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SOME ASPECTS OF WATER BALANCE IN TENEBRIONID BEETLES AND A THYSANURAN FROM THE NAMIB DESERT OF SOUTHERN AFRICA[1]

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INTRODUCTION

The richness of the arthropod fauna in vegetationless sand dunes of the Namib Desert in S.W. Africa has recently received comment (Lawrence 1959; Koch 1961, 1962). This fauna together with that of the dry riverbed and of the stony plains, all near Gobabeb, provide exceptional material for investigation of the various adaptations of arthropods to extreme desert conditions. In an attempt to take advantage of some of these opportunities, I visited the Namib Desert Research Station at Gobabeb during the summer and again during the winter of 1969 and made observations both there and at the University of Cape Town on certain aspects of the physiological ecology of some of the commoner arthropods. The present paper reports the results of those experiments which were concerned with water exchange. Experiments on body temperature and on activity in relation to microclimatic conditions will be reported elsewhere.

On the whole, desert arthropods are exposed to a highly desiccatory environment, and one important aspect of their physiology concerns the extent to which evaporative water loss may be reduced and water conserved. The pres-

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[1] The late Dr. C. Koch kindly provided facilities at the Namib Desert Research Station in South West Africa. My thanks are due to Prof. John Day for facilities in his department at the University of Cape Town. Mrs. Gay Youthed kindly sent beetles from Grahamstown and Mr. Eric Holm not only collected for me in the Namib Desert when I was away, but gave a great deal of valuable assistance and information while I was working in the desert. Grateful acknowledgments are also made to the Guggenheim Foundation and the National Science Foundation (GB 7931 and 8700) for financial support.

ent work was done to obtain comparative data about total water loss in a variety of species and to see whether, and if so how, this may be correlated with different habitats and different activity patterns. Several arthropods are now known to reverse the direction of overall water movement and to show a gain of water in unsaturated air provided the relative humidity is above a level specific for each species (Edney 1967, 1970). The existence of such an ability would presumably be advantageous in desert situations—it has been shown in a desert cockroach (Edney 1966)—and the present work was designed to find whether it occurs in any of the species now studied.

MATERIAL AND METHODS

The species used were chosen to represent as far as possible the three main habitats in the vicinity of the research station at Gobabeb: the vegetationless sand dunes to the southwest, the Kuiseb riverbed which runs approximately from southeast to northwest, and the gravel plains on the northeast of the river.

Brief ecological information about each of the species studied is given in table 1; for further information see Holm (1970). The sand dune habitat contains several subhabitats: the dune slopes, slip faces and crests (which are vegetationless), the dune bases, and interdune valleys where small clumps of the grass *Stipagrostis sabulicola* and the cucurbit *Acanthosicyos horridus* provide some protection. The Kuiseb riverbed is quite richly vegetated, including the large trees *Acacia giraffae* and *A. albida*. The gravel plains again are virtually without vegetation.

As a control insect *Trigonopus* sp., a tenebrionid beetle from a more mesic area near Grahamstown in the Cape Province, was used. This beetle is common under stones on hillsides lightly wooded with pine trees. The insects were either caught by hand or in pitfall traps, were kept in the laboratory in metal boxes with sand, and were fed on corn flakes, dog biscuit, carrot, and occasionally lettuce.

TABLE 1

MAIN ACTIVITY PERIODS AND MAIN HABITATS OF SPECIES STUDIED

SPECIES	ACTIVITY				HABITAT
	Winter	Summer	Day	Night	
Onymacris plana Peringuey	+	++	+	...	Dune and slip face bases
Onymacris laeviceps Gebien	...	+	Twilight	...	Dunes and feet of dunes
Onymacris rugatipennis Haag	+	++	+	...	Riverbed
Gyrosis moralesi Koch	...	+	+	...	Interdune valleys
Calosis amabilis Deyrolle	...	+	+	...	Gravel plains
Lepidochora porti Koch	+	+	...	+	Dune crests and slip faces
Lepidochora argentogrisea Koch	+	+	...	+	Dunes and dune feet
Ctenolepisma terebrans Silvestri	...	+	...	+	Dune feet and dune slopes (fairly ubiquitous)

Some preliminary measurements were made in the laboratory at Gobabeb, but the greater part of the work was done in the zoölogy department at the University of Cape Town. For the main experiments the insects were exposed singly in open glass vials to air over freshly dried calcium chloride (a nominal 0% relative humidity) in desiccators. The desiccators were kept at 27 C ± 0.5 C, except for about 10 min. each day when the insects were weighed. Weighings were made to the nearest 0.1 mg, and provided the vials were at laboratory air temperature, repeatability to 0.2 mg was readily achieved. Where possible 25 or more individuals of each species were used, and they were weighed once a day for 5 days while in dry air. After this, 10 insects of each species were put into 90% relative humidity and weighed for a further 2 days, to find whether they reabsorbed water vapor.

To reduce the output of fecal pellets as far as possible, all insects were fasted for 24 hr before use. Nevertheless, a few pellets were sometimes produced, but their weight was never more than 5% of the weight lost by evaporation of water from the whole insect. Loss of water from the pellets was unknown but must have been comparatively small, and the few pellets that were produced were therefore left in the vials and weighed with the insects. However, on the fifth day the pellets were discarded and the insects reweighed before being placed in 90% relative humidity, since dry fecal pellets might have absorbed considerable amounts of water.

