Physiological Studies on the Namib Fauna: A Brief Critique

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The general status of physiology is examined in a modern zoological context to provide a background for critically reviewing physiological studies on the Namib fauna. The review highlights several excellent studies but concludes that many physiological studies on the Namib fauna have been too fragmentary. The necessity for sound natural history research and ecophysiological studies in the future is emphasized. The excellent research opportunities that exist in plant physiology, nitrogen cycling and the testing of various physiological hypotheses are also reviewed under the general title of recommended future research.

THE STATUS OF PHYSIOLOGY

While not wishing to encumber the start of this paper with a pointless semantic argument, it may nevertheless be useful to first reflect on what we mean by some very familiar terms such as physiology, environmental physiology, comparative physiology and physiological ecology, also known as ecophysiology. The zoology student in the period between the Great Wars still received a classic training in systematics and comparative anatomy. The study of the functions of animal organs, tissues and cells (physiology) was very much in its infancy and mostly confined to medical schools. This situation changed markedly after World War II, when the few pre-war schools of comparative physiology began to thrive and extend their influences across North America and Europe. Comparative physiology became the fashionable discipline within zoology and attracted imaginative and gifted students who were also well versed in another burgeoning sister discipline, namely biochemistry.

Comparative physiology at this time was meant to complement comparative anatomy and provide the golden thread to explain evolution in terms of chemistry and physics. Now, some forty years later, this discipline is being criticized. It is maintained, for example, that comparative physiology has merely assembled an encyclopaedia of facts and has contributed minimally to the important principles of zoology, particularly those involved in evolutionary theory. It is also true that the number of students now attracted to post-graduate study in this field is declining, whereas those attracted to ecology, behavioural ecology, conservation biology, evolutionary biology and biotechnology are increasing rapidly. Is this modern criticism of comparative physiology justified? Yes, in many instances it is valid: many of us are guilty of concentrating on snippets of biological understanding with insufficient academic or practical relevance. On the other hand, many examples can be gleaned from the comparative physiology literature which are of great fundamental significance and which have contributed to the grand intellectual sweep of evolutionary theory, a criterion which appears to have become a *sine qua non* in so many modern zoological circles (Feder, Bennet, Burggren and Huey, 1987). One need only mention the work on the evolution of endothermy or on comparative mechanisms of osmoregulation and obligatory nitrogen excretion, so ably described in *From Fish to Philosopher* by Homer Smith. More recently, the discovery of molecular clocks, the explanation of the molecular evolution of brain hormones, and many other examples can be used to soften these criticisms of comparative physiology. It has also been argued that the advent of environmental physiology has made comparative physiology more relevant and meaningful to zoology. This is, however, seldom the case as environmental physiology, strictly speaking, merely explains the effect of environmental influences on the physiological responses of an organism. In contrast, ecophysiology explores the physiological interaction between an organism (species) and its environment, with the specific goal of using this information to explain the distribution and abundance of the particular species, thereby moving much closer towards ecology and evolutionary biology. Using this background let us now critically examine some of the physiological studies carried out on the Namib fauna during the past two decades. How can they be classified and how do they rate against these criteria? No attempt will be made to review all the literature.

NAMIB STUDIES

Probably the first serious physiological study carried out on the Namib fauna was by Eric Edney (1971), who clearly showed that various species of Namib Tenebrionidae were highly tolerant to desiccation. This study provided a pattern for the rather biased approach of subsequent physiological studies. The investigator, faced with a quintessential desert of endless sand dunes, barren gravel plains, overwhelming sunshine and almost no rain, firmly believed that all Namib animals were physiologically magically different to other animals and set out to prove it. In this way, another early study examined the physiological and behavioural ecology of the sand-diving lizard *Aporosaura anchietae* (Louw and Holm, 1972); we were able to show that this species was partially herbivorous, that it engaged in a thermoregulatory dance upon the dune slipface to extend its surface activity and, most significant of all, that it stored large amounts of fog water in its digestive tract. The study was biased towards the concept of desert animals being

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entirely different, and misconstrued the colon as the water-storing organ. In fact, a delicate abdominal bladder serves this function. Nevertheless, it explained the restricted distribution of this species to aeolian sand and its occurrence in the fog belt of the Namib Desert, thereby qualifying as ecophysiology. In fact, most of the physiological studies on the Namib fauna have qualified as ecophysiology or at least environmental physiology. Nevertheless, certain Namib species have also proved to be ideal subjects for pure electrophysiological research on the membranes of Malpighian tubules (e.g., Nicolson and Isaacson, 1987), but only ecologically orientated studies will be considered here.

