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Standard energy metabolism of a desert harvester ant, *Pogonomyrmex rugosus*: Effects of temperature, body mass, group size, and humidity

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ABSTRACT **_Pogonomyrmex rugosus_ (Hymenoptera: Formicidae) is an important seed predator in the Mojave Desert of the southwestern United States. Its standard rate of O_2 consumption ($\dot{V}O_2$) varied significantly with temperature ($\dot{V}O_2 = 10^{(-1.588 + 0.0315T)}$, where $\dot{V}O_2$ is $ml \cdot g^{-1} \cdot hr^{-1}$ and T is body temperature in °C). The ratio of the $\dot{V}O_2$ values at 10°C increments in body temperature, Q_{10}, also varied with temperature; methods of calculating $\dot{V}O_2$ from temperature with a shifting Q_{10} are described. $\dot{V}O_2$ also varied with body mass ($\dot{V}O_2 = 0.0462M^{0.669}$, where $\dot{V}O_2$ is $ml \cdot hr^{-1}$ and M is body mass in g). $\dot{V}O_2$ was inversely related to relative humidity and was independent of group size. The rise in $\dot{V}O_2$ at low relative humidities was caused by increased activity and resulted in higher rates of net water loss. The primary metabolic adaptation to xeric conditions in _P. rugosus_ appears to be a lower-than-predicted metabolic rate.**

Ants are attractive organisms for the study of foraging behavior. They have a wide array of strategies, yet their foraging behavior can be accurately quantified because the workers are flightless and relatively indifferent to observers. Moreover, they are often of major importance in their communities.

Without reliable data on the energetic transactions involved, foraging theories remain intellectual exercises. A quantitative ecological evaluation of foraging behavior requires reliable data on the metabolic rates of individuals while motionless in the colony and while engaged in the various activities associated with nest maintenance and food acquisition (1, 2). However, because ants are very small animals and their physiology is strongly affected by social interactions, reliable information on the energetics is fragmented and incomplete. The authors of a recent compendium of the metabolic rates of inactive ants (3) remarked that the scatter in the published data was so great that it made little difference whether metabolic rates were expressed per gram live body mass or per gram dry body mass. Metabolic rates of ants have been measured under conditions ranging from continuous activity (4, 5) to anesthetically induced immobility (6) at a variety of temperatures and have been reported in many different units.

Because of the ecological importance of ants in natural communities, the effects of erroneous estimates of their energy metabolism can be far-reaching. For example, when Golley and Gentry (7) reported extremely high metabolic rates for a species of harvester ant, a school of ecological thought developed that concluded that ants acted as energy sinks in ecosystems (8, 9). However, it has recently been shown (10) that Golley and Gentry overestimated the metabolic rates they measured by at least a factor of 30.

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The present study examines the energy metabolism of ants under conditions of minimal activity. However, even when the manifold complications associated with activity are ignored, quantification of the energy metabolism of ant colonies faces many constraints: (*i*) The methods used should afford the requisite accuracy. (*ii*) The ants should be minimally active—a state of affairs relevant to colony energetics, but not always easy to achieve in respirometers. (*iii*) "Group effects"—i.e., differences in mass-specific metabolic rates between solitary and grouped workers (11, 12)—should be taken into account. (*iv*) The effects of body mass and temperature should be rigorously defined. (*v*) Variations in metabolic rate related to the vertical stratification of workers in the nest (13) should be quantified. (*vi*) Effects of humidity on metabolic rates (14) should be quantified. (*vii*) Information on temperature profiles, distribution of workers within the nest, and population size and structure should be available.

MATERIALS AND METHODS

Harvester ants of the genus *Pogonomyrmex* are widespread and have often been used in foraging studies. The species considered in the present study, *Pogonomyrmex rugosus*, is a conspicuous member of the harvester ant guild in the Mojave Desert of southwestern North America (15), and it is an important seed predator in the areas where it occurs. The relatively large size of the workers (12–25 mg) and their amenability to captivity make them suitable for physiological study. Groups of about 300 workers were collected at the entrances of their nests in the Mojave Desert near Pearblossom and Rosamond, Los Angeles County, California, during August, September, and October, 1987. They were maintained in a laboratory at the University of California, Los Angeles, on a normal photoperiod at a temperature of 22 ± 2°C. Water and food consisting of rolled oats and wheat germ were supplied ad lib. Experiments were carried out within 3 weeks of capture.

