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REPORT OF WORK ON THE ADAPTATIONS OF INSECTS TO DESERT ENVIRONMENTS

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Introduction

The work reported below was undertaken during a sabbatical leave in South Africa. The purpose was to get to know something about the insect fauna of the Namib Desert and to carry out observations and experiments on some of the adaptations shown by these animals to their environment.

I was prepared to find a great variety of niches (in a wide sense) occupied by insects, and a parallel diversity of morphological, behavioral and physiological adaptations. These expectations were fully born out. However, in the time available I was able to open up enquiries only in a few areas. I decided to leave the question of morphological adaptations entirely to others and to concentrate on aspects of water and heat relationships.

While I was there, Mr. Erik Holm was accumulating a lot of useful information on the activity patterns of dune species. Dr. Gideon Louw, of the University of Stellenbosch and Dr. William Hamilton, of the University of California at Davis, had obtained some useful data on water and heat balance in certain species. All these workers generously put their information at my disposal. None of it is published so far as I know.

My own work was concerned with three aspects of the problem:

1. Measurements of microclimates in the immediate habitats of the insects and correlation of this with activity.

2. A comparative study of overall rates of water loss in species occupying different niches and of water vapor uptake in a thysanuran.
3. Comparative work on the upper lethal temperatures and factors controlling the body temperatures of certain species in the field.

The work under Section 1 was done entirely at the Namib Desert Research Station, Gobabeb, S. W. Africa during two visits, from January 12 to February 12 and from June 15 to June 25, 1969. The work described in Sections 2 and 3 was done partly at Gobabeb and partly in the Zoology Department at the University of Cape Town.

#### 1. Microclimates in relation to activity

The microclimate was studied in three different habitats a) the bed of the Kuiseb River, b) the plains to the east of the river, and c) the large sand dunes to the west of the river.

##### a) The Kuiseb river bed

Temperatures and humidities were measured during a complete 24 hour cycle in several places within an area occupied by Oryzopsis pergandensis and Physosterna cribripes (the former being present in greater numbers). The sites chosen were below, at and above the sand surface, inside and on top of an Eragrostis bush, and at the base of a large Acacia giraffae tree. Readings were taken every hour during the day and at longer intervals during the following night. I shall not attempt to describe the results in detail in this report, but the following features are worth mentioning. The highest temperatures occurred on the open sand surface in direct sunlight at 2.0 p.m., when 66°C was reached. At this time, however, a temperature of 37°C was recorded only 10 cm below the surface, 32°C at the base of a tree trunk (in the shade) and 40°C

near the top of an Eragrostis bush. Lowest temperatures were recorded at 6.30 a.m., just before sunrise, when the open sand surface was 16°C.

Maximum beetle activity occurred between 9.0 and 10.0 a.m. when the surface temperature was 58°C in the sun and 37°C in the shade. There was very little activity even in the shade at 2.0 p.m. when the sunlit surface was 66°C and the shade surface 37°C. A second, lesser peak of activity occurred at 6.0 p.m. when the surface temperature in the sun was 43°C, and in the shade, 34°C. At this time of the year the records showed a distinctly bimodal activity cycle. When they were not active, the beetles retired into Eragrostis bushes or into the sand.

At a similar habitat in the river bed in the winter month of July, beetle activity (again Onymacris rugatipennis and Physosterna cribripes) was unimodal, with an activity peak at 3.0 p.m. At this time the ground sun temperature varied from 41° to 46°C on different days. Censuses of active beetles were taken each hour of the day by walking a pre-determined path of 375 paces in 6 minutes and counting the beetles seen. Activity commenced at 9.0 a.m. (when a mean of 1 beetle per round was seen), rose rapidly to 18 beetles per round at 11.0 a.m., and then more slowly to 26 beetles per round at 3.0 p.m. There followed a rapid drop to 3 beetles per round at 6.0 p.m. and none thereafter. For both species the curves were unimodal.

Body temperatures of some of these beetles was measured and will be considered further below.

b) The plains to the east of the Kuisab river

The only habitat studied here was that of the thysanuran insect Gtenolepisma, probably pauliani. This insect lives in the crevices of exfoliated granite

rocks and stones which occur on the desert surface. Measurements of temperatures and humidities were made above and below the stones and in other relevant places. The insects were present below the stones from 8.0 a.m. to 9.0 p.m., after which they were very scarce, most of them having moved out, presumably to feed, until they reappeared under the stones again the next morning. The activity of Ctenoplectisma, unlike that of Onymacris rugatipennis, is nocturnal.