Very nearly all the insects were apparently healthy at the end of the experiment, and the few that showed any indication to the contrary (e.g., if they were unnaturally inactive or unresponsive) were discarded. Loss or gain of weight during the experimental period was interpreted as loss or gain of water, respectively. No doubt the insects' dry weight fell as a result of oxidation of reserves during this time, and it is unlikely that the resulting water of oxidation would offset this loss precisely, so that some error will have been introduced. However, for comparison between species the observations are probably acceptable as measures of water leaving the insect (not as measures of overall change in water content). Measurements of RQ were not made, but if fats and polysaccharides were metabolized in equal proportions and O_2 uptake was 0.4 ml g^{-1} hr^{-1} (based on values for *Schistocerca, Tenebrio molitor* and other insects quoted by Keister and Buck 1964), calculation shows the error to be 5% in an insect that loses only 2% of its weight per day. If more fat were metabolized, or weight lost more rapidly, the error would be less.

RESULTS

Besides getting information about comparative water loss, I also wanted to know whether the rate of loss from any one individual varied with time, and whether size affected the rate of loss per unit weight. The results will be considered from these points of view.

A. VARIATION IN RATE OF LOSS WITH DURATION OF EXPOSURE

The daily weights of 10 *Onymacris plana* over an 8-day period (5 in dry air followed by 3 in 90% relative humidity) are plotted in figure 1 in order to show individual behavior and variability. After the first 5 days, weights of individual insects varied from 94.8% to 96.8% of original wet weight, and

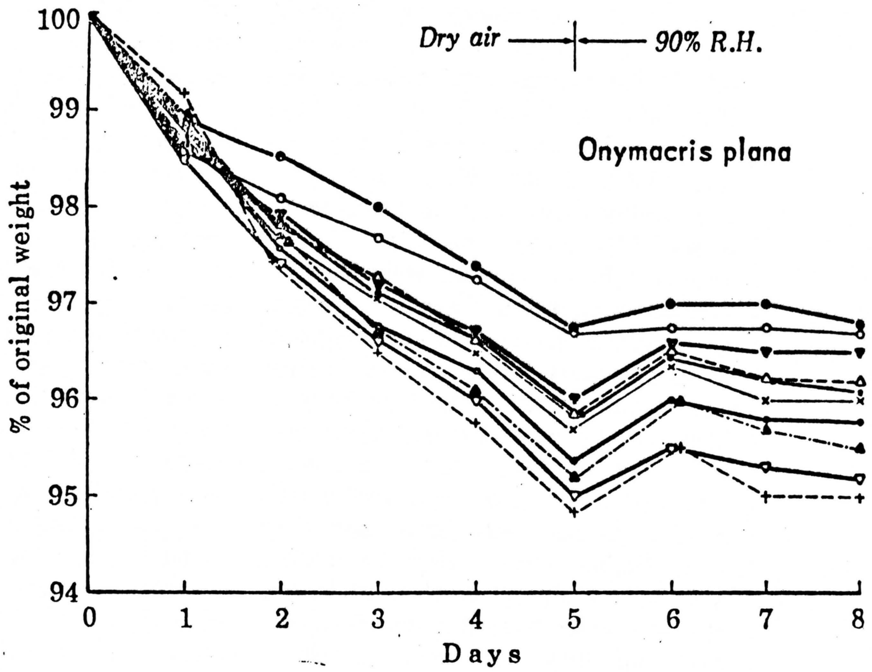

FIG. 1.—Loss of weight (presumed to be water loss) by 10 individual *Onymacris plana* during 5 days in dry air, followed by 3 days at 90% relative humidity. The rate of loss falls off slightly with time in dry air. Gain on the sixth day is probably due to cuticular adsorption.

after some initial variability an insect which lost comparatively rapidly on one day did so fairly consistently on other days. There was a slight decrease in the mean rate of loss on successive days: from 1.2% on the first day to 0.8% on the fifth. On day 6 there was an increase in mean weight, from 95.7% to 96.3% of original, and this was probably due to adsorption of water onto the dry cuticle, for on the following two days further slight drops occurred such as might be expected in 90% relative humidity. Ahearn and Hadley (1969) found a similar effect in the tenebrionid *Cryptoglossa verrucosa*.

As we shall see later, some of the variance between individuals may be accounted for by a size effect. At present, however, we are concerned with average rates of loss, and in view of the generally consistent behavior of individuals from day to day in other species as well as in *O. plana*, little information will be lost if the results for all species are expressed simply as daily means with individual limits, and this has been done in figure 2, where the species are divided into three groups only for the sake of clarity.

These results show that the mean rate of loss varied greatly from one species to another, and that the rate of loss in most species declined slightly from day to day up to five days in dry air. Subsequent behavior in 90% relative humidity was also quite consistent: there was sometimes a gain during the sixth day (probably the result of cuticular adsorption as mentioned above), but on the seventh and eighth days there was always a slight loss.

