

females, resulted in the paradoxical situation of low-ranking females enjoying longer drinking times than high-ranking females. The adult male responsible for most supplantings of high-ranking females was either a shadow male of uncertain troop status or a new immigrant. A further finding was that for high-ranking females, multiple drinks appeared to be required at each drinking session.

The environmental and social pressures on this troop of baboons, and particularly on females, may contribute to the extremely poor infant survival rate (two infants in approximately eight years). Findings reported here suggest that the low-ranking female baboons make better use of the limited available water than high-ranking females. This could prove significant in the future as the only surviving juveniles in the last 9 years have been born to low-ranking females. I am currently investigating this hypothesis.

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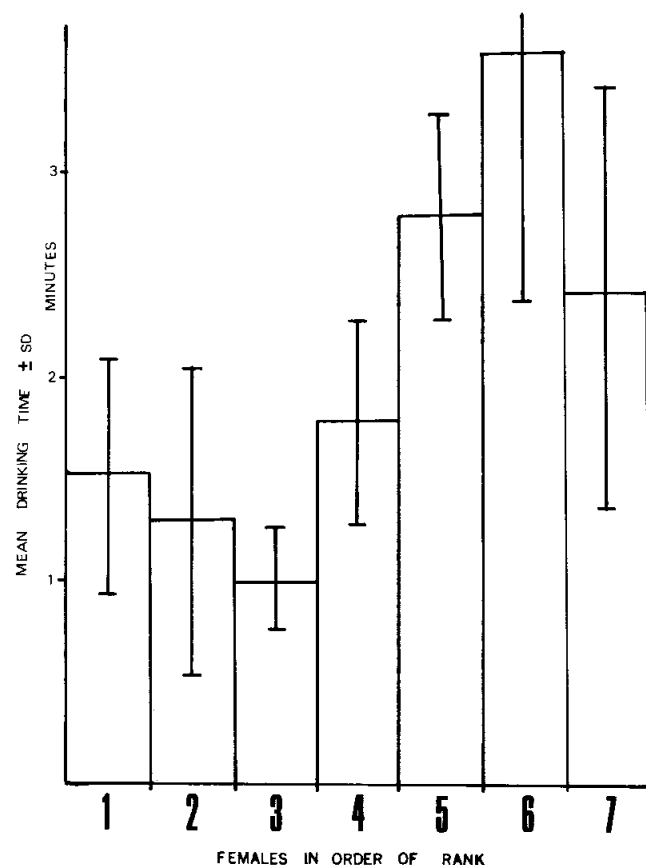


Fig. 3 Mean drinking times for seven adult female baboons as recorded during 11 drinking sessions.

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Water Relations of the Namib Tenebrionid Beetles

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Physiological research on water balance in the Namib tenebrionid beetles is reviewed. Most of the work described has been published in the last 10 years and concerns a single genus, *Onymacris*. Drinking of fog water is probably the main avenue of water gain in the adult insects, while the larvae depend on active uptake of atmospheric water. Metabolic water may be significant under certain conditions, and *Onymacris* species are efficient osmoregulators when water-stressed. Adaptations to minimize water loss via the cuticular, respiratory and excretory routes are well developed, although the function of the diuretic hormone in this genus is not clear. None of these adaptations is unique: it is rather the combination of them that contributes to the success of the flightless tenebrionids in the desert environment.

INTRODUCTION

Much of the research carried out on the tenebrionid beetles of the Namib Desert has focussed, naturally, on their thermal and water relationships. This review summarizes physiological research on the water relations of these beetles, most of it published in the last 10 years. Although work in this field has tended to be environmentally oriented, some more specialized studies have used the desert tenebrionids to examine fundamental biological principles. The emphasis is almost exclusively on a single genus, *Onymacris*, of the tribe Adesmiini (Penrith, 1984). The 14 species are all psammophilous and form a conspicuous element of the dune fauna. They are flightless, long-legged, fast-moving diurnal beetles that have a long lifespan and may be locally very abundant.

For all desert arthropods, the problems of living in a hot, dry environment are exacerbated by small size and relatively large surface areas, which lead to rapid exchanges of heat and water with the surroundings. In addition, the water activity of insect haemolymph (about 300 mOsm) is equivalent to 99.5% r.h., with the result that the net gradient for water movement is invariably outwards, except in saturated atmospheres (Edney, 1977). This applies to all terrestrial insects, not just desert forms. Water is exchanged with the environment through various avenues, in both liquid and vapour states (Fig. 1). Continuous loss of water through the body surface and the respiratory and excretory systems must be balanced by water intake from food and drinking, by metabolic water and by uptake from the atmosphere.