The Namib tenebrionid beetles have been the subjects of most of the physiological studies carried out on the Namib fauna and they have provided a wealth of useful knowledge, particularly with regard to respiration, water balance and the chemistry of the cuticle. It is also noteworthy that, without any preconceived research plan, the various studies on these beetles fit spontaneously into a surprisingly logical sequence: we have gained a good understanding of their nutrition (Hanrahan and Seely, this volume), osmoregulation (Coutchie and Crowe, 1979*b*; Nicolson, 1980), water collection (Seely and Hamilton, 1976; Hamilton and Seely, 1976; Coutchie and Crowe, 1979*a*), reproduction (De Villiers, 1985), respiration (Bartholomew, Lighton and Louw, 1985; Louw, Nicolson and Seely, 1986), temperature regulation (Seely, Roberts and Mitchell, 1988) and waterproofing of the cuticle (McClain, Seely, Hadley and Gray, 1985). Some of these studies could be criticized as being too fragmentary by the 'high priests' of ecological and evolutionary theory, but taking them as a whole we can now piece together the ecophysiology of several tenebrionid species, thereby contributing to a more complete picture of the ecology of the Namib. Moreover, several of the papers, for example the brilliant field observations by Hamilton and Seely (1976) on fog basking and the elegant studies by Coutchie and Crowe (1979*a*) on the uptake of water vapour by *Onymacris* larvae, are outstanding in their own right. The logical way in which these papers fit together also warrants comment. For example, Nicolson's (1980) simple but well executed laboratory experiments on osmoregulation in *Onymacris plana* showed clearly that this species loses water, albeit slowly, at high vapour pressure deficits while osmoregulating efficiently. A suite of adaptations is therefore present in these animals to minimize water loss, such as waxy blooms, sunken spiracles, intermittent respiration and low metabolic rates. Because these are not sufficient to maintain a positive balance, water collection is consequently maximized by some form of fog imbibition. The larvae that do not normally appear on the surface and are not able to use fog water directly, have the remarkable ability to absorb water vapour from unsaturated air via the rectum (Coutchie and Crowe, 1979*a*).

The purist may object to my inclusion of Seely and Hamilton's (1976) and Hamilton and Seely's (1976) observations on trench building and fog basking by tenebrionid beetles, because they are behavioural and not physiological phenomena. A response to this criticism is required because, in my opinion, too many authors dwell too heavily on the relative importance of behavioural versus physiological adaptations in the desert and other extreme environments. In higher vertebrates we used to make a convenient distinction between behaviour and physiology by referring to the brain centres involved. If the higher cortical centres were involved, the response of the animal was described as behavioural, whereas a lower centre response was designated as physiological. If we now consider the relative simplicity of the cerebral ganglia of insects, this approach cannot be used, yet the osmoregulatory behaviour in insects and reptiles is frequently classed as physiological whereas courtship responses are considered behavioural. While I shall concede that a distinction can be made between extreme differences, particularly among higher vertebrates, the arguments and debates on the relative importance of these phenomena are largely semantic and not very productive. Both physiology and behaviour ultimately become the physics and chemistry of cells.

While the tenebrionid studies combine to make a unifying theme, physiological studies on other species have been more sporadic. Marsh (1986) and Curtis (1985) have shown the importance of social insects in the general ecology of the Namib and how well they are adapted physiologically to survival in the desert environment. Marsh's (1985) demonstration of how the heat-running ant *Ocymyrmex barbiger* uses its high surface area to volume ratio to off-load heat while resting in a thermal refuge is an excellent example of how careful field studies can sometimes provide critical information for unravelling the life history of a species (see also Marsh in this volume).

