1' copy 07/04
10933
Mary

Libyan Studies 24 (1993)

Successful Desert Animals — Scorpions, Beetles and Lizards

By J. L. Cloudsley-Thompson*

Namib
sand

Abstract

Whereas the reactions of animals to heat are largely behavioural, responses to water shortage are primarily physiological. These characters are exhibited in all terrestrial biomes, but are enhanced in the desert. Desert animals, in general, are either cryptically sand-coloured or else black when distasteful or poisonous. This applies to all three taxa under discussion; most beetles are black, most lizards cryptic. Scorpions, paradoxically, may be either black or cryptic. Examples of mimicry and protective resemblance are also cited. It is concluded that scorpions, beetles and lizards are especially successful desert animals, not so much on account of unique adaptations to the harsh and variable environment as to their innate qualities which have adapted them for life in hot, dry and unpredictable habitats.

Introduction

The extreme physical and climatic conditions of the desert biome have engendered or enhanced a number of inter-related morphological, behavioural and physiological characters, many of which are paralleled in various quite unrelated groups or taxa of animals and even of plants. The basic problem for all desert organisms is the maintenance of an equable temperature without the expenditure of an excessive amount of water for evaporative cooling. To smaller animals, such as arthropods and reptiles (whose surface to volume ratio is correspondingly high), this problem — always present on land — becomes especially acute. It is significant that the integuments of desert arthropods and the cuticles of desert angiosperms both possess unusually impervious wax layers. There is also a positive correlation between the high critical temperatures (at which the monomolecular layers of epicuticular wax of arthropods become disorientated) and the high ambient temperature that the animals experience in their natural habitats. Below this critical temperature, the rate of water loss is especially low in scorpions and beetles (Edney 1977). Xeromorphic desert plants are characterized by having their stomata buried in the epicuticle below the general level of the plant surface or superficially depressed due to the extremely thick surrounding cuticle, while the spiracles of desert arthropods are similarly often sunken or hidden below the surface of the integument (Fig. 1) (Hadley 1972).

To give another example of parallelism between diverse organisms, locusts orient their bodies at right angles to the sun's rays in the morning and evening. At midday, however, when the heat is great, they turn their heads towards the sun, thereby reducing the surface exposed to radiation. Lizards do the same. So do beetles, ostriches, camels, wildebeest, springbok and probably many other species of antelope, while the movements of plant leaves and petioles, due to turgor changes, can likewise reduce the effective area so that excessive transpiration and wilting are avoided. Many other examples of parallelism between plants and animals could be cited.

Different taxa of animals respond to environmental factors in remarkably similar ways. When quite unrelated species come to look alike as a result of parallel evolution in unconnected geographical regions, they are known as 'ecological equivalents' or, more accurately, as 'ecological analogues'. One of the best known examples is provided by the fennec fox of the Sahara, which has a number of adaptive characters that match those of the American kit foxes. Likewise there is a close structural similarity between the kangaroo-rats of North America and the jerboas of the Great Palaearctic desert

