WATER ECONOMY OF CERTAIN NAMIB DESERT ANIMALS

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INTRODUCTION

IN recent years increasing interest in arid regions has developed as a result of expanding populations and congestion in the temperate areas of the world. This interest is naturally directed towards exploitation of these regions and modern advances in technology, such as desalination with nuclear power, have increased the feasibility of exploitation although serious economic hurdles still remain. In any event, if desert areas are to be exploited either for productive purposes or as recreational areas, a thorough understanding of their ecology is essential. For this reason a knowledge of the physiological ecology and particularly the water economy of the plants and animals is of primary importance.

In addition to practical considerations a study of desert animals is also of absorbing academic interest to the zoologist. The reason for this is that the desert, because of its extreme aridity and frequent searing temperatures, provides an ideal testing ground for the stratagems of evolution to produce animals adapted to the hostile environment. In this respect it should be realized that the environmental temperatures and humidities experienced in deserts are frequently outside the tolerance limits of cellular and therefore animal life.

In view, then, of the academic interest of desert animals, zoologists in Southern Africa are most fortunate in having the Namib Desert as a study area. This desert, judging by the high degree of specialization exhibited by the indigenous animals, must be among the oldest in the world, although geologists are not as convinced as biologists in this respect. Moreover, the Namib has suffered minimum interference from human activity and it is still possible to study animals there in completely undisturbed, natural conditions.

In the following discussion an attempt will be made to illustrate some of the stratagems employed by certain Namib Desert animals to survive in the desert environment. In doing so examples will be selected to show progressive adaptation from semi-arid conditions to the extreme hostility of the desert dunes. In addition, the examples will illustrate how smaller animals, the dassie and sand-diving lizard, adapt largely by behavioural means in escaping to a favourable micro-climate, while larger animals such as the ostrich and the oryx are unable to do so and therefore exhibit interesting physiological adaptations. The discussion will be in general terms and is directed towards the non-specialist.

BEHAVIOURAL ADAPTATION

The dassie or hyrax

The dassie *(Procavia capensis)*, although successful in semi-arid regions, is not a true desert animal and is not restricted to the Namib. Nevertheless, it occurs on the periphery of the desert and is a good starting point to illustrate progressive degrees of adaptation to the desert environment.

It is popularly believed in South Africa that the dassie can exist without drinking water and for this reason we have examined its water balance and temperature regulation in some detail (Louw *et al.*, 1970). We have found that when these animals are housed at comfortable temperatures (20^{o} C) and fed on air-dry food that they will drink very little water, namely 45.7 ml per kg. of body weight. If we compare this figure with 146 ml/kg for the laboratory rat and 186 ml/kg for growing pigs it would seem that the dassie makes efficient use of its drinking water. This is indeed the case but we have also found that the dassie cannot exist on dry food indefinitely without water. After eight days without water, food intake ceases and the animals begin to lose weight. The dassie is therefore not as efficient as the kangaroo rat, found in North America, which can exist indefinitely without water and the reason is to be found in differences in their kidney function.

A useful measure of the concentrating ability of the kidney is the osmotic concentration of the urine which is expressed in milliosmoles per kg of solvent (mOsm/kg) This value is a reflection of the total concentration of all dissolved substances in a solution and will be used in the following discussion. For example, if we compare the maximum urine concentration we obtained in the dassie (3 088 mOsm) with maximum concentrations reported for the beaver (520 mOsm) and man (1 160 mOsm) it is clear that the dassie possesses very superior renal efficiency which is approximately equal to that of the desert camel. Renal efficiency in the dassie is, however, not nearly as spectacular as that of the kangaroo rat (6 500 mOsm) which explains the ability of the latter to exist without water. Under natural conditions, however, the dassie would not be restricted to air-dry food and it is quite probable that given sufficient succulent food that it could exist without free drinking water.

Before leaving the subject of kidney function in the dassie it is of interest to note that we found large amounts of undissolved calcium carbonate in the urine of these animals. This is a most unusual phenomenon as excess calcium is usually eliminated in mammals via the digestive tract. This clacium carbonate collects on rocks at the communal urinating sites of dassies and sometimes even in the form of stalagmites. These deposits were known as *klipsweet* to pioneer settlers in South Africa and were used as a home remedy by them for various complaints including rheumatism. Any physiological advantage of excreting calcium in large quantities via the urine to the dassie is, however, not known.

Control of body temperature is intimately associated with the water economy of desert animals and any attempt to control body temperature under conditions of high atmospheric temperature involves considerable water loss. For this reason we examined temperature regulation in the dassie and found these animals to have poor control over body temperature and surprisingly low heat tolerance. Their body temperatures fluctuated over a wide range depending upon the environmental temperature and heat prostration occurred between 35°C and 40°C.

