

# ASPECTS OF ANIMAL ECOLOGY IN THE KALAHARI

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I was very surprised on my first visit in May 1956 to the Kalahari Gemsbok National Park, described as a semi-desert, to find the ground well covered with grass and bush, and to see the teeming life of big and small animals. It was not until I realised the absence of permanent water and the extreme temperatures that I began to wonder how life under such conditions is possible. The problems that at once presented themselves were:

- (a) How is it possible for animals to obtain enough water without drinking, and what measures have they taken to economise with the water.
- (b) How well are they adapted to the extreme and usually very fluctuating temperatures.

Apart from the birds, which I have so far left out of consideration, and the bigger mammals, most animals can retire to holes in the ground if the microclimatic condition above should become too extreme. Moreover, there is a very sharp division of the animal population into a diurnal and a nocturnal fauna. These factors simplify matters, but are not sufficient to explain how life has become possible. A physiological adaptation must also have taken place.

## MICROCLIMA

Before entering upon a discussion of their adaptation to the life in deserts and particularly in the Kalahari, it is desirable to consider the microclima in which the animals live.

A considerable daily and yearly range of temperatures is characteristic of areas away from the sea. The Kalahari is no exception in this respect. The clear, often cloudless sky, allows for great radiation and the sparse vegetation allows the sun rays to strike directly on the soil. The soil is rapidly warmed during the day but loses its heat as rapidly during the night, receiving no effective protection from the vegetation. There are no official figures available for the temperatures of the Kalahari, but I am informed that they can rise to above 50°C. Buxton (1923) mentions similar temperatures from the near and middle East, and so does Williams (1954) from Egypt. In the Kalahari in May -5°C was measured at 7.30 a.m. Similarly there are great variations in the humidity. The highest humidity measured with a whirling hygrometer in February 1957 at 7.5 a.m., six feet from the ground, was 79% R.H. During the day it fell to about 25% R.H. Williams (1954) registered an annual maximum variation from 97% to 16% R.H. in Egypt.

Fig. 1.

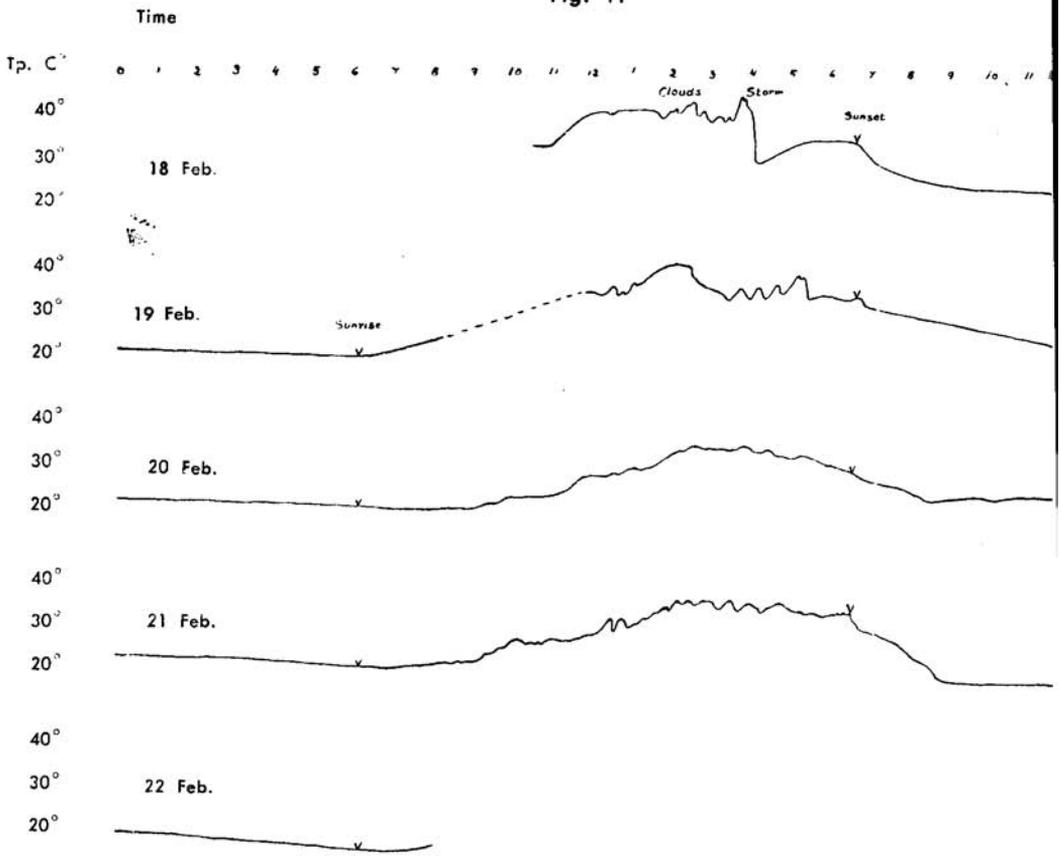
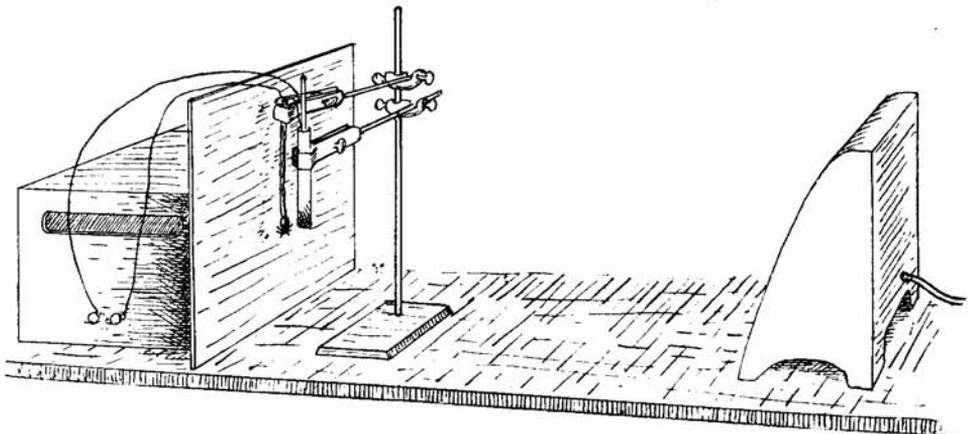


