

## THE ENERGETICS OF LOCOMOTION AND LOAD CARRIAGE IN THE DESERT HARVESTER ANT *POGONOMYRMEX* *RUGOSUS*

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### Summary

The locomotion and load carriage energetics of the southwestern American harvester ant, *Pogonomyrmex rugosus*, were quantified at several temperatures within their normal foraging temperature range using a voluntary locomotion regime ('running tube respirometer'). In a metabolic rate (MR) *versus* running speed regression, the intercepts for the individual ants differed significantly, so data were evaluated using analysis of covariance (ANCOVA) rather than the more common pooling of individuals. Unladen cost of transport was  $158 \text{ J kg}^{-1} \text{ m}^{-1}$ . The mean y-axis intercept did not differ significantly from zero after temperature-corrected standard MR (SMR) had been subtracted from MR; i.e. the y-axis intercept was not elevated above SMR. When the data were pooled, standard tests of the cost of load carriage showed that the costs of load and body carriage were statistically equivalent. However, using ANCOVA to regress MR–SMR against the product of running speed and load ratio showed that the cost of load carriage in *P. rugosus* is approximately 40% lower per unit mass than is the cost of body mass carriage (load ratio range 1.06–2.27). General methods are developed and described for evaluating and predicting locomotion and load carriage costs in small insects using data spanning a variety of temperatures and load ratios.

### Introduction

Ants are among the most successful and ecologically significant of all insects, themselves the most speciose, diverse, abundant and widespread of all terrestrial animals. Ants owe much of their success to the social or multiple-entity structure of their colonies, which implement a 'massively parallel' approach to the common problems of existence, such as locating shelter and food. This contrasts with the serial approach of single-entity species. However, the parallel approach is not without cost. The nest in which a large colony lives and protects its brood is energetically and temporally expensive to build and maintain. This precludes its relocation except in emergencies. Consequently, most ant species are 'central-place foragers': they forage from their nests and use complex behavioural and chemical cues to locate food sources and to communicate navigational information during subsequent recruitment (Hölldobler and Wilson, 1990). The best

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known exceptions that prove this rule are the army ants, which forage to such devastating effect that a nomadic existence is forced upon them by recurrent shortages of prey; in this sense they are victims of their own success.

The fitness of a colony is directly related to its success at locating and transporting food. Foraging success is a complex function of nutritional requirements, food availability and composition, unit food size, foraging distance, locomotion costs and load carriage costs, among other variables. The energy costs of locomotion and load carriage may be important components of overall foraging energy transactions (but see Fewell, 1988). To further our understanding of this aspect of colony function, it is vital to predict the costs of locomotion accurately for any realistic combination of speed, temperature, body mass and load mass. Such predictions have not been feasible until now because the interactions between body mass, body temperature, cost of transport and cost of load carriage have not been quantified in small insects. Our paper addresses this lack of data and describes new general approaches for measuring locomotion and load carriage energetics in small arthropods.

The cost of locomotion can be expressed in three main ways, all of which share the same units; the energetic cost (J) of transporting a unit mass of organism (1kg) a unit distance (1m). The most direct measure is the gross cost of transport (GCOT), obtained by dividing metabolic rate (MR, in  $\text{J s}^{-1} \text{kg}^{-1} = \text{Wkg}^{-1}$ ) by speed in  $\text{m s}^{-1}$ . This is perhaps the most ecologically relevant measure, but it suffers two key disadvantages: it is dependent on the animal's standard metabolic rate (SMR, or the MR while inactive) and its running speed. The net cost of transport (NCOT) addresses the SMR problem by subtracting SMR from MR measured while running, but NCOT is still speed-dependent. The minimum cost of transport (MCOT), in contrast, is dependent on neither speed nor SMR: it is the slope of the regression line relating MR to running speed. This makes it possible to compare, for example, a large endothermic homeotherm such as a horse running at  $3\text{--}15 \text{ m s}^{-1}$  with a small ectothermic heterotherm such as an insect running at  $0.03\text{--}0.15 \text{ m s}^{-1}$ , in spite of their very different speeds and SMRs. MCOT is not temperature-dependent in ectotherms such as insects (Herreid *et al.* 1981; Lighton and Feener, 1989) and can, in principle, be measured easily by allowing insects to run on treadmills.

