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# THE ROLE OF ADVECTIVE FOG IN THE WATER ECONOMY OF CERTAIN NAMIB DESERT ANIMALS

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## SYNOPSIS

The Namib desert is a long narrow coastal desert on the southwestern coast of Africa. The presence of the cold Benguella current on the western margin of the desert has a profound effect upon the climate of the Namib and is responsible for the frequent occurrence of advective sea fog over the desert. The frequency of fog and the accumulation of wind-blown plant detritus in those areas of the desert which are almost devoid of vegetation, provides sufficient water and energy to support a surprisingly varied endemic fauna. Certain of these animals, such as the tenebrionid beetle *Lepidochora argentogrisea* and the psammophilous lizard *Aporosaura anchietae*, have evolved a physiological dependence upon fog water and are capable of a considerable degree of water storage. Other animals within the ecosystem such as the ostrich and Namib gerbil, are physiologically well adapted to desert life but are not able to store water or exist indefinitely on dry food. These animals, are, however, indirectly dependent on fog water by feeding on succulent plants which are sustained by the regular condensation of fog.

## INTRODUCTION

The Namib is a desert on the southwestern coast of Africa. In length it is over 16 000 km and it extends southwards from Mossamedes in Angola to below the mouth of the Orange River (lat. 15 to 30°S). In contrast with this great length the Namib is comparatively narrow, seldom extending for more than 130 km into the interior of the continent. The eastern border of the desert is demarcated by the foothills of the Western Escarpment which rises to an undulating plateau at 1200-1800 m above sea level. The Atlantic Ocean forms the western margin of the desert and the northern and southern halves of the Namib can be roughly divided on geomorphological criteria at the Kuiseb River. The northern half consists of flat gravel plains occasionally interrupted by *Inselberge*, while in the southern portion the plain is overlain by a massive dune system which extends southwards from the Kuiseb without interruption for over 320 km. These physiographic features are illustrated in Fig. 1. They exert a profound effect on the climate of the desert and consequently on the ecology and physiology of the endemic fauna and therefore warrant further brief description.

The cold Benguella current which sweeps up the western coast of southern Africa is indirectly responsible for the extreme aridity of the

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FIG. 1. A view of the central Namib Desert taken from outer space. The massive parallel dunes which end abruptly along the Kuseb River bed are clearly visible, as are the foothills of the escarpment on the right (Courtesy, United States Information Service).

Namib. In this respect it is important to note that in the western half of the desert, the area in which the present investigations were conducted, the rainfall is so low and variable that it can be considered negligible for the purposes of this discussion. As a result vegetation in the western half of the desert is extremely sparse and limited to a few specialized species such as *Zygophyllum*. In contrast the eastern half of the desert receives some rain (25–50 mm per annum), although very sporadically. These sporadic thunderstorms result in a dramatic growth

of the grass cover, predominately *Stipagrostis* species, on the gravel plains and between the parallel dunes on the so-called dune streets. The escarpment on the eastern border of the desert receives sufficient rainfall to support a mixed plant cover of shrubs and perennial grasses.

An additional and equally important effect of the proximity of the cold Benguella current is the regular occurrence of advective sea fog and the cool, moist southwesterly sea breeze. Fog occurs most frequently on the coast but has also been recorded infrequently as far as 130 km from the coast. The frequency of fog at Gobabeb, some 56 km east of the coast, has been summarized in Fig. 2. These data were originally compiled by Schulze (1969) over a five year period and show

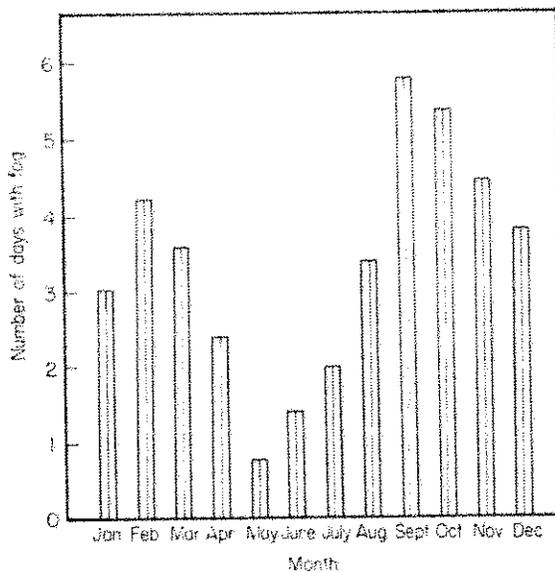


FIG. 2. Mean number of days per month on which fog occurs at Gobabeb, some 56 km East of the Atlantic coast. (Compiled from data in Schulze, 1969.)

that fog can be expected at least once per month throughout the year. The fog frequently, although not always, condenses on the surface and on wind-blown plant detritus in the form of fine droplets of water. We have collected fog water in glass containers and from the surface of plants and wind-blown detritus. The osmolality of these samples ranged from 14–38 m-osmole/l which is surprisingly low and emphasizes the suitability of fog as a source of water for the endemic Namib fauna.