The dassie is therefore a poor thermoregulator and relies upon a well defined behaviour pattern for avoiding temperature stress. This behaviour pattern has been documented by Sale (1970) and consists essentially of retreating to rock crevices to avoid unusually high or low atmospheric temperatures. In other words the animals escape to a favourable micro-climate and emerge only for brief periods in the morning and afternoon unless conditions are favourable throughout the day.

The behaviour pattern of the dassie, supported by efficient renal function, are thought to be the main contributing factors to its success in hot arid regions.

The sand-diving lizard.

In contrast to the dassie, the sand-diving lizard *(Aporosaura anchietae)* is a true desert animal and, although relying largely on escape beneath the sand for its survival, is highly specialized for desert life. It is confined largely to the soft sand on the slipfaces of the high dunes of the Namib and even a cursory examination of the external anatomy reveals how well it is adapted to living in sand. The head and body have a flat appearance allowing maximum contact with the sand. The lateral abdominal folds are voluminous allowing marked distention of the digestive tract which will later be seen to be of great importance. The snout is broad, depressed and spatulate and this shovel-like form assists the animal in diving beneath the sand. The colouring is fairly cryptic and the digits are attenuated and denticulated to facilitate sprinting on soft wind-blown sand. In view of this specialization and their highly specialized habitat we decided to examine temperature regulation and water economy in these animals (Louw & Holm, 1970).

A study of their temperature regulation revealed that the animals escaped the extreme surface temperatures by diving beneath the sand. They emerge from the sand only when the surface temperature approaches 30°C which usually occurs several hours after sunrise. Upon emerging they flatten their bodies upon the sand and raise all four limbs into the air in order to achieve maximum contact with the sand and thus raise their temperatures as quickly as possible to the preferred level for activity. Once this is achieved they forage upon the dune face until the temperature approaches 40°C. Temperatures rise rapidly on the dune face and the interval of time between 30°C and 40°C is short and the lizards must make maximum use of this period. Therefore, as the surface temperatures approach 40°C the animals move their bodies as far as possible from the surface of the sand by straightening their limbs. Periodically they will interrupt this stilt-like walk to raise diagonally opposite limbs into the air while the base of the tail is used for support. This is presumably done to assist radiant and convective cooling. At surface temperatures above 40°C the animals dive beneath the sand, disappearing within a fraction of a second to the cooler depths below. This peculiar thermoregulatory dance is repeated in the afternoon as the surface temperatures cool between 40°C and 30°C and although this behaviour pattern protects the animals from extremely high temperatures they are nevertheless exposed to high temperatures and low humidities which means they must lose a considerable amount of moisture on the dune face. This loss is further aggravated by the nature of their diet which, in the inland dunes, consists mainly of dry grass seed. The question now arises as to how the animals obtain moisture and an obvious choice would be condensed sea fog ± 15 mOsm) which is a regular feature of the Namib climate.

Although the lizards have not been observed to drink condensed fog we have obtained strong circumstantial evidence that they do. For example, they have been trapped in time registering traps during heavy fog when surface temperatures were well below their preferred range of 30° 40°C and in captivity they will emerge from beneath the sand to drink water droplets which have been aerosol sprayed upon plant material in the terrarium. Moreover, when animals are captured and dissected shortly after a heavy condensing fog has occurred, their stomachs are found to be tremendously distended and filled with water. This large volume of water then passes into the caecum which expands proportionately and acts as a reservoir of water upon which the animal can draw for several weeks until the next fog occurs.

It is very rare for desert animals to store water and the water storing mechanism exhibited by this species illustrates remarkable adaptation to the fog belt of the Namib. It would also seem that, judged from an evolutionary viewpoint, the weather pattern of the Namib which is dominated by the cold Benguella current must be very ancient in geological time.

PHYSIOLOGICAL ADAPTATION

The ostrich.

Unlike the sand-diving lizard and dassie, discussed previously, the ostrich is too large to escape to a favourable micro-climate and must therefore depend more on physiological adaptation. For this reason we have examined water economy and temperature regulation in this animal (Louw *et al.* 1969)

The ostrich shares two important physiological advantages with the sand-diving lizard when compared with mammals such as the dassie or oryx. Firstly it does not sweat which represents a considerable saving in moisture loss and secondly, like all birds and most reptiles, its nitrogenous waste is excreted in the form of uric acid and not urea. Uric acid is almost insoluble and as a result can be excreted with minimal water loss, while urea is highly soluble and removes large amounts of water from the body as it is excreted. In addition we have found large numbers of specialized cells in the ureters of ostriches which produce a lubricant to facilitate the expulsion of the insoluble uric acid and thus minimize water loss via this pathway. A further advantage which the ostrich enjoys over any reptile, such as the sand-diving lizard, is its ability to produce a urine which is more concentrated than its blood plasma and in this way excretes excessive amounts of electrolytes from its body without large water loss. For example, we found that the ostrich could produce urine with an osmotic concentration of 800 mOsm. This is nowhere near the value of 3 000 mOsm for the dassie but is nevertheless much higher than the plasma which measured 300 mOsm.

