

Water balance in insects of the Namib Desert

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One of the reasons why insects as a group are so biologically successful is that they possess highly efficient mechanisms for maintaining water balance, often in very dry surroundings. Deserts provide very good material for the study of these mechanisms, because the extremely hot, dry conditions that occur there have led to a maximum expression of the adaptations concerned. In South West Africa (Namibia) the geologically old Namib Desert contains a rich fauna of tenebrionid beetles, the various species of which are specialised in different ways to live in the different biological niches that the desert affords. During the past decade or so, interest in these problems has been developing, and the facilities for field study afforded by the Namib Desert Research Station at Gobabeb<sup>1</sup> have attracted several insect biologists to work in the area. I have visited Gobabeb several times, and with the valuable cooperation of Mr. Erik Holm, Professor Gideon Louw, and Dr. Mary Seely (the present Director of the Station) I have worked on some of the numerous problems that call for investigation. The National Geographic Society kindly supported my visit in November and December 1973 - the subject of this report.

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<sup>1</sup> Founded by the late Dr. C. Koch, whose studies on the taxonomy of African tenebrionids is basic to all the subsequent ecological and physiological work on the group.

The beetle fauna can be divided into three ecologically more or less distinct groups: those in the 'stony' desert to the north-east of the (usually dry) Kuiseb River bed, those in the river bed and the bordering vegetation, and those in the vast, virtually plant-free sand dune country between the river and the coast, some forty miles distant. The fauna in the dunes is nourished largely by plant detritus which is blown into the area, sometimes from great distances. Food is important to these beetles not only for energy and nourishment but also for the free water that it contains (albeit in small quantities), and as a source of metabolic water which results when even completely dry food is oxidised in the body.

Holm and Edney (1972) observed that the behavior of the sand dune species is such that each takes advantage of the food resource in its own way. Activity patterns (though annual as well as daily cycles) are distinct - different species using different times of the day and of the year to forage, the patterns varying seasonally. Thus a diurnal species such as Onymacris plana shows a bimodal daily activity pattern in the summer, but this becomes unimodal in the winter as mid-day temperatures become less extreme. Furthermore, the activity patterns correspond well with physiological attributes of the species concerned - thus species with higher cuticular water loss rates are active only by night (e.g., the species of Lepidochora). In this connection, Seely and Hamilton (1976a) have recently shown that Lepidochora spp. drink the water that condenses from advective fog on small sand ridges built by the beetles themselves. Onymacris unguicularis on the other hand, although normally diurnal, may emerge

at night when fog is present, and drink the water that is formed by condensation on their bodies (Hamilton and Seely 1976b). In 1973, Mary Seely and I extended my earlier work to a study of the biology of Onymacris plana, and a common riverine species, Onymacris rugatipennis. O. plana lives in the dunes, but is usually associated with clumps of the cucurbitaceous plant Acanthosicyos horrida, (whose vernacular name is 'nara') and we were interested in finding its food preferences. By labelling various possible food materials with radioactive  $^{32}\text{P}$ , we found that plana always prefers fresh flower buds to other parts of the plant or to nara detritus (although it will eat the latter). In our experiments the beetles did not feed on wind blown fibrous grass detritus when this was offered although it was common in the area. Fresh flower buds contain about 83% water, while dry buds as detritus contain only 5%. Adult O. plana beetles lose about 10 mg per gram per day by transpiration (measured in dry air at  $27^{\circ}\text{C}$  - unfortunately we do not have data for such loss in natural conditions) and calculations based on reasonable assumptions for fecal water loss and metabolic water show that a 1 gram beetle would have to eat only about 12 mg of nara buds per day to remain in water balance. Beetles were allowed to feed on radioactive buds for 48 hours and then counted for radioactivity (in whole body Anton counters). These counts indicated a mean ingestion of

96.85 mg per gram of beetle, but the actual amounts were certainly larger than this because of the quenching effect of the beetles' bodies, and of loss by defecation. Thus for these desert sand dune beetles, water balance is readily maintained provided Acanthosicyos

is available.

Earlier work (Holm and Edney, 1973) had determined the temperatures and humidities to which certain sand dune species are exposed both at and below the surface during a 24 hour cycle in the summer. In 1973 I extended these observations by measuring conditions in the habitat of O. plana (a large, nara-topped sand hillock). As might be expected, both temperature and humidity 30 cm below the surface were relatively equable, even though surface temperatures rose to 41° C and humidities fell to below 10%. These beetles therefore have a comfortable retreat in which they may avoid the harsh ambient conditions.

During my 1973 visit, Mary Seely and I also obtained information about the feeding habits of the common riverine species, Onymacris rugatipennis. First we measured the water content of various available food materials. This was about 61.7% (S.D. 3.26%) for detritus (mostly flowers) of Acacia albida collected at 11:15 a.m., and about 3.5% higher for the same material collected early in the morning at 6:30 a.m. Detritus collected at 5:00 p.m. and left overnight in 100% relative humidity gained 16.9% by absorbing water. Fresh Nicotiana leaves had a water content of about 88%, and radioactive labelling showed that beetles preferred this food over other offerings, although they fed quite readily on Acacia giraffae and Euclea flower and fruit detritus.

I had already observed the activity patterns, water loss rates, and body temperature relationships of this species, and in 1973 we recorded the distribution of detritus feeding activity during a

24 hour cycle. Such information may be important because, as we had found, in nature the moisture content of the detritus changes with immediate climatic conditions. The feeding distribution was measured by labelling artificial food (we used corn flakes) with  $^{32}\text{P}$  and offering it to successive groups of 4, 5 or 6 beetles, at each hour from 6:00 a.m. to 6:00 p.m. (We knew that the beetles are inactive at night.) Each group was allowed to feed for 2 hours, after which individuals were counted for radioactivity. Numbers were small and variances large, but there was a significant trend: feeding increased from a low in the 6:00 a.m. group to a maximum during the two hours after noon, and fell again to a low in the 6:00 p.m. group. This feeding pattern would not seem to be optimal for water uptake, having regard to observed changes in water content, but our work was done in the laboratory, and further observations in nature, and at other times of the year, are necessary.

Finally we wanted to know whether beetles take more food either when it is moist rather than dry, or when the beetles themselves are dehydrated rather than in good water balance. For these experiments we used rugatipennis and the artificial food (corn flakes) labelled with  $^{32}\text{P}$ . The answers were quite clear: the beetles always took more moist than dry food, irrespective of whether they themselves were fasted or were short of water. Such behavior could be advantageous if the amount of water present in dry food is less than the water content of the feces produced. This has been shown by Loveridge (1974) to be true for desert locusts, but we do not yet have sufficient information for a conclusion in the case of O. rugatipennis.

Conclusion

This research answered a few questions and uncovered several others, and the results will be incorporated in a book to be published shortly (Edney, in press). We now know a little more about the water problems of desert insects and the adaptations by which they are solved. From this and other work the overall impression that emerges is one of a multiplicity of solutions to the same general problem (how to remain in water balance in a hot dry desert). Differences in size, color, micro-habitat, behavior and physiological attributes combine to determine the particular strategy adopted by each species. In all probability adaptations in reproductive mechanisms also play an important part, but of these little or nothing is yet known.

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