---

**Department of Biology, University College London.*

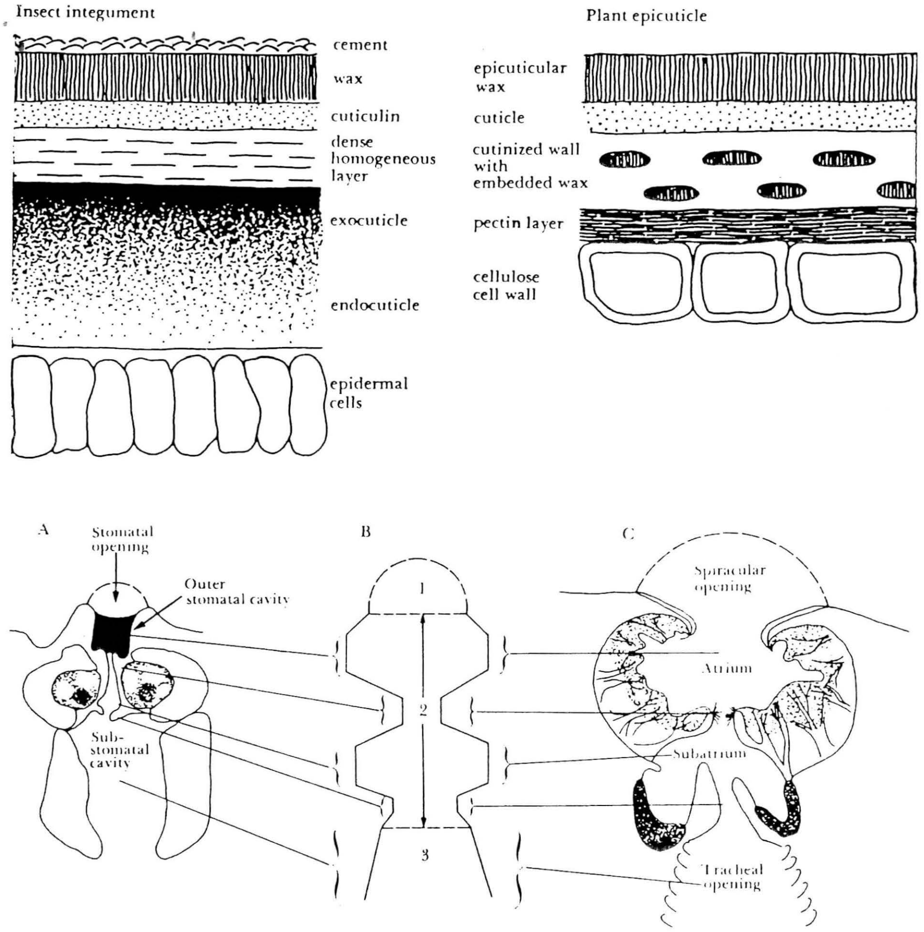

Figure 1. Above: diagrammatic structure of the insect integument compared with that of a plant cuticle. Below: comparison of drought resistance within and outside a plant stoma and insect spiracle. A. Cross-section of stoma Yucca*; B. Schematic representation of relative resistance to diffusion through an aperture of varying diameters: 1. External resistance (boundary layer); 2. Stomatal (spiracular) resistance; 3. Sub-stomatal (tracheal) resistance; C. Horizontal section through left spiracle of a desert beetle. (From Cloudsley-Thompson 1988, from Hadley 1972.)*

(Cloudsley-Thompson 1993). Reptilian examples include the Australian thorny devil (*Moloch horridus*) and its ecological analogue, the horned lizard (*Phrynosoma platyrhinos*) of the North American deserts which also exploits a diet of ants (Fig. 2). These are anatomically closer to one another than either is to any other member of its own lizard taxon (Pianka 1986). Another well-known example is provided by the North-American sidewinder rattlesnake (*Crotalus cerastes*) and its counterpart, the Saharan sand viper (*Cerastes cerastes*) (Fig. 3). Both species are so much alike in appearance that, but for the rattle of *C. cerastes* and the pits between its eyes and nostrils, the two species might easily be confused.

No taxon of arthropods appears to have been investigated in the way that desert lizards have been studied by Pianka (1986), but most desert regions are characterized by the presence of large, black tenebrionid beetles. *Eleodes armata* in North America might, for

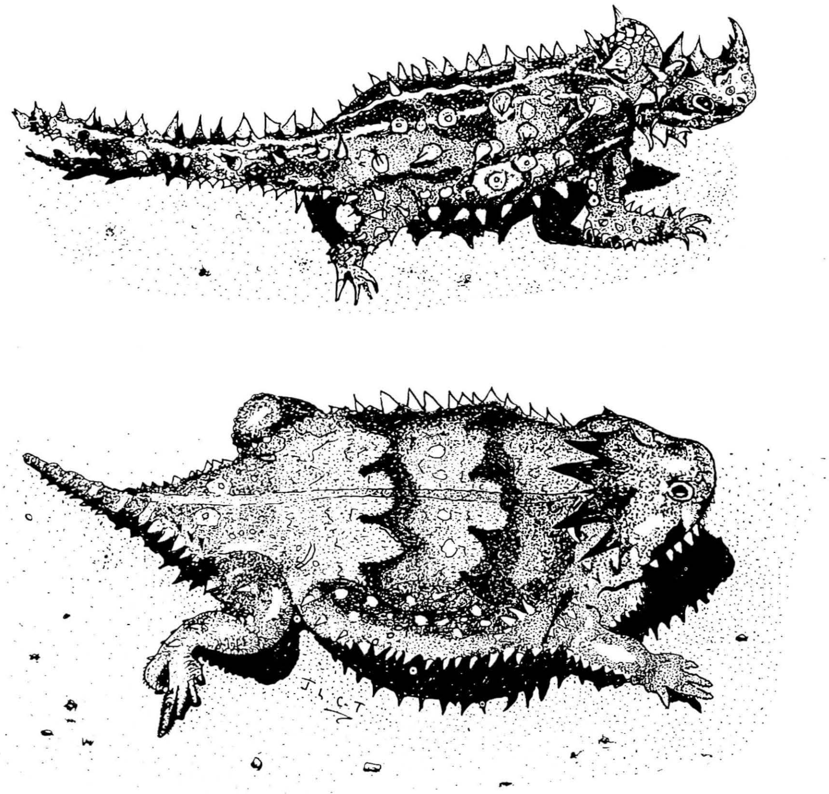

Figure 2. Above: Moloch horridus *(Agamidae), the thorny devil of the Australian deserts. Below:* Phrynosoma *sp. (Iguanidae), the horned toad of the North American deserts. (From Cloudsley-Thompson 1991.)*

instance, be regarded as an ecological analogue of *Blaps inflata* in the northern Sahara. Convergence is less marked among arthropods than among reptiles, probably because the former are smaller, more diverse, and therefore occupy less generalized ecological niches. Nevertheless, when comparisons are made between the scorpion fauna of the Kalahari and Namib deserts and that of the northern Sahara, it is found that, in contrast to the preponderant species richness of seven genera of Scorpionidae in southern Africa, there is only one species in the north, namely *Scorpio maurus* (Fig. 4) which is represented by numerous subspecies, each with differing life-styles, depending upon the texture of the soil. These subspecies, however, are comparable with analogous species of the genus *Opisthophthalmus* (Fig. 5) in southern Africa (Cloudsley-Thompson 1991; Vachon 1952).

The existence of ecological equivalents sheds light upon the selective factors that operate on desert organisms. Arthropods (especially scorpions and beetles) and reptiles (especially lizards) are uniquely successful desert animals, not so much on account of specific environmental adaptations as to their innate characters which pre-adapted them to life in hot, dry regions. They tend to avoid the extremes of the midday heat behaviourally by escaping into shelter or deep burrows, while conservation of water is primarily physiological. It can truly be argued that the ecology of these and other desert animals is affected less by thermal instability and the scarcity of water than it is by environmental unpredictability (Safriel *et al.* 1989).