Highest and lowest temperatures and humidities recorded were as follows:

	<u>Temperature °C</u>			
	<u>High</u>	<u>Time</u>	<u>Low</u>	<u>Time</u>
Below granite stone	43	3.0 p.m.	24	6.0 a.m.
Surface of stone	58	3.0 p.m.	22	6.0 a.m.
Air above stone	38	2.0 p.m.	18	6.0 p.m.

	<u>Relative humidity %</u>			
	<u>Low</u>	<u>Time</u>	<u>High</u>	<u>Time</u>
Below granite stone	17	3.0 p.m.	49	6.0 a.m.
Air above stone	32	3.0 p.m.	75	6.0 a.m.

A feature of some interest is the fact that although the humidity was never higher than 75% and usually much lower, this would be sufficient to permit the insects to absorb water vapor and thus to remain in water balance. (The experimental evidence for this statement will be referred to below).

c) In the sand dunes area - Caravan Dune

Sand dunes formed the third habitat in which the microclimate was investigated. Here temperatures and humidities were recorded every hour for a complete 24 hour

cycle in the following places: on the dune lee side at -80, -40, -20, 0, +0.3, +3 cm., and on the dune slope at -40, -20, -10, 0, +0.3, +1, +5 cm. (the minus sign indicates depth below the surface). Readings were also taken near the top of an Aristida clump.

The following readings are of interest:

	<u>Time</u>	<u>Temp °C</u>	<u>R. H. %</u>	<u>Time</u>	<u>Temp. °C</u>	<u>R. H. %</u>
Surface of dune slope	1.0 p.m.	57	10	6.0 a.m.	17.5	78
20 cm. below surface	10 p.m.	34	35	12 noon	31	31

In each case the time chosen is that at which the highest or lowest temperatures and humidities occurred. Only 20 cm. below the surface the temperature varied some 3°C throughout the 24 hours (and was warmest some 10 hours after the warmest time at the surface). The humidity there was also rather constant. At greater depths temperatures and humidities showed even less daily fluctuation.

Mr. Erik Holm has information about the activities of various species at these places, during both summer and winter. For example, while the above readings were being taken, Onymacris laeviceps was active at 7.0 and 8.0 a.m. and again from 6.0 to 8.0 p.m., while O. plana was active from 9.0 to 12.0 noon and from 4.0 to 6.0 p.m. Both were bimodal in activity, but the modes were at different times.

## 2. Water balance in certain beetles and in Stenolepisma

Total water loss during starvation was measured in dry air at  $27^{\circ}\text{C} \pm 0.5^{\circ}\text{C}$ . Most of these measurements were made in the laboratory at Cape Town. Preliminary measurements were also made at Gobabab, but the temperature there was not controlled and varied between  $25^{\circ}$  and  $30^{\circ}\text{C}$ . In comparison, similar measurements were made

on three species of Trigonopus - pedinine tenabrionid beetles from the more mesic environment of Grahamstown in the Eastern Cape Province.

Beetles were weighed individually each day for five days. The results show that in most species water was lost more rapidly at first than later (an effect which is quite general in arthropods, although the explanation is not certain) and secondly that if water loss is expressed as a percentage of original wet weight, there was a clear effect of size, in that smaller individuals lost a greater percentage than larger ones did. This effect appears to be absent in the larger size classes of Onymacris rugatipennis and O. plana (which are themselves the largest beetles studied), but my results have not yet been analysed to the extent that a firm statement about this can be made.

The number of beetles used was at least 30 for each species, and the mean losses were as follows: (as percentages of original weight)

		<u>Original Weight Range of Beetles Used (g)</u>
<u>Onymacris plana</u>	6.4	0.6 - 1.2
<u>O. rugatipennis</u>	7.3	0.3 - 0.7
<u>Calosis snabilis</u>	8.5	0.05 - 0.022
<u>Gtenolepisma pauliana</u>	10.0	0.004 - 0.021
<u>Onymacris laeviceps</u>	10.6	0.3 - 0.6
<u>Gyrosis moralesi</u>	12.6	0.06 - 0.15
<u>Lepidochora porti</u>	14.0	0.12 - 0.22
<u>Lepidochora argentogrisea</u>	15.9	0.06 - 0.12

The above may be compared with the losses shown by more mesic beetles:

<u>Species</u>	<u>% Original Wt. Lost</u>	<u>Original Weight Range of Beetles Used (g)</u>
<u>Trigonopus</u> sp. near <u>capicola</u>	21.6 (10 only)	0.30 - 0.45
<u>T. spinipes</u>	13.6 (5 only)	0.31 - 0.35
<u>T. sp.</u>	25.7 (20 only)	0.10 - 0.18

All the mesic tenebrionids lost water more rapidly than all but two species (both active by night) of the desert forms. Of the desert species, those active by day lost less than those active by night, and the two largest species lost less than any of the others. Ctenolepisma, the thysanuran, seems to be remarkably well waterproofed, as indeed it needs to be to live where it does.

