

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 *Aporosaurus 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

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 xerophytic, 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 free-

dom 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 environmental, 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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