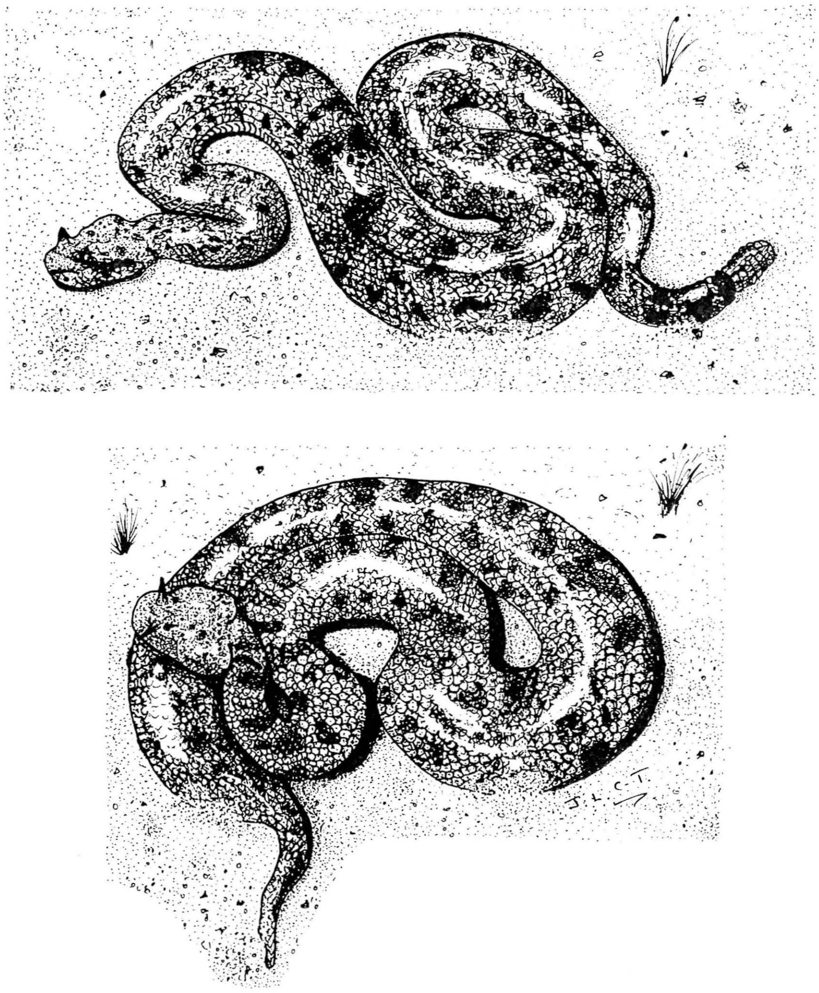

Figure 3. Above: Crotalus cerastes *(Crotalinae), the American side-winding rattlesnake. Below:* Cerastes cerastes *(Viperinae), the side-winding horned viper of the Great Palaearctic desert. (From Cloudsley-Thompson 1991.)*

Responses to Heat

Arthropods and reptiles are ectothermal — metabolic rates are low and most of their body heat is obtained from the environment. When their temperatures reach or exceed the optimum, however, they seek cooler microclimates (Fig. 6). Desert forms tend to avoid the heat on summer days by sheltering in burrows or in cool, shady retreats from which they emerge at dusk, dawn, or during the night. Even day-active species take shelter when their temperatures begin to reach lethal levels. The family Tenebrionidae contains the most conspicuous ground-living desert beetles. One of these, *Onymacris plana*, is a large black day-active species of the Namib desert. The fastest pedestrian insect known, with an average speed of 90 cm s^{-1}, *O. plana* runs swiftly across the hot dune sand from the shade of one plant to another without its body temperature becoming unduly elevated. Another Namibian tenebrionid, *Stenocara phalangium* (Fig. 7), carries its body well above the scorching sand on elongated legs. In contrast, the nocturnal *Stips stali* (Fig. 7) has a flattened body and short legs well adapted for burrowing in sand (reviewed in Cloudsley-Thompson 1991). Nocturnal species comprise the majority of desert beetles, but why the