Constant-volume O_2 and CO_2 respirometry was carried out during daylight hours on individual ants as previously described (16). An automated version of the same technique was used to measure the rates of oxygen consumption ($\dot{V}O_2$) and CO_2 production ($\dot{V}CO_2$) of groups of ants. Ten to 30 ants were put in a respirometer chamber (volume 15 ml) that was part of a system through which a stream of outside air, scrubbed of H_2O and CO_2, flowed continuously at a rate of 50 $ml \cdot min^{-1}$. The input and output ports of the chamber were connected to solenoid-controlled changeover valves. When closed, the solenoid valves shut off both ports, allowing the animals in the respirometer chamber to alter the concentrations of O_2 and CO_2 in it. When the changeover valves closed off the chamber, they opened up a bypass circuit, causing the airstream to flow through it. When the solenoid valves were open, the airstream passed through the respirometer chamber rather than through the bypass. Thus, the airstream was used alternately to establish a reference base line and to measure

respiratory gas exchange. The concentrations of O_2 and CO_2 in the airstream were monitored continuously with an S-3A O_2 analyzer from Applied Electrochemistry (Ametek Thermox, Pittsburgh) and an AR-50 CO_2 analyzer from Anarad (Santa Barbara, CA). After the respirometer chamber had been isolated for a controlled interval, the solenoid changeover valves were energized, and the air inside the respirometer chamber was drawn through a H_2O scrubber and then through the gas analysis instruments. After the respirometer chamber had been completely flushed with reference air, the two solenoid valves were deenergized, again sealing off the respirometer chamber, and the cycle of measurement was repeated. The entire operation was computer controlled, including the timing and energizing of the solenoids and the regulation of the temperature of the respirometer chamber to within 0.5°C at any level between 10 and 45°C.

The computer also continuously recorded O_2 and CO_2 concentrations in the airstream. It calculated the volumes of O_2 consumed and CO_2 produced by integrating the concentration profiles, using the reference airstream as a baseline. It also determined rates of O_2 consumption and CO_2 production by using the calculated gas volumes and enclosure times, correcting $\dot{V}O_2$ for the presence of CO_2 (17), and converting the values to STPD (standard temperature and pressure, dry).

The effects of temperature at 5°C increments from 10 to 45°C on $\dot{V}O_2$ and $\dot{V}CO_2$ were determined on groups of workers in humidified air. Group size at 45°C was 10; at the other temperatures it was 30. Successive readings of $\dot{V}O_2$ and $\dot{V}CO_2$ were made until the ants were almost completely inactive, and the readings had stabilized at a minimal level (ca. 3 hr). Thereafter, repeated determinations were made, at 30-min intervals, for 6–8 hr. The means of four or five of the minimal readings were used for analysis. The relative humidity in the respirometer chamber was maintained near saturation [the situation experienced by ants in their underground nests (18)] by a water-saturated wad of cotton wool. To determine the losses in body mass during the experiments the ants were weighed individually to 0.1 mg prior to respirometry; after respirometry, the ants were reweighed in groups. Changes in body mass were calculated by subtracting the final mass of the group from the summed masses of the individual ants at the start of the experiment.

The effects at 24°C of low and high humidities on $\dot{V}CO_2$ were measured with a changeover valve system like that described above. However, during alternate 40-min periods the 50-ml·min^{-1} stream of dried CO_2-free air was humidified under computer control by bubbling it through a 30-cm column of water containing 2% KOH. The humidity change had no effect on CO_2 concentration readings when there were no ants in the respirometer chamber. The relative humidity of the air entering the chamber was monitored with a Brady Array humidity sensor (Thunder Scientific PC-2101C; Albuquerque, NM). In most of the experiments, the activity of the ants was monitored with a photoelectric system as described elsewhere (16).

Regression equations were calculated by the method of least squares and tested for significance with analysis of variance. Differences between means were tested with Student's t test. Means are accompanied by standard deviations and sample sizes.