The prevailing winds of the Namib are the cool, southwesterly sea breeze and the desiccating, easterly *berg* wind. These winds are responsible for sculpting the large parallel sand dunes of the southern Namib. As a result of wind action the sand on the windward side of the dunes becomes compacted while the leeward side consists of soft wind-blown

sand which is an ideal medium in which burrowing animals can escape from extremely high or extremely low surface temperatures. For example, while studying the temperature profile of a dune we found that the temperature of the sand 7.5 cm below the surface was 38°C at 14.00 h compared with 60°C on the surface. Conversely, at 18.00 h the temperature on the surface had dropped to 20°C while at a depth of 7.5 cm below the surface the temperature was 33°C.

In addition to the sculpting effect of the prevailing winds they have other extremely important influences. The southwesterly sea wind, which usually begins to blow in the early afternoon in response to the intense insolation of the fore-noon, cools the surface of the sand rapidly and raises the relative humidity of the air. In this way more favourable conditions are created for diurnal animals. The easterly *berg* wind, on the other hand, originates over the escarpment on the eastern border of the desert and, because of the sudden drop in altitude between the escarpment and the desert plain, the temperature of the air mass increases rapidly giving rise to a very strong, hot and desiccating wind. The strength of this wind is such that dry grass stems and seeds are lifted into the air and blown into the vegetationless dune system where they accumulate in the form of cushions of detritus. This detritus has a gross energy value of approximately 3800 cal/g and represents a very important source of energy for the dune fauna.

In summary, then, the Namib Desert is a true desert of extreme aridity which experiences very high temperatures at times. These hostile conditions are, however, tempered by a cool moist sea wind and the fairly frequent occurrence of advective fog. In addition, some of the areas without vegetation receive a secondary supply of food energy in the form of wind-blown plant detritus. As a result the apparently lifeless, barren dunes and gravel plains support a surprising variety of animal life. The first authoritative description of this fauna was written by Koch (1961). Until recently, however, no attempts have been made to correlate the physiology of any of these species with the unusual, if not unique, habitat provided by the Namib. This paper, then, is a brief summary of physiological studies carried out over the past three years on several key species inhabiting the Namib. Special attention has been given to water economy and thermoregulation in an attempt to elucidate the physiology of adaptation of these species to the desert environment.

#### METHODS

The methods employed were all of a standard nature and require little elaboration. Field observations of thermoregulatory and feeding

behaviour were supplemented by laboratory observations in a temperature controlled chamber and in artificially constructed enclosures in the open air. Blood, urine and haemolymph samples were collected from freshly killed animals in the field and from animals kept in the laboratory. These were analysed by standard methods using flame photometry for determining electrolyte concentrations and an osmometer (Advanced Instruments) for determining the osmolality of large samples and the method of Gross (1954) for small samples. Temperatures were recorded with a variety of instruments including fast registering cloacal thermometers, a YSI telethermometer and radiotelemetry.

The studies were conducted mostly at the Namib Desert Research Station, Gobabeb, South West Africa.

#### RESULTS AND DISCUSSION

The selection of suitable species to illustrate physiological adaptation to the Namib environment is difficult because of the large variety of interesting examples. For instance, the organisms inhabiting the bare gravel plains in the western half of the desert exhibit interesting adaptations and occupy unusual microhabitats. On first inspection, however, this habitat appears to be a lifeless plain covered with scattered quartz stones. Closer examination of these stones, nevertheless, reveals that the regular occurrence of advective fog and the presence of wind-blown detritus have created suitable conditions for animal life beneath the stones. The sea fog condenses frequently upon the stones and provides water for lichens which grow on the upper surface. If the condensation of fog water is sufficiently heavy, the water will reach the lower surface of the stone, thus creating a moist environment which is sufficiently cool for the growth of green algae. In addition, wind-blown grass frequently collects on the eastern side of the stones and in this way an ideal microhabitat and niche is created for arthropod life (Fig. 3).

In spite of the interesting adaptations encountered on the gravel plains the vegetationless dunes represent the most unusual habitat and it is from this ecosystem that five samples will be taken to illustrate physiological dovetailing with the previously described habitat.

#### *The tenebrionid beetle Lepidochora argentogrisea*

The wind-blown grass or detritus which collects on the leeward side of the vegetationless dunes represents the most important primary source of energy to the psammophilous fauna inhabiting the soft wind-blown sand on the leeward side or slip-face of the dune. One of the most important direct utilizers of this energy is the tenebrionid beetle

Fog on  
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*Lepidochora argentogrisea*. For this reason we have examined thermo-regulation, digestion, metabolism and water economy in this species (Louw & Hamilton, 1971).