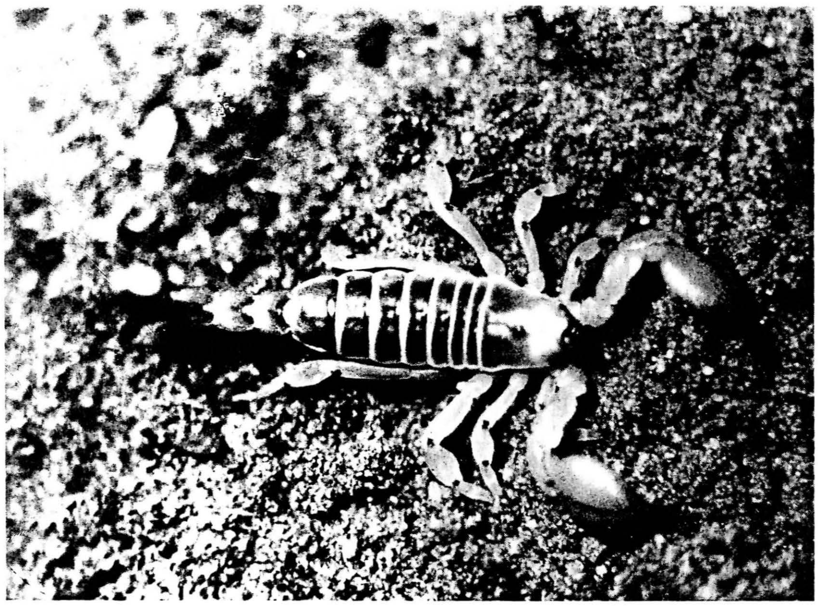

Figure 4. Scorpio maurus *(Scorpionidae). Great Palaearctic desert.*

Figure 5. Opisthophthalmus flavescens *(Scorpionidae). Namib desert.*

common Saharan *Adesmia antiqua* should be day-active while the sympatric *Trachyderma hispida* and *Pimelia grandis* are nocturnal (Cloudsley-Thompson 1963), has never been satisfactorily explained. It may possibly be related to the avoidance of competition.

In contrast to beetles, all desert scorpions are nocturnal, only emerging from their burrows and retreats at night. Yet they, like beetles, have surprisingly high lethal tempera-

Figure 6. Trachyderma philistina *(Tenebrionidae) of Kuwait, retreating into shade. (From Cloudsley-Thompson 1991.)*

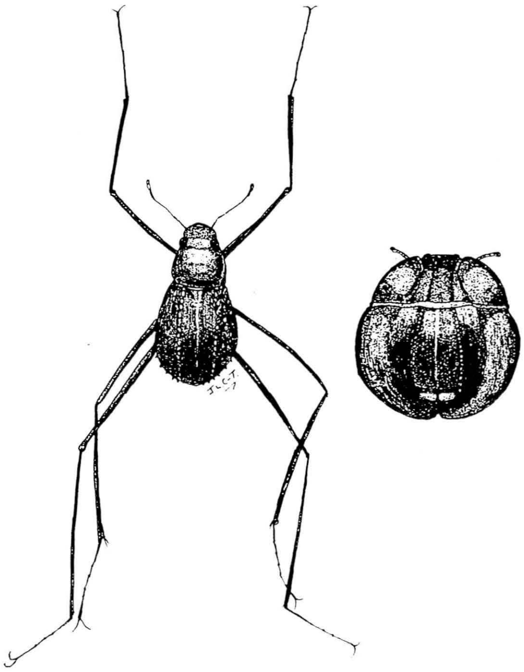

Figure 7. Namib desert Tenebrionidae. Left: Stenocara phalangium. *Right:* Stips stali. *(From Cloudsley-Thompson 1991, after C. Koch.)*

tures (reviewed in Cloudsley-Thompson 1991; Edney 1974). Several years ago, I postulated that scorpions may be nocturnal chiefly as an adaptation that enables them to evade large vertebrate enemies. Desert beetles, on the other hand, are conspicuous and distasteful to potential predators. Their conspicuous black coloration has a warning or aposematic function (see below) and they are not compelled to be nocturnal as an adjustment to avoid predation (Cloudsley-Thompson 1961).

The majority of lizards are day-active, but they maintain remarkably constant body temperatures by shuttling between sunlight and shade (Cloudsley-Thompson 1971). The ultra-psammophilous *Aporosaura anchietae*, for example, inhabits inland dunes of the Namib desert, feeding mostly on dry grass seeds. When surface temperatures approach 30°C on the slip-face, the lizards emerge from beneath the sand and press the ventral surface of their bodies against the substrate. As their body temperatures begin to rise they forage on the slip-face but, when the temperature of the surface approaches 40°C, they dive beneath the surface to reach a cooler environment (Louw 1972).

Emergence from burrows and retreats, with their equable microclimates, is controlled both by responses to environmental factors and by 'biological clocks' which synchronize the activities of burrow-dwellers with changing conditions in the outside world (Applin *et al.* 1987). Most arthropods and reptiles show circadian rhythms of locomotory activity, but those of desert species tend to be especially well marked. This subjective impression is difficult to prove experimentally, but there is evidence that desert centipedes, scorpions and mygalomorph spiders (tarantulas) are not only more strictly nocturnal than temperate and tropical forest species, but they are generally much more active (Cloudsley-Thompson 1981). The physiology of rhythmic locomotory activity in desert arthropods and reptiles has been reviewed in many books and reviews (see Cloudsley-Thompson 1991), so I will not discuss it again here.

Although the reactions of desert animals to heat are largely behavioural, it should not be imagined that physiological responses do not also occur. Scorpions, beetles and lizards of hot deserts are able to withstand considerably higher body temperatures than those tolerated by the inhabitants of cooler regions. Although small invertebrates are seldom able to afford the expenditure of energy necessary to raise their body temperatures metabolically, reptiles produce metabolic heat which may be conserved by shunting blood from superficial tissues and by decreasing the heart rate. The American horned lizard *Phrynosoma coronatum* (Fig. 2) shows a complex pattern of inter-relationships, both behavioural and physiological, that are combined in thermal regulation. Emergence from the sand during hours of normal activity depends upon a high head temperature and is independent of the temperature of the body, but the difference diminishes at higher body temperatures (Heath 1966). This means that the lizards emerge to bask in the sun and raise their body temperatures as soon as their brains are warm and they are fully alert. Moreover, the temperature of the head is regulated by opening lateral vessels that shunt blood from the cephalic sinuses to the external jugular veins, thereby bypassing a counter-current exchange of heat between the internal jugular veins and the internal carotid arteries (Fig. 8) (Heath 1965). At higher body temperatures, animals that are unable to seek shade or burrow, begin to pant and like tortoises, discharge liquid from the cloaca which cools them by evaporation.