RESULTS

Standard Energy Metabolism: Effects of Temperature. The $\dot{V}O_2$ and $\dot{V}CO_2$ of grouped ants (mean mass = 15.1 ± 1.5 mg, n = 8, means of ca. 60 ants each) were strongly dependent on ambient temperature (Fig. 1). The body masses of the ants did not change significantly during the periods of measurement (paired t = 0.16, $P > 0.4$). The relations of $\dot{V}O_2$ and

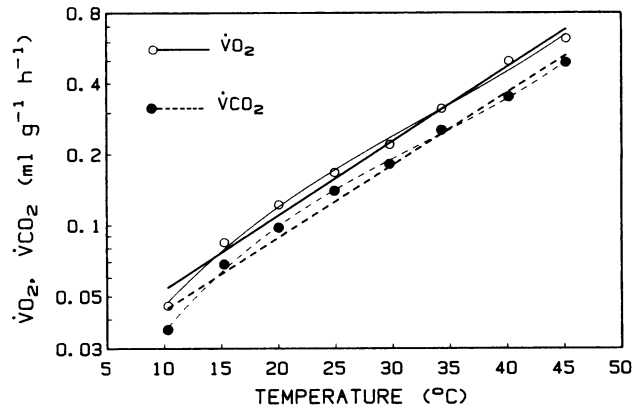

FIG. 1. Effect of body temperature on standard rates of O_2 consumption ($\dot{V}O_2$) and CO_2 production ($\dot{V}CO_2$) in *P. rugosus*. Open circles and unbroken lines are $\dot{V}O_2$; closed circles and broken lines are $\dot{V}CO_2$. Heavy lines are linear regressions. Light traces are polynomial regressions. See text for equations.

$\dot{V}CO_2$ to body mass can be described by linear regressions on semilogarithmic plots,

$$\dot{V}O_2 = 10^{(-1.588 + 0.0315T)}$$
$$r^2 = 0.998;\ F = 512;\ P < 0.0001 \quad [1]$$

$$\dot{V}CO_2 = 10^{(-1.667 + 0.0308T)}$$
$$r^2 = 0.985;\ F = 386;\ P < 0.0001, \quad [2]$$

where $\dot{V}O_2$ is ml·g^{-1}·hr^{-1} and T is body temperature in °C. However, inspection of Fig. 1 reveals systematic deviations from these exponential models. The deviations are eliminated when polynomial regressions are used.

$$\log \dot{V}O_2 = -1.968 + 0.0762(T) - 0.0015(T^2) + 0.000015(T^3)$$
$$r^2 = 0.998 \quad [3]$$

$$\log \dot{V}CO_2 = -2.18 + 0.092(T) - 0.002(T^2) + 0.00002(T^3)$$
$$r^2 = 0.999. \quad [4]$$

The improved fit afforded by the polynomial model results from the fact that the Q_{10} (the ratio of the $\dot{V}O_2$ values at 10°C increments in body temperature) varies systematically with temperature. Based on the exponential model, the mean Q_{10} for $\dot{V}O_2$ was 2.06 ($= 10^{(0.0315 \times 10)}$), and for $\dot{V}CO_2$ it was 2.03 ($= 10^{(0.0308 \times 10)}$). Differentiation of the polynomial regression allows the changes in Q_{10} as a function of temperature to be calculated (19). For both $\dot{V}O_2$ and $\dot{V}CO_2$, Q_{10} was maximal at low temperatures, decreased to a minimum of about 1.9 near 33°C, and increased again at higher temperatures (Fig. 2). Clearly, for accurate predictions of the effects of temperature on $\dot{V}O_2$ and $\dot{V}CO_2$, the polynomial equations should be used.

The respiratory quotient (RQ), 0.796 ± 0.040 (six groups), was not significantly temperature dependent. The energy equivalence of O_2 at this RQ is approximately 20.08 J·(ml of O_2)$^{-1}$ (20).

Standard Energy Metabolism: Effects of Body Mass. The $\dot{V}O_2$ and $\dot{V}CO_2$ of individual ants, measured at 25°C at a relative humidity of 70–80%, varied with body mass (Fig. 3) according to the equation

$$\dot{V}O_2 = 0.0462M^{0.669}, \quad [5]$$

where $\dot{V}O_2$ is ml·hr^{-1} and M is body mass in g.