Fig. 2.



These figures, however, originate from measurements six feet above the ground, which is above the strata in which most animals live. A study of the climate close to the ground as well as in the warrens of the animals, is therefore necessary.

Due to the sparse vegetation in deserts the surface of the sand is exposed to intense radiation from the sun, which heats it up to a temperature which can even exceed 60°C. (Buxton, 1924b; Williams 1954). In a cool period of February 1957, I recorded 57°C 5 mm. below the surface of the sand in the Kalahari. Parry (1951) has made recordings in Cambridge with blackened discs and found that the temperature of a disc at the top of the grass was 5°C warmer than one 30 inches above the ground. If placed on the ground it rose to 15°C above the one at a height of 30 inches. It is obvious that in places with a temperature gradient as steep as this one, strong air currents must be created. Both radiation from the sky as well as from the ground, and convection must play an important part in the microclimate in which small animals live. Recent recordings from the Belgian Congo (Noirfalise, 1956) gave similar results. Buxton (1923) draws the attention to the great local variations in the microclimate not only from hour to hour but also simultaneously. These variations always make it possible for the animals to select suitable places for their activities. Williams (1954) has made very careful recordings in Egypt and confirmed this. The soil temperature which fluctuates much on the surface soon becomes constant when digging down. In a jeboa's burrow 75 cm. from the entrance the fluctuations on two days in August was about 4°C, while in a bird's nest it was about 21°C. K. Schmidt-Nielsen, B. Schmidt-Nielsen and Brokaw (1948) registered somewhat greater fluctuations in the nest chamber of *Dipodomys*.

Recordings from the Kalahari have so far shown a great similarity to those of Williams in Egypt. In a cool period in February the temperatures 12 cm. above the ground were recorded to vary between 16°-46°C (Fig. 1). In a burrow of *Parotomys*, 18 inches from the entrance and 18 inches below the surface the temperatures varied 2°C only — from 29° to 31°C. In May 1956 the variations in the burrows were recorded to be from 16° to 22°C. Probably these latter recordings are slightly too low due to disturbances of the holes. The lowest part of the burrows are about 2' 6" to 2' 9" below surface and one can reckon that the temperature here must be almost constant, probably about 26°C. These recordings are considerably higher than those made by Davis (1939) in artificial warrens.

It has been mentioned in the introduction that it frequently rains in the Kalahari. The water, however, sinks in immediately and puddles remain in the dry river beds only for a very short time. The result of the rain is that the sand is always moist some distance below the surface. Recordings by Williams (1954) in Egypt and by K. Schmidt-Nielsen, B. Schmidt-Nielsen & Brokaw (1948) show that the air of caves and warrens can have a humidity

considerably higher than that of the air outside. The latter found that the air humidity of the soil could be 100% R.H. With an outside humidity that fell right down to 1% R.H. the nest chamber of *Dipodomys* could maintain a humidity of about 30% R.H. The much lower humidity of the nest chamber than of the soil they thought was due to a through draught of the warrens. It would probably be useful if some measurement of the air circulation of the warrens of small rodents were made. In the Kalahari in May 1956 up to 95% R.H. in warrens of *Parotomys* and *Gerbillus* 24 inches from the entrance was registered. This can probably be partly contributed to the fact that much sand invariably fell on the recorder and partly covered it but it is probably also due to a lower rate of air circulation. That this is so is indicated by the smaller fluctuations of temperatures in the warrens of these two Kalahari rodents. In the warrens of some of the other rodents one can even expect a still poorer ventilation. Although many more recordings from the Kalahari are required there is reason to believe that the air humidity of most warrens there averages well above 50% R.H.

In summarising the above one can say that the temperatures and the humidity in the Kalahari show great fluctuations, particularly in the strata in which most animals live. This holds good for day as well as for night throughout the year. Even if the temperatures or the lack of humidity become extreme in some places, it is always possible for the animals to find a locality, however limited it may be, where the climatic conditions are tolerable. If it is too cold, hot or dry on the ground, most animals will always be able to find shelter underground. The need of special adaptation for life in deserts has, therefore, become lessened considerably at least among the burrowing animals.