Responses to Aridity

All aspects of ecophysiology are inter-related but, in hot deserts, none more closely than thermal and water relations. Because the drying power of the air is so greatly increased at higher temperatures, heat and drought are the two most important elements of the climate. Both arthropods, such as scorpions and beetles, and lizards are endowed with relatively impermeable outer surfaces. The epicuticular wax layer, characteristic of arthropods, is

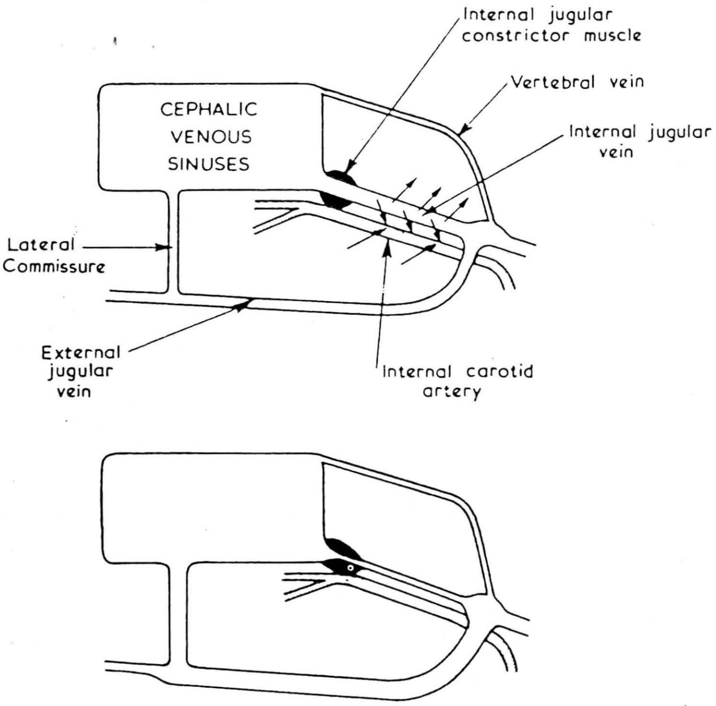

Figure 8. Diagram to show the relations of the major vessels in the head of the horned lizard Phrynosoma coronatum. *The venous spaces are abstracted to a single space. Above: Internal jugular vein is open. Arrows indicate heat exchange between internal jugular veins, internal carotid artery, and tissues of the neck. Below: Closure of the internal jugular constrictor muscle causes collapse of the internal jugular vein. Venous blood returns through a shunt to the external jugular vein. Cool blood enters the head while warm blood flows through the external jugular to the body. (From Cloudsley-Thompson 1971, after Heath 1966.)*

extremely impervious, and loss of water through lung-books and spiracles is kept to a minimum, as already mentioned. Although cutaneous water loss is actually somewhat higher than was previously thought to be the case, it is nevertheless lower in desert than in mesic species (see Cloudsley-Thompson 1991; Edney 1977).

Both arthropods and reptiles produce non-toxic insoluble, nitrogenous excretory compounds — guanine in the case of scorpions, uric acid in insects and reptiles. These appeared along with 'cleidoic' or enclosed eggs with impermeable shells, at the time of the conquest of the land, and are retained throughout the lives of the animals concerned. (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 (Cloudsley-Thompson 1988).) Consequently arachnids, insects and reptiles are pre-adapted for life in arid environments and further desert adaptation can only be a matter of degree.

Desert arthropods and reptiles are able to withstand a considerable degree of dehydration without ill effects, and must therefore be endowed with marked powers of osmotic and ionic regulation (Edney 1974). Some never drink, obtaining all the water they need from their food. Others drink when water is available. The beetles of coastal deserts, such as the Atacama and Namib, not only obtain water absorbed hygroscopically by dry vegetation, but drink droplets of moisture from fog condensed on their bodies. 'Fog basking' was

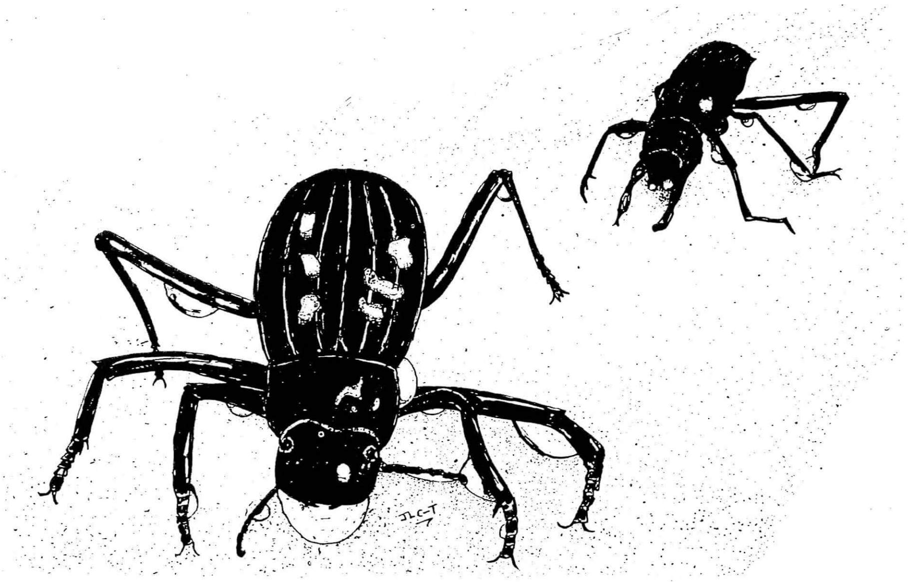

Figure 9. Fog-basking by Onymacris unguicularis *(Tenebrionidae) in the Namib desert. (From Cloudsley-Thompson 1991.)*