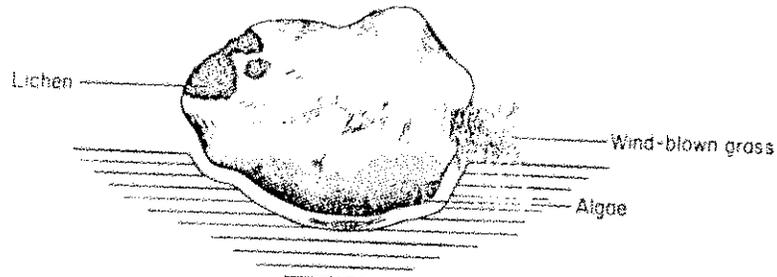


FIG. 3. Diagrammatic representation of the effect of fog on stones covering the vegetationless gravel plains. Lichens grow on the upper surface of the stone while condensed fog water reaching the lower surface creates a suitable microhabitat for algae and arthropods, the latter feed upon wind-blown grass collecting on the windward side.

These beetles are morphologically very well adapted to their ultra-psammophilous existence (Fig. 4) and as they are largely nocturnal in habit they escape from the extremely high surface temperatures, experienced on the slip-face during the day, by burrowing beneath the sand. Their strict nocturnal activity pattern can be changed by a facultative response to surface wind. Whenever strong winds occur the surface of the sand is cooled and the beetles emerge in large numbers to feed upon the detritus brought in by the wind. Nevertheless, this species appears to have a wide temperature tolerance since active individuals have been observed on the surface of the sand when the surface temperature was as low as 6°C. They seldom emerge, however, at surface temperatures approaching 40°C and for the most part are exposed only to cool night temperatures. In this way excessive water loss experienced during high temperature conditions is avoided.

The ability of *L. argentogrisea* to digest the wind-blown detritus was examined and it was found that they were able to obtain sufficient nutrients from the detritus to satisfy their calorific requirements, which were determined in a separate metabolism experiment. The digestible cellulose and other nutrients obtained from digestion can, after absorption, naturally serve as an important source of metabolic water. This fact, coupled with the ability of *L. argentogrisea* to withstand desiccation at 0% rh, as efficiently as the familiar *Tenebrio molitor*, would lead one to believe that they are independent of free water. This was not found to be the case since the animals slowly lose weight on air dry food.

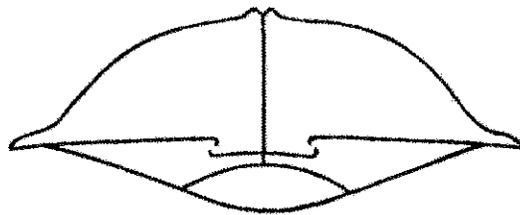
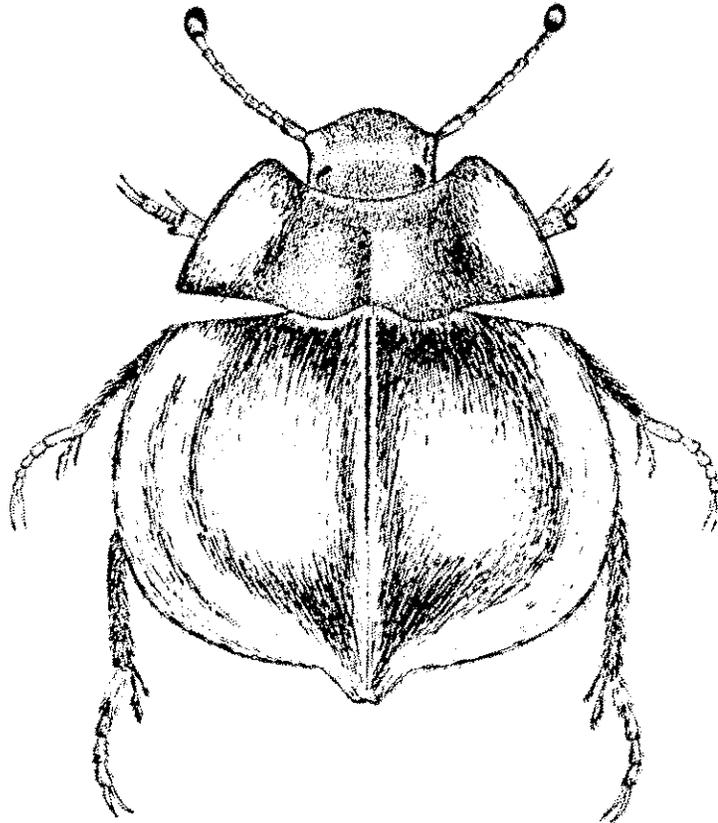


FIG. 4. Dorsal view of the psammophilous tenebrionid *Lepidochora argentogrisea*. The body outline (below) shows the projecting epipleura, beneath which droplets of fog water collect. (Adapted from original by Koch, 1962.)