The ratio of the mean rate of loss

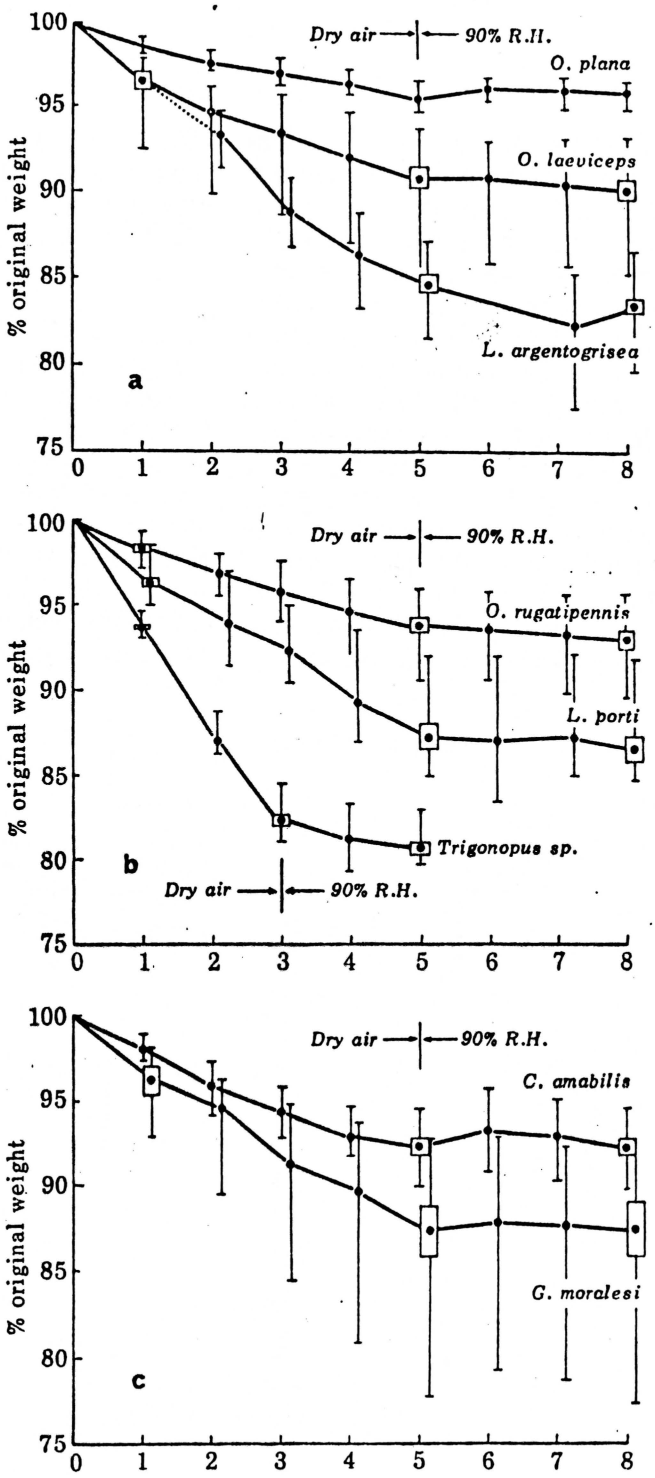

FIG. 2.—Loss of weight (presumed to be water) by eight species of tenebrionid beetles duri days in dry air. *Trigonopus* sp. comes from a mesic habitat, the rest are desert forms. Means limits are shown, and the height of the rectangles, where included, represents 1 SE each side o

during the last day in dry air to that during the second day in 90% relative humidity varied from 2.5 for *Calosis amabilis* to 4.5 for the mesic species of *Trigonopus*. If the rate of loss were determined solely by the ambient vapor pressure deficit, evaporative loss in dry air would be 10 times that in 90% relative humidity. The fact that it is much less than 10 times suggests that the insects in dry air reduced the rate of loss, perhaps by spiracular control.

There is one important exception to the generally observed slight loss of weight in 90% relative humidity: as shown in figure 3, *Ctenolepisma terebrans,* after losing weight rather rapidly in dry air, gained weight when subsequently exposed to 80% relative humidity. Experiments to explore this fact in more detail are reported below.

B. THE EFFECT OF SIZE ON EVAPORATIVE WATER LOSS

If the amount of water lost by individuals of one species is a fixed proportion of their original weight, the relation between *L* (weight lost per unit time) and *W* (original weight) will be linear. However, if a significant proportion of the water loss occurs through the insects' cuticle, such a relationship would not be expected to hold, and weight loss might vary as a

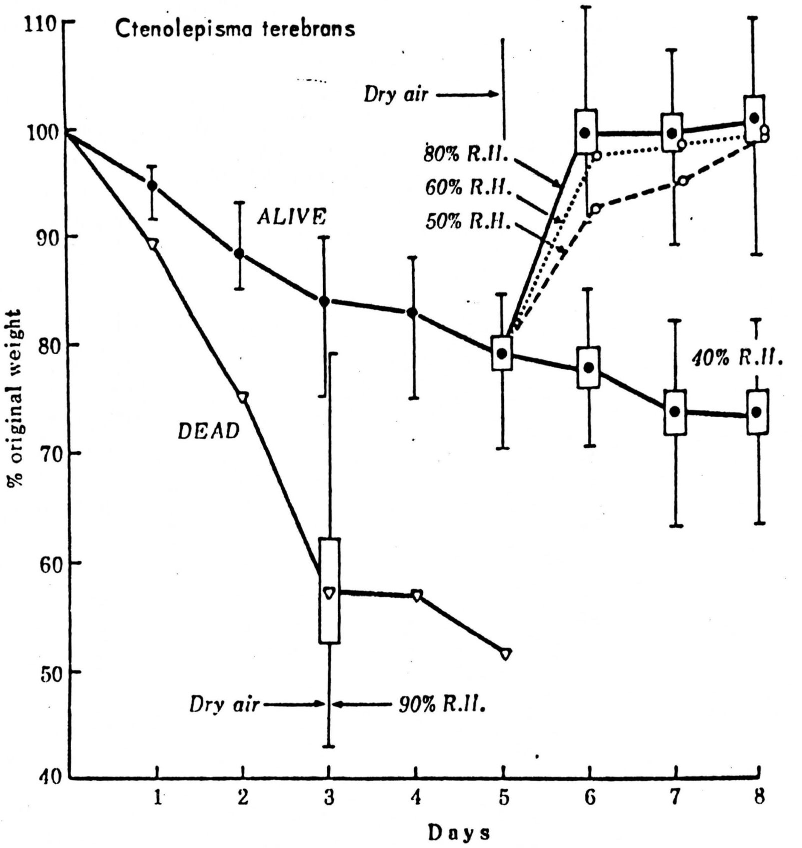

FIG. 3.—Changes in weight (presumed water) in the desert thysanuran *Ctenolepisma terebrans.* Dead insects lose much faster than living ones, and the latter gain water in 50% relative humidity or above after dehydration. Means, limits, and standard errors as in fig. 2.

fractional power of the original weight, so that $L = aW^b$, or $\log(L) = \log(a) + b \log(W)$.