#### WATER INTAKE AND ECONOMY

The water required by animals can be obtained in various ways. It can be free or chemically bound. The free water can be gained by drinking and by licking moist soil, or objects, by diffusion through the body wall and from food such as green plants, other animals and dead organic material containing free water. The first and the last of these methods are familiar to most people while it is not so generally known that for example some wolf spiders (*Lycosidae*) have been found able to drink water from soil against a capillary pressure up to 600 mm. mercury (Parry, 1954). It is equally surprising that the cuticle, which in some insects forms a very effective protection against evaporation, permits water to pass through into the body from the surroundings. Some syrphid larvae have been found to suck up liquid water through their anal papillae (Schneider, 1948, quoted from Edney, 1957), and the cutworms *Agrotis* can take up water from the surrounding soil (Evans, 1944). Water absorption from the air is possible in meal-worms (*Tenebrio*

molitor, — Buxton, 1930, and Mellanby, 1932a). Below a relative humidity of 88% the larvae were able to regulate their water content; at a higher humidity they absorbed water (Mellanby, 1932). Experiments with ticks have shown that *Ixodes ricinus* is able to absorb water from the air (Lee, 1946, 1947). Lee's suggestion that the process is physiological has been confirmed by Browning's experiment on *Ornithodoros moubata* (1954). The flea *Xenopsylla brasiliensis* has been found to be able to absorb water from the air at its prepupal stage only, but can do so in a humidity as low as 50% R.H. (Edney, 1947).

It is perhaps significant that among the insects of the desert none is more common than the tenebrionid beetles, and that fleas are common ectoparasites of the bigger and smaller vertebrates.

Of interest for our understanding of the sources of water available it is also worth mentioning that dead plant material is hygroscopic but it seems necessary that the relative humidity goes above 80% if it shall be of any value to animals (Buxton 1924a). Also B. Schmidt-Nielsen and K. Schmidt-Nielsen (1951) mention that seeds are hygroscopic and that the water they absorb from the air in the warrens may be beneficial to rodents.

The only known methods in which mammals can take up water is through the mouth either as free water or as water chemically bound. Vorhies & Taylor (1922) who studied the Kangaroo rat *Dipodomys spectabilis spectabilis* drew the attention to the fact that "during the long dry periods characteristic of Southern Arizona no evidence that the animal seeks a supply of succulent food such as cactus is found; and if it may go for two, three, or six months without water or succulent food, it is reasonable to suppose that it may do so indefinitely. In the laboratory, *D. spectabilis* ordinarily does not drink, but rather shows a dislike for getting its nose wet." *Dipodomys* is a nocturnal animal and therefore less exposed to dry air than the diurnal rodents. B. & K. Schmidt-Nielsen (1950 a & b) who also worked on *Dipodomys* found that when the animals breathe the fairly moist air in their burrows the formation of metabolic water will lead to an ultimate gain in water thus making drinking unnecessary. There seems, however, to be comparatively few rodents that are as well adapted as *Dipodomys*. *Neotoma albigula*, the pack rat, has shallow warrens in shaded places. Its nest is slightly deeper. Living in more shallow burrows than *Dipodomys* one can assume that *Neotoma* is less well protected against heat and evaporation and, therefore, will require more water. Vorhies & Taylor (1922) never saw this rat drink but they found that 44% of its food was cactus which contains nearly 90% water. K. Schmidt-Nielsen, B. Schmidt-Nielsen and Brokaw (1948) concluded from their experiments that *Neotoma* is biologically not physiologically adapted to life in the desert. The diurnal ground squirrel *Citellus tereticaudus* which is exposed to even more extreme conditions than *Neotoma* was found to drink when water is available. The food it consumes

may contain 60 to 80% free water. (K. & B. Schmidt-Nielsen, 1952). An analysis of stomach contents from rodents from the Kalahari is given in Table 1.

TABLE 1

DIURNAL		DRY		MOIST	
		Straw	Seeds	Cucumber & fresh cucumber seeds	Green grass and leaves
Geosciurus ... ..	May 1956	1	3		
"	May 1956	1	2	3	
"	Feb. 1957				3
"	Feb. 1957				3
"	Feb. 1957				3
Parotomys ... ..	May 1956	1	3		
"	Feb. 1957				3
"	Feb. 1957		2		3
"	Feb. 1957	1			3
Rhabdomys ... ..	May 1956	1			3
"	May 1956				3
"	May 1956	1	1		3
"	Feb. 1957		3		2
"	Feb. 1957		2		3
NOCTURNAL					
Desmodillus ... ..	May 1956	1	3		
"	Feb. 1957		3		
Thallomys ... ..	May 1956		2		3
"	May 1956		2		3
"	May 1956		1		3
"	May 1956	1	3		1
Gerbillus	Feb. 1957		3		
Spring Hare ... ..	Feb. 1957				3

This table only gives a rough idea of the proportion of the various foods and will not stand up to a statistical analysis, but it may give an indication of the tendency. The figures 1.2.3. indicate little, some much of the material found in the stomach. All the rodents tabulated, with the exception of *Desmodillus* and perhaps *Gerbillus*, seem fond of green or moist plant material; the diurnal more so than the nocturnal. This is what could be expected, because the animals active by day are exposed, not only to a hotter, but also to a drier climate than those active by night. It is possible that a study of *Desmodillus*, *Gerbillus* and related forms will show an adaptation similar to that of *Dipodomys*.

An interesting discovery made by Pearsons (1947) which may be mentioned here is that the feeding time of nocturnal animals is shorter than that of diurnal forms. The periods of activity in nocturnal rodents may be reduced to one hour duration only. The metabolism of these animals drops, however, low enough during the day to make the food gathered in their restricted feeding periods last the full 24 hours. This probably explains why it is among the nocturnal rodents, and not among the diurnal forms that the greatest physiological adaptation to the existence on dry food has developed. Low temperatures can be expected to curtail their periods of activity. If sufficient food with much free water such as green leaves was to be consumed in these short periods, its bulk would easily exceed the capacity of their stomachs.

