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 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 low-ranking females. I am currently investigating this hypothesis.

ACKNOWLEDGEMENTS

I am grateful to Dr Mary Seely, Mr Eckart Pfeffer and the staff of the Desert Ecological Research Unit of Namibia for their encouragement and logistical support; to Mrs Linda Malen, Dr Gin Watson, and Mrs Theresa Bolton for their help in preparing the manuscript; Prof. W. J. Hamilton III and Prof. D. Mitchell for their advice and the Department of Nature Conservation, especially Dr Eugene Joubert, for permission to work in the Namib Naukluft Park. My parents enormous support helped make the study possible and for this I am most grateful.

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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, Ochymas. 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 Ochymas species are efficient stomatoglyphs when water-stressed. Adaptations to maximize water loss via cuticular and respiratory and excretory routes are well developed, although the function of the diuretic hormone in this genus is not clear. The most remarkable example is the ability to recombine the combination of water from fog and deep rainwater.

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

INTRODUCTION

Much of the research carried out on the tenebrionid beetles of the Namib Desert has focused, 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, Ochymas of the tribe Aedimembra (Porntree, 1984). The 14 species are all psammophiles and form a conspicuous element of the dune fauna. They are flightless, long-lived, fast-moving diurnal beetles that have a long lifespan and might 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 (Eldredge, 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 by 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 (Eldredge, 1977). This is not a consequence of living in a desert, but is due to the relatively heavy insect 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 basing in Ochymas uncinctus (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 is substantial; for example, up to 34 % of pre-fog weight in O. uncinctus (Hamilton and Seely, 1976). The subcuticular cilia of these flightless tenebrionids permits body expansion after imbibition of large quantities of water at irregular intervals (Stobodnikbok and Wissman, 1981). When O. plana are dehydrated slowly under laboratory conditions, and then provided with free water, they 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 aphids 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. uncinctus, drinking represented 50 % of water intake.

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 protein-rich water because it is often less nutritious than water 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 as they feed, they consume detritus with the water contents of 6% (Seely and Hamilton, 1978). There is apparently no quantitative information on the water intake of Namib tenebrionids during feeding. In contrast to herbivorous insects in other deserts and arid 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 insect species. More detail is available for the mealworm Tenebrio than for other desert larvae. 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, which are produced by metabolism may account for a third to a half of that lost by transpiration (Nicolson, 1980; Cooper, 1982). Two recent measurements confirm that O. unguicularis from 4.12 mg g⁻¹ h⁻¹ during fasting run 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 these estimates to be 0.84 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 Ommatius. 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 vapour through body surfaces is a 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 tenebrionid. 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 Ommatius plana and O. marginipennis gain weight when exposed to relative humidities above 83% (Coutchle and Crowe, 1979a). Active water vapour uptake has been closely studied in the familiar mealworm Tenebrio, but Ommatius larvae have the experimental advantage of much larger size and have been a useful model for investigation of the mechanism of absorption (Coutchle and Crowe, 1979a; Machin, 1981; Coutchle and Machin, 1984). Uptake rates of Ommatius are over double those of Tenebrio in larvae of the same size at identical humidities. Tenebrionid larvae possess a crenulated complex, in which the distal portions of the six Malpighian tubules form a sheath around the rectum. This complicated, crenulated surface is arranged in such a way that the driving force for water movement from the rectal contents (Ramsay, 1984), but it 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 biological osmometer 9 Osmol for Ommatius (Machin, 1981). This runs down to haemolymph levels (about 0.6 Osmol) at the time of moulting, so that the complex undergoes seasonal 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 in the same exchange ratio. This also applies to the adults, except that water intake is in the form of fog moisture. For the Namib tenebrionid, 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 Coutchle and Crowe (1979b), O. marginipennis is probably the only insect surviving a wider 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 Ommatius are also excellent osmoregulators. Twelve days of dehydration resulted in a 60% decline in a haemolymph volume in O. plana, although the tissue water remained unchanged and the haemolymph osmolality rose by only 14% (Nicolson, 1980). This was achieved by rapid dehydration. From work on other Namib tenebrionids (Cooper, 1982; Hattingh, Ganho and Naidu, 1984; Naidu and Hattingh, 1986), it seems that efficient crenulation is characteristic of at least the desert representatives of the family. Even in the destituation-resistant Peripalinae, in which ion regulation has been studied most, tissue water declines along with haemolymph water during dehydration (Hyatt and Marshall, 1985). Ommatius 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 involve reversible sequestration of ions in the fat body (Nicolson, 1980). Desert tenebrionids would be an 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 (Cloudley-Thompson, 1970). 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 titrated 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 waves. 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 tenebrionids 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. Loukky 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, 1962). 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 flamentous 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 Ommatius (Perrin, 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 closed 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 at the tip of the subelytral cavity (Ahearn, 1970). Functions suggested for the subelytral cavity include reduction of respiratory water loss, thermal buffering, and providing space for water storage (Cloudley-Thompson, 1975; Slobodnikoff and Wissmann, 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 respirator
system suggests that the humid microenvironment surround-
ing most of the spores 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 centipedes appear to avoid this problem; we have used the ventilated capsule technique (Nicolson et al., 1984) to measure subterral water loss in O. plana. In immobilized beetles, cuticular and subterral water losses were both extremely low at about 0.1 mg 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 subterral cavity, and excludes any water which may leave the remaining spiracles.