In such a case, if the loss of weight is expressed as a percentage of the original weight, that is, as weight-specific weight loss, then we might expect,

$$\frac{L}{W} = aW^{b-1} \quad (1)$$

or

$$\log\left(\frac{L}{W}\right) = \log(a) + (b-1)\log(W). \quad (2)$$

If a relationship indicated by (1) holds, it is better to transform the data to the logarithmic form of (2), as Lasiewski and Dawson (1969) have pointed out in connection with standard metabolic rate and body weight in birds, because such transformation lowers the variance of the higher values and thus permits the calculation of a more reliable value for b.

The transformed values for all available individuals in each of three species are plotted in figure 4. The three species chosen are illustrative of the rest

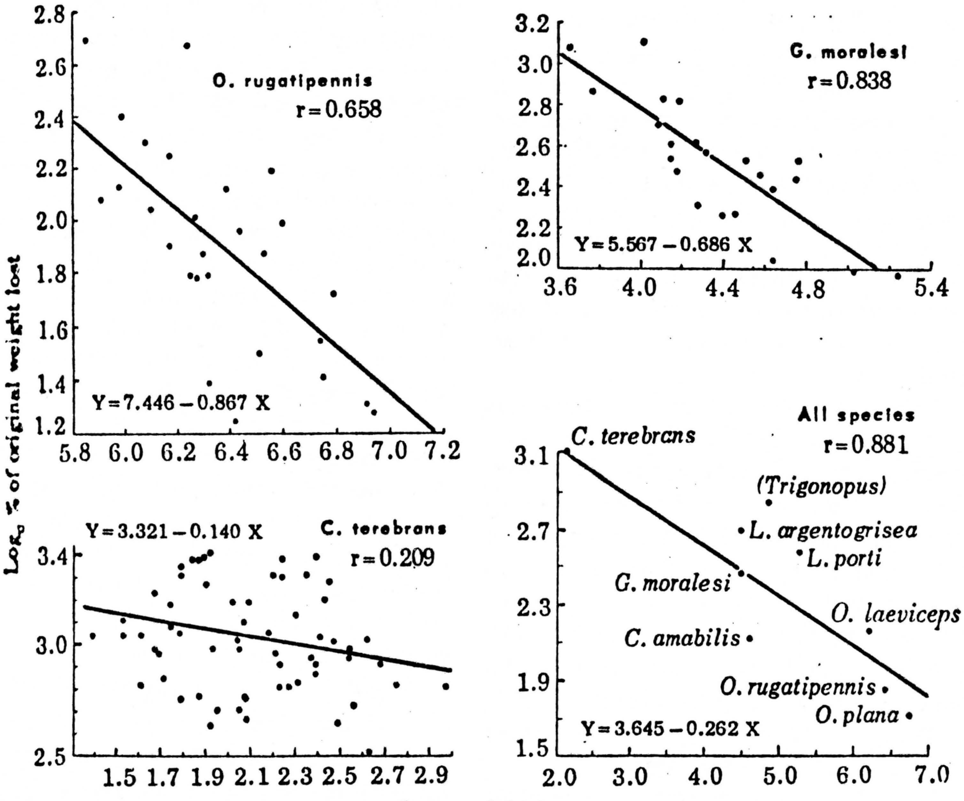

FIG. 4.—The relationship between weight (*W*) and weight specific loss of weight (presumed water) (*L*/*W*), both on a logarithmic scale. In *O. rugatipennis* and *G. moralesi* there is a highly significant negative correlation with a regression coefficient of less than 1, showing that water loss is proportional to a fractional power of the original weight of individuals. The much smaller thysanuran *C. terebrans* shows no significant correlation. A negative correlation also exists between mean weight and water loss (both logarithmic) in different species when these are compared, as in lower right-hand graph of figure. Differences between mean rates of loss in species of approximately the same weight are probably due to differences in cuticle permeability or to spiracular control efficiency.

and include one of the largest, *O. rugatipennis;* one of the smallest *Gyrosis moralesi;* and the thysanuran *C. terebrans*. The two beetle species show a significant negative correlation between weight-specific loss and original weight, while *Ctenolepisma* shows no such correlation. To graph the individual values for all the other species would be unduly repetitious, and consequently the full results are shown in tabular form (table 2).

Correlation coefficients and regression coefficients of log (specific weight loss) on log (weight) were calculated for each species, and all are significant at least at the .05 level (with the exception of *Ctenolepisma* as mentioned above). The same statistics were also calculated for each species using log (L) on log (W), but the results showed no significant correlation in the five species, *O. plana, O. rugatipennis, O. laeviceps, Lepidochora porti* and *Trigonopus* sp. although correlations were present in the others. We may conclude that there is a better correlation between weight-specific weight loss and size, and these values have been used in table 2.

Values for $(b-1)$ in (2) above derived from all available data for each species vary rather widely between species. In *Calosis amabilis* the $(b-1)$ value is -0.34, which is equivalent to a b value of $+0.66$, so that total evaporative water loss is closely proportional to surface area. In other species, however, particularly the larger ones, such proportionality is obscured, presumably by the interaction of other factors affecting water loss.