The water content of Namib tenebrionids is lower than the average of about 70% for arthropods in general (Edney, 1977). This is not a consequence of living in a desert, but is due to the relatively heavy integument and sometimes extensive fat reserves. Water content of the insects remains constant as long as water intake is sufficient to balance water expenditure: if not, dehydration is inevitable and osmoregulatory mechanisms are necessary until body water can be replenished.

WATER GAIN THROUGH DRINKING, FOOD AND METABOLISM

As described elsewhere in this volume, the aridity of the Namib Desert is tempered by the fairly frequent occurrence of advective fog. The importance of fog in the water economy of various animals inhabiting the Namib dunes was first described by Louw (1972).

Two unusual behavioural responses, involving the direct collection of fog, appear to be unique to the Namib Desert: fog basking in *Onymacris unguicularis* (Hamilton and Seely, 1976), and trench building in species of the genus *Lepidochora* (Seely and Hamilton, 1976). Most Namib beetles, however, rely simply on drinking fog water that has condensed on vegetation, detritus or stones (Seely, 1979). Such water has a surprisingly low osmotic concentration (14-38 mOsm; Louw, 1972). The amount imbibed may be substantial; for example, up to 34% of pre-fog weight in *O. unguicularis* (Hamilton and Seely, 1976). The subelytral cavity of these flightless tenebrionids permits body expansion after imbibition of large quantities of water at irregular intervals (Slobodchikoff and Wisman, 1981). When *O. plana* are dehydrated slowly under laboratory conditions, and then provided with free water, they will drink approximately 100 mg in a few minutes, restoring their body weight to its original value (Nicolson, 1980). The physiological control of drinking behaviour is complex and not necessarily the same in different insect species: so far, it has been examined only in acridids and flies. In *Locusta migratoria* a decrease in abdominal volume leads to a positive response to water, while a rapid drop in haemolymph osmotic concentration stops the drinking response (Bernays, 1977). Desert tenebrionids might be good material for this type of research.

The only quantitative estimate of the importance of drinking to Namib tenebrionids is that of Cooper (1982), who found that in active *O. unguicularis*, drinking represented 50% of water input.

The rich beetle fauna in the Namib dunes depends not only

on water in the form of advective fog, but also on food in the form of wind-blown plant detritus. Detritus is not a good source of pre-formed water for the beetles because, unlike those observed by Broza (1979) in Israel, they do not appear to take advantage of the hygroscopic absorption of water by detritus. Feeding occurs only during the diurnal surface activity period (Seely, 1979). For example, *Lepidochora* feed on detritus with a water content of about 2%. Instead of constructing sand trenches during fogs, they could be consuming detritus with a water content of 60% (Seely and Hamilton, 1976). There is apparently no quantitative information on the water intake of Namib tenebrionids during feeding. In contrast to herbivorous insects in other deserts and carnivorous arachnids, these essentially detritivorous beetles acquire little pre-formed water in their food, hence the relative importance of drinking in their overall water balance.

Metabolic or oxidation water may be an especially important component of water gain when no free water is available and the water content of the food is low, as in arthropods living in stored grain (Edney, 1977). It is also important during flight, but this is not applicable to the majority of desert insects. More detail is available for the mealworm *Tenebrio* than for its desert relatives. During 12 days of dehydration *O. plana* metabolized sufficient lipid to maintain a constant water content (Nicolson, 1980). In this species and in *O. unguicularis*, water produced by metabolism may account for a third to a half of that lost by transpiration (Nicolson, 1980; Cooper, 1982). Two recent measurements of metabolic rate in *Onymacris* (Bartholomew, Lighton and Louw, 1985; Louw, Nicolson and Seely, 1986) permit calculation of the extremes of metabolic water production in these beetles: these extend from 4.12 mg g⁻¹ h⁻¹ during fast running in *O. plana* down to 0.02 mg g⁻¹ h⁻¹ in resting *O. unguicularis*, a 200-fold range. Cooper (1982) calculated metabolic water production in free-ranging *O. unguicularis* to be 8.4 mg g⁻¹ day⁻¹ or 0.35 mg g⁻¹ h⁻¹, a value intermediate between these extremes.