From the above it is obvious that it is not sufficient to study the intake but also the loss of water. Water can be lost in three ways: (a) by evaporation through the skin, lungs and respiratory tracts, (b) it can be given off as an essential part of the urine and (c) it can be contained in the faeces.

Animals adapted to life in deserts can be expected to economise with their water in one or more ways. The possibilities are: (a) The animals may reduce their evaporation by reducing their number of sweat glands and by decreasing their evaporation through the lungs. The latter can be done by cooling the air on its passage out through the nose. This is done by the American Kangaroo rat, *Dipodomys*, which has a temperature of its nose of about 10°C lower than that of the body (B. Schmidt-Nielsen & K. Schmidt-Nielsen, 1951, B. Schmidt-Nielsen, 1954). Experiments by Lindeborg (1952) with other American rodents showed that *Perognathus penicillatus* "is able to prevent loss of water through the skin and lungs; in completely dry air it lost an average of only 0.80 c.c. of water per day, whereas *Peromyscus leucopus tonillo* lost 2.33 c.c. daily and *P. l. noveboracensis* slightly more". (b) Water can also be saved by desert animals by producing a more concentrated urine than others. The maximum concentration of electrolytes in the urine of man is 0.37 mol., in white rats it is 0.60 mol., in *Neotoma* 0.7 mol., and in the kangaroo rat it is 1.2 mol. (B. & K. Schmidt-Nielsen, 1949, 1951, 1952, B. Schmidt-Nielsen, 1954).

As will be seen the kangaroo rat can produce a much more concentrated urine than man and white rat.

In order to see if the experience with regard to the water economy gained elsewhere applies to the rodents of the Kalahari, it was attempted to measure the water intake and the water loss of white laboratory rats and ground squirrels (*Geosciurus inauris*).

The experiments were carried out in a room with an almost constant temperature of 23°C.

The animals were kept in cages with a wire bottom so that droppings and remnants of food could be collected in trays and weighed. Water was supplied from a flask from which a tube led down to a small bowl from which the animals could drink. The evaporation was measured daily from control drinking bowls and subtracted from the loss of water from the bowls in the cages. The only food supplied was maize. Each experiment lasted for 12 days, and the animals were fed on maize only. Measurements were not started until the third day to make sure that the animals had rid themselves of food other than maize. The content of water in the faeces was measured by collecting pellets from the animals as soon as they were produced, weighing them, drying them at about 110°C, and calculating their loss in weight.

Attempts to sample urine were made in a separate experiment. In this the animals were confined to very small cages with a wire bottom under which was a funnel to catch the urine and lead it down into a measuring glass. Much debris fell unavoidably into the urine, and the readings gave no more than an approximate idea of the amount produced.

Also the rate of evaporation was measured in a separate experiment in which single animals were placed under a glass bell with a wire bottom. Under the bell was a glass funnel through which some ventilation could take place. The joint between the glass bell and the funnel was closed with cellotape. In the top of the bell was placed a large piece of filter paper that had been soaked in a solution of  $\text{CaCl}_2$  and thereafter dried in an oven placed in a room with about 35% R.H. The temperature of the oven was 35°C. Eight experiments were made in all with each animal (1 rat and 1 squirrel, both the same as those used in the other experiments). With the exception of three experiments with the rat, which lasted for 3 hours each, all experiments had a duration of 20 minutes each.

The filter paper was weighed before and after each experiment and the increase in weight was taken as the water evaporated from the animal. To make sure no water of importance diffused in through the funnel, a control experiment was made with the empty apparatus. After 3 hours no additional weight of the filter paper could be measured.

The results expressed in the average intake and output per 24 hours are shown in *Table 2*.

TABLE 2

Maize contains 9% free water

RAT: 560 g.

Consumption	Output
12.5 g. maize consumed per day	1.7 g. dry faeces per day. (Fresh faeces contained 62% free H <sub>2</sub> O).
Food contained 1.1 g. free water 6.3 g. bound water	faeces contained 2.9 g. free water 1.0 g. bound water
drank 19.0 g.	urine 4.1 g.
	evaporated 18.1 g.
Total 26.4 g.	Total 26.1 g.

SQUIRREL: 915 g.

Consumption	Output
16.2 g. maize per day	1.4 g. dry faeces per day. (Fresh faeces contained 52.8% free water).
Food contained 1.5 g. free water 8.2 g. bound water	faeces contained 1.6 g. free water 0.8 g. bound water
drank 17.1 g.	evaporated 23.6 g.
Total 26.8 g.	Total 26.0 g.

no urine was recovered.

In order to make comparison easier the intake and output were calculated per 100 g. food consumed. (Table 3)

TABLE 3.

RAT: 560 g.

Intake	Output
100 g. maize eaten	13.9 g. dry faeces
Food contained 9.0 g. free water 49.2 g. bound water	faeces contained 23.1 g. free water 7.7 g. bound water
drank 152.3 g.	urine 32.8 g.
	evaporated 144.8 g.
Total 210.5 g.	Total 208.4 g.

SQUIRREL: 915 g.