Insects and vertebrates that run on treadmills do, however, share a peculiar idiosyncrasy. When extrapolated to zero running speed, their estimated MR is well above SMR (Herreid *et al.* 1981; Herreid and Full, 1984; Lighton, 1985; Lighton and Feener, 1989), an effect usually referred to as 'y-axis intercept elevation'. This is sometimes stated to be a 'postural cost' but its real cause is still unknown. In any event, it frustrates attempts to predict the total metabolic cost of locomotion, particularly because the mass scaling and temperature-dependence of y-axis intercept elevation in insects are unclear at best.

There is a further complication. To quantify load carriage energetics, the effect on MCOT of carrying loads of given masses must be known. The cost of load carriage is usually measured by loading an animal with a known mass and then allowing it to run on a treadmill. The hypothesis tested in most studies (e.g. Herreid and Full, 1986; Maloiy

*et al.* 1986) is that the ratio of laden over unladen O<sub>2</sub> consumption rate will increase linearly with unity slope when plotted against load ratio [LR=(body mass+load mass)/body mass]. This is roughly congruous with the more rigorous hypothesis that the cost of load mass carriage is equivalent, per unit mass, to the cost of body mass carriage. These two hypotheses are not entirely congruent because SMR is presumably not affected by load ratio, but is included in the overall rate of O<sub>2</sub> consumption. Because MCOT is a speed-independent measure of the energy cost of transport (which must increase with added load mass), it is well-suited to testing the hypothesis that the cost of load and body mass carriage are equivalent. This is especially so because it is insensitive to changes in running speed that may result from loading.

Information on the subject of COT in ants started with the pioneering study of Jensen and Holm-Jensen (1980) and continued with the studies of Lighton *et al.* (1987), Fewell (1988), Bartholomew *et al.* (1988) and Nielsen and Baroni-Urbani (1990). These studies generally employed closed-system respirometry. This technique depends on a single, integrated measurement made over several minutes or tens of minutes and, therefore, cannot differentiate between different running speeds during a single experiment. This poor temporal resolution may explain the considerable scatter in the results, which are usually presented in terms of GCOT and NCOT only. In general, NCOT increased proportionately with increasing load ratios. The hypothesis that load and body carriage costs are equivalent could not be disproved, except in the case of *Messor capitatus*, for which Nielsen and Baroni-Urbani (1990) suggested that load carriage costs may be lower. Lighton *et al.* (1987) succeeded in running *Atta colombica* on a treadmill, and thus obtained the first MCOT values for an ant. However, these ants were unladen so the effect of the load ratio on MCOT was unclear. Ants, and small insects in general, run poorly on treadmills, so a better method for determining their COT was obviously necessary.

Lighton and Feener (1989) pursued this question using a new approach; the 'running tube respirometer' (see Materials and methods). Because this method uses only voluntary locomotion, it is free of the problems associated with forcing insects (and perhaps animals in general) to run at pre-defined speeds on treadmills. By using running tube respirometers and treadmills at four temperatures each, Lighton and Feener (1989) showed, that although MCOT remained constant across technique and temperature, the y-intercept elevation above SMR was significant with the treadmill technique, but disappeared when the running tube respirometer was employed.

This effect of voluntary locomotion allows us to employ new analytical methods, in conjunction with running tube respirometry, to determine the energy costs of locomotion and load carriage in the ant *Pogonomyrmex rugosus* (Emery) over its foraging temperature range. *P. rugosus* is a member of a fairly diverse guild of seed-harvesters in arid areas of the southwestern United States that includes other ant species with different food preferences, foraging strategies and temporal and thermal preferences. The abundance and relatively large size of *P. rugosus* make it a convenient and ecologically important model organism with which to explore the relationships between body morphology, locomotion energetics, load carriage energetics and foraging strategies in ants in general.

## Materials and methods

### *Animals*

Samples of 300–400 workers from *Pogonomyrmex rugosus* colonies were collected from Lytle Ranch Preserve in southwestern Utah, USA, between May and August of 1991, and kept at  $25\pm 2^\circ\text{C}$  in a laboratory at the University of Utah. They were maintained in earth-filled buckets and were supplied with water *ad libitum*, and fed on millet seeds and sliced mealworms. They remained in apparently healthy condition for several weeks after capture.