In addition to the pressure for the spiracles afforded by the subterral cavity, discontinuous respiration may further reduce respiratory water loss in terenbinth beetles. With the develop-
ment of sophisticated respiration techniques, it has be-
come apparent that discontinuous respiration is widespread among insects. Bartholomew et al. (1985) found oxygen con-
sumption to be strongly cyclical in three Namib centipedes. The pattern persisted when the elytra were perfused, i.e., it depended on ventilatory movements and spiracular opening rather than on periodic opening of the subterral cavity. The same authors found that intermittent respiration was still ap-
parent when the beetles were running on a treadmill at 35 °C. One of the planarians rarely cyclically gasped, and its respiratory water loss could then be potentially serious.

Because many of the adult terenbinth species spend a consider-
able amount of time on the sand, we examined patterns of gas exchange in O. uroglaucus under such conditions (Louw et al., 1986). We found an extremely low metabolic rate, and very long inactivity periods of up to 60 min between cyclical peaks of CO₂ release and O₂ uptake. Periodic CO₂ release as a mechanism for reducing respiratory water loss may be a feature of two groups of insects: diapause pupae of large Lepidoptera (see Edney, 1977) and quiescent cockroaches (reviewed by Kestler, 1984). Kestler discussed physiological properties of some insects, and his review demonstrates the range of finding that ventilation is favor-
able 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 possible to separate cuticular and respiratory water losses, as we have done under these conditions (Kestler, 1984). It is obvious that desert terenbinth beetles are excel-
lent material for further research in this still largely unexplored field, but more measurement of respiratory water loss during activity and at high body temperatures seems techni-
cally impossible at present.

EXCRETORY WATER LOSS

Water conservation would be expected to enhance the excre-
tory physiology of the Namib terenbinth. It was therefore suprising to find that the Malagbibian tubules of O. plana were dramatically stimulated by a diuretic hormone (Nicolson and Harrana, 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 body water. This would reflect the existence of a free-living anatrophous organism and its environment (Edney, 1977). Labelled water has now made it possible to study water and energy turnover in O. plana females. The only application of this technique has been to O. uroglaucus (Nicolson, 1986). The field situation is complex and also constantly changing; for example, a more detailed study on seasonal water budgets in American terenbinth (Cooper, 1985) demonstrated that, although the largest component of water loss was always evaporative, food, drink or passive variation in the environment. 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 condu-
ctive to water conservation. Flightiness is of great signifi-
cance here: overheating and desiccation are potentially seri-
ous disadvantages of flight in desert insects (Hennig, 1975). Avoidance of the same problems by retiring to the sub-
face thermal refuge in the middle of the day also contributes to the conspicuous success of the Namib terenbinth.

ACKNOWLEDGEMENTS

This owes much to Gideon Louw's enthusiasm for the Namib Desert and for physiology. Financial support was

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Fever 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 poisons. In a few species, the elevated temperature has been demonstrated to have positive survival value for the host. Representatives of a group of vertebrate ectotherms have been reported to develop fever, as have representatives of the Anopheles and Aedes genera, but not the Mosquito. We do not think that fever is naturally advantageous to vertebrate ectotherms; however, we have not been able to obtain fever in seven African reptile species we have tested.

Studies of reactions of Namb ectotherms to potential poisons are important for several reasons. One is that some Namb species have selected body temperatures in the mammalian range, higher than most ectothermic species. Another is that the Namb Desert provides a suitable environment for studying endemic ectotherms in their natural habitat. The tenebroid beetle Onymacris plana selected warmer than normal subadult temperatures, in a thermal gradient chamber, following administration of large doses of the endotoxin of gram-negative bacteria. However, the endemic lizard species Agama agama and Angolohyrax skocgi showed no thermoregulatory responses to potential poisons. 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 (Helton, 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) (Dinarello, Camenisch and Wolf, 1988). Fever is also associated with gross behavioural changes, for example somnolence in several mammals, and both somnolence and malaise in humans (Rife, 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 incom-
Namib Ecology
25 Years of Namib Research

Edited by

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December 1990 Desember
Transvaal Museum Monograph No. 7
Transvaal Museum Monografie Nr. 7
Transvaal Museum, Pretoria