Intake	Output
100 g. maize eaten	8.7 g. dry faeces
Food contained 9.0 g. free water 49.2 g. bound water	faeces contained 9.9 g. free water 4.8 g. bound water
drank 105.6 g.	evaporated 145.7 g.
Total 163.8 g.	Total 160.4 g. + xg urine

Figures show that the amount of water required by the squirrel is considerably lower than that by the rat. The water drunk by the squirrel is considerably lower than that by the rat. The water drunk by the squirrel is just over two thirds of that drunk by the rat. The rate of evaporation in the two animals is approximately the same. In the case of the rat, the loss of water through the faeces is almost double that from the squirrel. This is due to a less effective utilisation of the eaten food and a less effective absorption of water in colon. While the rat produces a considerable

amount of urine, the squirrel voids very little. Measuring the concentration of the urine of rats and squirrels, it has been found that in the case of rats it often fell so low that its vapour pressure corresponded to that of a 0.1 — 0.2 molar solution of NaCl. In the case of the squirrel I have not measured a concentration less than that corresponding to a salt solution of 0.7—0.8 molar.

Samples of urine taken from animals in the Kalahari showed that their concentrations had a vapour pressure corresponding to salt solutions as listed in table 4.

TABLE 4

Squirrel less than 1 molar	
Squirrel	0.8 molar
Squirrel	0.8 molar
Desmodillius	0.5 molar
Malacothrix	1.0 molar
Spring hare	0.6-0.7 molar
Springbuck	1.0 molar

These figures show that the animals adapted to life in arid areas have a more effective re-absorption of water from their renal tubules than the laboratory rats.

Since the principal reabsorption of water from the faeces takes place in colon it could be expected that this section of the alimentary tract would be longer in animals from the Kalahari than in those from other places. Therefore the length of the colon of various rodents was measured in comparison with the head-body length of the animals. The results are listed in Table 5.

TABLE 5

	Length in mm. of colon/Head-body	Approximate proportion
White mouse ( <i>Mus musculus</i> )	93/85	1
<i>Leggada minutoides</i>	62/62	1
White Rat ( <i>Rattus norvegicus</i> )	190/180	1
<i>Aethomys namaquensis</i>	176/109	1 $\frac{2}{3}$
<i>Rhabdomys pumito</i>	142/99	1 $\frac{1}{2}$
<i>Malacontrix typicus</i>	95/70	1 $\frac{1}{3}$
<i>Desmodillus auriculares</i>	143/105	1 $\frac{1}{3}$
<i>Gerbillus paebea</i>	129/93	1 $\frac{1}{3}$
<i>Otomys</i> sp.	263/150	1 $\frac{2}{3}$
<i>Parotomys brantsii</i>	337/166	2
Ground squirrel ( <i>Geosciurus inauris</i> )	647/230	3
Spring hare ( <i>Pedetes cafer</i> )	1620/360	4 $\frac{1}{2}$

As will be seen the figures give no reason to presume there is any relation between the length of colon and the adaptation to life in arid areas.

Attempts made by me to rear white rats and mice on dry food and vegetables only, without giving them anything to drink, have proved successful. The animals, however, never reach the size of animals allowed to drink and the number of litters is greatly reduced. From my observations I feel no doubt that rats (*Rattus norvegicus*) can uphold its life in the less extreme parts of the Kalahari, but I doubt if they will be able to breed there. This is probably the reason why they never have been able to establish themselves. Also Lindeborg (1950) is of the opinion that in many mammals it may be the female's ability or disability to conserve sufficient water for pregnancy and lactation, which is the limiting factor in the distribution of mammals in arid zones. This may rest on very small morphological, physiological or biological differences only. The dwarf mouse *Leggada* which belongs to the Muridae — the same family as the laboratory rats and mice — is well established in the Kalahari and I am informed that rats (*Rattus* sp.) are common in the desert of Southern Madagascar (personal communication from Dr. R. M. A. Paulian).

The laboratory rats show great individual variations and a strain of rats, able to live in the Kalahari may sooner or later develop. Experiments are at the moment in progress with the aim of producing laboratory rats with a greater resistance to arid conditions.

## TEMPERATURE REGULATION

Although the microclimate of the Kalahari fluctuates greatly with regard to temperature, the animals will always be able to retreat to localities where the temperatures are not extreme. Their search for food will, however, from time to time compel them to leave these sheltered places. It has already been pointed out that the day and night animals are faced with different problems. This particularly holds good when the question of temperature arises. The animals active by day may be exposed to excessive heat, those out by night may have to suffer very low temperatures. It is, therefore, obvious that a special adaptation is required.

Poikilothermic animals active by night undoubtedly have a much lower optimum temperature than the day forms. Judging from observations in the Kalahari, most of them seem to disappear underground in excessive cold or heat. A few remain above, where they shelter by day in the shade of the vegetation and by night may be overcome by stupor.

Attempts to find the temperature preference of the nocturnal beetle *Gonopus* sp. failed, but it was definitely low, much lower than that of beetles active by day, probably well below 20°C. The diurnal beetles

*Onymacris multistriata* from the Kalahari and *Onymacris bicolor marshalli* from S.W. Africa, both had a preference for 38—39°C. *Adesmea* sp., a more tropical form collected in N. Transvaal, seemed even to prefer a temperature slightly higher.

During my visits to the Kalahari I have paid very little attention to the nocturnal poikilothermic animals, although they were more plentiful than those with diurnal habits. Obviously the latter are faced with by far the greatest problems.