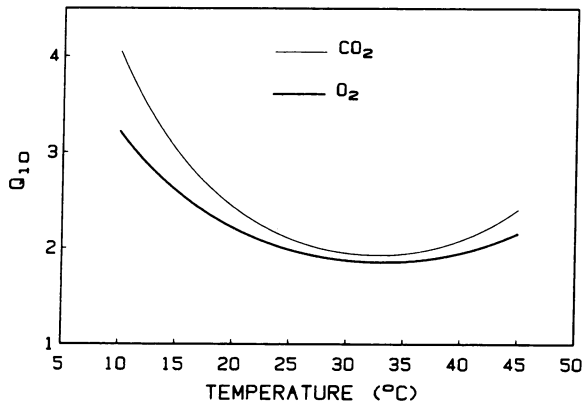

FIG. 2. Q_{10} as a function of temperature in *P. rugosus*. See text for equations.

To test for the existence of a group effect on $\dot{V}O_2$, we used this equation to predict the mass-specific $\dot{V}O_2$ of a group of ants, using the body masses of the ants that generated the data point for $\dot{V}O_2$ at 25°C in the experiments on the temperature dependence of energy metabolism (Fig. 1). The predicted mass-specific value for the group (0.1862 ml·g^{-1}·hr^{-1}) does not differ from the value predicted for an individual by Eq. 5 (0.1576 ml·g^{-1}·hr^{-1}, 95% confidence interval 0.1283–0.1936 ml·g^{-1}·hr^{-1}). From this we infer that the group effect on $\dot{V}O_2$ and $\dot{V}CO_2$ in *P. rugosus* is negligible.

The equations relating $\dot{V}O_2$ to body mass (Eq. 5) and to temperature (Eqs. 1–4) are based on different sets of data and do not afford quick calculation of $\dot{V}O_2$ from both temperature and body mass. However, if the mass scaling exponent (b in the equation $\dot{V}O_2 = aM^b$; = 0.699, Eq. 1; see Fig. 3) is assumed to be independent of temperature, then the body masses and $\dot{V}O_2$ values of the workers in the temperature experiments can be used to calculate the value of the proportionality constant (a in the equation $\dot{V}O_2 = aM^b$). This constant can then be regressed against temperature by using an exponential regression model. The resulting equation relates $\dot{V}O_2$ of *P. rugosus* directly to both temperature and body mass,

$$\dot{V}O_2 = (10^{-2.168 + 0.0307T})M^{0.669}$$
$$r^2 = 0.97,\ n = 8, \qquad [6]$$

where $\dot{V}O_2$ is ml·hr^{-1}, T is body temperature in °C, and M is body mass in g. Eq. 6 assumes a constant Q_{10} of 2.03. For improved accuracy, the changes of Q_{10} with temperature

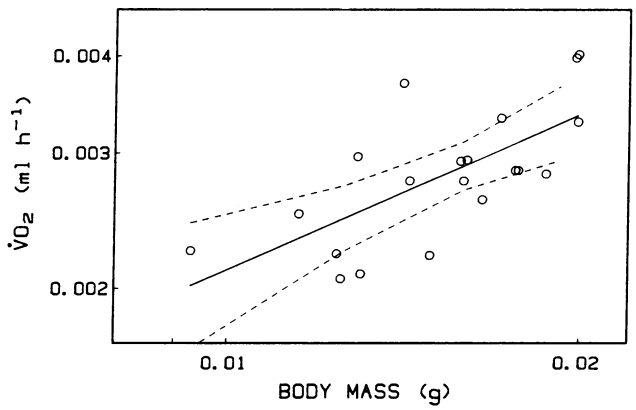

FIG. 3. $\dot{V}O_2$ as a function of body mass in *P. rugosus*. See text for equation. The broken curves enclose the 95% confidence limits of the line. $r^2 = 0.47$; $F = 19.9$; df = 1, 18; $P < 0.001$.

Table 1. Effect of relative humidity on $\dot{V}CO_2$ in *P. rugosus*

Exp.	Mass, mg	WL, %·hr^{-1}	M, %	IMR, %	MWP, % WLR
1	14.1	1.18	95	87	0.81
2	14.5	0.69	100	28	1.32
3	13.9	0.82	92	22	1.01
4	14.5	0.76	100	27	1.09
5	15.0	1.30	100	65	0.85
6	15.3	1.05	102	48	0.92

There were 50 ants in each experiment; ambient temperature was 24°C; and mean experiment duration was 18 hr. WL, water loss (corrected for loss of respiratory substrate) as percent original body mass per hr; M, body mass as percent original mass after free access to water for 90 min; IMR, percent increase in $\dot{V}CO_2$ caused by increase in relative humidity from 10% to 86%; MWP, rate of metabolic water production as percent of rate of total water loss, lipid substrate assumed (table 2 of ref. 21).