An impression of the potential importance of metabolic water may be gained from dissecting larvae or adults of *Onymacris*. Both life stages are able to accumulate remarkable reserves of fat. The relationship between lipid reserves, water balance and reproduction certainly merits further study in the Namib beetles.

UPTAKE OF WATER VAPOUR

Another source of water for insects is the atmosphere. It is important to distinguish between passive and active absorption of water vapour. Passive vapour influx occurs in all insects in direct proportion to ambient humidity (Wharton, 1985). The net loss of water through the body surface is the difference between efflux and a sometimes substantial influx. The latter component of an insect's water balance has been much neglected, and no measurements exist for the Namib tenebrionids.

More is known about active absorption of water vapour, which occurs via specialized processes and is restricted to certain wingless arthropods (Edney, 1977). For desert forms, the adaptive significance of this ability is obvious, and the Namib tenebrionids have been the subject of quite extensive research in this area. Larvae of *Onymacris plana* and

O. marginipennis gain weight when exposed to relative humidities above 83% (Coutchie and Crowe, 1979a). Active water vapour uptake has been closely studied in the familiar mealworm *Tenebrio*, but *Onymacris* larvae have the experimental advantage of much larger size and have been a useful model for investigation of the mechanism of absorption (Coutchie and Crowe, 1979a; Machin, 1981; Coutchie and Machin, 1984). Uptake rates of *Onymacris* are over double those of *Tenebrio* in larvae of the same size at identical humidities.

Tenebrionid larvae possess a cryptonephric complex, in which the distal portions of the six Malpighian tubules form a sheath around the rectum. This complicated, concentrically arranged structure apparently evolved as a powerful mechanism for withdrawing water from the rectal contents (Ramsay, 1964), but is also used for the uptake of water vapour from unsaturated air. Space does not permit description of the process here: Wharton (1985) gives a concise summary. Whether water is being resorbed from faecal material or from air, the mechanism is solute-dependent, with a unidirectional gradient causing water movement from rectal lumen to tubule lumen. The driving force is the osmotic pressure generated by the Malpighian tubules, a biologically extraordinary 9 Osmol for *Onymacris* (Machin, 1981). This runs down to haemolymph levels (about 0.6 Osmol) at the time of moulting, so that the complex undergoes cycles of transport activity. The epithelial cells possess remarkable abilities in terms of volume regulation (Machin, 1981).

OSMOREGULATION

As Machin (1981) has observed, in larvae of tenebrionid beetles all the problems of water regulation come together: they can survive prolonged dehydration as well as rapid water vapour intake without exchanging solutes with their environments. (This also applies to the adults, except that water intake is in the form of fog moisture.) For the Namib tenebrionids, osmoregulation is unfortunately the only other aspect of water balance that has been examined in the larval stages. As a result of the thorough study of Coutchie and Crowe (1979b), *O. marginipennis* is probably the only insect surviving a wide range of water contents in which all major osmotically active solutes have been analysed (Machin, 1981). In these larvae, all the components of the haemolymph (roughly equal proportions of sodium, chloride, trehalose and amino acids) were found to participate in osmoregulation.

Adult *Onymacris* are also excellent osmoregulators. Twelve days of dehydration resulted in a 60% decline in haemolymph volume in *O. plana*, although the tissue water remained unchanged and the haemolymph osmolarity rose by only 14% (Nicolson, 1980). Regulation was equally good during rapid rehydration. From work on other Namib tenebrionids (Cooper, 1982; Hattingh, Ganhao and Naidu, 1984; Naidu and Hattingh, 1986), it seems that efficient osmoregulation is characteristic of at least the desert representatives of the family.