Various authors have in the past treated the question of heat regulation of diurnal insects living in hot places. The heating has been found to be affected by the colour of the animal (Strel'nikov, 1932; Parry, 1951).

The radiation load depends on the shape of the body and may be affected by changes in the orientation (Parry, 1951). Locusts, *Schistocerca gregaria*, place themselves perpendicularly to the sun rays in the morning, thereby receiving the maximum heat radiation (Fraenkel, 1929, 1930; Fraenkel & Gunn, 1940; Gunn, 1942). In dry air the insects can maintain a body temperature below that of the surroundings. This is done by transpiration (Buxton, 1924a) and it applies particularly to large insects which, in hot air above 40°C can keep their bodies cool. (Mellanby, 1932). Gunn, (1942), believes that there is no reason to think this cooling is an active regulating mechanism. It can be useful over a short period but is harmful during a longer one.

Most animals in deserts have a paler colouration than those living in a more moderate climate. Tenebrionid beetles form an exception to this rule. In moderate climates they are usually dark brown, in deserts they become jet black. This is a fact to which Buxton (1923) has already drawn attention. Only a few of these beetles I know of deviate in this respect. *Onymacris bicolor marshalli*, which I am told lives in extremely hot places in South West Africa, forms such an exception, having white elytra. The closely related *Onymacris multistriata* is jet black with only a narrow yellow edging of its prothorax. The biological significance of this blackening is difficult to understand. Bodenheimer et al. (Bodenheimer 1953, 1954, and Bodenheimer Halperin & Swirski 1953) point out that the pigment protects against ultraviolet light but, as they also point out, this protection is similarly found in animals with other body colouration and various integumental structures. Since black is reckoned to absorb heat rays, it is difficult to understand why black and not another colour has become the predominant colour. To make sure that the rule of black absorbing the heat rays also applies to beetles from the Kalahari, a number of species was exposed to infra-red radiation and the reflected rays were observed on the screen of a converter. It was found that the black chiten absorbs all heat rays.

Unfortunately it was not possible for me to study the body temperature

of the beetles during my stay in the Kalahari. I, therefore, decided to copy the extreme climatic conditions as well as I could in the laboratory and there measure the body temperature of the black and the white species of *Onymacris* mentioned above.

The technique employed for measuring the effect of heat radiation on the body temperature of the beetles was the simplest possible. The radiation was produced by an electric heater. The beetle was suspended about 25 cm. above the table with its dorsal side facing the heater and with a thermo-couple in its body. During the first experiments the thermo-couples were inserted from the dorsal side into the thorax. Later on the couples were inserted from the ventral side of the abdomen, thus providing a better screening of the wires against the radiation. An effective protection of the wires was also provided by a rubber tube which surrounded them. Next to the beetle was a blackened test tube with a thermometer and the other thermo-couple. In the bottom of the test tube was a little water. The water, together with the inserted bulb of the thermometer, was kept at a volume approximately the same as that of the beetle.

### *Absorbtion of heat in tenebrionid beetles*

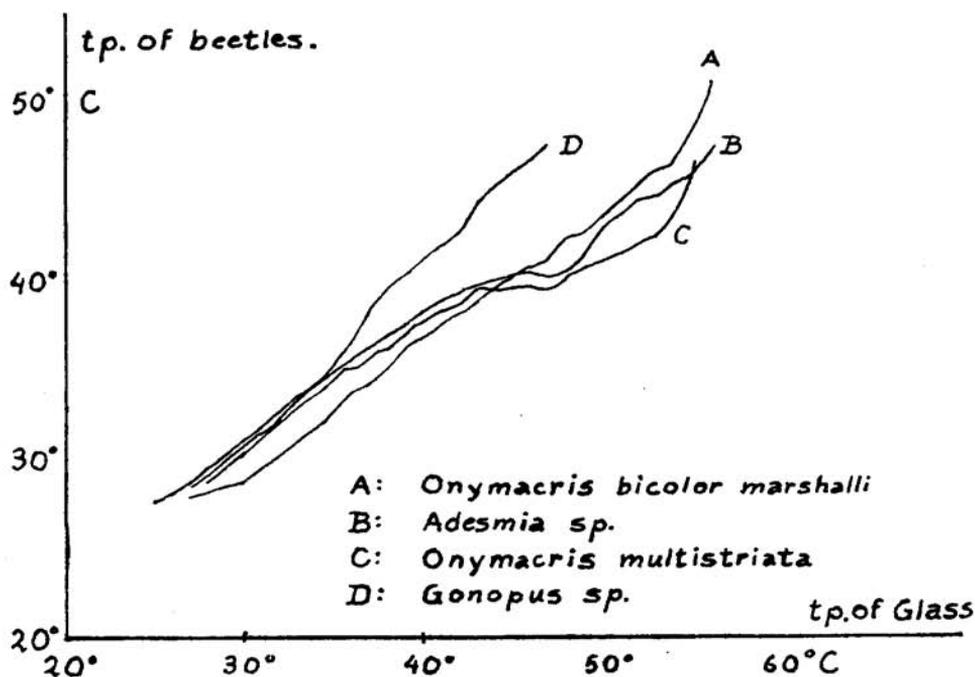


Fig. 3.