Ctenolepisma terebrans is egregious in this as in some other respects. It shows no correlation between log (L/W) and log (W). Instead, there is a strong negative correlation between log (L) and log (W), for which $r = -.80$.

C. INTERSPECIFIC DIFFERENCES IN RATE OF WATER LOSS

Apart from the effect of size on water loss intraspecifically, we may also ask whether the observed specific differences in rates of loss (expressed as percentages of original weight lost in unit time) may themselves be ascribed to interspecific size differences. If so, then we need not postulate any difference in (for example) cuticular permeability between the species. To answer this question a specific rate of water loss was obtained for each species by calculating the rate for an average sized individual from the appropriate relationship: $\log (W/L) = \log (a) + (b-1) \log (W)$. These values, in terms of percentage loss in 5 days, were graphed against log (W) for each species, as shown on the lower right graph in figure 4. A correlation coefficient of $-.8$ obtains, and the $(b-1)$ value is -0.262. In general, therefore, smaller species do indeed show higher specific weight losses than larger ones. However, such a conclusion is not very informative: of more importance is the fact that there exist large differences in loss rate between rather similarly sized species. For example, *C. amabilis*, a beetle active by day in the summer on open gravel plains, has a lower weight-specific loss rate than the two species of *Lepidochora, argentogrisea* which is mostly nocturnal and *porti* which is strictly nocturnal; while a much higher loss rate is shown by the mesic *Trigonopus* sp., although all four species are rather similar in individual weights. The matter is discussed further below.

TABLE 2

COMPARATIVE RATES OF WEIGHT LOSS (PRESUMED WATER LOSS) IN VARIOUS SPECIES, AS PERCENTAGE OF ORIGINAL WEIGHT AND AS RATES PER UNIT SURFACE AREA

	SPECIES								
	Onymacris plana	*Onymacris laeviceps*	*Onymacris rugatipennis*	*Gyrosis moralesi*	*Calosis amabilis*	*Lepidochora porti*	*Lepidochora argentogrisea*	*Ctenolepisma terebrans*	*Trigonopus sp.*
N	26	19	28	22	27	27	16	63	18
Mean weight in mg	838.5	483.9	601.5	85.2	96.7	187.5	86.7	8.7	125.8
Mean weight lost in 5 days as % of original weight	5.6	9.1	7.2	12.8	8.8	14.2	15.0	21.1	29.5
Correlation between log (% weight lost) and log (original weight) (all individuals):									
r	−0.425	−0.668	−0.658	−0.834	−0.588	−0.630	−0.631	−0.209	−0.817
p^a	<0.05	<0.01	<0.001	<0.001	<0.01	<0.001	<0.01	>0.1	<0.001
$(b-1)^b$	−0.494 ±0.444	−0.901 ±0.514	−0.867 ±0.400	−0.686 ±0.208	−0.342 ±0.193	−0.719 ±0.365	−0.465 ±0.328	−0.140 ±0.168	−0.875 ±0.327
Mean weight lost in 1 hr as % of original weight[c]	0.052	0.139	0.071	0.163	0.076	0.195	0.138	0.228	0.264
Mean surface area in cm^2	10.64	7.38	8.54	2.32	2.53	3.92	2.35	1.10	3.01
Mean rate of loss of weight—(presumed water) in μg cm^{-2} hr^{-1} mmHg^{-1}	1.53	3.41	1.87	2.24	1.09	3.49	1.91	0.68	4.13

[a] The probability that the correlation coefficient, r, does not differ from 0.

[b] Where $(b-1)$ is the exponent in the equation $\frac{L}{W} = aW^{(b-1)}$, ± 95% confidence limits.

[c] Calculated as 1/24 of the loss during the first day.

D. THE EFFECT OF CO_2 AND DEATH ON WATER LOSS BY ONYMACRIS PLANA

Thirty beetles were prepared by fasting for 1 day as before and then divided into three groups. The first group was kept in dry air for 2 days, the second group was in 20% CO_2 in dry air, and the third group was killed in H_2S and then kept in dry air for 2 days. The weights of individuals in each group were measured each day, and the results are shown in table 3.

While the beetles in dry air lost 1.95% of their original weight, those in CO_2 lost 6.78% and those that were dead lost 7.41%. The difference between those in air and those in CO_2 is significant ($P < .001$), and since CO_2 generally causes spiracles to be kept open we can attribute the extra water loss to this channel. The difference between dead and living beetles was also highly significant ($P < .001$), but that between dead beetles and living ones in CO_2 is not significant ($P > .1$), so that the high rate of loss in the dead beetles may have been due to their dying with the piracles open, although the evidence or this is not, of course, conclusive.

E. WATER VAPOR ABSORPTION BY CTENOLEPISMA TEREBRANS

As mentioned above, *C. terebrans* behaves differently in several ways from the beetles studied. Its weight-specific water loss is high and is not affected by weight. Furthermore, after dehydration this species gains weight by absorption of water vapor in high humidity.

TABLE 3

EFFECT OF 20% CO_2 AND OF DEATH ON WATER LOSS IN "ONYMACRIS PLANA"

Conditions	N	Mean Loss of Weight in 2 Days as Percentage of Original Weight ± Standard Error
live in dry air	10	1.95 ± 0.20
		$P < .001$
live in 20% CO_2 in dry air	10	6.78 ± 0.50
		$P > .1$
ead in dry air	10	7.41 ± 0.56

Such water vapor absorption has now been observed in several arthropods, and the limiting conditions for its occurrence are various, so that an experiment was designed to define the process and its effects in this species.