### *Respirometry*

We carried out flow-through respirometry on active *P. rugosus* using a Sable Systems TR-2 respirometry system (Sable Systems, 476 E South Temple, Salt Lake City, Utah 84111) together with Sable Systems data acquisition and analysis software and hardware. The respirometric methods and equations that we used are described in Lighton (1991).

To measure the energetic cost of pedestrian locomotion, we employed a 'running tube respirometer' similar in principle to that described by Lighton and Feener (1989). This method takes advantage of the stereotypical escape behaviour that many insects and other arthropods exhibit when they are confined in a tube with constricted ends. The trapped insect often spends long periods running or walking from one end of the tube to the other; on finding one end blocked, it usually turns around rapidly and proceeds to the other end where it repeats the process, sometimes for several hours.

The running tube was constructed of square glass tubing, 1.2m long, internal width 10mm, floored with 2mm thick ground glass. Its volume was approximately  $100\text{cm}^3$ . The ants had no difficulty running on the ground-glass surface. An array of 64 infrared light paths allowed us to determine the position of the ant within the running tube to a resolution of 2cm. This position information was continuously recorded, together with running tube temperature (averaged over four equally spaced points on the running tube surface) and rate of  $\text{CO}_2$  production ( $\dot{V}_{\text{CO}_2}$ , determined by flow-through respirometry at a flow rate of  $250\text{cm}^3\text{min}^{-1}$ ). The temperature of the running tube was regulated at 34, 37, 40 or  $43\pm 0.25^\circ\text{C}$  by computer control. Ants were weighed to 0.01mg before and after each recording.

### *Data analysis*

A sign-insensitive cumulative differentiation of the position trace yielded the total distance travelled by the ant as a function of time. The distance trace was examined to find sections of consistent locomotion, defined as a coefficient of determination ( $r^2$ ) of at least 0.98 over an interval of at least 3min. Ants, like most highly tracheate insects, are fully aerobic at normal running speeds (Lighton *et al.* 1987; see also Herreid and Full, 1984). This is confirmed by their consistently high level of locomotion during trail foraging over distances of 100m and durations of 30min or more. A relatively short interval of steady-state locomotory performance and  $\text{CO}_2$  output was therefore sufficient to quantify the energetic cost of locomotion at a single speed. We determined the speed in metres per second over each selected interval by regression analysis. Typically, the

standard error of the slope (where slope=speed) was less than 5% of the speed; this compares favourably with the performance of many treadmills. We calculated the ant's  $\dot{V}_{CO_2}$  over the same interval and converted it to metabolic rate (MR) in watts per kilogram, using the known joule equivalent for carbon dioxide of this species (Lighton and Bartholomew, 1988; Lighton and Feener, 1989).

It is generally accepted that MR is related to speed ( $V$ ), MCOT, SMR and the  $y$ -axis intercept elevation ( $y_{el}$ ) by the equation:

$$MR = SMR + y_{el} + (MCOT \times V). \quad (1)$$

The disappearance, or at least reduction to statistical insignificance, of  $y_{el}$  under conditions of voluntary locomotion (Lighton and Feener, 1989) allows the following simplification:

$$MR = SMR + (MCOT \times V). \quad (2)$$

SMR can be calculated from standard equations relating ant MR to body mass. We used the equation  $MR=1143M^{0.933}$ , where MR is in  $\mu W$  and body mass,  $M$ , is live mass in grams at 25°C (Lighton and Wehner, 1993). SMR can readily be temperature-corrected, assuming a  $Q_{10}$  of 2.0 (Lighton, 1988, 1989; Lighton and Bartholomew, 1988), but overall MR (which is a function of temperature-sensitive and temperature-insensitive components; Lighton and Feener, 1989) cannot. Thus, if SMR at the temperature of the running ant is subtracted from MR (which thus becomes the *Adjusted Metabolic Rate* or AMR), then:

$$AMR = MCOT \times V. \quad (3)$$

Equation 3 allows the determination of MCOT from data collected at any reasonable temperature, provided that the SMR of the animal and its temperature sensitivity are known. If laden MCOT increases in direct proportion to loading ratio (LR), then:

$$AMR = MCOT \times V \times LR, \quad (4)$$

where MCOT is the value obtained for unladen ants; multiplying it by LR should increase it to the correct value for laden ants, assuming equivalent costs of load and body carriage. It follows that MCOT can be calculated by regressing AMR against  $V$  in equation 3 or AMR against  $V \times LR$  in equation 4. In each case, the slope will be equal to unladen MCOT as determined in equation 3 if MCOT increases directly in proportion to LR; in other words, if the cost of carrying a unit mass of load is equivalent to carrying a unit of body mass, which is the general hypothesis (see Maloiy *et al.* 1986).