(Fig. 2) can be incorporated into the equation by employing a polynomial equation to predict the proportionality constant from temperature,

$$Z = -2.799 + 0.1052\,T - 0.002512T^2 + 0.00002555T^3$$
$$\dot{V}O_2 = 10^Z M^{0.669}$$
$$r^2 = 0.998. \qquad [7]$$

Effects of Humidity on Energy Metabolism. A reduction in relative humidity from 86.3% ± 3.8% to 10.4 ± 2.1% (six groups of 12–14 measurements) caused an increase in $\dot{V}CO_2$ that was large (46.2 ± 25%) and significant (paired $t = 3.34$, $P = 0.02$; Table 1). The immediate cause of this rise in $\dot{V}CO_2$ was increased activity. The ants became more active as soon as the relative humidity of the incoming airstream began to fall. This visually obvious behavioral change was confirmed by photoelectric monitoring of the activity of the ants (Fig. 4). The elevation in $\dot{V}CO_2$ was accompanied by increased water loss rates. The correlation between $\dot{V}CO_2$ in dry air expressed as a percentage increase over $\dot{V}CO_2$ in moist air, and the percent mass loss per hour after compensation for loss of respiratory substrate and production of metabolic water (Table 1), was significant ($r = 0.872$, df = 4, $P = 0.02$). Metabolic water production compensated for less than 1.3% of total water loss, and the ants became dehydrated during the experiments. After each experiment the ants were weighed and then allowed to rehydrate by drinking from

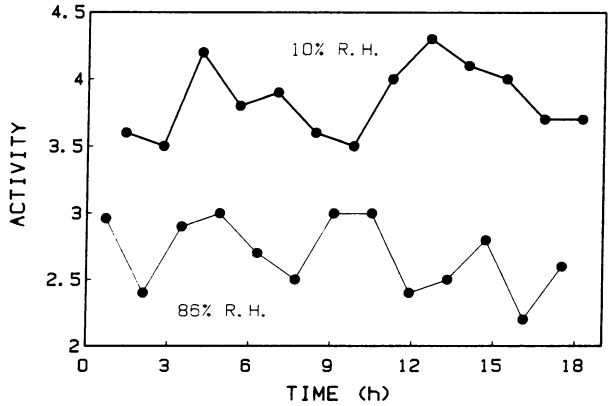

FIG. 4. Activity (arbitrary units) of *P. rugosus*, measured with a photoelectric activity monitor, as a function of relative humidity (R.H.). The ants ($n = 50$) were exposed alternately for 40 min to airstreams at 86% and 10% relative humidity. Ambient temperature = 24°C. The activities at high relative humidity are significantly less than those at the low ($t = 10.83$; df = 24; $P < 0.0001$).

water-saturated cotton wool, which they did immediately. When reweighed 90 min later, they had rehydrated to 98.2 ± 3.8% (six groups) of their original body masses.

DISCUSSION

P. rugosus lives in an exceedingly arid region characterized by wide fluctuations in temperature and food availability. One would expect to find adaptations to this stringent environmental regime in the physiological parameters that we measured. Certainly, the production of increased quantities of metabolic water when dehydrating conditions develop, as proposed by Ettershank and Whitford (14), would be adaptive. However, on a given diet it is not possible to increase production of metabolic water without increasing metabolic rate, and an increase in metabolic rate, other things being equal, necessarily increases respiratory water loss (ref. 22, p. 190).

We have found that *P. rugosus* does indeed increase its metabolic rate in dry air, as Ettershank and Whitford reported (14). However, we cannot accept their inference that this increase is an adaptation for enhancing metabolic water production. They reported in table 3 of their paper that although the energy metabolism of *P. rugosus* increased in dry air, its level of activity decreased. In contrast, we found that the increase of $\dot{V}O_2$ in dry air was not accompanied by a diminution in activity, but, in fact, was caused by increased activity (Table 1; Fig. 4). Ettershank and Whitford based their estimates of intensity of activity on 1-min periods of observation at the end of 30-min periods of respirometry, whereas we based ours on continuous monitoring of activity.