first observed by Hamilton and Seely (1976) in the Namibian *Onymacris unguicularis.* A characteristic head-down stance facing the wind is adopted and water trickles down the body to the mouth (Fig. 9). Although *Physadesmia globosa* is not a fog-basking species, it also emerges on foggy nights and sucks moisture from damp sand. The posture that it adopts whilst drinking is similar to that of *O. unguicularis,* which may provide an explanation of the origin of the adaptive behaviour of the latter (Cloudsley-Thompson 1991).

Avoidance and Deterrence of Predators

The three factors of the desert environment that influence its inhabitants most are heat, drought, and exposure to enemies. During their daily sojourn in retreats and burrows, nocturnal animals avoid the extremes of all these parameters. Even so, they do not escape them entirely, for the desert may still be hot at night, or it can be cold. It can be very dry, or even flooded, and enemies are never absent. Nor is there security in darkness, for light from the stars and moon in the clear desert sky is so bright that adaptive colouration is important at all times.

Adaptations for burrowing include the unusually thick and heavy pedipalps (claws) of scorpions of the families Diplocentridae, Vejovidae, Chactidae and Scorpionidae (Figs 4 and 5) although, even among these, digging is carried out mainly by the legs — the pedipalps being used chiefly for support. Most members of the family Buthidae, in which the claws are slender, do not burrow. Instead, they inhabit scrapes beneath rocks and surface litter. Exceptions include *Leiurus quinquestriatus* (Fig. 10) which ranges throughout the eastern part of the Sahara and the Middle East, and *Parabuthus hunteri* of the Sudan. These normally dwell in holes dug deeply into the ground. Four different life styles, with appropriate morphological adaptations, are recognised among scorpions: (a) lithophiles, adapted to life in cracks and crevices in rocks. These have flattened, elongated bodies and curved claws which provide the legs with a strong grip on rough surfaces; (b) psammophiles, with long tarsal claws for digging in loose sand; (c) fossorial scorpions which spend almost their entire existence in burrows, from the entrances to which they

Figure 10. Leiurus quinquestriatus *(Buthidae). Sahara.*

move actively whilst foraging. These have large, slender bodies and pedipalps (Polis 1990b).

It is worth remembering that, of almost 1500 known species of scorpions, there are less than 50 whose venom can be dangerous to human beings, and all of these are Buthidae with slender claws. Colour is no guide as to toxicity of the venom. *Leiurus quinquestriatus* (Fig. 10) has probably the most toxic venom of any scorpion in the world. Fortunately, the amount of poison that it produces is so small that adult human lives are seldom endangered, although *L. quinquestriatus* is a significant cause of death among young children (Simrad and Watt 1990).

Desert beetles, represented most strongly by members of the family Tenebrionidae, take refuge from heat and enemies beneath rocks and detritus (Fig. 6) or down the burrows of lizards and scorpions. They do not dig into hard soil, but dune species, such as *Lepidochora discoidalis* of the Namib, are saucer-shaped and readily burrow into loose sand. The tibial spurs, especially those of the hind legs, are long and flattened so as to be well adapted for raking. The adaptations of lizards for burrowing and swimming in sand include modification of the limbs for digging, shielding breathing movements from the surrounding sand, valvelike closure of the eyes, nostrils and mouth, and so on.

Most of the inhabitants of arid regions are either black or pale — resembling the background colour of the desert in which they live. This applies almost equally to nocturnal and day-active species, no doubt as a result of predatory selection at all times. The hypothesis is supported by the fact that more scorpions are active on nights with little or no moon, in comparison with nights when the moon is full (Hadley and Williams 1968; Polis 1990a and b). Desert lizards, both diurnal and nocturnal, are usually cryptic, their colour matching that of the background (Fig. 11). Many are able, to some extent, to change colour as chameleons do. They also become pale when overheated so that less solar radiation is absorbed. An exception is provided by the black lizards of the lava flows of New Mexico, which would become lethally conspicuous and vulnerable if they were to do so. The Gila monster and Mexican beaded lizard (*Heloderma* spp.) are the only lizards

Figure 11. Amphibolurus fordi *(Agamidae) of the arid regions of Australia. (From Cloudsley-Thompson 1991.)*

known to be venomous. Not surprisingly, they are also exceptional in possessing conspicuous colouration — black, with pink or yellow, respectively.