Multiplying speed by LR has two fundamental advantages over other methods. First, animals with different loads can be tested, and the loading ratio can even be varied as the run progresses, while maintaining the capability of incorporating all LR conditions into the analysis. Second, there is no need to obtain an MCOT value for each individual animal, provided that the MR-speed data can be legitimately pooled.

The ants did not carry loads voluntarily under the conditions of our experiments. To simulate load carriage, we attached a small piece of platinum to the top of the ant's head capsule with a tiny amount of water-soluble polyvinylchloride glue. This allowed us to

add more than 100% of the ant's body mass without adverse effects on locomotion ability or stability. In order to minimize any such effects, however, we restricted load masses to approximately 0.1–1 times body mass, equivalent to load ratios of 1.1–2. This is similar to load ratios observed in laden *P. rugosus* workers in the field (mean=1.14±0.28, range 1.00–2.78,  $N=62$ ; J. A. Weier, unpublished data).

### Statistics

All means are accompanied by standard deviations (s.d.) and sample sizes ( $N$ ). Regression analysis was by least squares, and slopes and intercepts are accompanied by standard errors (s.e.m.) where appropriate. Regression significance was tested by analysis of variance, and regressions were compared by analysis of covariance (ANCOVA).

### Results

We obtained data on the cost of unladen transport in a total of 25 *Pogonomyrmex rugosus* (mean mass 12.96±1.25mg). Approximately equal numbers were tested at 34, 37, 40 and 43°C. The ants ran reasonably consistently in the running tubes (Fig. 1). We analyzed data only from those ants that ran consistently for at least 3min at each of several speeds. Each ant yielded 6–20 data points of MR *versus* speed (total points 288).

Most studies of COT combine data from several individuals and calculate MCOT from the resulting pooled data (Herreid *et al.* 1981; Herreid and Full, 1984; Lighton, 1985). We employed this approach as well, but supplemented it with an ANCOVA across individuals, thus obtaining information about the significance of differences in MCOT and y-intercept between individuals.

#### *Unladen ants: MCOT, y-intercept and temperature effects*

Our sample of unladen ants ran at a mean speed of 3.39±0.92cm s<sup>-1</sup> (range 0.50–4.77cm s<sup>-1</sup>). Most recordings lasted a total of approximately 75min. In terms of water loss, the runs were moderately stressful to the ants, which lost significant body mass, ranging from 9.8±1.6% h<sup>-1</sup> at 34°C to 15.4±4.1% h<sup>-1</sup> at 43°C. Because of this alteration in mass, we calculated mass-specific MR for each data point for each ant on the basis of a linear mass reduction (Lighton and Feener, 1989) over the duration of the recording.

MCOT was not affected by temperature: all unladen ants at all measured temperatures shared a common MCOT of 158.0±7.0J kg<sup>-1</sup> m<sup>-1</sup> [ANCOVA; homogeneity of slopes,  $F(24, 238)=1.35$ ;  $P>0.1$ ]. The coefficient of determination ( $r^2$ ) for this ANCOVA, given common slopes, was 0.72. However, the intercepts did differ significantly between individual ants [ $F(24, 262)=28.5$ ;  $P<0.001$ ]. Our MCOT value is within 15% of those previously measured in *P. rugosus* (Lighton and Feener, 1989).

The statistically different intercepts of individual ants (Fig. 2) complicate a conventional pooled-data analysis because the data cannot, strictly speaking, be combined into a single regression. If this is done, however, MCOT drops to 147.4±11.4J kg<sup>-1</sup> m<sup>-1</sup> (regression  $r^2=0.38$ ;  $P<0.0001$ ).