It is therefore not surprising that the ostrich is a successful inhabitant of some of the most arid regions of the Namib. We were, however, surprised to find that they cannot exist indefinitely on dry feed. After 11 days they cease eating and lose weight steadily. The reason for this is to be found in the fact that the ostrich maintains its body temperature at a constant level and in order to do this at high atmospheric temperatures it is compelled to employ evaporative cooling from the respiratory system by panting which represents a considerable water loss. Nevertheless, this loss is kept to an absolute minimum by a behavioural mechanism which allows the birds to make maximum use of radiant and convective cooling. This consists of manipulating the wings and feathers in such a way as to expose the skin surface as much as possible to air currents moving across the body. For example when high atmospheric temperatures are experienced the animals, unlike other birds, erect their feathers and move their wings forwards and away from the body thus exposing the rib cage and thighs which are without feathers. In this way the slightest breeze is exploited and the temperature threshold at which panting occurs is raised considerably.

We were able to confirm the importance of this mechanism by continuous measurement of skin temperatures, body temperatures and the temperature of the air space between the skin and feathers. Finally, it should be emphasized that under natural conditions in the Namib the ostrich is not compelled to exist on air-dry food as in our experiment. In the early morning plants absorb considerable hygroscopic moisture and occasionally they are covered with either dew or condensed fog. In these circumstances they are probably able to survive for long periods without ever drinking.

The oryx

Although the springbok occurs in the Namib, the oryx is the only antelope which penetrates into the entirely arid dune system. It must therefore be able to survive indefinitely without ever drinking and in doing so it is faced with several serious physiological disadvantages. For example, it is of too large a size to escape to a burrow or other favourable micro-climate and being a mammal it excretes nitrogen waste in the form of urea with its attendant water loss. Moreover, like all mammals it should sweat to maintain body temperature and will lose considerable moisture from its respiratory system. How then is it able to survive in the face of these disadvantages?

Although no physiological studies have been done on the Namib oryx the answer to this question can be found in a series of admirable experiments carried out by Taylor (1969) on the oryx in East Africa.

Taylor has found that when the oryx has free access to water it will sweat to maintain a constant body temperature under hot conditions. If water intake is restricted, however, it will not sweat and allows its body temperature to rise as high as 45°C. At night, when atmospheric temperatures drop sharply the animal loses this heat load by radiant cooling and thus a considerable saving in moisture is effected. In addition these animals lose minimal amounts of water in the faeces and urine by producing dry faecal pellets and a concentrated urine.

The sharp drop in temperature which these animals experience at night, which is a feature of the desert climate, poses a problem to the oryx as it is poorly insulated with sub-cutaneous fat. As a result it must increase its metabolic rate to maintain its body temperature and must therefore increase its oxygen consumption to support the increase in metabolism. This could result in a considerable loss of moisture from the respiratory tract but is largely circumvented by physiological adaption in the oryx. For example, the dehydrated oryx shows a distinct reduction in oxygen consumption when compared with the hydrated animal. Moreover, although oxygen consumption increases at at low temperatures, respiration rate decreases. This is achieved by increasing the depth of inspiration and therefore no increase in ventilation of the dead space occurs. This is a distinct advantage as ventilation of the dead space removes moisture from the animal but does not contribute to oxygen exchange.

In the Namib high relative humidities are frequently experienced at night and, as we have seen, even condensing advective sea fog. It is quite probable therefore that certain desert plants may absorb this moisture hygroscopically during the night as Taylor found to be the case with *Disperma* species in East Africa. Consequently if the oryx were to regulate their grazing periods to night and early morning, their moisture intake could be reasonably high.

In conclusion, it can be seen from this superficial review that it is seldom a single dramatic factor which allows animals to survive in the desert but rather a series of small adaptations which, acting in concert, ensure perfect dovetailing of the animal with its environment.

REFERENCES

LOUW, G.N., BELONJE, P.C. & COETZEE, H.J. 1969. Renal function, respiration, heart rate and thermoregulation in the ostrich *(Struthio camelus). Scient. Pap. Namib Desert Res. Stn* 42, 43.

LOUW, E., LOUW, G.N. & RETIEF, C.P. 1970. Thermolability, heat tolerance and renal function in the dassie or hyrax, *Procavia capensis. Zool. afr.* (In press).

LOUW, G.N. & HOLM, E. 1970. Physiological, Morphological and behavioural adaptations of the ultrapsammophilous, Namib desert lizard *Aporosaura anchietae. Scient. Pap. Namib Desert Res. Stn.* (In press).

SALE, J.B. 1970. The behaviour of the resting rock hyrax in relation to its environment. *Zool. afr.* 5, 87.

TAYLOR, C.R. 1969. The eland and the oryx. *Sci. American*. 220. 88.