I made a few measurements in an attempt to determine the relative importance of the general integument and the spiracles for water loss in O. plana. When the spiracles of these were kept open by about 20% CO<sub>2</sub> in dry air their weight fell by 6.8% of original in 2 days, while a control group fell by 2.7%. The CO<sub>2</sub>-treated beetles were allowed to recover for one day after which they again lost only 1.3% of their weight in a day. O. plana which had been killed by exposure to chloroform lost 7.4% in two days. It is not clear, however, whether the dead insects lost a lot of water because their spiracles were open, or for some other reason.

Uptake of water vapor by Ctenolepisma

Forty Ctenolepisma were kept in dry air at 27°C until their weight fell to a mean of 79.8% of original weight. Ten animals were then put in each of the humidities 40, 50, 60, and 80% for two days, after which their weights were as follows:

<u>R. H. %</u>	<u>% of Original Weight</u>
40	72.8
50	98.8
60	100.4
80	100.3

Those that had been at 40% R. H. were held at 45% for a further 2 days, when their weight fell to 65.8%, then at 47.5% for 2 days when their mean weight rose to 68% (4 gained, 3 lost and 1 remained constant); then to 50% for 4 days when their weight rose to 86.2% and finally for 1 day at 90% when the weight rose to 101%. One insect finished with a weight equal to 139% of its original weight, and this after two weeks starvation.

In a further experiment, 45% R. H. was again found to be too low for vapor uptake, while at 47.5% this was just possible.

Experiments were then made to find whether the state of hydration of these insects affects the rate of water loss and gain. This appears to be so, for a fully hydrated group of insects lost 14% of their original weight in 2 days at 20% R. H. while a control group of partly dehydrated insects lost only 5%; and again, hydrated animals gained only 1% during 2 days at 90% while dehydrated ones gained 20% in the same conditions. As mentioned above, these insects live in an environment which at times is very hot and very dry. Doubtless some of the



water they need is derived from the oxidation of foodstuffs (they feed on plant detritus blown into their otherwise lifeless habitat). However, there probably are times when food is very scarce or absent, and then it seems that the ability to absorb water vapor from relative humidities as low as 47.5% is a very useful adaptation.

### 3. Body temperatures

#### a) Body temperatures in the field.

All the body temperatures to be reported were measured by means of fine copper-constantan thermocouples made from 46 S.W.G. wire, using a potentiometer sensitive to 0.005 mV. (A copper/constantan junction generates about 0.04 mV per 1°C difference). With care the thermocouples could be relied upon to the nearest 0.2°C.

Insertion of a fine thermocouple into the thorax of even a small beetle such as Stenocara eburnea did not appear to incommode it at all.

Temperatures of beetles in the field were measured by exposing the insects either in such a way that they could move relatively freely while the observer followed their movements with a stick which carried the thermocouple leads. Alternatively, the beetle was mounted on a small slip of wood by slips of adhesive tape over each tarsus, the wood was covered with sand to provide the appropriate substrate reflectivity, and the main thermocouple leads were attached firmly to one end of the mount. Such a 'probe' could be placed wherever it was desired to measure the insects' temperature.

The highest body temperature observed in a situation where other completely free beetles were also present (and presumably had about the same body temperature) was 44.5°C in Onymacris rugatipennis at 11.30 a.m. on January 27 on sand.

When tethered in direct sunlight for experimental purposes, O. rugatipennis frequently reached 50°C for several minutes and survived. However, no free beetles were present at those times so that it cannot be said that O. rugatipennis reaches 50°C in nature.

Such records are not particularly informative. Of greater interest is valuable information concerning the effect of various factors on body temperature, and some information on this was obtained. For example the importance of orientation of the body towards the sun's rays was very clearly observed. The following example of a beetle's thoracic temperature is typical of several records:

July 18. 2.06 p.m. Kuiseb river bed.