These beetles thus require a source of free water and the most obvious choice would be fog water. It was not surprising, therefore, to find beetles above the surface of the sand during a heavy condensing fog. The fog had condensed on the dorsal surface of the elytra in the form of fine drops. Moreover, in the afternoon of the same day, several hours after

TABLE I

*The effect of hydration upon the osmolality of the haemolymph of L. argentogrisea\**

Group	N	Osmolality of the haemolymph (m-osmole/l)		
		Mean	SD	% difference
Hydrated beetles	12	339	± 20.3	
Dehydrated beetles	12	427	± 15.9	+ 26%

\* From Louw & Hamilton (1971).

the fog had cleared, water drops were still found on the ventral surface of beetles which had been removed from beneath the sand. These drops were found to be clinging to the ventral surface of the epipleura. Subsequent laboratory studies showed that water drops, sprayed on to the dorsal surface of the elytra, are not directly absorbed through the cuticle. Nevertheless, these drops do not evaporate as quickly as similar sized drops placed on an inert ceramic surface, which may mean that the water drops coming into contact with the cuticle are surrounded by a lipid layer.

Laboratory studies did, however, show that water sprayed on dehydrated beetles entered the digestive tract and subsequently caused a marked reduction in the osmolality of the haemolymph (Table I). In this way water is stored in the soft tissues of the insect until the next fog occurs.

#### *The sand-diving lizard Aporosaura anchietae*

These lizards inhabit the soft wind-blown sand of the dune slip-face. Unlike the *Lepidochora* beetles they are diurnal animals but, nevertheless, escape extremely high and low surface temperatures by adopting a bimodal activity rhythm which coincides with surface sand temperatures between 30–40°C. Because of the prevalence of these animals on the dune slip-face we have examined their feeding habits, thermoregulation and water economy in some detail (Louw & Holm, 1971).

In their feeding habits *Aporosaura* are opportunistic. For example, on the dunes immediately adjacent to the Atlantic Ocean they feed almost exclusively on kelp flies. The flies have a high moisture content which is sustained by the precipitation of fog water upon their wings.

On the other hand, *Aporosaura* which inhabit the inland dunes feed mostly on dry grass seed which is an important constituent of the wind-blown detritus which collects on the vegetationless dunes. The latter group therefore, although they will capture the occasional arthropod when the opportunity arises, are, as a result of the nature of their diet, exposed to a greater risk of dehydration.

This risk of dehydration is further aggravated by their preferred temperature range of 30–40°C. Temperatures within this range are experienced for a relatively short period on the dune slip-face but the animals make maximum use of this short period by employing a characteristic thigmothermic behaviour pattern. 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. In order to achieve maximum contact with the substrate all four limbs and the tail are raised off the surface of the sand and the body temperature of the animal rises swiftly. The lizards then begin to forage on the slip-face but, as the temperature of the surface approaches 40°C, they move the body as far as possible away from the surface of the substrate by straightening the limbs. They will occasionally interrupt this stilt-like walk to raise diagonally opposite limbs while using the base of the tail for support (Fig. 5). This thermoregulatory dance allows the lizards to remain above the surface for as long as possible but when the surface temperature exceeds 40°C they dive beneath the surface to reach a cooler environment.

The exposure of the lizards, although only briefly, to the strong insolation on the slip-face at temperatures between 30–40°C must result in a considerable loss of moisture. Moreover, the nature of their diet, which contains a large percentage of dry grass seed, aggravates the situation further and they are therefore compelled to utilize a source of free water. The most obvious source is again fog water and, although we have never observed the animals drinking fog water, we have strong circumstantial evidence that they do. For example, when the animals are killed and dissected shortly after the occurrence of a heavy condensing fog, the stomach is enormously distended and filled with water. Subsequently this water is transferred to the caecum which expands to accommodate it and even after eight weeks there is a significant amount of fluid still present in the caecum. Moreover, in captivity the animals drink readily when water is sprayed in the form of fine drops on the glass side of the terrarium. In doing so they consume about 10% of their body weight in water and exhibit twisting and writhing movements of the body during the last phases of drinking. These movements presumably facilitate the consumption of an abnormally large volume of



FIG. 5. The psammophilous lizard *Aporosaura anchietae* engaged in thermoregulation on the dune slip-face. (See text for explanation.)

fluid. In Table II the effect of dehydration upon the plasma osmolality of *Aporosaura* is illustrated. These data show that, similar to *Lepidochora*, the plasma osmolality of *Aporosaura* appears to be fairly labile and is influenced by the degree of dehydration. It would appear, then, as if *Aporosaura* is capable of a considerable degree of water storage and that its physiology in this respect is well adapted to dependence upon the peculiar Namib weather pattern of regular advective sea fog. It is also important to note in this respect that the known distribution of *Aporosaura* is limited to the fog belt of the Namib.