First, a pilot experiment was carried out to find the approximate lower limit of relative humidity in which absorption would occur. Noble-Nesbitt (1969) found that another thysanuran, *Thermobia domestica,* absorbed water vapor at 63% relative humidity but lost water at 43%, and Heeg (1967) observed absorption by *C. longicaudata* from 60%. Accordingly, 80%, 60%, 50%, and 40% were chosen for the pilot experiment. Dead *C. terebrans* were used as controls. The result in 80% relative humidity has been briefly referred to above—all results are graphed in figure 3—and we now consider them further.

After dehydration to a mean of 79.6% of original weight during 5 days, *C. terebrans* increased in weight by water-vapor absorption to 101%, 99.1%, and 99.1% of original weight during a further 3 days at 80%, 60%, and 50% relative humidity, respectively, but decreased to 73.4% in 3 days at 40%. Dead *C. terebrans* lost water more rapidly than living ones, dropping to 57.6% of original in 3 days in dry air, after which they did not reabsorb water vapor even at 90% relative humidity.

A further experiment permitted the more precise definition of conditions necessary for absorption. Insects were dehydrated as before for 5 days, during which time their weight was reduced to a mean of 79.5% of original. Thereafter they were divided into three groups of

10 each. The first group was kept at 45% relative humidity and lost weight from 79.7% to 77.6% in 2 days; the second group at 47.5% relative humidity rose from 80.3% to 91.5% of original in 2 days, and the third group at 50% relative humidity gained weight, from 78.5% to 91.1% in the same time. These results are shown graphically in figure 5, and we may conclude from them that the lower limit for uptake of water vapor by *C. terebrans* lies between 45% and 47.5% relative humidity.

F. THE EFFECT OF PRECONDITIONING ON WATER EXCHANGE IN CTENOLEPISMA TEREBRANS

A further question concerns the extent to which loss of water may be regulated according to need. For example, if the body water content is low, does an insect then reduce its rate of loss in dry air below the level characteristic of one with normal water content? The contrary question may also be asked in the case of an insect such as *C. terebrans,* namely, is the extent of absorption at high humidities lower in insects with high water contents?

To answer these questions, the following experiment was done. Twenty insects were kept at 90% relative humidity without food for 7 days, after which, when they were presumably fully hydrated, half were transferred to 20% relative humidity, the remainder being retained at 90%. A further 20 insects were kept at 20% relative humidity for 7 days, after which 10 were kept at 90% and 10 at 20%.

The results are shown in figure 6, and the effect of the preconditioning is very clear. During one day in 90% relativ humidity, insects gained 0.8% weigh if they had been previously in high hu midity and 20% if they had been i low humidity. Contrariwise, in one da at 20% relative humidity, insects los 3.2% weight if previously dry, but 9% if previously wet. Both differences ar significant ($P < .01$). During the secon day's exposures these trends were i general repeated.

DISCUSSION

Some information already exists abo water loss in desert arthropods, and th is referred to by Edney (1967, 1971 The work of Warburg (1965) on is pods; of Cloudsley-Thompson (1961 1961*b*; 1968, and other papers) on va

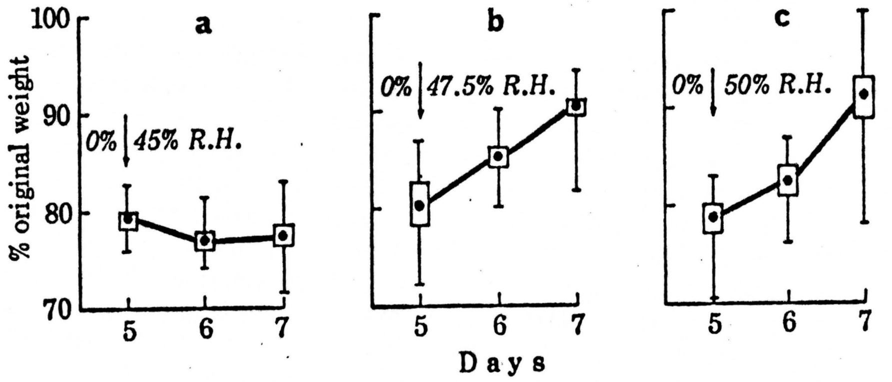

FIG. 5.—The critical humidity for water vapor absorption by *Ctenolepisma terebrans.* At 45% r tive humidity there is little change, at 47.5% rehydration occurs. Means, limits and standard error in fig. 2.