Our findings directly contradict the conclusions of Ettershank and Whitford about the adaptive role of changes in metabolic rate with regard to maintenance of water balance. Our data show that in dry air metabolic water production compensates for a negligibly small proportion of total water loss (circa 1%) in *P. rugosus* (Table 1). For metabolic water production to match total water loss in our sample of *P. rugosus*, metabolic rates would have to increase 100-fold even if respiratory water loss remained constant, which it would not. This metabolic rate corresponds to a $\dot{V}O_2$ of 14 $ml \cdot g^{-1} \cdot hr^{-1}$, a level that could hardly be achieved in the absence of flight.

We conclude that the increase of $\dot{V}O_2$ in low humidity noted in *P. rugosus*, and probably in other ants (14, 23), is caused by increased activity and is not an adaptation for maintaining water balance. Further, we suggest that the increased activity shown by *P. rugosus* when exposed to dry air represents an attempt to escape from a desiccating situation. Under natural conditions when facing the challenge of dehydration the ant would return to the humid environment supplied by its underground nest.

Ettershank and Whitford stated that *P. rugosus* ". . . does not accept water when it is offered experimentally either in the laboratory or in the field." Again we disagree. During the dry season we have found water to be an effective means of luring the ants from their nests for capture. Within seconds of pouring *ca.* 20 ml of water into and around the nest entrance, large numbers of workers swarm out, and many appear to drink. In the laboratory workers drink readily, particularly when dehydrated.

MacKay (13) proposed that the $\dot{V}O_2$ of *P. rugosus* workers decreases with the depth of their location within the nest. This is consistent with his observation that the workers deepest in the nest are callows. However, he provided no statistical tests of the procedures on which the proposal was based. We did not gather new data to test this hypothesis, but we digitized the relevant data (figure 1 in MacKay's paper), and recalculated the linear regression of $\dot{V}O_2$ on depth in the nest. We found that the slope of the regression does not differ significantly from zero ($r^2 = 0.042$; $t = 0.86$; df = 16; $P > 0.4$). For the present we must, therefore, reject MacKay's statement that in the nests of *P. rugosus* "respiratory rates decrease with depth." Available data indicate that estimations of colony metabolism in *P. rugosus* require no depth correction, other than correction for temperature changes that accompany depth.

Published records indicate that group effects on metabolic rate are important in some social insects (2, 11, 12) but not in others (19). In *P. rugosus* we found that the mass-specific energy metabolism of individual ants did not differ significantly from that of groups of ants. It is reasonable, therefore, to extrapolate metabolic rates based on single workers of this species to include all the workers in a colony.

We have defined the relation of standard metabolic rate to temperature and to body mass in *P. rugosus* precisely enough to estimate realistically the metabolic rates of inactive workers in the field over a wide range of temperatures. For best results, the polynomial regressions (Eqs. 3, 4, and 7) should be used. Our measurements indicate that previous investigations (5, 13, 14, 24) have substantially overestimated the inactive metabolic rate of *P. rugosus*, probably because levels of activity during the periods of measurement were inadequately controlled for.

One physiological adaptation to the desert environment that can ameliorate the impact of aridity and sparse and unpredictable food supply is a reduction in rate of energy metabolism. This option has been exploited by some desert mammals and a few desert birds (for references see refs. 25 and 26). Data on the occurrence of reduced metabolism in desert insects is limited, but it is clearly demonstrated by the tenebrionid beetles of the deserts of southern Africa (27). In the case of *P. rugosus*, in which respiratory water loss greatly exceeds metabolic water production, it is reasonable to assume that natural selection might favor reduction of energy metabolism. The most complete data set on ant energy metabolism in relation to body mass (28) as updated (1) can be fitted by an allometric equation,

$$\dot{V}O_2 = 0.137M^{0.84}$$
$$r^2 = 0.8, \qquad [8]$$

where $\dot{V}O_2$ is $ml \cdot hr^{-1}$ at 20°C, and M is body mass in g. According to this equation, an ant with the mean body mass of *P. rugosus* (15.1 mg) should consume 0.2818 ml of O_2 $g^{-1} \cdot hr^{-1}$. At 20°C the $\dot{V}O_2$ of *P. rugosus* (Eq. 1) is 0.1101 $ml \cdot g^{-1} \cdot hr^{-1}$, or 39% of the predicted value. We conclude that one of the adaptations of *P. rugosus* to its arid habitat may be a reduction in $\dot{V}O_2$, which affords a reduction in food requirements and respiratory water loss.

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