Even in the desiccation-resistant *Periplaneta*, in which ion regulation has been best studied, tissue water declines along with haemolymph water during dehydration (Hyatt and Marshall, 1985). *Onymacris* is thus an unusually good example of an insect's haemolymph acting as a water reservoir for its tissues, and the mechanism, as in cockroaches, appears to

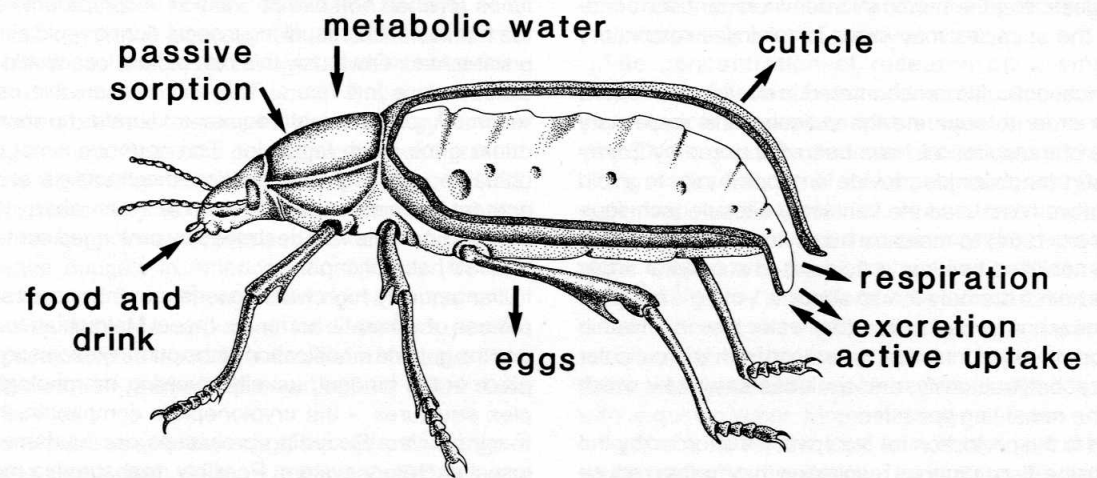


Fig. 1

Avenues of water gain and loss in a tenebrionid beetle. Beetle silhouette, showing the subelytral cavity, after Ahearn (1970)

involve reversible sequestration of ions in the fat body (Nicolson, 1980). Desert tenebrionids would be appropriate material for detailed study of the redistributions of solutes and water between different compartments of the body during water stress.

CUTICULAR WATER LOSS

Low rates of evaporative water loss are characteristic of desert arthropods (Cloudsley-Thompson, 1975). The first such study of the Namib tenebrionids was that of Edney (1971), who took advantage of the variety of species by comparing rates of water loss in beetles of different sizes. He found that their evaporative water loss was very low, that it was inversely proportional to body size, and that differences between the species correlated well with their behaviour and ecology.

Evaporative water loss in arthropods has traditionally been measured gravimetrically, on the assumption that weight loss represents water loss. However, during slow dehydration the loss of dry matter may be considerable in relation to water loss (e.g., Nicolson, 1980). Also, gravimetric methods measure only net flux and lead to difficulties in separating the cuticular and respiratory components of transpiration. We therefore developed an alternative technique using tritiated water and ventilated capsules, and applied it to *O. plana* (Nicolson, Louw and Edney, 1984). Water loss through the elytra, expressed in terms of surface area and vapour pressure difference, was 0.75 µg cm⁻² h⁻¹ mm Hg⁻¹. This is almost the lowest cuticular permeability ever reported for an insect, and is comparable to that of desert scorpions (Edney, 1977), which usually have the advantage of larger size.

Cuticular water loss of the Namib tenebrionids has also been examined from another perspective, emphasizing the surface waxes. The arthropod cuticle has been the subject of extensive research, and its impermeability is known to be due to lipids associated with the outer epicuticular layer. Hadley (1981) has

reviewed the waterproofing function of surface lipids in both plants and arthropods. Various studies on desert tenebrionid beetles have attempted to relate the quantity and chemistry of the epicuticular lipids to cuticular permeability: an example from the Namib Desert is the work of Hadley and Louw (1980) on *O. plana* and *Lepidochora discoidalis*. Lockey has examined the chemistry of the epicuticular lipids from another point of view, attempting to demonstrate taxonomic differences in tenebrionids from the Namib and elsewhere (e.g., Lockey, 1982). If such differences exist, the Namib is obviously a good place to look for them.

In addition to the normal epicuticular waxes, some insects extrude additional wax in a powdery or filamentous form, thus giving rise to 'wax blooms'. This ability is exceptionally well developed in the Namib tenebrionids (McClain, Seely, Hadley and Gray, 1985), including some species of *Onymacris* (Penrith, 1984), and is described in detail by McClain elsewhere in this volume. The significance for the water balance of these insects is that the wax blooms develop at low humidities and presumably increase the resistance to water vapour diffusion from the cuticle (Hadley, 1979).

