THE SAND-DUNE FAUNA OF THE NAMIB DESERT*

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THE sand-dunes of the South West African coastline at their first appearance would seem to be a region quite unable to support life. As bare as one's hand, these evermoving turbulent dunes, which rise in places to almost a thousand feet in height, resemble an endless sea of undulating sand stretching to the horizon. In these mindless and impersonal surroundings man becomes only an accidental occurrence, an unimportant and indeed unnecessary intruder, an utterly unnoticed and insignificant part of the landscape.

Between Walfisch Bay and Luderitzbucht this vast sand-dune desert stretches for about 300 miles and with an approximate width of 70; it is almost completely without water though in occasional years there may be a single sudden downpour of an inch or two. The last time a river came down in flood in this region was 1942.

How illusory this appearance of lifelessness is has been amply proved recently by the visit of an expedition, organised by the Transvaal Museum and Mr Bernard Carp of Cape Town, to the dunes at Gobabeb on the Kuiseb river below Walfisch Bay. An amazing fauna has come to light including about 40 species unknown to science, of Insects, Arachnida and Reptiles and this material can only be described as a sample or an assay of the total animal life of the dunes, and which was also taken at a rather unfavourable period of the year.

Fig. 1—The personnel of the Namib desert expedition, 7th–24th May, 1959. Standing, left to right: Messrs Herre, Port, Carp, Koch, Paulian, Prozeski, Lawrence, Vari and Brown.

(Photo: C. K. Brain)

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THE FAUNAL CONSTITUENTS

Desert sand provides a unique and unusual ecological background for a number of both nocturnal and diurnal animals. It might be of interest to record first the main groups which are not to be found on them. Among the vertebrates the amphibia are of course absent, and no tortoises are found. Among the invertebrates the absence of certain large and small groups is perhaps more significant. Insects more directly dependent on vegetation could not be expected and thus only a few of the strongly flying orders, such as flies and bees, were seen. Most orders of insects were represented by only a handful of species. No terrestrial crustacea, no mollusca and no earthworms were seen, though no doubt a few of these may later be found to occur there.

Of the other invertebrates all the Myriopoda, i.e. centipedes and millipedes, were conspicuously lacking, among the Arachnids certain widespread orders such as the Whip-Scorpions, Harvestmen and Pseudoscorpions.

The Sand-dune fauna can be divided almost entirely among three groups of animals, Insects, Arachnida and Reptiles.

The insects are predominantly composed of a single family of beetles well represented in deserts, the Tenebrionidae or Toktokkies; the members of this family are by far the most specialized of all the animals living in the dunes and in number of species and individuals they exceed those of all the other groups combined. The Arachnida are represented by spiders, of which there are a fair number, a few Solifuges and a single species of scorpion. The reptiles consist of 5 highly specialized forms, four lizards and one snake.

THE EFFECTS OF DESERT ENVIRONMENT ON THE INVERTEBRATES

When any animal has to face the austere and extreme conditions of heat and aridity which one finds in the Namib, it can do one of a number of things; it can take refuge from the savage heat by burrowing beneath the surface of the hot sand or seek temporary shelter under the sparse vegetation of the dunes, or it can feed in the early morning or late afternoon when it is cooler; others may go the whole hog and become nocturnal in habit.

The digging or burrowing habit is very widely developed in both vertebrates and invertebrates. The silver-fish or *Lepisma* insect is one of the last named; this humble insect (commonly called a primitive wingless insect) plays a very important economic role in the sand-dunes; it is extremely numerous in the Namib and takes refuge at the base of tussocks of the grass Aristida where it wriggles or almost swims with fish-like movements in the sand. At least one species of Hemiptera has the same habit. Even a species of the large powerful ant, *Camponotus detritus*, seems to show no objection to being buried in the sand and soon makes its way out. At least 3 genera and perhaps 6 species of Tenebrionid beetles have become flattened and platelike in appearance, with short legs and the thorax and abdomen expanded into wide but thin plates with sharp edges; they disappear rapidly into the sand with alternate sideways movements, as when a plate is thrown into water and can be seen descending with alternate lateral movements. Dr C. Koch of the Transvaal Museum, the authority on this family, found the dunes at night virtually covered with the slow-moving *Lepidochora*, a large flat-ivory coloured beetle; this was a species which during the day burrowed very deeply to avoid the heat of the surface stratum of sand.