TABLE II

*The effect of dehydration upon the plasma osmolality of the lizard Aporosaura anchietae\**

Group	N	Plasma osmolality (m-osmole/l)	
		Mean	Range
Freshly captured after recent fog	8	312	275-320
Dehydrated in captivity for three weeks	5	420	410-435

\* Adapted from Louw & Holm (1971)

*The side-winding viper Bitis peringueyi*

This viper with its characteristic side-winding mode of locomotion is fairly common in the dune ecosystem of the Namib. They have been observed to be active on the surface of the sand both during the day and at night. It is, however, not yet known whether they are diurnal or nocturnal. In any event, the ease with which they are able to submerge themselves beneath the sand allows them to escape the dehydrating effect of extremely high temperatures. Moreover, they have been seen to feed upon *Aporosaura* lizards which would ensure a high moisture content of their diet. It is not surprising therefore that these animals have been successfully kept for over four months in captivity without access to water. Nevertheless, acting on an original observation of K. Schaer in 1969 I was interested in determining whether these animals made use of fog water. In order to determine this, two individuals were placed in an enclosure which prevented fog condensing either on the snakes or near them. They were regularly fed on small live lizards.

After two months the snakes were sprayed with water in the form of a fine mist which settled on the dorsal surface of the animals. As soon as a snake became aware of the water droplets it became excited and immediately flattened its body against the substrate in order to increase the surface area exposed to the spray. At the same time the snakes coiled up and the head moved back and forth over the dorsal surface of the body as the animal licked off the water droplets. This behaviour was interrupted every few minutes to raise the head some 10 cm above the ground to assist the flow of water into the digestive tract by gravity (Fig. 6). This well defined behaviour pattern would appear to indicate that *Bitis peringueyi* makes regular use of condensing fog water under natural conditions. It is also of significance in this respect that the distribution of *B. peringueyi*, like *Aporosaura* is confined to the Namib fog belt.

#### *The ostrich* *Struthio camelus*

The ostrich, unlike the species described previously, cannot escape to a favourable microclimate to avoid excessively high temperatures. Moreover it has the added disadvantage of maintaining a fairly constant body temperature (Crawford & Schmidt-Nielsen, 1967). Nevertheless, it successfully inhabits some of the most arid regions of the Namib and for this reason we have examined thermoregulation and renal function in these birds (Louw, Belonje & Coetzee, 1969).

Although the ostrich maintains a fairly constant body temperature of 38–40°C it makes maximum use of convective and radiant cooling in order to reduce water loss to a minimum. This is achieved by erecting the feathers over the body and moving the wings away from the body to expose the thorax and thighs which are not covered by feathers. In this way the convective cooling action of the slightest breeze is utilized and the temperature of the air space between the feathers and the skin is reduced sufficiently to allow loss of body heat. Only as a last resort, when there is no wind will the ostrich employ evaporative cooling by raising its respiration rate suddenly from approximately 4 to 40/min. Conversely, at low ambient temperatures the feathers are folded closely against the skin and the temperature of the air space between the feathers and the skin rises rapidly to form an insulative layer (Fig. 7).

The ostrich also has efficient renal function. When deprived of water and fed only on air dry food (9% water) the urine volume decreased dramatically and the osmolality rose sharply to reach a maximum of 800 m-osmole/l. The concentration of potassium in the urine rose to a value of 139 m-equiv/l while the concentration of sodium fell from 76 to 30 m-equiv/l indicating efficient aldosterone control. Concurrently