RESPIRATORY WATER LOSS

A special feature of flightless tenebrionids of arid environments is the subelytral cavity, an air-filled space between the fused elytra and the abdomen (Fig. 1). Instead of opening directly to the exterior, the abdominal spiracles open into the subelytral cavity, and expired air leaves through a single aperture above the anus (Ahearn, 1970). Functions suggested for the subelytral cavity include reduction of respiratory water loss, thermal buffering, and providing space for water storage (Cloudsley-Thompson, 1975; Slobodchikoff and Wismann, 1981). Of course there is no reason why these possible functions should be mutually exclusive. Although experimental evidence is not yet available, the anatomy of the respiratory

system suggests that the humid microenvironment surrounding most of the spiracles may serve to minimize respiratory water loss.

The technical difficulties encountered in sealing an insect's spiracles, in order to separate the cuticular and respiratory components of transpiration, have been discussed by Edney (1977). Desert tenebrionids provide an opportunity to avoid this problem; we have used the ventilated capsule technique (Nicolson *et al.*, 1984) to measure subelytral water loss in *O. plana*. In immobilized beetles, cuticular and subelytral water losses were both extremely low at about $0.1 \text{ mg g}^{-1} \text{ h}^{-1}$. This is the only measurement of respiratory water loss in a Namib beetle. Unfortunately it includes water lost from the cuticular lining of the subelytral cavity, and excludes any water which may leave the remaining spiracles.

In addition to the protection for the spiracles afforded by the subelytral cavity, discontinuous respiration may further reduce respiratory water loss in tenebrionid beetles. With the development of sophisticated respirometry techniques, it has become apparent that discontinuous respiration is widespread among insects. Bartholomew *et al.* (1985) found oxygen consumption to be strongly cyclical in three Namib tenebrionids. The pattern persisted when the elytra were perforated, i.e., it depended on ventilatory movements and spiracular opening rather than on periodic opening of the subelytral cavity. The same authors found that intermittent respiration was still apparent when the beetles were running on a treadmill at 35°C . One of the species, *O. plana*, runs very rapidly in the field and its respiratory water loss could then be potentially serious.

Because many of the adult tenebrionids spend a considerable part of each day submerged beneath the sand, we examined patterns of gas exchange in *O. unguicularis* under such conditions (Louw *et al.*, 1986). We found an extremely low metabolic rate, and very long intervals (up to 60 min) between cyclical peaks of CO_2 release and O_2 uptake. Periodic CO_2 release as a mechanism for reducing respiratory water loss has been thoroughly investigated in two groups of insects: diapause pupae of large Lepidoptera (see Edney, 1977) and quiescent cockroaches (reviewed by Kestler, 1984). Kestler discusses physical principles in some detail, and has demonstrated the unexpected finding that ventilation is favourable for water retention, especially in small insects and at low metabolic rates. He stresses the importance of studying gas exchange and the associated water loss in undisturbed insects in their natural environment. By waiting until the insect closes its spiracles, it is even possible to separate cuticular and respiratory water losses under these conditions (Kestler, 1984). It is obvious that desert tenebrionid beetles are excellent material for further research in this still largely unexplored field, but accurate measurement of respiratory water loss during activity and at high body temperatures seems technically impossible at present.

EXCRETORY WATER LOSS

Water conservation would be expected to dominate the excretory physiology of the Namib tenebrionids. It was therefore surprising to find that the Malpighian tubules of *O. plana* were dramatically stimulated by a diuretic hormone (Nicolson and Hanrahan, 1986). Secretion rates of isolated tubules some-

times reached 100 nl min^{-1} , which is comparable to those of the tubules of bloodsucking insects during rapid elimination of a water load. Obviously this rate of fluid loss would dehydrate a beetle in a few hours. The only conceivable occasion on which *O. plana* might require a diuretic hormone is after drinking too much fog water. The hormone is not particularly unstable, although inactivation mechanisms are probably present for finer control: Nicolson and Hanrahan (1986) found that the hormone was destroyed by prolonged contact with the beetle's haemolymph.