Some of these flattened Tenebrionids which feed on the leeward side of the dunes on the slopes of loose, moving sand, can orientate themselves horizontally so that the smallest digging movements of the legs starts a cascade of sand from above, promoting a very rapid concealment in a covering of sand; other species of Tenebrionids have rounded bodies with very tough cuticles or extremely long spidery legs for rapid running over the sand.

Spiders belonging to at least three different families and about 6 species also burrow; they have strong fairly short legs with powerful combs of spines of various shapes and sizes for raking the sand. Most of them dig themselves completely into the sand; one of the *Zodariidae*, *Caesetius*, can cover itself in a few seconds, the large, rather obese abdomen being the last to disappear.

In addition the spiders, which are almost all white or pale yellow without markings of any kind, have enormous brushes of flattened hairs or bristles on the under sides of the tarsi which act like snow-shoes and facilitate their movements on the sandy surface. These structures are found in very many different arthropods, such as the silver-fish already mentioned (*Lepisma*), and a large nocturnal Gryllid (*Comicus namibensis*). At least one of the larger spiders, *Cerbalus*, digs a rough tube diagonally in the sand, cementing the sand grains with rough criss-cross webbing,

Fig. 2—The large white Sparassid dune-spider, Cerbalus, **a genus originally described from North African deserts.**
(Photo: C. K. Brain)

the spider lying at the bottom of the tube with its limbs contracted; the broad flat chelicerae, lying side by side, form a bull-dozer with which from time to time a fall of sand is pushed up the slope of the tube to its mouth.

The Solifuges and a single species of Scorpion were found in sand at the base of Aristida grass tussocks; both of these Arachnid orders make tubular burrows for themselves in other desert habitats and there is little doubt that they are sand dwellers in the Namib.

THE EFFECT OF THE ENVIRONMENT ON THE VERTEBRATES

Five species of reptiles live in the sand-dunes, four lizards and one snake; of these one lizard seems to be nocturnal in habit, the rest diurnal.

As in the case of the spiders and insects, many of the reptiles have some special adaptation for rapid burrowing; the shovel-snouted lizard *Aporosaura* and the Sand lizard *Scaptira* have shovel-like snouts and when hard pressed may literally dive head first into the loose sand, which becomes in effect a medium almost like water. The limbless Skink, *Typhlosaurus,* also has a sharp-edged snout and burrows quickly with serpent-like movements in the sand, where it seems to live almost permanently. Further adaptations for living in sand are to be found in the nostrils which are tubular and usually mounted on a raised swelling, with the openings pointed sideways or backwards rather than forwards; the ear openings are either protected by a grill of special scales or are strongly reduced in size; many of these lizards which have to contend against the eternal wind-driven sand of the dunes have a transparent lower eyelid, a sort of window surrounded by a ring of black pigment which, when raised, enables them to see with the eyes shut as it were.

Both the diurnal lizards *Scaptira* and *Aporosaura* have flattened scales at the sides of the toes which act like snow-shoes, enabling them to run quickly over the sand; this ability to move quickly over sand is of the greatest importance to lizards since for them it is often (to paraphrase Darwin) a question of the survival of the fleetest. The snow-shoe habit of locomotion is however most highly

Fig. 3—The web-footed dune Gecko, Palmatogecko rangei **preyed upon by the spider** Cerbalus. (Photo: C. K. Brain)

developed in the frail-looking nocturnal Gecko, *Palmatogecko,* which has a complete webbing between the fingers and toes for supporting it on loose sand. *Palmatogecko* is a small, weak and rather defenceless type of lizard, much more so than the quick-moving and fairly robust *Scaptira* and *Aporosaura,* so that a nocturnal habit of life would doubtless constitute its best form of defence against the perils of desert existence.

The extreme nature of the environment in the desert is probably as great a hazard to the lizards of the sand-dunes as the struggle to obtain sufficient food or to escape from their enemies. Though it is popularly assumed that reptiles can withstand very high temperatures (perhaps in view of their sun-bathing or basking habits), this is not so and they are even more susceptible to extremes of temperature than mammals and birds. Most lizards prefer temperatures ranging between 35° and 82° Fahrenheit, but are unable to tolerate for very long any rise above 117°, while the temperature of the desert sands may soar to 145° in summer time. If exposed for any length of time at 117° or above they are stricken with paralysis which attacks first the hind limbs and then the front ones; the respiratory centres are affected, they are unable to breathe, and death speedily follows. Bogert working in the Californian desert describes how he released a shade-loving nocturnal lizard so that it ran out into the

sunlight on a day when the sand temperature was 135°. On reaching the sun it stopped abruptly, opened its mouth and succumbed immediately.

