

ECOPHYSIOLOGY OF DESERT ANIMALS

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الفسيولوجيا البيئية للحيوانات الصحراوية

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توضح الدراسة بأن المشاكل البيئية الرئيسية التي تواجهها النباتات والحيوانات الصحراوية تنحصر في شح الماء (أو فيضه في بعض المواسم) والتطرف في درجات الحرارة وانعدام الغطاء. وتشمل أساليب التكيف لهذه العوامل تخفيض معدلات الأيض والكمون والبيات الفصلي والحفاظ على ماء الجسم وامتصاص الماء من الهواء الرطب. وتفقد الحيوانات الصحراوية الماء بسبب عمليات النتح والتنفس والأخراج، وتتحاشى تلك الحيوانات التطرف في درجات الحرارة والأفتراس بالاختباء في الجحور والملازات الآمنة والظليلة إضافة للأيقاع الليلي للنشاط وابتداع عدة طرق دفاعية لتفادي الأفتراس.

INTRODUCTION

The principal environmental problems that confront both plants and animals in the desert are water shortage and flooding, thermal extremes, and the absence of cover. Adaptational responses to these include cryptobiosis, diapause, seasonal quiescence, water conservation, and the uptake of atmospheric moisture. The major avenues of water loss from animals are in transpiration, respiration and excretion. Both thermal extremes and predatory enemies are avoided by taking shelter in burrows, rock crevices, or shade, combined with nocturnal activity rhythms and various anti-predator devices.

WATER SHORTAGE

All living organisms utilise water at some stage of their life cycles, even if they are able to survive for long periods without it. Survival without water can occur either in a state of cryptobiosis or, more usually, in diapause. In their active stages, some arthropods are able to obtain sufficient moisture for their needs from water vapour, while many desert animals, especially carnivores, receive enough from the products of metabolism and the preformed water in

their food.

CRYPTOBIOSIS

The word "cryptobiosis" was proposed by Keilin in [1] to replace the terms anabiosis and abiosis, which refer to states in which "metabolic activity becomes hardly measurable, or comes reversibly to a standstill". Hinton [2], distinguished between a very low level of metabolism, as is found during diapause, and a total absence of metabolism. For this reason, he restricted the term cryptobiosis to the persistence of life among desiccated cells in which metabolism had temporarily ceased. He pointed out that completely dehydrated rotifers, nematodes, tardigrades and crustaceans may revive and grow normally after being subjected to temperatures as low as that of liquid helium (-270°C). In the cryptobiotic state, all the chemical reactions responsible for the maintenance and growth of an organism cease. Although viability decreases over time, it is associated with chemical reactions that have nothing to do with metabolism.

The best known example of cryptobiosis among higher invertebrates is provided by *Polypedilum vanderplanki*, a

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West African Sahelian chironomid midge whose larvae inhabit the small pools that form in shallow depressions on unshaded rocks during the rainy season. These depressions may fill and dry several times each year, but the larvae are well adapted to their unstable environment. They can become almost completely desiccated many times without harm, absorbing water again when it is present. They may persist for decades in a dehydrated state, and during such periods are able to survive exposure to temperatures of up to 106°C for 3 hours or as low as -270°C, and yet produce apparently normal adults. In the active hydrated state, on the other hand, their tolerances are no different from those of any other midge larvae [2].

Some of the inhabitants of temporary desert rainpools also pass the dry season in a state of cryptobiosis. Cysts of the cosmopolitan brine shrimp, *Artemia salina*, can survive in a dry state for as long as 28 years. The capacity to tolerate total dehydration at developmental temperatures appears to be a primitive feature of protoplasm. It is necessary because the molecules of respiratory gases are larger than water molecules. Consequently, if an organism is to exchange gases through its epidermal layers it must also lose water when the ambient environment is drier than its own protoplasm [3].

DIAPAUSE

Comparatively few animals employ cryptobiosis as a means of survival during periods of drought. More commonly, they endure unfavourable climatic conditions in diapause. In this state, metabolism is reduced to a very low level, so that little moisture is lost in respiration. The term diapause was originally restricted in its usage to describe the resting stage during insect development but, today, it is generally applied to most cases of arrested development.