Behind the beetle was a linoleum screen. The readings were made on a low-resistance galvanometer. They gave the difference in temperature between the water in the test tube and the body of the beetle, but they were calculated into the actual temperatures. The temperature of the beetle was, in most experiments, taken every time that the water in the test tube had risen one centigrade. The results were plotted on sheets of graph paper. A typical example is shown in *fig. 3*, where the temperatures of white and black beetles tested simultaneously are shown.

A glance at the reproduced graph shows clearly that the black beetle has an active mechanism which sets in when the body temperature reaches 40°C, and which helps to prevent it from rising above this level. The white beetle has not got this mechanism. Its white elytra, however, offers some protection by reflecting the rays falling on its dorsal side. When the temperature of the body of the beetles approaches 40°C they begin to aerate their tracheal system and the space under their elytra. This is done by protruding and retracting the head and by moving the abdomen. Also the genitalia are often exposed.

Similar experiments were made with the diurnal *Adesmia* sp. and the nocturnal *Gonopus* sp., both collected in Northern Transvaal. The results are illustrated in *fig. 3*. It is obvious that *Adesmia* has a mechanism similar to that of *Onymacris multistriata*, while this is lacking in *Gonopus*. The latter showed the first sign of injury from the heat at a body temperature of 37°C, which is even below the temperature preference of the other beetles. At 48°C it was dead. Death did not occur in the other beetles until they had reached a temperature above 50°C.

These experiments contradict Gunn when he denies the existence of an active temperature regulating mechanism.

Small homoiothermic animals are faced with problems that are no less formidable than those of the poikilothermic forms. Very little seems known about their tolerance of variation of body temperature but it is known that most mammals have a "normal" body temperature which is fairly constant and which in most mammals lies between 34.5° and 38.5°C. It has been shown that there is a nearly linear relation between the basal heat production and the body surface of a homoiothermic animal. In other words: they have the same heat dissipation per unit of surface. From this it follows that small animals will have a loss of heat per unit of body weight much larger than that of bigger animals.

The loss of heat can be counteracted in (a) increasing the metabolism, (b) sheltering in nests or underground and (c) reducing the dissipation by growing a thicker fur, and also by reducing the surface by curling up into a ball, and by raising the hairs; (Scholander Al. 1950a, b and c, Gulick, 1937). Increase of metabolism is possible as a short termed precaution but

not over a prolonged period and it has been found (Scholander et al. 1950 c.) that the basic metabolic rate of arctic and tropic animals is the same. Gulick (1937), found that white rats 25 days old could maintain a body temperature of 34°C by rolling into a ball. We know that the small mammals of the Kalahari all shelter underground and that they can withdraw to moderate climates at any time. Up till now we know nothing about the insulation offered by their fur.

To my knowledge very little is known about the measures taken by the small mammals to counteract the effect of high temperatures. There are, however, various precautions they can take although none of them can be effective over long periods. In the Kalahari they can protect themselves against the high day temperatures (a) by sheltering underground and (b) by increasing their evaporation through the respiratory tracts and by sweating. A thick fur may offer protection over a very short period. Decreased metabolism can only be effective as long as the surrounding temperature is well below that of the body.

Direct observations show that the small rodents of the Kalahari do not tolerate high or low temperatures over lengthy periods. Four *Melacothrix*, which are nocturnal in habits, died from exposure when the temperature of the room fell from 23°C to 16°C. The same happened to a certain strain of white mice. On an earlier occasion a newly-caught *Parotomys* died from the same cause and six ground squirrels which had also just arrived were in a light stupor.

All these animals, except for the white mice, are diurnal.

Deep rectal temperatures of animals just removed from their nesting box were taken. The results were as listed in Table 6.

TABLE 6

White mouse	36.8
White rat	38.3
<i>Mastomys</i>	38.7
<i>Rhabdomys</i>	34.9 — 38.7
<i>Melacothrix</i>	34.5 — 36.0
Ground squirrel	37.9

All the animals had been kept in a room with a temperature of more or less 22°C. These results correspond well with those of Fuller & Heistand (1947), Gulick (1937), and of Erikson (1957).

When the temperatures of these rodents were taken it was found that if delayed the readings became lower. The animals were, therefore, put into cylinders of a fine wire mesh so that they could not move, and a thermocouple fastened 1—1½ inches up their rectums. Thus fixed, the

animals were placed in a thermostatically controlled cupboard at 10°C and their body temperatures were read every five minutes. In the case of a small mouse the body temperature fell to 20°C after 20 minutes, while in *Mastomys* (ca. 45g) it only fell to 31°C after one hour. *Rhabdomys* (45g) seemed to have greater difficulties in maintaining its body temperature although there seem to be individual differences. The results obtained with *Rhabdomys* are given in Fig. 4.

The animals' reaction to high temperatures were recorded in a similar way and it was found that in temperatures of 40°—41°C their body temperatures rose in one case even to the lethal point. Even the much bigger squirrel was unable to keep down its body temperature. The results obtained with *Rhabdomys* are plotted in Fig. 4. Control experiments were made with a dead mouse.