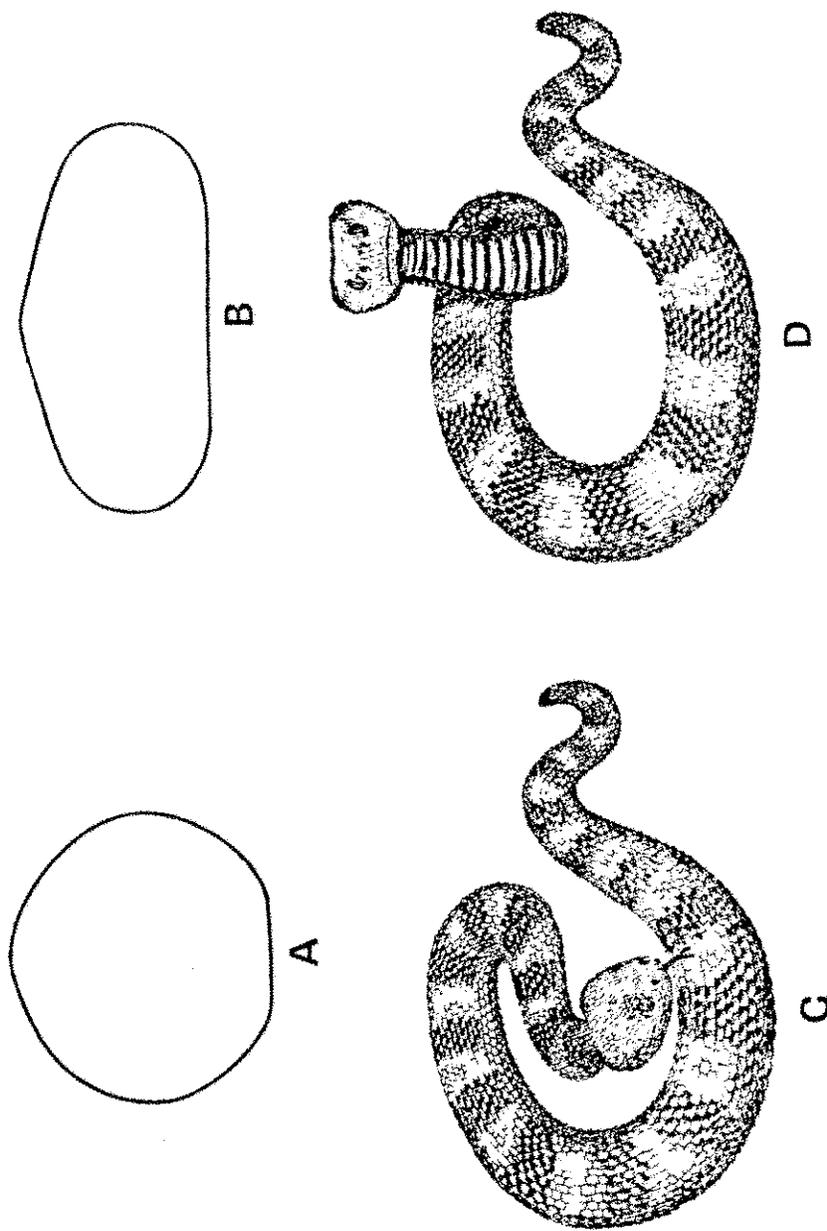


FIG. 6. The side-winding viper *Bitis peringueyi* responds to a water spray by flattening the body (A-B), drinking the water droplets (C) and finally raising the head to assist the flow of fluid into the digestive tract (D).