The eggs of tadpole shrimps (*Triops spp.*) survive the hot, dry, Saharan summer in a state of diapause. These eggs can tolerate 98 °C for 16 hours whilst dry, but the lethal temperature for the active adults is only about 40 °C for 2 hours or 34 °C for 24 hours [4]. A function of their diapause, is to ensure that all the individuals of a population do not become activated simultaneously. If all the eggs of *Triops granarius*, for example, were to hatch the moment they were wetted, a brief shower that did not provide a pool deep enough to last through their entire development cycle would prove fatal to the population. This is one way in which diapause differs from cryptobiosis.

The fauna of tropical rainpools fringing the Sahara is dominated by primitive filter-feeding phyllopod (Nostraca and Anostraca) whose life span is compressed into a couple of weeks; this is much shorter period than that of related species from temperate waters. Indeed, their life seems to be a veritable race against time, for they must reach maturity and lay their eggs before the pools dry up. It is interesting to observe among these animals, perhaps

more conspicuously than in many others, that the death of the individual is essential to the survival of the race. For, in more permanent waters where the adults could, theoretically, live a normal span of life and not be killed by the drying up of their environment, they do not survive predation from more advanced animals such as fishes [5].

Any stage of an arthropod's life-cycle can enter diapause, but the egg is the one that most frequently does so. Whilst in diapause, the eggs of insects, like those of crustaceans, are resistant to drought, heat and cold, but are nevertheless metabolising, albeit slowly.

Ephemeral life is by no means limited to desert animals, but the irregularity of desert precipitation naturally favours species with a protracted diapause. In some, this is obligatory, occurs in every generation, and is controlled endogenously. In others, it is facultative, and evoked by environmental factors that predict a change to unfavourable conditions [6].

QUIESCENCE

Many desert organisms evade the adverse conditions of drought and heat by aestivating in a quiescent state of suspended animation which, like facultative diapause, is engendered by environmental conditions. Quiescence, however, is reversed automatically on the return of favourable conditions. The difference between quiescence and diapause is physiological and can often only be determined experimentally. Indeed, on occasions there does not appear to be a very clear-cut distinction between them. During aestivation, the mouth of the shell of desert snails is closed by a thick epiphragm of calcified slime which reduces water loss by evaporation to such an extent that snails have been known to remain in this state for over 5 years and yet recover when wetted. Their low metabolic rate assures survival during these long periods of dormancy [7].

Unlike North American and Australian deserts, the Great Palaeartic desert is not inhabited by drought-resistant amphibians which aestivate in cocoons of mud or dead skin while lying deeply buried in the soil. Such cocoons are relatively impervious to water. The animals remain in a state of suspended animation, during which the metabolic rate is greatly reduced and they depend upon reserves in fat bodies within the abdominal cavity. Some also accumulate urea in their tissues, which increases osmotic pressure above that of the surrounding soil, so that any moisture tends to pass into the animals' bodies.

Many desert reptiles hibernate in winter, when food is scarce and ambient temperatures are too low for them to be active. Others aestivate during the hot summer. Among homeotherms, aestivation with reduced metabolism is common among rodents, but has also been recorded in an Australian marsupial (*Cercaetus nenus*) and in the Californian poorwill (*Phalaenoptilus nuttallii*) during the dry season when food is scarce.

WATER CONSERVATION

In order to exist with minimal water intake, desert organisms that are not in a state of cryptobiosis need to conserve moisture as far as is possible. Survival in the desert is achieved by numerous devices, usually employed in combination. These have been analysed in numerous books and reviews (e.g. [3,5,7-10,14]). I shall not attempt to discuss them in detail. They can, however, be summarised as follows:

(1) Evasion of drought and heat by completing the life cycle before the onset of stressful conditions which are endured in suspended animation.

(2) Avoidance and escape from heat and drought. This is achieved by morphological and physiological characters that reduce heat gain and water loss, and behavioural strategies which include retreating into burrows and shelters during the day.

Arthropods are able, to some extent, to avoid dehydration because they possess outer coverings of wax which reduce the amount of water lost through transpiration. Economy in respiratory moisture is achieved by keeping stomata, spiracles or lung books closed as far as possible. Tortoises hold their breath when desiccated, while jerboas and other small desert rodents have narrow nasal passages with large surface areas, so that they are cooled by evaporation when air is inhaled; water then recondenses during exhalation. The saw-scaled viper (*Echis carinatus*) stridulates by rubbing together the keels of its lateral scales, thereby avoiding the loss of respiratory moisture through hissing [4]. Desert animals have further reduced water loss through the evolution of extremely efficient excretory systems. Among insects and arachnids the production of uric acid and guanine, respectively, is related to the development of a 'cleidoic' or enclosed egg surrounded by relatively impermeable membranes and egg shell. Within such an egg, ammonia would soon accumulate and become toxic, while a concentration of urea would upset the osmotic relations of the developing embryo. Insects, like egg-laying reptiles and birds, are therefore uricotelic and develop the necessary machinery to excrete uric acid during the egg stage. They retain this ability throughout their lives, which preadapts them to desert life. Even where it is available, most arthropods are too small to be able to drink liquid water without becoming trapped by its surface tension. This, combined with their enormous surface to volume ratio, dictates the necessity for extreme economy in the use of water.