The correction of MR to yield AMR by subtraction of estimated SMR at the

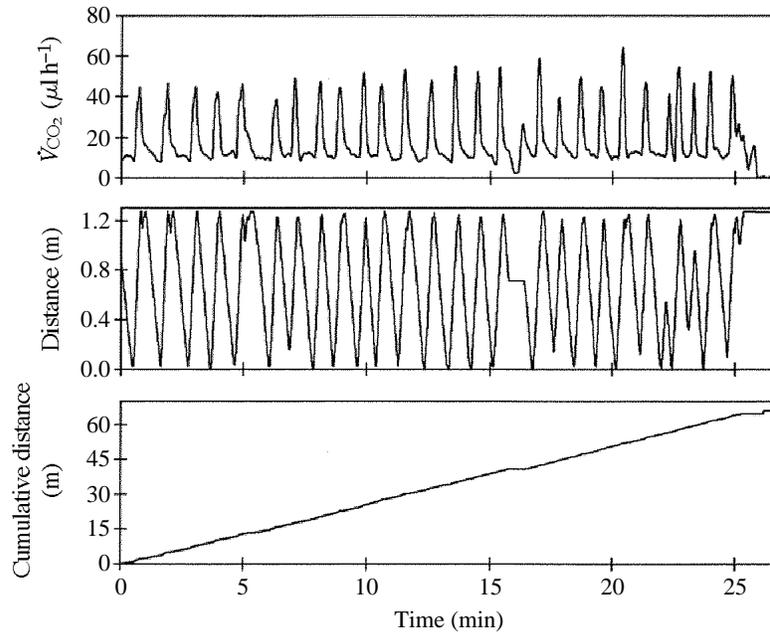


Fig. 1. A typical recording of  $\dot{V}_{\text{CO}_2}$  (top), position of the ant in the running tube respirometer (middle) and cumulative distance travelled (bottom) of a *Pogonomyrmex rugosus* worker, mass 13mg. The end of the  $\dot{V}_{\text{CO}_2}$  trace shows the system's baseline. The MR is calculated from  $\dot{V}_{\text{CO}_2}$ , which varies considerably over a short time scale depending on the ant's ventilation status and whether the ant is running with the airstream or against it, thus alternately rarefying or amplifying the  $\dot{V}_{\text{CO}_2}$  signal. In practice, the effect of these fluctuations is negligible if the time lag of the  $\dot{V}_{\text{CO}_2}$  signal is corrected for, and if intervals of 2–3min or more are averaged.

temperature of the trial successfully removed temperature effects: no correlation was observed between temperature and the intercepts of the individual 'by-ant' regression lines ( $r < 0.002$ ;  $P = 0.4$ ). If the estimated SMR was not subtracted, intercepts were significantly greater than zero ( $P < 0.01$ ) and were affected by temperature ( $P < 0.02$ ) with a  $Q_{10}$  of approximately 2. Subtracting SMR from MR successfully eliminated the overall y-axis intercept elevation; the mean intercept was  $2.03 \pm 2.11 \text{ W kg}^{-1}$ , which does not differ significantly from zero. However, about half of the individual regression lines still showed significant intercept elevations. We cannot assign biological explanations for the observed intercept differences between individuals. Because our major goal is to derive a predictive equation that is valid for *P. rugosus* as a species, we consider the mean of all measured intercepts to be the best estimate of this variable.

The cost of transport, expressed as NCOT rather than MCOT, was  $231.0 \pm 81.3 \text{ J kg}^{-1} \text{ m}^{-1}$  ( $N = 25$ ). Towards the upper range of running speeds (at or above  $3 \text{ cm s}^{-1}$ ), NCOT fell to  $205.4 \pm 64.0 \text{ J kg}^{-1} \text{ m}^{-1}$ . There was no statistically significant effect of body mass on MCOT, NCOT or running speed.