How do the desert reptiles avoid these lethal temperatures in nature? There are several ways: first by retreating to cooler depths in the sand or in burrows in the ground, or by becoming nocturnal in habit. Secondly by using as a shelter any suitable vegetation or rock, and in this case speed of movement is an advantage in running from one sheltering retreat to another. Thirdly they can meet the extremes of temperature by pigmentary changes; with contraction of the pigment cells their skins become lighter and thus present more of a reflective and less of an absorbent surface, which is really what we do when we change into white linens on warm days. Under really extreme conditions reptiles may resort to respiratory movements, opening their mouths and gasping, as dogs pant in hot weather.

Some interesting pioneer work on the temperature preferences of South African desert reptiles and birds has already been begun by Dr C. K. Brain of the Transvaal Museum. He has found, during the expedition I have referred to, that the temperatures lethal for reptiles in the Namib desert agree largely with those noted by American workers for reptiles living in the Arizona and Mexican deserts.

The desert is probably more favourable to small lizards and snakes since small species can take greater advantages of short favourable exposures and of the numerous small shelters which occur in their surroundings; their activities will be more restricted however under conditions of long exposure, since they have a larger heat conducting and absorbing surface in proportion to their volume, than the larger lizards. Certainly all of the reptiles of the Namib sand-dunes can be considered small rather than large forms. Temperature regulation has given the mammals and birds an infinite advantage over the reptiles which today are forced to rely upon solar heat for bodily warmth; probably in the early mezozoic 170 million years ago, when the skull was becoming larger in the Karroo mammal-like reptiles, centres were arising in the brain which were to control their mechanisms for maintaining the constant heat of the body.

Yet not all the mammals have efficient heat regulating mechanisms since for all intents and purposes the sloth and the platypus are cold-blooded animals. There are also compensations in being a reptile; a large percentage of the food consumed by mammals and birds is used up in the oxidising process of keeping the body warm; this waste of energy is unnecessary in reptiles; thus they can go for long periods without eating and often one meal a week is quite sufficient to maintain them in good health, while they also save the energy spent in stalking and catching the meal. The reptiles, though they will never rule the earth again, are an old persistent stock, with plenty of stamina.

FOOD AND FOOD CHAINS

In studying an ecological habitat it is frequently useful to compile an Animal's "Who eats who" and "Who eats what". It was at first thought that the large population of Tenebrionid beetles with its numerous forms and individuals, comprising as it does a preponderance of the total fauna, would represent the basis of the food chain or at least provide the bulk of the food for such insectivorous vertebrates as lizards. This does not however seem to be the case. The only droppings found on the dunes composed almost entirely of Tenebrionid remains were obviously those of some small mammal, perhaps a mongoose or small felid, which, while not living on the dunes, would pay nocturnal visits to them from some more sheltered neighbourhood. None of the lizards would have strong enough teeth to crack the powerful shells of the larger black Tenebrionids, such as *Onymacris* or *Physosterna*, though they might be able to deal with the smaller flattened kinds like *Stips stali*. An exception should be made in the case of Gray's lark which was seen to feed near the sand-dunes from about 10 to 12 in the morning on the fast-running long-legged spider beetle *Stenocara*.

The basis of the food chain for most animals seems without doubt to be the seeds and other edible parts of the tough dune grass *Aristida amabilis* which is almost the

only plant able to grow there and constitutes the main binder of the sand. The tussocks of this extremely thick bamboo-like grass form oases providing both food and shelter for a small but varied biocoenosis.

These edible parts of the grass are blown down the slopes of the sand-dunes and moulded by the eddies of the almost unending wind into a more or less rounded, compact ball of vegetable matter, as the islands of weed are formed in a Sargasso sea. These masses of vegetable debris mixed with particles of dead animal matter collect in the hollows of the dunes, but this work is undone again by a change in the direction of the wind and the mass is again disintegrated and scattered over the dunes; much of its food content becomes gradually mingled with the upper layers of the sand on the leeward side of the dunes, where it is sought out by a number of species of Tenebrionid beetles and other insects. A few species of Hemiptera, various beetle larvae and perhaps some termites may actually feed upon the roots or stem of the grass itself, especially after it has been softened by decay.