The ability to minimize excretory water loss among reptiles is associated with the absence of a loop of Henle in the nephrons of the kidney - consequently, they cannot produce hypertonic urine. Urine is concentrated in the cloaca, however, and not in the kidney as it is in birds and mammals. Most desert reptiles are either partially or completely uricotelic, although urate may not be excreted solely as uric

acid. Tortoises, in particular, show considerable temporal variations in the ratio of urea to uric acid excreted. In several species, changes from predominantly uric acid to urea metabolism and vice versa may occur within a single individual. Ostriches, and some desert lizards, possess extra-renal excretory organs in the form of nasal salt glands which secrete fluids rich in potassium. Thanks to these, they are able to drink very saline water.

All birds probably need to drink, but jerboas and gerbils can survive indefinitely upon dry seeds. They avoid the midday heat by burrowing, and are able to excrete large amounts of salt and urea whilst maintaining normal water balance. Camels and other large desert mammals are also able to excrete very concentrated urine. Camels do not need to drink while grazing in the cool season, but working camels must be watered every 3-4 days during the Saharan summer. Addax and oryx antelope, on the other hand, can survive without drinking in the wild, at an average maximum daily temperature of 40 °C, as long as their diet contains as little as 50% moisture. Like gazelles, they feed at night - when the leaves of acacia trees and grasses are actively transpiring and full of sap - and seek shelter during the hours of daylight. If this is not available, they take up a position facing the sun, thereby exposing a minimum of their body surface to incoming radiation. The same behaviour is observed in camels, lizards, locusts and many other taxa ([7,8,10]).

UPTAKE OF ATMOSPHERIC MOISTURE

Most desert animals live far from any source of open water, and inhabit regions that are totally dry throughout most of the year. Insectivorous and carnivorous animals can obtain sufficient moisture from the body fluids of their prey, while herbivores benefit from the moisture in their vegetable food. Seed eaters often gain little preformed water, however, and have to make do with metabolic water, unless, like birds, they can travel to distant oases and other water places. Sandgrouse, which nest far away from rivers or lakes, have adopted an extraordinary method of bringing water to their young. The male rubs his breast on the ground before drinking, so that his specially-adapted feathers are awry and easily saturated as he bends over the water to drink. He then flies back to the nestlings who pass the wet feathers through their beaks to obtain the trapped water.

Many desert beetles and other insects obtain moisture by chewing hygroscopic plant material which has absorbed atmospheric moisture during the night. Mists and fog also provide a source of moisture in some regions of the Great Palaeartic desert, but are a much more dependable source of water in the Namib and Atacama deserts. These cool coastal deserts enjoy regular mists engendered by the Benguela and Humboldt currents, respectively.

Some arthropods are able to absorb water vapour directly from unsaturated air. These include ticks, Thysanura, Psocoptera, Siphonaptera, Orthoptera and Coleoptera. The subject has been reviewed in detail by Edney [11], who

points out that only wingless insects are involved, and this sometimes means that the faculty is restricted to the immature stages. Except in ticks and the North American desert cockroach *Arenivaga investigator*, in which the mouthparts and buccal structures are implicated, the rectum appears to be the site of water vapour intake. The mechanism by which this takes place is still unknown. The phenomenon has not been demonstrated among Saharan Tenebrionidae, possibly because these have already evolved such low rates of water loss as to render it unnecessary. It could, perhaps, take place beneath the sub-elytral cavity. Some arthropods are also able to utilise soil moisture [4,11].

RISK OF FLOODING

Whilst heavy rainfall stimulates the emergence of many desert animals that have been aestivating in cryptobiosis, diapause or quiescence, it can be a danger to others too immobile to escape. Burrowing species, in particular, are at risk from sheet flooding and Australian trapdoor spiders, in particular, have countered this with a variety of burrow structures and impregnable entrances. Many Ctenizidae and Dipluridae seal their burrows with plugs, or have collapsible silk collars at the entrances: these can be drawn tightly closed to avoid flooding of the spiders' tubes [12].