Studies on small mammals have followed the usual pattern by demonstrating the extremely high urine concentrating ability of their kidneys (Louw, 1972; Withers, Louw and Henschel, 1980). The latter study showed that water was so efficiently used by some of these small Namib mammals that the ratio of their daily energy expenditure to their daily water turnover rate actually approached the theoretical stoichiometric minimum values, calculated from the complete oxidation of protein, fats and carbohydrates. These studies have been complemented by Buffenstein, Campbell and Jarvis (1985) who showed that cricetid rodents excrete large amounts of allantoin as a nitrogenous end-product in the urine. While these small mammal studies have undoubtedly contributed to our knowledge, they were mostly short-term studies. What needs to be done in the future is to tackle a long-term field study, backed up by excellent laboratory facilities, to unravel the whole life history of a species through a study of its physiological ecology. Alternatively, a very thorough laboratory study in a carefully controlled environment of a complete water balance in the mould of Schmidt-Nielsen's (1964) much quoted study on the kangaroo rat should be rewarding.

Physiological research on large animals in the Namib has been conspicuous by its virtual absence. The logistics for carrying out this research have been very difficult to arrange and these factors, combined with the wealth of opportunities for studying smaller animals, have brought about this situation. Nevertheless, the behavioural studies on baboons by Hamilton (1986) contain a great deal of useful information on their nutrition and water use in the Kuiseb River bed during severe drought conditions, and make fascinating reading. Also, studies by Louw, Belonje and Coetzee (1969) on the ostrich, although performed outside the Namib, have explained how these animals reduce water loss by efficient kidney function and very refined use of feather erection and body orientation to maximize convective and radiant cooling. A second study on the ostrich by Withers, Siegfried and Louw (1981) provided convincing evidence that, under conditions of rest while not engaged in thermal panting, ostriches exhaled air that was not saturated with water vapour, thereby effecting very significant water savings. A similar phenomenon has been described in the camel by Shkolnik, Schroter and Schmidt-Nielsen (1980) and it remains to be seen how widespread this phenomenon is in large birds and ungulates. The springbok and the gemsbok are the most common large ungulates of the Namib Desert, yet we know very little about their ecophysiology. In the case of the gemsbok we still rely on Taylor's (1969) early studies in Kenya which suggested that the animals exhibit an extreme form of adaptive hyperthermia when dehydrated. These conclusions require verification in the field. In the case of the springbok, apart from the studies of Skinner, Dott, van Aarde, Davies and Conroy, (1987), the only desert-orientated study is that of Hofmeyer and Louw (1987). The latter study raises some intriguing questions about how the springbok can survive the temperature extremes of the desert with its relatively small body mass and very thin pelage, but it does not answer the crucial question of how the animals can survive without access to drinking water. In general then, these few studies have mostly been incomplete. They have, however, shown that interesting questions exist and that ecophysiological studies on these large species, as well as on some of our 'indigenous' sheep and goat breeds, in the mould of Shkolnik's research should prove very rewarding.

This brief review has revealed that many of the physiological studies have been worthwhile and that they have mostly been biased towards the genre of ecophysiology. In view of the unique environmental influences operating in the Namib, this trend should be encouraged. They have also been useful in supporting other studies and providing a more complete picture of this very well-studied area of our planet. Most of the physiological studies have set out to test hypotheses even if the hypotheses were simple, thereby avoiding being branded as 'only' a series of descriptive studies. The latter criticism should not be taken too seriously as there are still opportunities for well-planned descriptive studies in the Namib. Every effort should, however, still be made in the ecophysiological sphere, not only to ask clear-cut questions and test hypotheses, but to test *important* hypotheses which are relevant either academically or in a practical goal-directed fashion. I shall enlarge on this latter suggestion when discussing future research. Before then, I wish to examine the question 'Are desert animals really special?' more closely.

ARE DESERT ANIMALS SPECIAL?

This question was first posed by Cloudsley-Thompson as early as 1964. Since then it has had several proponents and in 1987 a whole conference was devoted to the theme 'What's special about desert ecology?' In his summing up of the conference, Dr Larry Slobodkin suggested 'that although the same basic physiological machinery is used by organisms that live in deserts, it is usually modified to cope with either the rich but episodic resources, or the more continuously available low quality resources that characterize desert ecosystems. In this context it would be interesting to know more about speciation in and around deserts, in particular to discover whether they act as sources of, or sieves for, evolutionary novelties' (Dobson and Crawley, 1987). Seely (1989) contributed an important paper to the same conference, using the ecophysiological studies on Namib tenebrionids to construct several interesting hypotheses. She also concluded that the physiological adaptations of desert invertebrates are not qualitatively different from those of 'some species from other environments' and that 'behavioural adaptations are an important adjunct to physiological ones'. I have already dealt with the difficulties encountered in attempting to make a distinction between physiological and behavioural phenomena and wish now to examine this alleged similarity of the 'basic physiological machinery used by organisms that live in deserts'. I do so because young physiologists, reading these papers superficially, may be discouraged from engaging in the rewarding field of desert ecophysiological research.

