively constant, predictable daily temperatures of McMurdo Sound in the Antarctic (Fig. 2*a*) offer little possibility for an organism to alter its temperature behaviourally by changing location, activity period or posture. In contrast, the predictable daily changes associated with almost no seasonality in equatorial Quito (Fig. 2*b*), changes which an organism could track on a circadian basis, negate the need for opportunistic behavioural temperature adjustments. If we compare these two situations with that prevailing in the Namib Desert (Fig. 2*c*), where the mean monthly temperatures vary little but daily temperatures vary widely and relatively unpredictably, the possibilities for behaviourally altering heat load, using a variety of microhabitats, are apparent. With large temperature variations within and between days, the temperature lag in established microrefuges offers small organisms a range of thermal conditions that continually varies spatially and temporally. Moreover, conditions appear too unpredictable to allow organisms to track the environment physiologically.

## Environmental unpredictability

The relative unpredictability of desert environmental conditions has manifold consequences influencing the contributions to adaptation of relatively fixed invertebrate physiology and relatively opportunistic invertebrate behaviour. Environmental

Table 2. Three levels of unpredictability of the desert environment and the importance of physiology and behaviour for an invertebrate in adapting to them.

| | *Predictable* | *Less predictable* | *Unpredictable* |
|---|---|---|---|
| Time scale | 'Macroscale' (decades, years, seasons) | 'Mesoscale' (days) | 'Microscale' (hours, minutes) |
| Duration of stimuli | Long term | Medium term | Short term |
| Duration of effects | Long term | Medium term | Immediate to long term |
| Factors involved | Aridity, high (and low) seasonal temperatures | Fog, diel temperatures | Rain |
| Mode of response | Physiology | Physiology and behaviour | Physiology (and behaviour) |