The bareness of the sand-dunes and the complete lack of food material, except for the tough and austere dune grass, is thus more apparent than real. There is in fact, though not an abundance, a fairly good supply of basic food, the organic vegetable and animal debris mingled with the sands, and thus not immediately perceived.

There are also the corpses of a number of flying insects such as large Orthoptera which have been blown out of their course, made forced landings among the dunes and then have died there; these serve as food for the scavengers, to which category many of the Tenebrionid beetles belong, and it may be assumed that nothing is left over from such windfalls by the more hard pressed inhabitants, many of which must live a border-line existence from the dietary point of view.

Certain species of these scavenger beetles appear to surface at a fairly fixed time and our observers noted the regular appearance of one species in the evening shortly before sunset; others may feed in the early morning so that the feeding times of different species would be spaced out like the successive sittings for meals in a crowded train.

With the sinking of the sun and the coming of the cold dank mist which blows in from the sea and deposits a thin mantle of moisture on the sands, a new and different set of life forms arises from the unending sand to pass the night feeding and preying upon each other.

An ideal food for many small insectivores accustomed to seek for their food in sand would be the small silver-fish insect *Lepisma*. This creature was very abundant in the sand near grass tussocks and it was considered to be one of the main foods for small reptiles, such as the limbless and blind sand skink, *Typhlosaurus*, and perhaps also the delicate and rather defenceless web-footed gecko, *Palmatogecko*.

The large, tough and extremely aggressive ant, *Camponotus detritus*, found only on the Aristida grass, was evidently considered to be edible by some lizards. These ants and some of the smaller Tenebrionid beetles would probably constitute the food of the more robust diurnal lizards, *Scaptira* and *Aporosaura*.

The spiders and other Arachnids, being habitual carnivores, would presumably feed on whatever insect or reptile they could overcome, following the same way of life that they practise in other situations. The largest of the dune spiders, *Cerbalus*, an almost entirely pale creature measuring 4 inches with extended legs, was mainly nocturnal and appeared to prey on the rather defenceless web-footed *Palmatogecko*. This theory was admittedly based on circumstancial evidence; after we became familiar with the tracks of both spider and Gecko it was noticed that these tracks sometimes met upon the dunes at night; in such a case it was also noted that there were obvious signs of a scuffle and then only the tracks of the spider leading away from the scene. It seems however a fairly reasonable conclusion judging from the fact that this large spider is extremely active and actually pugnacious; its curious aggressive attitudes on the sand were responsible for the rather fanciful name given to it by Cape Town newspapers of the "White dancing spider of the sand-dunes".

In Natal another large wandering spider, *Palystes*, with a close family relationship to

this dune spider, often catches and feeds upon the small wall gecko *Lygodactylus*, a fact which was first noted many years ago at the Natal Museum by its first Director, Dr E. Warren.

The aggressive attitudes of the dune spider, which are far more developed than in any spider I have met with, can probably be ascribed to the fact that it is a large predatory arachnid with few opportunities of obtaining prey, living in a perpetual state of semi-starvation. Though very little is yet known about the food and feeding habits of the dune inhabitants, in this case the sequence of predator and prey, or food chain, seems to be as follows:—

Spider—Gecko	Ants Lepismids	Animal and vegetable debris in the sand

AFFINITIES OF THE FAUNA WITH THAT OF OTHER DESERTS

Mighty must be the power of environment when it can not only influence the mould of form but also the fashion of life of the organism. Apart from the faunal similarities between the North African and South West African deserts, for we find at least the dune spider, *Cerbalus*, and one genus of lizard common to both regions, each type of lizard or snake found in the dunes of the New World deserts can be duplicated by one found in the Sahara, and one in the Namib desert.

All the structures that have been developed by reptiles to contend with the exigencies of life in deserts of wind-blown sand are found equally in those of the Old and the New World; the snow-shoe type of flattened scales on the feet, the valve-like closure of the nostrils and the transparent lower eyelids of lizards are almost exactly similar in both hemispheres.

These convergences may be applied not only to the structures but to the habits of desert reptiles as well. The sand adders of the North American deserts are really small rattle-snakes or pit-vipers, those of the Sahara and South West Africa are true vipers, but they have all developed precisely the same peculiar and unique side-winding habit as a means of progressing over loose yielding sand. It is used by 3 species of adder in the Sahara, 1 Crotalid in California and 3 small adders in South West Africa. The side-winding habit has been photographed and analysed in the case of *Bitis peringueyi* by Dr C. Brain of the Transvaal Museum.