To argue that all organisms, both temperate and xerophylic, are physiologically similar is obviously true. For example, we accept that all insects have six legs, breathe via tracheae, extrude hydrocarbons on the surface of the cuticle, employ the tricarboxylic acid cycle and cytochrome system for respiration. But are we justified in exaggerating small physiological differences, such as a low metabolic rate or a few extra layers of long-chain hydrocarbons on the cuticle of a desert insect, as being profoundly different to the universal norm? Nevertheless, it is misleading to deny the very real differences between an animal which produces urine with a maximum concentration of 600 mOsm and one which is able to concentrate its urine to 7000 mOsm. This is not merely a quantitative difference: it requires a different 'kind' of kidney. Similarly, the spectacular ability of *Onymacris* to absorb water vapour from unsaturated air in its gut using a Malpighian tubule fluid with an osmolality of 9 Osm is indeed 'special' (Machin, 1981).

The argument against special attributes of desert animals could include the close physiological similarities among various tiger beetle species collected from a wide variety of habitats by Hadley and Schultz (1988), or the similarity in the high thermal tolerance of desert and temperate ant lion larvae established by Marsh (1987). To my mind, however, further debate on this issue is of limited value as the argument must eventually revolve around the strict philosophical definition of the word 'difference' and for this reason eventually becomes merely semantic. Nevertheless, the debate has been useful in cautioning physiologists against approaching the design and interpretation of their experiments with too strong a bias by expecting profound physiological differences in desert animals. It has also provided the evolutionists with interesting examples for speculating whether physiological mechanisms are sufficiently 'plastic' so that they do not place strict constraints on the distribution of animals, or whether distribution and abundance are perhaps more likely to be closely constrained by other ecological factors, such as competition and predation.

FUTURE RESEARCH

The Desert Ecological Research Unit of Namibia owes its success to various factors, not least among these being the fact that individual senior scientists have had complete freedom to pursue their own specialized interests. Far be it from me therefore to be prescriptive about future research in any way. I merely wish to share some thoughts on the basis of my long association with the research station. The following topics could to my mind offer some productive avenues of enquiry:

Physiology of desert plants

Recent personal experience, while studying the Nara plant, has convinced me that exceptional opportunities exist for physiological studies on Namib Desert plants. It is a neglected field and we have many endemic species growing under unusual environmental conditions that will provide ideal study material. These studies could follow the successful approach used by Park Nobel and his colleagues at the University of California, Los Angeles, by first concentrating on heat and water balances (e.g., Smith and Nobel, 1986) and then moving to the unravelling of the mechanism of fog or water vapour imbibition, which appears to be essential for the survival of many Namib plants. Hormonal control of dormancy and recovery after rain in desert perennials should provide excellent opportunities for basic studies in plant physiology.

Protein and nitrogen cycling

Much has been written about the reliable source of food energy (detritus) and free water (fog) in the dune ecosystem and how these factors sustain the remarkable variety of endemic animals (Louw and Seely, 1982). In contrast, we know almost nothing about how and where the plants obtain their nitrogen and the animals their protein. This is a difficult field, requiring a long-term fundamental study, but I feel confident it will yield important results leading to new concepts in nitrogen cycling because of the relatively simple ecosystem involved.

Physiological ecology or natural history

Many of the plants and animals in the Namib, as well as the communities they form, are so isolated that very little is known about them. There is therefore still a great need for natural history research in the Namib, particularly long-term research to eventually provide reliable data for the ecologists to either build their predictive models or explain the palaeoecological history of the region. With a little effort, these natural history studies can be designed to test specific hypotheses and, if necessary, be provided with suitable laboratory back-up to elevate them to the status of ecophysiological studies. In fact, many consider ecophysiology as merely a modern form of natural history. I anticipate that studies of this nature will continue to be an important part of the general research pattern on the Namib fauna. Recent successful studies of this nature include investigations on the ecophysiology and behaviour of the desert lizard *Angolosaurus skoogi* (e.g., Pietruszka, Hanrahan, Mitchell and Seely, 1986; Mitchell, Seely, Roberts, Pietruszka, McClain, Griffin and Yeaton, 1987).