#### Loading effects

The ants were tested with load ratios ranging from 1.07 to 2.27 (mean  $1.51 \pm 0.37$ ,

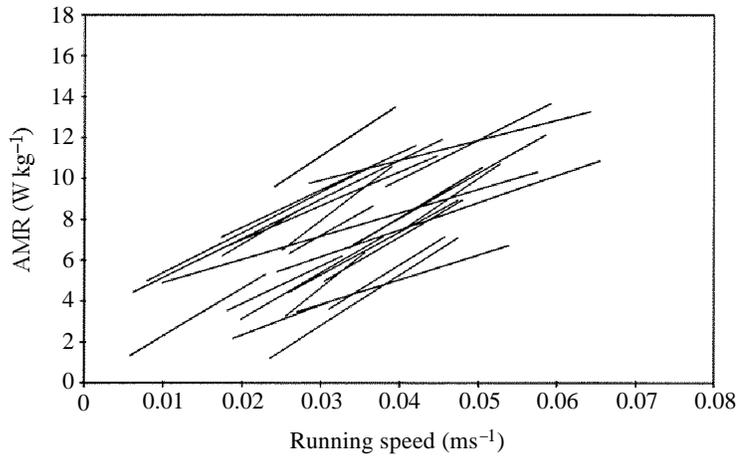


Fig. 2. The relationship between adjusted metabolic rate (AMR; obtained by subtracting SMR at the temperature of the measurement from measured MR) and running speed. Only the individual, raw regression lines are shown; they share a statistically common slope of  $158 \text{ J kg}^{-1} \text{ m}^{-1}$  (or  $\text{W kg}^{-1} \text{ m}^{-1} \text{ s}^{-1}$ ). The lines are calculated from 288 data points obtained from 25 unladen *Pogonomyrmex rugosus*, mean mass  $12.96 \pm 1.25 \text{ mg}$ .

$N=19$ ; mean body mass  $14.41 \pm 1.33 \text{ mg}$ ). The mean running speed of laden ants was  $2.04 \pm 0.50 \text{ cm s}^{-1}$ , which is significantly less than that of unladen ants ( $t=33.2$ ;  $P<0.001$ ). A reduction of running speed in laden ants is well known (Rissing, 1982; Lighton *et al.* 1987; Bartholomew *et al.* 1988).

Our data suggest that load carriage is less expensive, per unit mass, than body carriage. All laden ants shared a common slope or MCOT [AMR *versus* (running speed  $\times$  load ratio)] of  $136.6 \pm 8.5 \text{ J kg}^{-1} \text{ m}^{-1}$  [ANCOVA: homogeneity of slopes,  $F(18, 286)=1.0$ ;  $P=0.4$ ].  $r^2$ , given common slopes, is 0.82. As described in the Materials and methods, a loaded MCOT equal to unladen MCOT would be predicted if the cost of carrying a unit of load mass was equivalent to the cost of carrying a unit of body mass. This MCOT is, however, significantly lower than the equivalent figure for unladen ants ( $t=2.5$ ;  $P<0.02$ ).

As in the case of the unladen ants, the y-axis intercepts of individual laden ants differed significantly [ANCOVA;  $F(18, 284)=28.8$ ,  $P<0.0001$ ]; they were not significantly greater than  $0 \text{ W kg}^{-1}$  ( $1.51 \pm 2.02 \text{ W kg}^{-1}$ ) and they were not significantly affected by temperature, body mass or load ratio ( $P>0.1$ ). Again, about half of the individual regression lines showed significant intercept elevation. As in unladen ants, the cause of these inter-individual intercept differences remains obscure.

Regressing AMR against (running speed  $\times$  load ratio) substantially increased the proportion of the variance in AMR that was explained by speed, when compared with simply regressing MR or AMR against running speed alone. For example, in the case of pooled data, it increased the percentage of AMR variance explained from 19% to 50%, a highly significant improvement [ $z$ -test, Sokal and Rohlf (1981);  $t=120.4$ ,  $P<0.0001$ ; Fig. 3]. The MCOT for pooled data was  $173.5 \pm 10.0 \text{ J kg}^{-1} \text{ m}^{-1}$ , which was significantly greater than unladen MCOT ( $t=3.1$ ,  $P<0.002$ ). Note that this slope is 27% larger than the common slope derived from the same unpooled data set, thus obscuring and, indeed,

