OXYGEN CONSUMPTION OF TWO SPECIES OF POGONOMYRMEX HARVESTER ANTS (HYMENOPTERA: FORMICIDAE)

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Abstract—1. The effects of temperature and vapour pressure deficit (VPD) on oxygen consumption in two species of harvester ants, *Pogonomyrmex rugosus* and *P. maricopa*, were evaluated.

2. P. maricopa had a higher rate of oxygen consumption per unit weight than P. rugosus.

3. Higher VPD resulted in an increase in oxygen consumption in *P. rugosus* but had no significant effect on oxygen consumption rate in *P. maricopa*.

4. The increased rate of oxygen consumption in *P. rugosus* at high VPD was not the result of increased activity.

INTRODUCTION

HARVESTER ants of the genus Pogonomyrmex are conspicuous components of the arthropod fauna of the Chihuahuan desert. This desert is inhabited by several species of Pogonomyrmex with some areas supporting as many as five sympatric species (Cole, 1968). The physiological responses of these species to variables such as temperature and water stress are important in the interpretation of the ecological relationships of these species. In addition, data on changes in oxygen consumption as a function of environmental variables are required in the development of ecosystem models in the Desert Biome Program. The only available data on oxygen consumption in harvester ants are those of Golley & Gentry (1964) for the southern harvester ant, Pogonomyrmex badius. In their study Golley & Gentry evaluated the effect of temperature on oxygen consumption in this species but did not vary humidity, a factor of potentially great significance in desert species. Therefore we selected two species of harvester ants, P. rugosus and P. maricopa, for studies of the effect of temperature and vapour pressure deficit on oxygen consumption. P. maricopa is a wide-ranging species through Arizona, New Mexico and northwestern Mexico (Cole, 1968). In southern New Mexico and west Texas this species is found in sandy areas where the water table is high. P. rugosus has a wider range than P. maricopa and is broadly sympatric with it. In

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southern New Mexico this species is found on the outwash slopes of the mountains which are composed of gravelly soils characterized by a dense, calcified layer (caliche) between 15 cm and 1 m below the surface.

MATERIALS AND METHODS

P. maricopa workers were collected in pitfall traps on the sides of the large nest mounds in an area approximately 10 miles east of El Paso, Texas. P. rugosus workers were collected by aspirator from colonies in the vicinity of Las Cruces, New Mexico.

Oxygen consumption was measured in a Gilson Respirometer (Arditti & Dunn, 1969). Measurements were made for 30 min, followed by 60 min of flushing with a stream of fresh air. At the lowest temperatures where oxygen consumption was low, measurement time was increased to 1 hr.

Evolved carbon dioxide was absorbed by a freshly prepared potassium hydroxide solution. Four concentrations were used; 5, 40, 70 and 100% (with excess granular KOH in the 100%), which provided a set of four humidity conditions when the atmospheric moisture in the chamber came into equilibrium with the solutions. The solutions were pipetted onto glass wool in the sidearm of each flask. The response of the atmosphere to the solutions was modelled in a larger flask in which the relative humidity was checked by a miniature wet-bulb thermistor which had been calibrated over salt solutions (Weast, 1967), and found to be quite rapid. Humidity in the experimental flasks was also checked using potassium thiocyanate paper (Solomon, 1945).

A thin smear of silicone oil was applied around the inner edge of the flask, just below the sidearm, to prevent ants from climbing into the sidearm and into the caustic absorbent. Ten ants were in each flask, and the flasks assigned at random to the treatments. The appropriate absorbent was pipetted into the sidearm and the long-stemmed stopper fitted in the "open" position so that the flasks could be flushed. The temperature was lowered to 5°C and worked up through the sequence to 45°C. At each temperature, the ants were given 1 hr of acclimation with fresh air flowing through at a rate such that the volume of air in the flasks was changed twice in the hour. The stoppers on the sidearms were then closed for an additional 30 min of acclimation, during which time humidity equilibration occurred. At the end of an experiment, the flasks were removed and examined. If any ants were dead, the set of data for that flask was rejected.

The ants were immobilized by chilling, and placed in perforated vials which were exposed to cyanide fumes overnight. The vials were then placed in a vacuum desiccator and the ants dried to constant weight.

The gas volumes were converted to μ l/hr at standard temperature and pressure, and humidity to vapour pressure deficit. The data were analyzed by multiple linear regression, with dry weight, saturation deficit and temperature as independent variables and oxygen consumption as the dependent variable.