Dangerously high water losses may not necessarily follow release of a diuretic hormone. Insect Malpighian tubules open into the gut and modification of the primary excretory fluid takes place in the hindgut, usually involving morphologically complex structures – the cryptonephric complex in the case of many beetles. Recycling processes are fundamental to the insect excretory system. Possibly, reabsorptive mechanisms in the cryptonephric complex of *Onymacris* are able to recover all the water produced during 'diuresis'. Also, since potassium concentrations are very high in the tubule fluid (Nicolson and Hanrahan, 1986), the cryptonephric complex may function in retention of this ion. Until further information is available, the excretory system of *O. plana* seems to be equipped with two conflicting adaptations: a potent diuretic hormone and a cryptonephric complex.

This research on the Malpighian tubules of *O. plana* (Nicolson and Hanrahan, 1986) was initiated because of the complete lack of physiological studies on beetle Malpighian tubules. However, because of their large size and pronounced secretory and electrical responses to stimulation, we have found them to be ideal experimental material for a detailed electrophysiological study of the mechanism and control of fluid secretion (Nicolson and Isaacson, 1987; Isaacson, Nicolson and Fisher, 1989). The Malpighian tubules of *O. plana* have also been the subject of a complementary ultrastructural study (Hanrahan and Nicolson, 1987), and have recently been used to demonstrate that the technique commonly used to measure transtubular potentials in insect epithelia is not valid (Isaacson and Nicolson, 1989). These studies, however, are too specialized for description in this review.

The functioning of the cryptonephric complex was briefly mentioned in the section above on water vapour uptake. From work on *Tenebrio* and its desert relatives, it has been assumed that this structure is an adaptation for producing dry faeces, and that it is secondarily used for atmospheric water uptake in larvae only. There have been no measurements of their faecal water loss, but in adult *Onymacris* faecal water loss is apparently only a small proportion (11–14 %) of total water loss (Nicolson, 1980; Cooper, 1982).

CONCLUSION

In her recent review of the environmental physiology of insects and its relationship to microclimate, Willmer (1982) has said that 'some of the most elegant and comprehensive studies ... have concerned the lives of beetles, particularly the desert tenebrionids and their strategies for maintaining a favourable hygrothermal state'. This remark is borne out by the research I have described. There are, however, deficiencies which need to be remedied by future investigations.

First, it is much easier to work on isolated aspects of an insect's physiology in the laboratory, than to attempt to integrate all the avenues of water exchange between a free-living organism and its environment (Edney, 1977). Labelled water has now made it possible to study water and energy turnover in free-living animals. So far the only application of this methodology to Namib beetles has been the study of Cooper (1982) on *O. unguicularis*. The field situation is complex and also constantly changing: for example, a more detailed study on seasonal water budgets in American tenebrionids (Cooper, 1985) demonstrated that, although the largest component of water loss was always evaporative, food, drink or passive vapour sorption could be the main avenue of water gain. More thorough studies along these lines would be very welcome for the Namib beetles.

Second, there are several aspects of the water exchange of desert beetles about which we know nothing at all. One is egg production, which probably represents a considerable water loss to the female. The egg itself must be very vulnerable to water stress, and in fact we have no information about the water relations of the eggs and pupae of these holometabolous insects, and only patchy information on their relatively inconspicuous larvae. As far as acquiring water is concerned, passive sorption of water vapour may be a significant avenue of water gain, because submerged beetles are surrounded by

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a boundary layer of still air and probably increased humidity, thus increasing rates of passive influx.

The concentration of research on a single genus, *Onymacris*, has led to a fundamental understanding of the physiological adaptations that are central to its water economy. On the gain side, the important features are rapid drinking of fog water, the use of metabolic water, and the uptake of water vapour. Tolerance of water stress involves efficient osmoregulation in which the haemolymph serves as a water store. Losses are minimized by a low cuticular permeability supplemented by waxy blooms, by the combined effects of the subelytral cavity, intermittent respiration and a low metabolic rate, and by the cryptonephric complex. It is apparent that these adaptations are concerned more with conserving than with acquiring water. Moreover, none of these adaptations is unique; it is rather the total assemblage and their efficiency which matter to this insect. The obvious discrepancy is the possession of a diuretic hormone, and of course fast running and a preference for high body temperatures are not conducive to water conservation. Flightlessness is of great significance here: overheating and desiccation are potentially serious disadvantages of flight in desert insects (Heinrich, 1975). Avoidance of the same problems by retreating to the sub-surface thermal refuge in the middle of the day also contributes to the conspicuous success of the Namib tenebrionids.