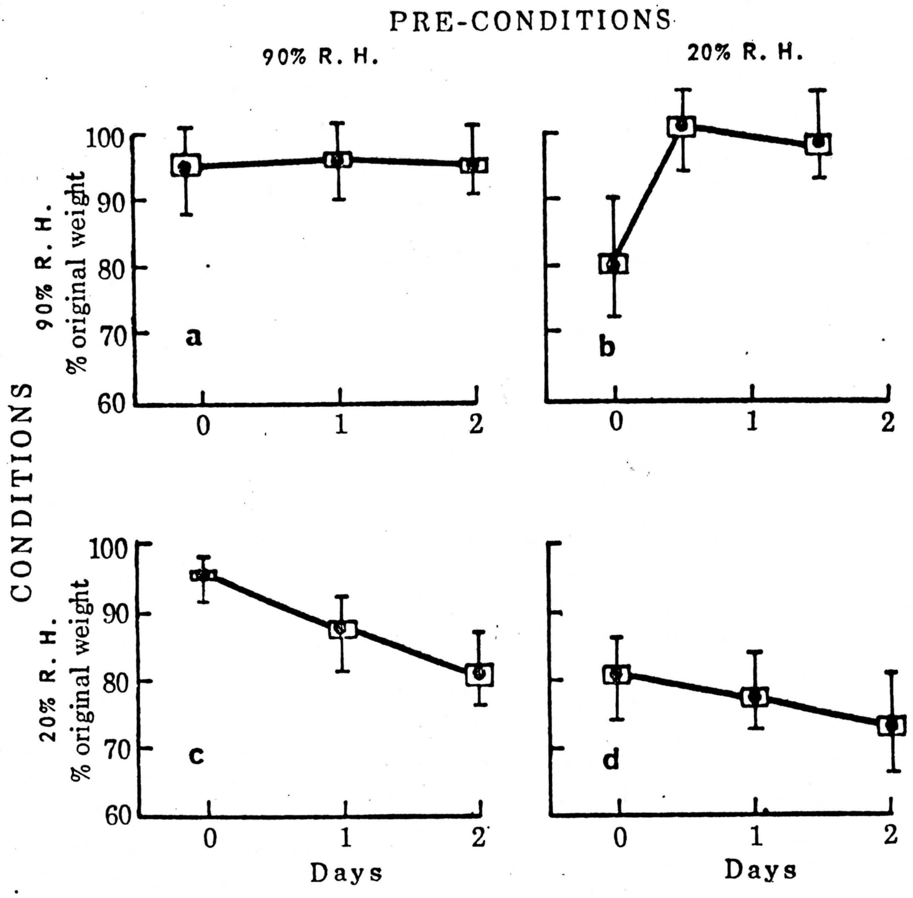

FIG. 6.—The effect of previous conditions (hydration or dehydration) on subsequent water exchange wet or dry air by *Ctenolepisma terebrans*. Previously dehydrated insects lose less water in dry air d gain more in 90% relative humidity. Means, limits, and standard errors as in fig. 2.

us arachnids; of Bursell (1958) on etse-fly pupae; of Ahearn and Hadley 1969) on beetles and of Herreid 1969) on arachnids, all goes to show at desert arthropods generally have ther low transpiration rates, and ere is little doubt that cuticular pereability and spiracular control of spiratory water loss are important mponents in the adaptation of many nall desert animals to their environent.

Direct comparison of transpiration tes is often difficult because authors ve expressed their results in different ıys, and also because even in one species the rate varies with stage of development, size, humidity of the environment (Loveridge 1968*a*, 1968*b*), the state of the individuals' water reserves, and of course with environmental and cuticular temperature. However, by transforming data and making a few assumptions such comparisons have been made (Bursell 1964; Edney 1967; Hadley 1970), and they prove to be instructive.

The present results show that so far as total transpiration is concerned, some of the beetles in the Namib Desert have some of the lowest rates recorded for any arthropod. Thus *Onymacris plana* lost a mean of 1.25% of body weight during the first day of exposure to dry air at 27 C. Its loss of weight was therefore 0.052% per hour, compared with 0.120% per hour for *Cryptoglossa verrucosa* and 0.245% per hour for *Eleodes armata* (Ahern and Hadley 1969), both American tenebrionid beetles. *Onymacris plana* does lose a rather greater proportion of its body weight per hour than the scorpion *Leiurus quinquestriatus,* which lost 0.03% (Cloudsley-Thompson 1961*a*) or the scorpion *Hadrurus arizonensis* weighing 4.0 g or more, which lost 0.028% per hour at 30 C (Hadley 1970). However, those scorpions were a good deal bigger than *O. plana,* and for specimens weighing from 0.5 to 1.0 g the rate (0.06%–0.11% per hour) was higher than that for comparable sized *O. plana.*

The mean weight of specimens of *O. plana* used was 0.838 g, and if we assume a value of 12 for k in the relation $S = k\ W^{2/3}$, an approximate figure of 10.64 cm^2 for surface area is obtained.[2] A little further calculation shows that the rate of loss by *O. plana* is about 1.53 μg cm^{-2} hr^{-1} mmHg^{-1}; and values for the other desert insects calculated in the same manner range from 0.68 (*Ctenolepisma terebrans*) to 3.49 (*Lepidochora porti*) μg cm^{-2} hr^{-1} mmHg^{-1}. These values are also shown in table 2. Not surprisingly, *Trigonopus* sp. (from a mesic habitat) has a higher rate of loss than any of the desert forms at 4.13 μg cm^{-2} hr^{-1} mmHg^{-1}.

Bursell (1958) found that the pupae of *Glossina morsitans* have a transpiration rate of 0.3 μg cm^{-2} hr^{-1} mmHg^{-1}, and this seems to be the lowest rate recorded, lower even than the well-waterproofed eggs of *Rhodnius prolixus* (Beament 1949).

Rates of transpiration expressed in this way (i.e., in terms of surface area) are of interest physiologically. From an ecological point of view, expression in terms of percentage of body weight lost per unit time is probably more meaningful, since a small insect may well reach its limit of dehydration before a larger one even though the latter has a higher rate of total transpiration per unit area of surface.