### *Temperatures of Rhabdomys pumilo.*

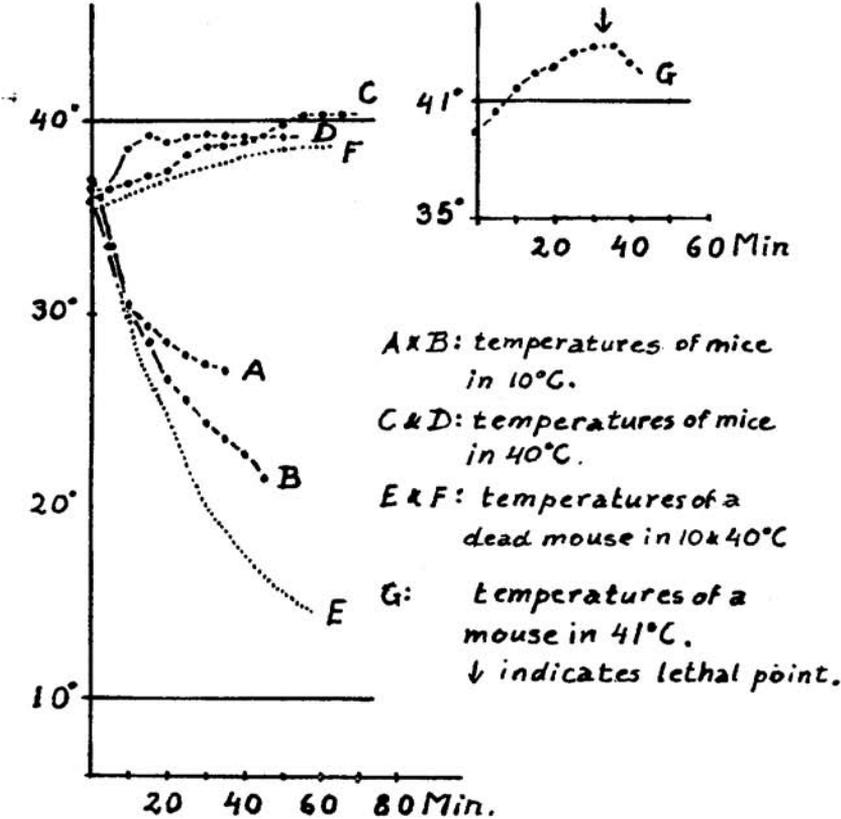


Fig. 4.

A glance at the graph shows that when *Rhabdomys* is exposed to a comparatively although not excessively low temperature the metabolism can delay but not prevent the cooling of the body. At temperatures above that "normal" to the body it can, provided the heat is not too excessive, at least for some time keep its body temperature down below the lethal one.

It should be pointed out that in all experiments the air in the thermostat was dry. By the end of the experiments with mice in cold air, the animals were shivering and at the lowest body temperatures they were semi-paralysed. At high temperatures they were panting and the capillaries in their nasal region filled with blood, giving the skin a reddish tint. When close to the lethal point the snout and the forehead become wet (Fig. 5). In case of the squirrel the whole body except for the lumbar and dorsal pelvic region was wet.

Experiments like these can easily be criticised because of the unnatural condition under which they were carried out. In nature when the animals are cooled down they will curl themselves up, thereby diminishing their exposed surface and they will raise their hairs, thereby thickening their insulating cover. The animals in the above experiments could do neither.



Figure 5 — Head of *Rhabdomys* showing the area that becomes wet when the animal is overheated.

This probably accounts for the great differences between the above results and those obtained by others. They do, however, show that the metabolism can only play a minor part in the maintenance of the body temperature when the air is cooled down. They show, too, that the high temperatures in which they move by day must be extremely dangerous, even to the diurnal animals, and that evaporation alone is not sufficient to keep their temperatures down.

#### SUMMARY

The microclimate in which most small animals in the Kalahari live has been described. Great annual as well as diurnal variations have been found. By day the air temperature 12 cm. from the ground can rise to about 50°C. The temperature of the surface of the sand can go up to

about 60°C. In the warrens of the animals the temperature is probably constant, about 26°C. Also the humidity of the air varies much above the ground; in the warrens it is close to saturation point.

The day and the night fauna is well defined.

Whether active by day or by night, most animals will be able to retire to a moderate microclimate.

The most important source of water in the Kalahari is from green leaves. There is some indication that diurnal animals need more green leaves than the nocturnal forms.

A comparison between the water economy of a white rat and of a ground squirrel showed that the squirrel utilises its food better than the rat, and it holds back more water in its kidneys and in its colon. It, therefore, needs to drink only two-thirds of what the rat requires per unit weight of food.

There is no evidence that animals adapted to life in a dry climate have developed a longer colon.

Most diurnal tenebrionid beetles in the Kalahari and other desert areas are darker than in other areas. An exception is formed by *Onymacris bicolor marshalli* which has white elytra.

The effect of heat radiation on *Onymacris bicolor marshalli* and on the black diurnal beetles *Onymacris multistriata* and *Adesmia* sp. was recorded. The white beetle heated up more slowly than the black ones, but the latter have a mechanism which sets in at a body temperature of 40—41°C, and keeps the temperature at this point for some time. The temperature preference of the three beetles was between 38 and 41°C.

The black nocturnal *Gonopus* sp. has a temperature preference much lower than the diurnal beetles. It was found to lack the same regulating mechanism as the black diurnal beetles. Already at 37°C it showed signs of heat injury.

The small mammals seem to tolerate great fluctuations of their body temperature. They were found unable to maintain a constant body temperature when exposed to cool or warm air. The experimental technique, however, suffers from obvious defects because the animals were kept immovable and had their fur pressed in against their bodies. In spite of this, it is clearly shown that changes in the metabolic rate alone can only play a minor part in the maintenance of the body temperature in cool air. Similarly the animals seem to be badly protected against heat for any length of time.

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