In contrast to lizards, desert Tenebrionidae and Scarabaeidae are frequently conspicuous, with black warning or aposematic colouration. This is associated with extremely tough integuments, unpleasant smell and taste. Scorpions seldom eat them unless starved for some months, but some camel-spiders (Solifugae) will readily devour them. North American darkling beetles of the genus *Eleodes* (Tenebrionidae) adopt a head down position when annoyed (Fig. 12) and spray their enemy with a smelly secretion containing benzoquinones. This irritates the skin, and has been found to repel a diversity of predators most effectively. No defence is perfect, however, and grasshopper mice learn to subdue these noxious beetles by holding them head up and forcing the tip of the abdomen downward so that the repugnant chemicals are discharged harmlessly into the sand (reviewed by Cloudsley-Thompson 1991).

Scorpions present a problem. As already mentioned, some are yellow, some black. Some are extremely venomous, others only mildly toxic to mammals, but all desert species appear to be nocturnal. I believe this to result from the vulnerability of these large, edible arthropods to vertebrate predators (Cloudsley-Thompson 1961). So, why are some yellow and some black? There is no correlation between colour and venom, so one cannot justifiably argue that, in one case, black is aposematic while, in the other, yellow is cryptic. Even congeneric, sympatric species may differ in colour. For instance, the Palaearctic *Androctonus australis* and *A. amoreuxi* are yellow, while *A. aeneas*, *A. bicolor*, *A. crassicauda* and *A. mauritanicus* are dark brown or black. They are all very large, with massive tails and slender claws, all extremely poisonous and capable of delivering large quantities of venom, yet their ranges frequently overlap, even though their habitats may differ (Vachon 1952). I am unable to offer any explanation for this apparent paradox.

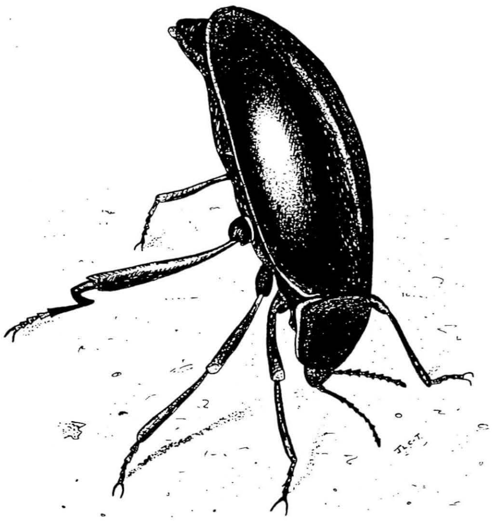

Figure 12. Eleodes *sp. (Tenebrionidae) of the North American desert spraying its defensive secretion. (From Cloudsley-Thompson 1991, after W. Wickler.)*

As in most environments, examples of mimicry and protective resemblance are to be found among the fauna of deserts. The universality of blackness among the beetles may well be an instance of müllerian mimicry (in which one or more distasteful species resemble one another, so that the numerical losses incurred in teaching enemies not to attack them are shared). Indeed, aposematic colours, other than black, are seldom if ever found in the desert (Cloudsley-Thompson 1971). Again, in a limited area of the Namib there is a complex of winged scarab beetles which have evolved orange elytra. The faster of these are believed to be müllerian mimics of one another: aposematic advertisement is correlated with speed and agility, and indicates that the beetles are not worth hunting. One species in the complex, however, is apterous and, therefore, a batesian mimic of the others. This is a rare example of speed mimicry in the desert (Holm and Kirsten 1979).

Although the adult lizards are cryptic, juvenile *Eremias lugubris* in the Kalahari are unusual in possessing a conspicuous pattern of black and white. In addition, they forage actively during the daytime with their backs arched, thus mimicking in colour, gait and size, carabid beetles of the genus *Thermophilum* (= *Anthia*) which spray a pungent acidic fluid when molested (Huey and Pianka 1977). The North American gecko *Coleonyx variegatus* arches the tail over its head when disturbed, and then, with its banded pattern, looks very much like the large scorpions (*Hadrurus* spp.) found in the same habitat (Parker and Pianka 1974). This may be a true case of batesian mimicry — for scorpions are by no means defenceless, even though it may pay them to avoid potential enemies. Alternatively, however, the posture may merely serve to divert the attack of predators from more vital parts of the body. The incidence of broken tails is high in this species. Some desert lizards in Australia elevate their heads, flatten their necks and actively strike at an enemy, thus mimicking poisonous snakes.

A fine example of protective resemblance is afforded by the round-tailed horned lizard *Phrynosoma modestum* (Iguanidae) of the Chihuahuan desert of North America. From a distance, this small species matches its background but, close up, it looks exactly like a stone. It is similar in size and colouration, and adopts a hunchbacked attitude (Sherbrooke and Montanucci 1988).

Discussion

Evidence for the success of scorpions, beetles and lizards in desert regions is demonstrated by the biodiversity there is of these taxa which, in the numbers both of species and individuals present, probably exceed all other macroscopic animals combined. Their success is due not so much to the possession of unique adaptations to the desert environment as to the innate qualities of the taxa concerned. These must have evolved very much earlier, and in relation to the conquest of the land. They pre-adapt their possessors to life in hot dry environments. Desert adaptations are not so much responses to the aridity and thermal instability of the environment as to its spatial patchiness, temporal variability, unpredictable water resources competition and exposure to predators (Safriel *et al.* 1989). Although the same basic physiological adaptations are employed by desert organisms as by related species elsewhere, they are usually modified in response to the extreme variability of environmental conditions.