In general the rates of total transpiration from insects studied in this work correspond rather well with their ecological niches. Thus *O. plana,* which is active by day in the summer and runs on open unprotected sand, has the lowest water-loss rate of all. *Calosis amabilis,* also active by day in the summer on gravel plains, approaches *O. plana* in water conservation. A form active by twilight, *O. laeviceps,* has a higher rate of loss, while the two species of *Lepidochora,* active by night only, have the highest rates of loss except for *C. terebrans,* and this insect can reabsorb water vapor. *Trigonopus* sp. from a mesic habitat shows a higher rate of loss than any of the desert forms. It is important to recognize, however, that these differential rates of water loss, correlated with habitat and behavior as they may be, result from the interaction of at least two different components. Thus *O. plana* has the lowest rate of loss per unit weight not only as a result of a relatively impermeable cuticle (although it is in fact more permeable than *C. terebrans* or *C. amabilis*) but also as a result of its comparatively large size. *Calosis amabilis,* being small and active by day in the summer, would be expected to show a very low rate of loss

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[2] Based on measured values for a variety of insects (Wigglesworth 1945) and other arthropods (Edney 1951). The aim is to take account of the two-thirds relationship, so that rates of loss may be seen in relation to surface area even if the units are somewhat arbitrary.

per unit surface area, and it does in fact have the lowest of all the beetles studied.

The thysanuran *Ctenolepisma* has a very low rate of loss per unit area, but on account of its size, it loses a greater proportion of its total weight per unit time than any of the desert beetles. It will be shown elsewhere that the microclimate in which *C. terebrans* lives is such that even at the height of summer the relative humidity rises at night to a level which permits the insects to absorb water vapor.

In the present work, analysis of the components of water loss has not been a major concern, but this is an important question and should receive attention in future work.

The fact that dead beetles lose more rapidly than living ones parallels observations by several authors on a variety of arthropods, although the causes of such effects are still not clear. That *O. plana* loses water rapidly when its spiracles are open (as in the CO_2 experiments reported above) is of interest, for this species characteristically runs very rapidly, sometimes for quite long distances, over the hot sand from one patch of shade to another. During such rapid movement the spiracles are probably wide open, and this raises the question as to whether water loss could act as a cooling mechanism during these excursions.

Information is presented which shows that, in *C. terebrans* at least, dehydration itself leads to more rigorous conservation of water, and the process of water-vapor absorption is regulatory insofar as it ceases when the normal water content has been restored. It is not clear whether more rigorous conservation is achieved by a change in the nature of the cuticle (as Loveridge [1968*a*, 1968*b*] suggests for *Locusta* and Bursell [1955] suggests for terrestrial isopods) or by more rigorous spiracular control, as seems to be the case in several insects (Bursell 1957 and references in Bursell 1964), but the process is not uncommon and is clearly adaptive.

As regards the absorption process in *C. terebrans,* the rate of uptake from moist air is greater than the rate of loss in dry air, as figure 3 shows, and this corresponds with the situation in *Thermobia* (Noble-Nesbitt 1969), *Tenebrio* larvae (Locke 1964); and *Xenopsylla* larvae (Knulle 1967). In *C. terebrans* the level to which the water content rises is independent of humidity as it is in *Thermobia,* but unlike the situation in the psocid *Liposcellis* (Knulle and Spadafora 1969), in the mite *Acarus* (Knulle 1962, 1965), and in *Xenopsylla* larvae (Knulle 1967).

Noble-Nesbitt (1969) working with *Thermobia,* has given good reason for believing that the main barrier to water loss at low humidities lies in the cuticle and is not dependent on the absorption mechanism being active. The same author (Noble-Nesbitt 1970*a,* 1970*b*) has also found that absorption does not occur if the anus of the insects is blocked, and he believes that the absorption mechanism may be located in the rectum, a proposal which would explain the apparent independence of the mechanisms involved in restriction of water loss and absorption of water vapor.

The present work on *C. terebrans* contains no data either confirming or denying the presence of this interesting mechanism in that species. The fact that *C. terebrans* loses water in dry air less rapidly when its water content is low (and the absorption mechanism is presumably switched on) is not decisive evidence, since many arthropods that do not possess the absorption mechanism nevertheless behave in this way.

Whatever the mechanism the result is clearly adaptive. To be able to remain in water balance at relative humidities as low as 47.5% in the absence of free water or food must permit these insects to occupy ecological niches that would be closed to other small species that do not possess such an ability.

SUMMARY

1. The rate of weight loss (assumed to be water loss) in dry air at 27 C was measured in seven species of tenebrionid beetles and a thysanuran from the Namib Desert in S.W. Africa and another tenebrionid species from a mesic habitat (Grahamstown) in the Cape Province.

2. The mean rate of loss in each species decreased slightly during 5 days' exposure. When the beetles were transferred to 90% relative humidity there was a slight increase in weight on the next day (perhaps the result of hygroscopic absorption by the cuticle) and a slight decrease during 2 subsequent days. The rate of loss was not proportional to vapor pressure deficit, but was lower than expected in dry air.

3. In each beetle species there was a significant correlation between weight (W) and water loss expressed as a percentage of original weight $(100\frac{L}{W})$ on a log/log scale. The thysanuran, *Ctenolepisma terebrans,* did not show such a correlation.

4. Mean rates of weight-specific water loss (percentage of original weight lost in unit time) in the various species were in general found to be adapted to their known habits and habitats. These differential rates result in part from differences in size, but they also reflect differences in rates of loss per unit surface area—the latter probably being due to different cuticle permeabilities.

5. The rate of water loss from the tenebrionid *Onymacris plana* in 20% CO_2 was more than three times the rate of loss in air. Dead *O. plana* also showed a similar increase in rate of loss. Perhaps both effects are due to loss of spiracular control over water loss from the respiratory surfaces.

6. *Ctenolepisma terebrans* gained weight by absorption of water vapor in relative humidities of 47.5% or above. The rate of uptake in high humidity was greater than the rate of loss in dry air and ceased when the normal water content was restored. This species lost water less rapidly if its water content was low than if it was fully hydrated.

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