It may be briefly described as follows: the snake lies with the body in a loose S-like curve; as the curves undulate most of the body is lifted off the ground and the snake rolls smoothly and with most unexpected rapidity sideways across the sand. There is no hesitation or pause in the even and continuous movement. This complex manoeuvre appears simple in action but is extremely difficult to describe. The tracks made by the snake can be reproduced artificially by coiling two loops of ordinary wire in a flattened helix and rolling them over the sand.

It is an extraordinary sight to watch the Namib sand adder, *Bitis peringueyi*, side-winding up the 45° slope of loose and flowing sand on the leeward side of a dune, a performance which it could never achieve by the ordinary forward method of progression used by most snakes.

A COMPARISON OF THE NAMIB WITH OTHER SAND-DUNE DESERTS

It is almost certain that the Namib desert, comparatively small though it is, supports a larger, more varied and probably older fauna than any desert in the world. In this respect we can compare it with the North American, Peruvian and Sahara deserts which owe their aridity largely to the same causes as those that have created the South West African deserts. We should like to know much more faunistically about the smaller dune desert at the Southern tip of Madagascar, but at the present we can hardly compare it with the larger deserts of the world.

Only 3 species of reptiles occur in the sand-dunes of the Arizona deserts, at least 5 in the Namib, while the Tenebrionid fauna with an approximate total of 50 species is one of the richest and most diverse that can be found anywhere in an area of the same size. To explain how the numerous life forms

which the Tenebrionids have developed and the various ecological niches which they have explored and occupied would in itself require volumes of print.

Such a large and variegated fauna can only mean one thing, that speciation and adaptation to the peculiar and unique desert environment must have been proceeding over a very long period of time, probably longer than in any of the larger deserts of the world. We know that the S.W. African deserts are very old geologically and that the structure of the Namib plain was roughed out at least 50 million years ago and has since remained fundamentally unaltered. During all this time various animals have migrated into it from the outer lands, most of them accidentally, as animals from the open have wandered into caves; in time they became fixed in the desert mode of life and were unable to return. Over this long period there must have been a slow but steady increase in the number of species able to inhabit the dunes, each newly arrived animal or plant indirectly providing more food for the biota as a whole and for other new settlers.

I would that I had the skill in the use of words to fire your minds with a burning desire for desert exploration. Fate has given South Africa, among her many natural gifts, one which is perhaps a mixed blessing, the Cold Benguella current which washes her Western shores. This on the one hand has given us the South-easter and the miseries of the Cape winter climate and moulded the desert landscape with its drought and desolation. But it has also been responsible for a healthy fishing industry and the colourful beauty of Namaqualand with its carpet of spring flowers. It has indeed influenced not only our geology and geography but our industry, agriculture, our very history itself.

It has also placed within the convenient reach of our biologists one of the most typical sand deserts of the world, where problems only applicable to deserts can be studied. It is however impossible to do the work required under canvas in a climate where sand storms often continue for days on end, and it is essential to have a more permanent station for such work. It would not require a very great outlay to provide a permanent sand-proof and largely heat-proof laboratory and living quarters at a station somewhere south of Walfisch-Bay. A water-hole sunk in the nearby riverbed and a windmill would solve the water supply question while the wind could be harnessed to provide lighting. Some kind of motor vehicle able to negotiate large sand-dunes would be essential for transporting workers to various sites in the desert without waste of time and energy.

There is a great deal to be done; we should require visiting meteorologists, geologists, botanists and zoologists at the very least and probably many other specialists. There would be innumerable projects on which to begin work: the organic and mineral composition of the sand, temperatures, humidities, rates of evaporation and precipitation, lists of the fauna and flora, food chains and stomach contents; all these apart from much essential experimental and physiological ground work. A course in practical desert biology could be arranged for advanced students at our Universities and I am convinced that motion pictures of desert life could be made which would far exceed Walt Disney's "Living Desert" in beauty and scientific interest, apart from the fact that funds could be earned in this way for the upkeep of the Station.

South Africa by erecting a permanent Station in the Namib would lead the states of Africa in the exploration of desert life and the problems connected with it. It seems to me a unique opportunity and a fitting time for establishing such a Station—indeed it is one that we cannot afford to miss.

I would therefore ask you, Mr President and Members of this Association, for your moral and practical support of this project.

NATAL MUSEUM,
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