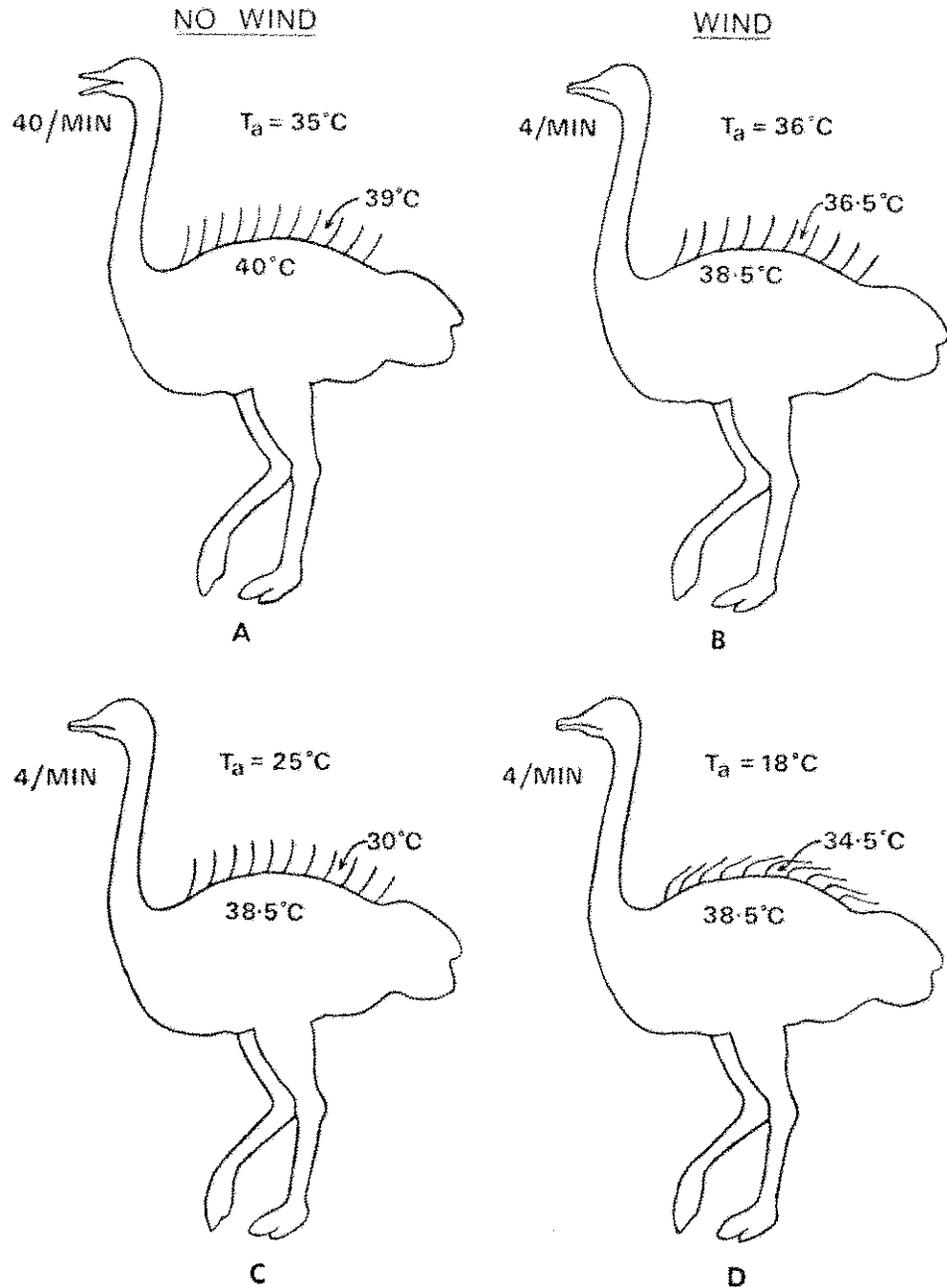


FIG. 7. Thermoregulation in the ostrich involves thermal panting and feather erection under conditions of no wind and high ambient temperature (A). In windy conditions feather erection alone is frequently sufficient to allow body cooling (B, C) while at low ambient temperatures at night the feathers are flattened to provide an insulating layer of air (D).

the undissolved uric acid content increased by approximately 1500% and its excretion was facilitated by copious mucus secretion from the epithelial lining of the ureter. Finally, during the dehydration period osmolality of the plasma remained remarkably constant.

With the above physiological background in view, it is therefore not surprising that the ostrich cannot exist indefinitely on dry food. After eight days they refuse to feed and lose weight steadily. Moreover, if they are forcibly hydrated by administering 11 l of water to them (10% of body wt), the excess water is rapidly excreted and the plasma osmolality is not significantly affected as it is in the species discussed previously. Very little, if any, water is therefore stored yet the animals survive in areas without surface water. The answer to the question of their means of survival is to be found in the high moisture content of certain plants, the frequent occurrence of condensing fog and the comparatively high relative humidity of the air at night in the Namib. For example, we have recently examined the effect of the relative humidity of the air on the moisture content of a dry perennial desert grass *Stipagrostis uniplumis* which is favoured by ostriches (M. K. Jensen & G. N. Louw, unpubl. obs.). The results are illustrated in Fig. 8 and show how closely the moisture content of the grass follows the humidity of the air. It is also clear that when grazing in the early hours of the morning the ostriches are feeding on grass with a moisture percentage of almost 27%. At 13.00 h the moisture percentage had dropped to below 10% but at the same time a succulent species of *Bohenia* which had been heavily grazed contained 68% moisture. Naturally after a heavy condensing fog the moisture intake during grazing would also be very high for several hours. Finally, when faced with extreme water deprivation the ability of the ostrich to move rapidly over long distances would allow it to visit isolated water holes.

It would appear then that, although the ostrich cannot use fog water as efficiently as the species described previously, it nevertheless is of direct importance and probably of secondary importance in sustaining succulent plants upon which the ostrich feeds.

#### *The Namib gerbil Gerbillus paeba*

The Namib gerbil is one of the very few mammals to be found in the dune ecosystem. It is strictly nocturnal and during the day remains hidden in fairly deep burrows which it frequently constructs in the fairly compact sand which surrounds the root system of the leafless but thorny narras plant *Acanthosicyos horrida*. The entrance to the burrow is always closed during the day and these animals are never exposed to the dehydrating effects of high temperatures. They are herbivorous and

never drink water. A study of their water economy was therefore undertaken.

It was found that when these animals are fed exclusively on a commercial mixture of bird seed, high in carbohydrate and low in protein and kept at an ambient temperature of 24°C and a relative