This type of study should, if possible, incorporate the latest technology, such as radio tracking, advanced radio-telemetry and the use of doubly-labelled water, to measure water turnover rates and field metabolic rates. In this way studies of truly excellent quality, similar to that of Nagy and Medica (1986) on desert tortoises, can be achieved. The opportunities for studying large animals, pointed out previously, should also be seriously considered in this context.

Meeting the criticisms of comparative physiology

The criticisms of comparative physiology outlined at the beginning of this paper are to my mind generally valid. Comparative physiologists, whether they be evironmental, eco- or general physiologists, must respond to these criticisms by carefully planning their investigations towards the testing of important hypotheses. I am not suggesting that we have to tackle profound hypotheses, such as the evolution of osmoregulation or endothermy, with every investigation we launch. Nevertheless, the scientific relevance and significance of the hypothesis should be carefully evaluated. For example, dozens of studies have examined the water relations of Namib animals but not one of these has attempted to construct a complete water balance which would allow the testing of several hypotheses. Also of crucial importance to the survival of certain desert animals that never drink free water is the balance between metabolic water produced and the concurrent loss of respiratory water vapour which accompanies the production of metabolic water, yet there are only a handful of studies worldwide that have measured metabolic rate and respiratory water loss simultaneously. This balance is a phenomenon which lends itself to the construction and testing of hypotheses; it has wide applicability and provides excellent opportunities for marrying physics and physiology. A similar study is suggested by the significant findings of Seely and Mitchell (1987) that water vapour pressures are generally higher on the dune surface at night than in the sand below the surface. Consequently they concluded that animals seeking refuge beneath the dune sand at night were doing so for reasons other than the seeking out of high water vapour pressures. This is probably true but Clarke (1988) has recently found that the desert lizard *Angolosaurus skoogi* lost water more rapidly when prevented from burying beneath the sand than when it was allowed to submerge, even when temperatures and humidities were similar below and above the sand surface. It is possible then that in the field, boundary air layers remain intact beneath the sand, whereas above the surface, in spite of higher water vapour pressures, air movement could disrupt boundary layers and lead to more rapid evaporative water loss. Clearly a series of physical thresholds must be involved and their measurement will provide physiologists with some challenging hypothesis-testing. Many other examples could be cited, but only at the risk of appearing prescriptive. The Namib offers excellent opportunities for ecophysiological research and is itself a splendid natural laboratory. These advantages can, however, be exploited optimally only by well-planned, disciplined research, preferably of a long-term and fundamental nature. In this way we can avoid merely proving that animals can survive in their natural habitats, and rather concentrate on asking more profound questions, preferably of an evolutionary nature

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REFERENCES

BARTHOLOMEW, G. A., LIGHTON, J. R. B. and LOUW, G. N., 1985. Energetics of locomotion and patterns of respiration in tenebrionid beetles from the Namib Desert. *Journal of Comparative Physiology* (B)**155**: 155–162.

BUFFENSTEIN, R., CAMPBELL, W. E. and JARVIS, J. U. M., 1985. Identification of crystalline allantoin in the urine of African Cricetidae (Rodentia) and its role in their water economy. *Journal of Comparative Physiology* (B)**155**: 493–499.

CLARKE, B. C., 1988. Department of Zoology, University of Cape Town. Unpublished results.

CLOUDSLEY-THOMPSON, J. L., 1964. Terrestrial animals in dry heat: introduction. *In:* DILL, D. B., ed., *Adaptation to the environment,* pp. 447–449. Handbook of Physiology, American Physiological Society, Washington, D.C.

COUTCHIE, P. A. and CROWE, J. H., 1979*a*. Transport of water vapor by tenebrionid beetles. I. Kinetics. *Physiological Zoology* **52**: 67–87.

COUTCHIE, P. A. and CROWE, J. H., 1979*b*. Transport of water vapor by tenebrionid beetles. II. Regulation of the osmolarity and composition of the hemolymph. *Physiological Zoology* **52**: 88–100.

CURTIS, B. A., 1985. Observations on the natural history and behaviour of the dune ant, *Camponotus detritus* Emery, in the central Namib Desert. *Madoqua* **14**: 279–289.