	<u>Temperature in °C</u>		
	<u>O. rugatipennis</u>	<u>Ground</u>	<u>Air at 1.0 cm.</u>
Insect head on to the sun	35.0	40.7	30.5
Insect's left side to sun	39.7	41.2	33.2
Insect's right side to sun	40.7	40.7	31.0

O. rugatipennis and P. cribripes were frequently observed to move between sun and shade. After a long exposure to the sun as they moved across an open area, beetles would pause in the shade of an Eragrostis bush (for example) before moving out into the sun again. I therefore made measurements to find the time taken for the body temperature to rise or fall as a result of movement between sun and shade. A beetle, attached to a fine thermocouple lead, was allowed to reach a constant temperature either in sun or shade and then transferred to the other condition. Immediately its body temperature was recorded at approximately 10 second intervals, while the substrate and air temperatures were recorded less frequently. A typical example of a move from shade to sun

is the following. The body temperature rose from 28.5°C to 41.0°C in 6 minutes while the ground temperature in the sun rose from 40.3° to 41.6°, and that in the shade remained at 28°C. In the reverse direction, the temperature of an insect placed in the shade after exposure to the sun fell from 38.1 to 28.5°C in 4 minutes while the air temperature varied between 27.5 and 29°C and the ground temperature in the sun was 41.0°C. On July 25, in the Kuiseb river bed, one O. rugatipennis was observed to walk in the sun for 15-20 second intervals, alternating with short sojourns of about 10 seconds in the shade. These conditions were mimicked as far as possible with captive beetles. Background conditions were as follows: Ground with direct sun, 42.5°C; ground in the shade, 22.5°C; air in sun 32.7°C, air in the shade (in Eragrostis bush) 22.5°C. One beetle in sunshine in these conditions varied between 42° and 43°C, while a second beetle, in the shade, was steady at 23°C. The second beetle was then exposed alternately to sun and shade for 15 seconds each. After eight such alternations the temperature of the beetle varied between 30° in the shade and 31.8°C in the sun.

It is therefore possible for beetles to thermoregulate satisfactorily in this manner. Whether or not this is the reason for the observed behavior cannot be said.

#### b) Lethal temperatures

Having observed rather high body temperatures in nature, it was of interest to establish upper lethal temperatures for the insects concerned. These determinations were made firstly in rising temperatures (about 1°C every 1.5 minutes). However, this gave rather erratic results because it was difficult to judge when heat coma occurred. Another method was therefore used, in which the beetles

were exposed to constant temperatures for a fixed period of time (30 min.) and their survival was determined on the following day. If at that time they were able to walk away from a 50 watt tungsten filament lamp in a metal shade suspended directly over them at a height of 6 inches, they were considered to have survived.

The beetles were exposed in moist air in a jar whose temperature was maintained by stirred water outside it. Thermocouples inserted into the beetles showed that even large species reached the air temperature in 7 minutes. Only 4 beetles were used at a time and their insertion into the jar caused only a brief (20 sec.) drop in the temperature of the air in the jar.

In constant temperatures: for 30 min. and moist air. (A signifies alive, D signifies dead, 24 hours after exposure)

Temp.	<u>Lepisma</u>	<u>O. plana</u>	<u>O. rugati</u>	<u>O. laeviceps</u>	<u>T. capicola</u>	<u>T. spinipes</u>	<u>T.sp (small)</u>
0°							
42.5	A	A	A	A	A	A	A
45	"	"	"	"	D	"	D
46	"	"	"	"	"	"	"
47	"	"	"	"	"	"	"
48	A/D	"	"	"	"	"	"
49	D	"	A A/D	D	"	D	"
50	"	"	A/D	"	"	"	"
51	"	D	D	"	"	"	"

Clearly two of the mesic tenebrionids have a much lower lethal temperature than all the desert insects examined. Of the latter, the most hardy seems to be

Onymacris plana, and this is reasonable because this species lives on the open dunes, is active and is exposed to higher temperatures than other species since it seeks cover later in the morning and emerges sooner in the afternoon.

c) The effect of surface color on body temperature

There is some doubt in the literature as to whether or not the surface colors of insects have an important effect upon their body temperatures. The experiments to be reported suggest that indeed black and white surfaces do have such an effect.

Preliminary experiments showed that the sub-elytral cavity of Onymacris brinki (a beetle with black head and prothorax and white elytra) was cooler than the thorax. The extent of the difference and the reasons for it were therefore investigated in this and in other species.

Fine thermocouples as described above were used to measure temperatures and they were inserted through small (0.5 mm) holes in the cuticle, and held in place by a water soluble white glue. The junction inserted through the elytron made contact with the abdominal surface below.