A rough measure of activity was obtained by counting the number of ants crossing a line on the base of each flask for 1 min towards the end of each run at each temperature.

RESULTS

The multiple regression equations and Figs. 1 and 2 summarize the data on the effects of temperature and vapour pressure deficit on oxygen consumption in P. maricopa and P. rugosus. These summaries are based on 290 data points for P. maricopa (10 lost due to death) and 200 for P. rugosus in which there were no deaths during the experiments.

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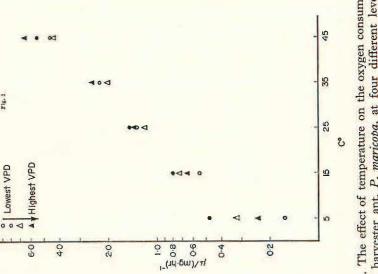
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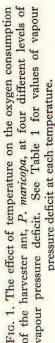
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P. maricopa had higher QO_2 than *P. rugosus* at all temperatures above 5°C except for the zero humidity conditions at 45°C (Figs. 1 and 2). Multiple regression analysis of these data showed that the slopes for temperature between the two species are highly significant (P < 0.01) (Table 2). There was a very highly significant partial regression coefficient for saturation deficit in *P. rugosus* but saturation deficit in *P. maricopa* had no significant effect on oxygen consumption (Table 2).

TABLE 1—POTASSIUM HYDROXIDE	SOLUTIONS US	ED TO	CONTROL	HUMIDITY	IN	EXPERIMENTAL
	FLAS	KS				

Concentration 5 KOH		Temp. (°C)								
	5		15		25		35		45	
%	RH	VPD	RH	VPD	RH	VPD	RH	VPD	RH	VPD
5	75	1.6	82	2.3	90	2.4	85	6.3	85	10.5
40	65	2.3	65	4.5	70	7.1	65	14.8	65	25.2
70	15	5.6	20	10.2	20	19.0	15	35.8	15	61.1
100	0	6.5	0	12.8	0	23.7	0	42·2	0	71.9

RH indicates relative humidity as a percentage and VPD indicates vapour pressure deficit in mm Hg.

TABLE 2-MULTIPLE	REGRESSION	ANALYSIS	OF VARIABLES	AFFECTING	OXYGEN	CONSUMPTION		
IN P. rugosus AND P. maricopa								

Independent variable	Regression coefficient	S.E. of R.C.	Computed <i>t</i> -value	d.f.	Probability
		P. ru	ugosus		
DW	0.01504	0.00251	5.99	286	< 0.0001
SD	0.00056	0.00069	0.82	286	0.579
Т	0.03202	0.00082	39.07	286	<0.0001
		P. ma	ricopa		
DW	0.00723	0.00237	3.05	196	0.003
SD	0.00574	0.00070	8.24	196	< 0.001
Т	0.02471	0.00096	25.84	196	<0.001

The regression line for P. rugosus may be expressed as

 $\log_{10}O_2 = 0.25561 + 0.01504DW + 0.00056SD + 0.03202T$

and for P. maricopa the regression line may be expressed as

 $\log_{10}O_2 = 0.46930 + 0.00723DW + 0.00574SD + 0.02471T,$

where DW is the dry weight in mg, SD the saturation deficit in mm Hg and T is the temperature in degrees Celsius.

The activity counts showed that in *P. maricopa*, activity approximately doubled for each 10 C deg. increment in temperature, but was apparently independent of vapour pressure deficit (Table 3). In *P. rugosus*, activity increased less rapidly with temperature, but within any one temperature, decreased with increasing vapour pressure deficit, as the activity indices show (Table 3).

TABLE 3—THE EFFECT OF TEMPERATURE AND SATURATION DEFICIT ON
ACTIVITY IN P. rugosus

	Temp. (°C)					
Vapour pressure deficit	5	15 Ad	25 ctivity in	35 dex	45	
	0	0	0	1	6	
1 (highest) 2	ŏ	ĩ	3	4	9	
2	1	2	5	7	10	
4 (lowest)	2	4	8	10	15	

The activity index is the number of times ants crossed a reference line on the respirometer flask in 1 min.