DE VILLIERS, P. S., 1985. Aspects of the reproductive biology of the Namib tenebrionid beetle, *Onymacris unguicularis* (Haag). Unpublished Ph.D. thesis, University of the Witwatersrand, Johannesburg.

DOBSON, A. P. and CRAWLEY, M. J., 1987. What's special about desert ecology? *Trends in ecology and evolution* **2**: 145–146.

EDNEY, E. B., 1971. Some aspects of water balance in tenebrionid beetles and a thysanuran from the Namib Desert of southern Africa. *Physiological Zoology* **44**: 61–76.

FEDER, M. E., BENNET, A. F., BURGGREN, W. W. and HUEY, R. B., eds, 1987. *New directions in ecological physiology.* Cambridge University Press, New York.

HADLEY, N. F. and SCHULTZ, T., 1988. Unpublished results, Zoology Department, Arizona State University.

HAMILTON, W. J., 1986. Namib desert chacma baboon (*Papio ursinus*) use of food and water resources during a food shortage. *Madoqua* **14**: 397–407.

HAMILTON, W. J. and SEELY, M. K., 1976. Fog basking by the Namib Desert beetle, *Onymacris unguicularis. Nature* **262**: 284–285.

HOFMEYER, M. D. and LOUW, G. N., 1987. Thermoregulation, pelage conductance and renal function in the desert-adapted springbok, *Antidorcas marsupialis. Journal of Arid Environments* **13**: 137–151.

LOUW, G. N., 1972. The role of advective fog in the water economy of certain Namib Desert animals. *Symposia of the Zoological Society of London* **31**: 297–314.

LOUW, G. N., BELONJE, P. C. and COETZEE, H. J., 1969. Renal function, respiration, heart rate and thermoregulation in the ostrich (*Struthio camelus*). *Scientific papers of the Namib Desert Research Station* **42**: 43–54.

LOUW, G. N. and HOLM, E., 1972. Physiological, morphological and behavioural adaptations in the ultrapsammophilous Namib Desert lizard, *Aporosaura anchietae. Madoqua* **1**: 67–85.

LOUW, G. N., NICOLSON, S. W. and SEELY, M. K., 1986. Respiration beneath desert sand: carbon dioxide diffusion and respiratory patterns in a tenebrionid beetle. *Journal of Experimental Biology* **120**: 443–447.

LOUW, G. N. and SEELY, M. K., 1982. *Ecology of desert organisms.* Longmans, London.

MACHIN, J., 1981. Water compartmentalisation in insects. *Journal of Experimental Zoology* **215**: 327–333.

MARSH, A. C., 1985. Thermal responses and temperature tolerance in a diurnal desert ant, *Ocymyrmex barbiger. Physiological Zoology* **58**: 629–636.

MARSH, A. C., 1986. Ant species richness along a climatic gradient in the Namib Desert. *Journal of Arid Environments* **11**: 235–241.

MARSH, A. C., 1987. Thermal responses and temperature tolerance of a desert ant-lion larva. *Journal of Thermal Biology* **12**: 293–300.

McCLAIN, E., SEELY, M. K., HADLEY, N. F. and GRAY, V., 1985. Wax blooms in tenebrionid beetles of the Namib Desert: correlations with environment. *Ecology* **66**: 112–118.

MITCHELL, D., SEELY, M. K., ROBBERTS, C. S., PIETRUSZKA, R. D., McCLAIN, E., GRIFFIN, M and YEATON, R. I., 1987. On the biology of the lizard *Angolosaurus skoogi* in the Namib Desert. *Madoqua* **15**(3): 201–216.

NAGY, K. A. and MEDICA, P. A., 1986. Physiological ecology of desert tortoises in southern Nevada. *Herpetologica* **42**: 73–92.

NICOLSON, S. W., 1980. Water balance and osmoregulation in *Onymacris plana,* a tenebrionid beetle from the Namib Desert. *Journal of Insect Physiology* **26**: 315–320.

NICOLSON, S. W. and ISAACSON, L. C., 1987. Transepithelial and intracellular potentials in isolated Malpighian tubules of tenebrionid beetle. *American Journal of Physiology* **252**: F645–F653.

PIETRUSZKA, R. D., HANRAHAN, S. A., MITCHELL, D. and SEELY, M. K., 1986. Lizard herbivory in a sand dune environment: the diet of *Angolosaurus skoogi. Oecologia* **70**: 587–591.