In direct sunshine at Gobabeb, when the energy of the radiation on a horizontal surface was about  $1.15 \text{ cal./cm}^2/\text{min.}$ , temperature differences up to  $4^\circ\text{C}$  were observed in O. brinki (the thorax being hotter). The differences were variable and depended very much on the orientation of the insect to the sun's rays. Air movement reduced the temperature difference.

In similar circumstances sub-elytral temperatures of Stenocara eburnea (a white species) were consistently about  $1^\circ\text{C}$  cooler than those of S. depressa (a black species). Both these insects are about 1 cm. long.

Differences were observed in dead as well as in living beetles, so that thoracic muscle contraction was not responsible for the difference. Differences

in temperature were also observed in models where only the elytra of O. brinki (white) and O. laeviceps (black) were used. In whole insects, the sub-elytral temperature of O. laeviceps was higher than that of O. brinki. Finally, the temperature of O. brinki was raised approximately to that of O. laeviceps when the elytra of brinki were coated with carbon black.

It can therefore be said that differences in reflectivity between the black and white elytral surfaces is responsible for the observed temperature differences.

The situation was analysed further in the laboratory at Cape Town, under more readily controlled conditions. This work was particularly useful in showing the extent of the orientation effect. Thus, in dead as well as in living O. brinki exposed to direct sunlight, the temperature of the abdomen below the elytra was equal to or cooler than that of the beetle's thorax except when the sun's rays fell at an elevation of 45° or less from behind the insect, when the abdomen was warmer. Contrariwise, in the all black beetle O. laeviceps, the sub-elytral temperature was equal to or higher than that of the thorax when the sun's direction was behind the animal and at any elevation up to 90°C.

By means of a recorder it was possible to follow the rate of heating and cooling below the black and white surfaces of beetles. In general black areas both gained and lost heat more rapidly.

Temperature differences in the expected direction were also observed between light and dark colored morphs of the diurnal beetle Calosis amabilis, even though this insect is a good deal smaller than O. brinki or O. laeviceps, (0.05 g. compared with 0.6 g. approximately).

The above experiments show that surface reflectivity in the visual range does have a significant effect on body temperature. Whether or not this has an ecological significance is another question. Beetles are able to move from one microhabitat to another, or to become active at different times of the day, and thus exercise considerable control over their temperatures. Perhaps the striking black and white contrast shown by (for example) Onymacris brinki or Stenocara eburnea have other functions, such as advertisement.

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### Summary

1. Microclimates in the immediate environments of the insects in three different habitats were measured. The data include temperatures and relative humidities in the dunes area, in the Kuiseb river bed and on the plains to the east of the river, during 24 hour cycles in January or February 1968. Some correlations are apparent between these factors and activity cycles. For example, the daily activity of Onymacris rugatipennis in the river bed is bimodal in the hot summer months but becomes unimodal in the winter.
2. Relative humidity in the habitat of the thysauran Ctenolepisma sp. near pauliana in the plains was always low, but sometimes high enough to permit the insect to absorb water vapor.
3. Overall water loss during 5 days in dry air at 27°C ranged from 6.4% of original weight in the diurnal beetle Onymacris plana to 15.9% in the nocturnal Lepidochora argentogrisea. Tenebrionids from more mesic habitats (Trigonopus spp. from Grahamstown) showed losses up to 25%.
4. Ctenolepisma sp. near pauliana absorbs water vapor from humidities down to 47.5%. It loses less rapidly (or gains more rapidly provided the R. H. is above the 47.5% threshold) when short of water after partial dehydration.
5. The body temperature of Onymacris rugatipennis rises to at least 44.5°C in nature. The temperature of these insects in the field depends upon their



orientation to the sun. The effect of direct sunlight and shade, and of various combinations of these, on body temperature was determined, using live insects and models. Possibly beetles thermoregulate by alternately visiting shaded and insolated areas.

6. Upper lethal temperatures were measured during exposures of 30 minutes in moist air. They range from 51°C for Onymacris plana to 49°C for O. laeviceps. The mesic tenebrionid beetle Trigonopus sp. near capicola died at 45°C.

7. During direct insolation Onymacris brinki, which has white elytra, has a lower sub-elytral temperature than does O. laeviceps which has black elytra. The sub-elytral temperature of brinki is cooler than that of the black prothorax in the same insect. Experiments in the field and in the laboratory, with live insects and with models, showed that surface reflectivity within the visual spectrum does significantly affect body temperature. Differences between sub-elytral and thoracic temperature of 2° - 3°C were commonly measured. The ecological significance of these facts is unclear.