DISCUSSION

Golley & Gentry (1964) presented data on oxygen consumption at different temperatures of workers and soldiers of *P. badius*. They found that workers of *P. badius* had a QO_2 about ten times greater than the soldiers which weighed approximately ten times more than workers (1.1 mg/ant vs. 9.9 mg/ant dry weight). This size relationship holds in comparisons between *P. maricopa* and *P. rugosus* in this study since the *P. rugosus* with a mean dry weight of 4.95 mg/ant had a lower QO_2 than *P. maricopa* with a mean dry weight of 3.69 mg/ant at temperatures above 5°C (Figs. 1 and 2). However, when *P. maricopa* and *P. rugosus* are compared with *P. badius*, the QO_2 of these species is lower than even the QO_2 of soldiers of *P. badius*. These differences in QO_2 ·may reflect part of the adaptation of the western species to markedly fluctuating food supplies characteristic of desert regions.

Vapour pressure deficit (VPD) is used instead of relative humidity because the latter gives no indication of the drying power of air at different temperatures. In desert animals, VPD may be as important as temperature as a factor influencing activity. We have shown that foraging behavior in harvester ants varies in response to combinations of temperature and vapour pressure deficit (Whitford & Ettershank, unpublished). At vapour pressure deficits greater than 45 mm Hg, the foraging activity of *P. rugosus* decreases significantly and virtually ceases at VPD 750 mm Hg.

The data in this study show that in *P. rugosus*, QO_2 increased significantly at high VPD but the QO_2 of *P. maricopa* was not similarly affected. This increase

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in oxygen consumption at higher VPD was not due to increased activity. This suggests that the increase QO_2 in *P. rugosus* may be elevating metabolism in response to high VPD to produce metabolic water.

Oxidation of all food yields a ration of water and some desert animals have become independent of other sources (e.g. the kangaroo rat, Schmidt-Nielsen, 1964). Edney (1967) points out that *Tenebrio* larvae survive successfully on grain with only 1% water. Fraenkel & Blewett (1943) reared *Tribolium confusum*, *Dermestes vulpinus* and *Ephestia kuhniella* on diets with very low water content. Larvae on drier diets took longer to grow. In addition, these larvae ate more food to achieve the same growth, which was assumed to indicate that the extra food was utilized to generate water. They considered this an answer to the contention of Mellanby (1936) that no increased production of metabolic water had ever been demonstrated, and that such an increase would be disadvantageous as it would lead to an increase in water loss from the respiratory system. Fraenkel & Blewett (1943) reasoned that the larva typically contains 60-70% water, and can be reared on a diet with 1% water—hence unless metabolic water is used, all the water in the larva plus that lost by evaporation and egestion must be obtained with the food, and this can readily be shown to be impossible.

Clearly, then, metabolic water is a normal component of the growth system of some insects. However, the major question, as Edney (1967) states, is whether "insects under water stress metabolize more food and thus derive more oxidation water than they otherwise would". Barton-Browne (1964) stated categorically that "some insects use metabolic water in a truly regulatory way", but regrettably gave no references to support this statement. Edney (1967) answers his own question by contending that "there is no unequivocal evidence that arthropods... metabolize faster as a result of water shortage". He goes on to point out that though *Tenebrio* larvae and tsetse flies use more oxygen in dry air, this may be due to their greater activity.

It is frequently stated, in discussion on metabolic water, that any gain is at the cost of an increased respiratory rate, and that the water profit would be lost by the concomitant increase in transpiration (e.g. Mellanby, 1936; Wigglesworth, 1965 and contained references). This proposition is hardly supported by more recent data. Bursell (1964) points out that increased respiration need not involve a proportionate increase in water loss. He states that during flight in dry air, *Glossina* increases its metabolic rate by a factor of twenty-two, but its water loss only increases by a factor of six.

P. rugosus inhabits an environment that is singularly lacking in free water for most of the year. Indeed, this species does not accept water when it is offered experimentally either in the laboratory or in the field. Its diet is mainly seeds and some insect fragments. Yet it successfully rears a brood each year on this low moisture diet. The increased metabolic rates observed at lower humidities in *P. rugosus* is not due to increased activity since these insects tend to become more quiescent at high VPD. This would seem to be the response where metabolism is facultatively increased in response to water loss. However, further investiga-

tion is needed into water loss rates and haemolymph concentrations before this evidence could be considered unequivocal. It is interesting to note that an exactly parallel situation occurs in a species pair of the Australian ant genus *Iridomyrmex* which is currently being investigated by one of us (G. E.).

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