THERMAL EXTREMES

Whereas most adaptations of desert animals to water shortage are physiological, thermal extremes are more often countered by the behavioural means by which drought is also evaded or avoided (see above).

HIGH TEMPERATURES

Only when body temperatures approach lethal limits is evaporative cooling evoked to reduce them. For instance, camels do not begin to sweat until their body temperature has increased about 6 °C [10]. Like the larger desert antelopes, they are thermolabile, storing heat during the day and losing it to the environment at night. Jerboas, gerbils and kangaroo-rats cannot afford to sweat at all but, if their body temperature approaches the lethal limit (42 °C), copious salivation occurs which wets the fur of the chin and throat. The cooling effect of this emergency regulatory process may keep experimental animals alive for up to half an hour at temperatures fatal to other small rodents.

Tortoises likewise salivate when overheated. They also urinate on their back legs, and it has been suggested that one function of the enlarged bladder may be to store urine for emergency thermoregulation [4]. Thermoregulatory panting is a common response of reptiles to overheating, as it is of birds and mammals. Cardiovascular responses, metabolic rates, and ventilation, interact in a vast complex with environmental factors [13].

Tolerance of heat by animals is not unlimited, but the

upper lethal temperatures of desert arthropods and reptiles are somewhat higher than those of allied species from other terrestrial ecobiomes. Lethal temperatures (LT50) as high as 50°C for exposures of 24 hours have been recorded for the solefiugid *Galeodes granti*, 47 °C for the scorpion *Leiurus quinquestriatus*, and 43 °C for tenebrionid beetles [4].

COLD TOLERANCE

In some desert regions the nights may be extremely cold, and adjustments such as freezing resistance and supercooling, typically associated with high latitude species, have been demonstrated in a number of desert organisms including arthropods and reptiles [3,14]. Desert arthropods also often show seasonal acclimation in their thermal relations, as do reptiles.

ANTI-PREDATOR ADAPTATIONS

Predation is one of the strongest of all selective factors in most ecobiomes and, because arid regions provide relatively little cover, the impact of predation is especially influential in them. Primary anti-predatory devices, which operate regardless of whether a predator is in the vicinity or not, include: - anachoresis (remaining hidden throughout life); hiding in burrows and retreats during the day - which is associated with rhythmic circadian behaviour - crypsis; protective resemblance and disguise; mimicry; integument, scales and armour; aposematic coloration; communal and social behaviour, and vigilance.

Secondary devices are called into play only in the presence of a potential predator. They include:- flight; thanatosis (death feigning); deflection of attack; autotomy; spines and urticating hairs; venoms and defensive fluids; warning sounds and deimatic or threatening displays; and retaliation.

In the co-evolutionary race between predators and prey, every defensive device has to be paid for in energy that might otherwise be channelled into reproduction. In desert regions, where sources of energy are scarce, there must be severe competition between the requirements of energy for defence and reproduction. Perhaps this is why the array of defensive adaptations is considerably less wide here than in the moist tropics. At the same time, however, because of the extent of exposure in arid regions, the devices that have been favoured by selection have evolved to a remarkable extent.

DISCUSSION

The specific morphological adaptations of desert animals to their environment are confined almost entirely to modifications for digging, burrowing in, and running across sand. This does not, however, imply that most desert regions are sandy: on the contrary, sandy stretches occupy only a small proportion of the world's deserts. The point is that habitats of clay, stone, and rock are by no means re-

stricted to deserts and have not therefore engendered many adaptations specific to arid regions.

Most desert animals survive because they avoid extreme conditions by exploiting favourable micro-climates within the desert ecosystem. Adaptations that enhance tolerance of heat and drought tend to be refinements of the morphological and physiological adaptations that are found in all terrestrial environments. These include impervious integuments, adaptations of the plumage of birds and pelage of mammals, water storage, adaptation of the size and shape of the extremities that facilitate heat loss, ectopic storage of fat in mammals, and so on. Physiological adaptations are concerned mainly with the conservation and uptake of water, tolerance of dehydration, osmoregulation, and the like [7]. Desert animals provide excellent material for the study of evolutionary adaptation and ecophysiology.

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