SCHMIDT-NIELSEN, K., 1964. *Desert animals: physiological problems of heat and water.* Oxford University Press.

SEELY, M. K., 1989. Desert invertebrate physiological ecology: what is special? *South African Journal of Science* **85**: 266–270.

SEELY, M. K. and HAMILTON, W. J., 1976. Fog catchment sand trenches constructed by tenebrionid beetles, *Lepidochora,* from the Namib Desert. *Science* **193**: 484–486.

SEELY, M. K. and MITCHELL, D., 1987. Is the subsurface environment of the Namib Desert dunes a thermal haven for chthonic beetles? *South African Journal of Zoology* **22**: 57–61.

SEELY, M. K., ROBERTS, C. S. and MITCHELL, D., 1988. High body temperatures of Namib dune tenebrionids – why? *Journal of Arid Environments* **14**: 135–143.

SHKOLNIK, A., SCHROTER, R. C. and SCHMIDT-NIELSEN, K., 1980. Exhalation of unsaturated air in camels (Abstract). *Proceedings of the XXVIII International Congress of Physiological Sciences, Budapest.*

SKINNER, J. D., DOTT, H. M., VAN AARDE, R. J., DAVIES, R. A. G. and CONROY, A. M., 1987. Observations on a population of springbok, *Antidorcas marsupialis,* prior to and during a severe drought. *Transactions of the Royal Society of South Africa* **46**: 191–197.

SMITH, J. A. C. and NOBEL, P. S., 1986. Water movement and storage in a desert succulent: anatomy and rehydration kinetics for leaves of *Agave deserti. Journal of Experimental Botany* **37**: 1044–1053

TAYLOR, C. R., 1969. The eland and the oryx. *Scientific American* **220**: 88–95.

WITHERS, P. C., LOUW, G. N. and HENSCHEL, J., 1980. Energetics and water relations in Namib Desert rodents. *South African Journal of Zoology* **15**: 131–137.

WITHERS, P. C., SIEGFRIED, W. R. and LOUW, G. N., 1981. Desert ostrich exhales unsaturated air. *South African Journal of Science* **77**: 569–570.

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LOCKE, M., 1960. The cuticle and wax secretion in *Calpodes ethlius* (Lepidoptera, Hesperiidae). *Quarterly Journal of Microscopical Science* **101**: 333–338.

LOCKE, M., 1974. The structure and formation of the integument of insects. *In:* ROCKSTEN, M., ed., *The physiology of insects,* Vol. 6, 2nd edn, pp. 123–313. Academic Press, New York.

McCLAIN, E., PRAETORIUS, R. L., HANRAHAN, S. A., and SEELY, M. K., 1984. Dynamics of the wax bloom of a seasonal Namib Desert tenebrionid, *Cauricara phalangium* (Coleoptera: Adesmiini). *Oecologia* **63**: 314–319.

McCLAIN, E., SEELY, M. K., HADLEY, N. F. and GRAY, V., 1985. Wax blooms in tenebrionid beetles of the Namib Desert: correlations with environment. *Ecology* **66**: 112–118.

McCLAIN, E., HANRAHAN, S. A. and GERNEKE, D., 1986. Extracuticular secretion on a Namib Desert tenebrionid, *Onymacris plana* (Peringuey): an indicator of aridity. *Madoqua* **14**: 363–367.

PENRITH, M. L., 1975. The species of *Onymacris* Allard (Coleoptera: Tenebrionidae). *Cimbebasia* **4**: 48–97.

POPE, R. D., 1979. Wax production by coccinellid larvae (Coleoptera). *Systematic Entomology* **4**: 171–196.

POPE, R. D., 1983. Some aphid waxes, their form and function. *Journal of Natural History* **17**: 489–506.

POPE, R. D., 1985. Visible insect waxes: form, function, and classification. *Bulletin of the Royal Entomological Society* **9**: 4–8.

RETNAKARAN, A., ENNIS, T., JOBIN, L. and GRANETT, J., 1979. Scanning electron microscopic study of wax distribution on the balsam woolly aphid, *Adelges piceae* (Homoptera: Adelgidae). *Canadian Entomologist* **111**: 67–72.

SEELY, M. K., 1978. The Namib Dune Desert: an unusual ecosystem. *Journal of Arid Environments* **1**: 117–128.