According to Louw (1990) the question 'are desert animals special?' was first posed by the present writer in 1964. Since then, the proposition has had several proponents and, in 1987, a whole conference was devoted to the theme 'What's special about desert ecology?' (Rubenstein 1989). The conclusion reached was that there is nothing unique about deserts, apart from their enormous variance in almost all conceivable dimensions and scales. The organisms that inhabit them demonstrate 'elegant and unpredictable adaptations and interactions that are either not needed or completely obscured in less extravagant parts of nature' (Slobodkin 1989). The pre-adaptations and adaptations of desert scorpions, beetles and lizards clearly exceed those of all other taxa in this respect, making them conspicuously successful desert animals.

Bibliography

Applin, D. G., Cloudsley-Thompson, J. L. and Constantinou, C. 1987. Molecular and physiological mechanisms in chronobiology — their manifestations in the desert ecosystem. *Journal of Arid Environments* 13: 187–197.

Cloudsley-Thompson, J. L. 1961. Adaptive functions of circadian rhythms. *Cold Spring Harbor Symposia on Quantitative Biology* (1960) 25: 345–355.

Cloudsley-Thompson, J. L. 1963. Light responses and diurnal rhythms in desert Tenebrionidae. *Entomologia Experimentalis et Applicata* 6: 75–78.

Cloudsley-Thompson, J. L. 1964. Terrestrial animals in dry heat — arthropods. In Dill, D. B. (ed.), *Handbook of Physiology*. Sect. 4, pp. 451–465, American Physiological Society, Washington, D.C.

Cloudsley-Thompson, J. L. 1971. *The Temperature and Water Relations of Reptiles.* Merrow, Watford, Herts.

Cloudsley-Thompson, J. L. 1981. A comparison of rhythmic locomotory activity in tropical forest Arthropoda with that in desert species. *Journal of Arid Environments* 4: 427–434.

Cloudsley-Thompson, J. L. 1988. *Evolution and Adaptation of Terrestrial Arthropods.* Springer, Heidelberg, Berlin, Tokyo.

Cloudsley-Thompson, J. L. 1991. *Ecophysiology of Desert Arthropods and Reptiles.* Springer, Heidelberg, Berlin, Tokyo.

Cloudsley-Thompson, J. L. 1993. *The Diversity of Desert Life.* Scientific Publishers, Jodhpur.

Edney, E. B. 1974. Desert arthropods. In Brown, G. W. (ed.), *Desert Biology* II: 311–384, Academic Press, New York.

Edney , E. B. 1977. *Water Balance in Land Arthropods.* Springer, Berlin, Heidelberg, New York.

Hadley, N. F. 1972. Desert species and adaptations. *American Scientist* 60: 338–347.

Hadley, N. F. and Williams, S. C. 1968. Surface activities of some North American scorpions in relation to feeding. *Ecology* 49: 726–734.

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

Heath, J. E. 1965. Temperature regulation and diurnal activity in horned lizards. *University of California (Berkeley) Publications in Zoology* 64: 97–136.

Heath, J. E. 1966. Venous shunts in the cephalic sinuses of horned lizards. *Physiological Zoölogy* 39: 30–35.

Holm, E. and Kirsten, J. F. 1974. Pre-adaptation and speed mimicry among Namib Desert scarabaeids with orange elytra. *Journal of Arid Environments* 2: 263–271.

Huey, R. B. and Pianka, E. R. 1977. Natural selection for juvenile lizards mimicking noxious beetles. *Science (New York)* 195: 201–203.

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* No. 31: 297–314.

Louw, G. N. 1990. Physiological studies on the Namib fauna: a brief critique. In Seely, M. K. (ed.), *Namib Ecology — 25 Years of Namib Research.* Transvaal Museum Monograph No. 7: 203–207.

Parker, W. S. and Pianka, E. R. 1974. Further ecological observations on the western banded gecko, *Coleonyx variegatus. Copeia* 1974 (3): 521–531.

Pianka, E. R. 1986. *Ecology and Natural History of Desert Lizards. Analyses of the Ecological Niche and Community Structure.* Princeton University Press, Princeton, New Jersey.

Polis, G. A. (ed.), 1990a. *The Biology of Scorpions.* Stanford University Press, Stanford, California.

Polis, G. A. 1990b. Ecology. In Polis, 1990a, pp. 247–293.

Rubenstein, D. I. (ed.) 1989. Proceedings of a joint U.S.–Israeli workshop 'What's special about desert ecology?' held at Sede Boqer, Israel, 14–22 March 1987, organised by The Mitrani Center for Desert Ecology at the Blaustein Institute for Desert Research of Ben-Gurion University of the Negev, Israel. *Journal of Arid Environments* 17: 125–292.

Safriel, U., Ayal, Y., Kotler, B. P., Lubin, Y., Okvig-Whittaker, L. and Pinshow, B. 1989. What's special about desert ecology? In Rubenstein, 1989, pp. 125–130.

Sherbrooke, W. C. and Montanucci, R. R. 1988. Stone mimicry in the round-tailed horned lizard, *Phrynosoma modestum* (Sauria: Iguanidae). *Journal of Arid Environments* 14: 275–284.

Simard, J. M. and Watt, D. D. 1990. Venoms and toxins. In Polis, 1990a, pp. 414–444.

Slobodkin, L. B. 1989. What have I learned about deserts? In Rubenstein, 1989, pp. 287–292.

Vachon, M. 1952. *Études sur les Scorpions.* Institut Pasteur d'Algérie, Alger.