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Fever in Namib and Other Ectotherms

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We examine the role of fever in the context of the evolutionary implications of host-pathogen interactions. Some ectotherms elevate their body temperatures behaviourally, following administration of pathogenic bacteria or other potential pyrogens. In a few species, the elevated temperature has been demonstrated to have positive survival value for the host. Representatives of all classes of vertebrate ectotherm have been reported to develop fever, as have representatives of the Arthropoda and Annelida, but not the Mollusca. We do not think that fever is ubiquitous amongst vertebrate ectotherms, however; we have not been able to obtain fever in seven African reptile species we have tested.

Studies of reactions of Namib ectotherms to potential pyrogens are important for several reasons. One is that some Namib species have selected body temperatures in the mammalian range, higher than most ectothermic species. Another is that the Namib Desert provides a suitable environment for studying endemic ectotherms in their natural habitat. The tenebrionid beetle *Onymacris plana* selected warmer than normal substrate temperatures, in a thermal gradient chamber, following administration of large doses of the endotoxin of gram-negative bacteria. However, the endemic lizard species *Aporosaura anchietae* and *Angolosaurus skoogi* showed no thermoregulatory responses to potential pyrogens. Future studies on the survival value of fever should include analysis of non-thermal as well as the traditional thermal components, which may have evolved separately. Also, studies are required of naturally-infected animals in their natural habitats.

FEVER AND EVOLUTION

Fever is a complex biological response of a host animal subjected to pathological insults, including infection, inflammation, tissue necrosis, antibody-antigen reactions and malignancy (Hellon, Townsend, Laburn and Mitchell, 1990). In addition to the characteristic rise in body temperature, the febrile response, at least in mammals, has several characteristic biochemical features: release of acute-phase proteins (e.g., C-reactive protein and fibrinogen), activation of lymphocytes and macrophages, and changes in serum metallic ion concentrations (decrease of iron and zinc, increase of copper) (Dinarelo, Cannon and Wolff, 1988). Fever is also associated with gross behavioural changes, for example somnolence in several mammals, and both somnolence and malaise in humans (Feldberg, 1975).

Fever is a metabolically costly phenomenon; for each degree Celsius rise in body temperature, energy requirements increase by 10 % or more (Kluger, 1986). Fever also suppresses appetite, so compensatory increases in food intake usually do not occur, and febrile animals enter negative nitrogen balance and tend to lose mass.

The biochemical and physiological features of the host response that occurs during fever are largely independent of the cause of the fever. For example, the same pattern of events occurs whether the host is responding to gram-negative infection, viral infection, protozoal infection, crush injury or incompatible blood transfusion. The similarity of features arises primarily because most, if not all, of the host defence reactions

have a common biochemical mediator, namely endogenous pyrogen (EP). EP is a hormone-like polypeptide, or family of polypeptides, released by macrophages, and other cells of the host, in response to any one of a variety of pathological stimuli. Four EPs have been identified, namely interleukin 1 (IL 1) and interleukin 6 (IL 6), tumour necrosis factor and interferon (Hellon *et al.*, 1990); they have little or no amino acid homology, but remarkably similar biochemical action (Dinarelo *et al.*, 1988).

From the neo-Darwinian point of view, it would be anomalous for a biological phenomenon to exist, which is metabolically costly and which has similar biochemical and physiological features irrespective of the stimulus and host species, unless the phenomenon has survival value for the host. Indeed, such philosophical arguments in favour of a survival value for fever have been expressed for at least 2000 years (Kluger, 1981). However, it has proved surprisingly difficult either to show quantitatively that fever indeed favours the host's survival, or to identify components of the febrile response beneficial to the host (Ewald, 1980). Only recently has it become clear that the release of EP contributes to the host's survival in infection, and in other conditions like malignancy (Dinarelo, Conti and Mier, 1986; Duff, 1986). What is still not established satisfactorily is whether pyrexia, the high body temperature characteristic of fever, *per se* has any survival value for the host (Banet, 1983; Kluger, 1986; Blatteis, 1986; Banet, 1986; Hellon *et al.*, 1990).

Pyrexia in endotherms is very different from other forms of hyperthermia (Stitt, 1979; Mitchell and Laburn, 1985). In



Dr Charles Koch, founder of the research station at Gobabeb, and first Director of the Desert Ecological Research Unit, examines one of his Namib pit-traps.

(Photo: Dr L. Prozesky-Schulze)

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