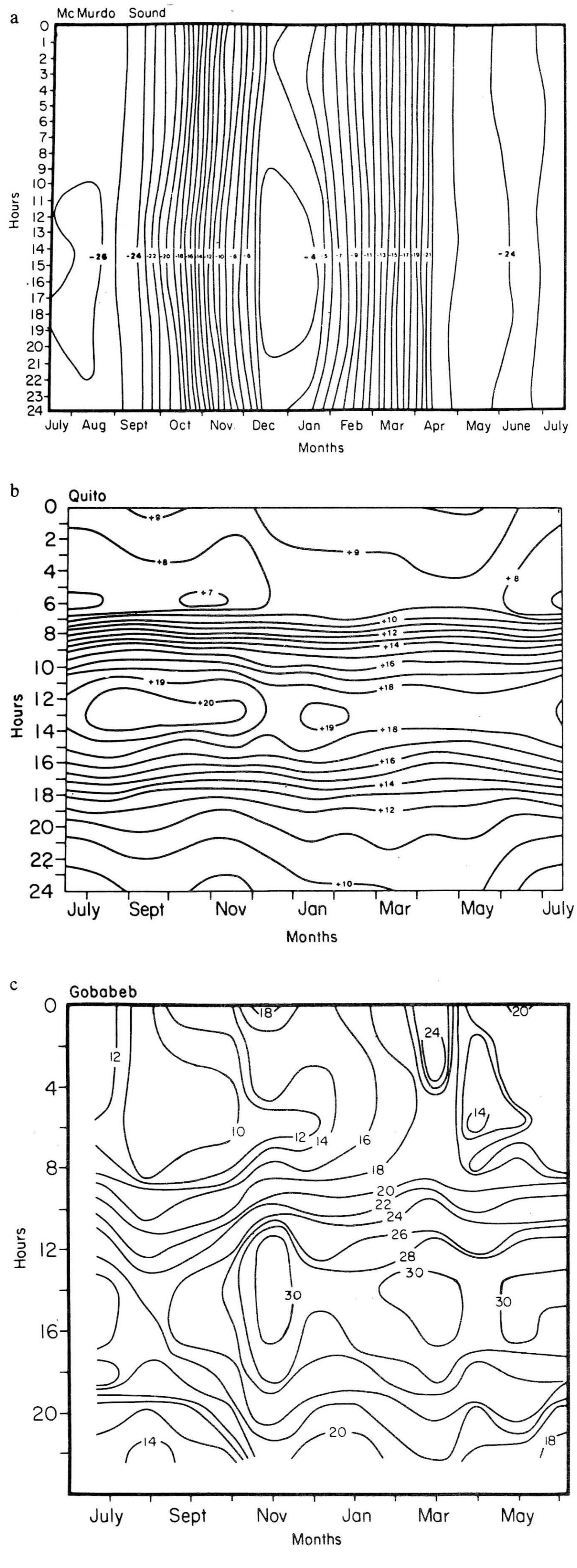


Fig. 2. Thermoisopleths from three different locations: *a*, McMurdo Sound, Antarctica (77°42′S, 165°35′E), with predictable seasonal temperature and little daily variation; *b*, Quito, Equador (0°14′S, 78°32′W), with predictable daily temperatures and little seasonal variation; *c*, Gobabeb, Namib Desert (23°34′S, 15°03′E), with less predictable daily and seasonal temperature variations. *a* and *b* from Troll[41] and Remmert;[42] *c*, original data.

unpredictability can be examined on three time scales (Table 2). Physical characteristics of aridity and high temperature and their biotic consequence—low primary productivity—are relatively constant and predictable on a macroscale of seasons, years or even decades. Adaptations to this scale of predictability are usually physiological, e.g. reduced water loss rates and high temperature tolerances and preferences.

In contrast is predictability on a daily basis or mesoscale level. Factors such as temperature and relative humidity may vary widely and rapidly on an hourly and daily basis which precludes physiological adaptation, particularly to extremes. These changes are not entirely unpredictable, however, as they are linked to the daily solar cycle. For example, although the absolute value of highest temperatures may vary by 15°C or more between successive days, the timing of highest temperature is relatively predictable. Similarly, highest relative humidity values, as well as dew and fog when they occur, are more likely to be measured during the nocturnal or early morning hours. Here adaptations of a behavioural nature, e.g. shifts between unimodal and bimodal activity periods[14,43] and facultative wind or fog response,[44] are of importance in avoiding daily extremes or taking advantage of temporarily favourable conditions.

The proximate environmental stimulus provided by rain initiates events which last from a few moments to a few hours in deserts. Such events are relatively unpredictable and intervals between them often may be much longer than the life cycle of an invertebrate. Behavioural responses to a short-lived event are limited, although nuptial flights of ants and termites and the emergence of spirostreptid millipedes or *Dinothrombium* mites[1] are two examples. In contrast, the after-effects of such an event in the form of vastly increased primary production may last for months or even years. Longer term responses may involve a direct reaction such as the breaking of dormancy and metamorphosis or activation of adult forms. These invertebrate responses are analogous to seed germination and the growth of annual plants following a pulse of rainfall.[45] Response may also be passive, such as decreased mortality of immature forms under improved moisture conditions.

## Ecological role of desert invertebrates

Given the suite of physiological and associated behavioural adaptations available to them, what particular role do invertebrates play in desert ecosystems? If one removed all invertebrates from the desert ecosystem, would there be a noticeable effect? For one important group which is almost always present, long-lived macrodetritivores, I believe the answer to the latter question is yes.

Because of the aridity which characterizes a desert, micro-decomposers such as bacteria and fungi, common in more mesic environments, are either scarce or absent[46] or show limited activity.[47] Insects and arachnids, however, are particularly conspicuous and common. Many insects feed upon wind-blown organic detritus. Termed macrodetritivores, they have several important functions thought to replace, at least partially, functions of micro-decomposers. In the warm, moist environment provided by their digestive tracts, they appear to be responsible for much of the decomposition and recycling of accumulated detritus. Macrodetritivores for which this function has been examined include camel crickets[47] and tenebrionid beetles,[48] although the magnitude of their role in the environment has not yet been satisfactorily determined.

On the other hand, large mammalian herbivores, even those adapted to desert conditions, tend to be precluded from living continuously in very arid parts of the desert, through lack of free water, insufficient energy or other reasons. Macrodetritivores are often present, however, and are able to replace at least some functions usually performed by large mammalian herbivores, such as the mechanical breakup and consumption of vegetation. In the Namib Desert dunes, tenebrionid beetles and thysanurans appear to be particularly important groups of macrodetritivores. In other deserts, other organisms, such as termites and camel crickets, appear to be more important.

Whatever the composition of the invertebrate assemblage, it would appear to be the suite of physiological and related behavioural adaptations exhibited by these organisms, adaptations not necessarily qualitatively special in themselves, that allows invertebrates to play a special role in desert environments.

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