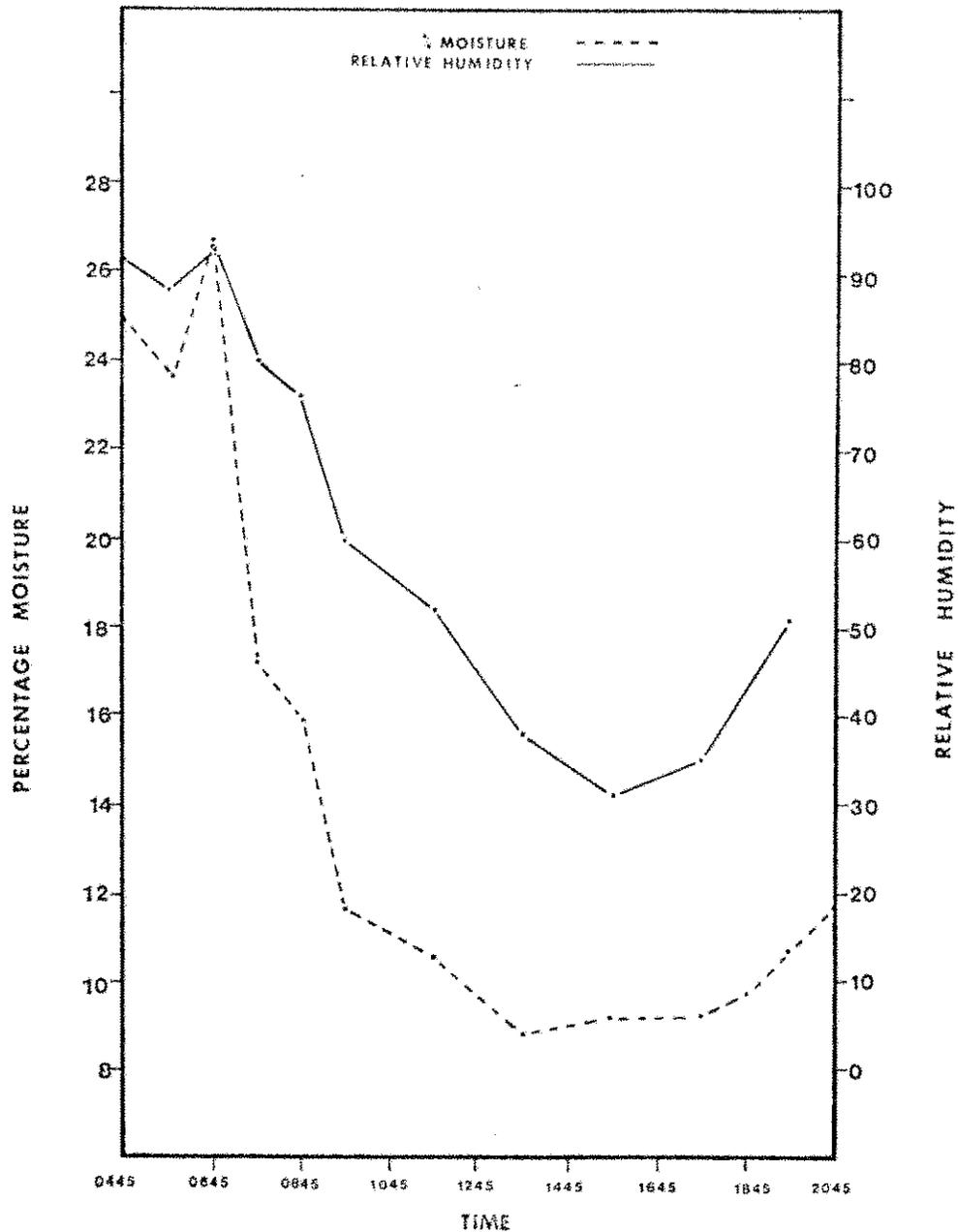


FIG. 8. The effect of the relative humidity of the air at various times of the day upon the moisture content of a perennial desert grass *Stipagrostis uniplumis*.

humidity of 50–55% that they lost weight rapidly. On the fifth day the mean percentage loss in weight of five animals was 22% and the experiment had to be terminated. The provision of fresh lettuce leaves at this stage swiftly restored the animals to their original body weight. In a similar experiment, also on five animals, but conducted at 19°C and 70–75% relative humidity the animals lost weight at a slower rate, taking seven days to lose 22% of their body weight. Nevertheless, the animals could not survive on the seed and the experiment again had to be terminated.

These results were confirmed by a third experiment in which five animals were again fed the same diet and kept overnight in metabolism cages which allowed for the collection of urine under mineral oil. Temperatures were kept constant at 19°C and relative humidity at 70–75%. When the animals received fresh lettuce leaves in their diet the mean osmolality of the urine was 2860 m-osmole/l (range 2246–3490 m-osmole/l) and the maximum mean osmolality achieved during dehydration was 4035 m-osmole/l (range 3767–4475 m-osmole/l). The Namib gerbil therefore has efficient renal function but not sufficiently spectacular to allow it to survive on dry grass seed. Moreover, unlike *Aporosaura* and *Lepidochora* it is not able to store water and cannot therefore rely on the periodic condensation of fog water. These animals must therefore obtain some source of succulent feed within their habitat and this supposition was confirmed by the presence of succulent plant material (*Trianthema hereroensis*) among the food stored in their burrows. It would appear, then, as if these gerbils, like the ostrich, are not directly dependent on fog water but indirectly on the few succulent plants sustained by the fog.

#### ACKNOWLEDGEMENTS

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