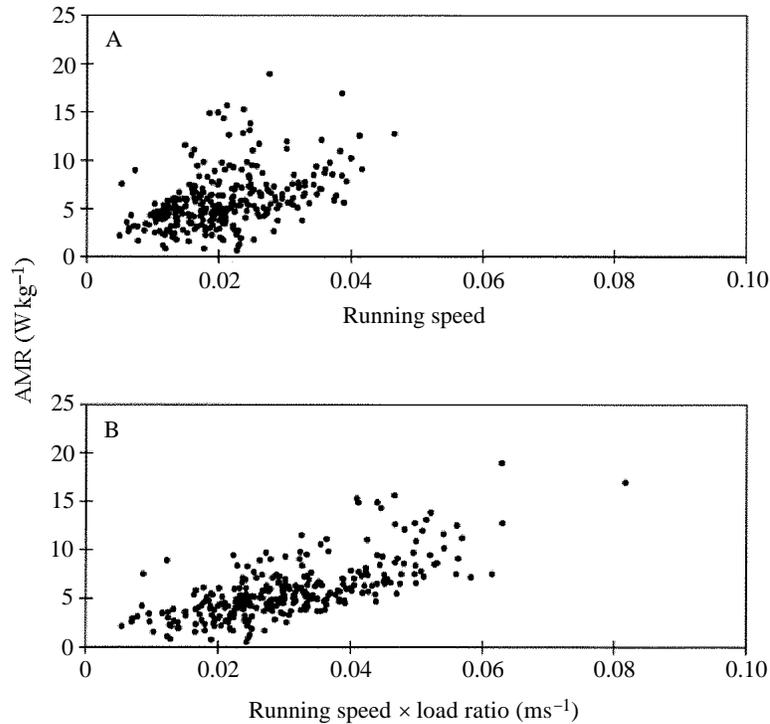


Fig. 3. The effect of regressing AMR against running speed (A) and running speed  $\times$  load ratio (B) for pooled data. This latter technique, which yields a slope equal to unladen MCOT if cost of body carriage equals cost of load carriage per unit mass, compensates for wide variations in load ratio and makes it feasible to analyze diverse data sets, provided that the data can be legitimately pooled (see text). The improvement of fit is highly significant, from 19% of AMR variance explained (A) to 50% explained (B;  $P < 0.0001$ ).

contradicting the lower cost of load carriage. This effect is caused by significant intercept differences between individuals.

COT while laden, if expressed as NCOT, is  $306.8 \pm 159.6 \text{ J kg}^{-1} \text{ m}^{-1}$ , which is significantly more than in the unladen ants ( $t = 4.19$ ;  $P < 0.001$ ); however, at least part of this increase was caused by the lower running speeds of the laden ants.

## Discussion

### *Locomotion energetics*

It is unclear whether the locomotion energetics of insects are systematically different from those of vertebrates. In one early study, Herreid *et al.* (1981) showed that the 5 g cockroach *Gromphadorhina portentosa* had an MCOT (measured by monitoring the cockroach's  $\text{O}_2$  consumption rate while it ran on a treadmill at various speeds), which fell close to the line relating MCOT to mass in vertebrates. In their pioneering work on ant locomotion energetics, Jensen and Holm-Jensen (1980) contended that NCOT in several species of ants fell close to a line extrapolated from vertebrate data. Herreid and Full

(1984) contended that insect MCOT values were significantly higher than those predicted for vertebrates of equivalent mass, whereas Lighton (1985) found that the existing data, when pooled with new data on three beetle species, fell exactly on the vertebrate line. The situation is equally confusing now. We confirm here, irrespective of the measurement methodology employed, the findings of Lighton and Feener (1989), which show extremely low MCOT values for *Pogonomyrmex rugosus*, some 50% lower than values predicted from the usual MCOT–mass regressions.

Plainly, it is premature to base new allometries on such a small number of data points. However, it is clear that substantial disparities exist between actual and predicted costs of transport for animals the size of small insects. More comparative data in this area are urgently required.

#### *Cost of load carriage*

The various techniques for evaluating the costs of load carriage have been covered in the Introduction and Results. It is our contention that the techniques in general use do not necessarily give valid results in the case of *P. rugosus*, nor perhaps in the case of ants in general.

For example, if laden NCOT is divided by unladen NCOT (or equivalent measurements) and the quotient is divided by LR (Herreid and Full, 1986), the result  $[(306.8/231.0)/1.51=0.88]$  is similar to that found in previous investigations (0.87 in *Atta colombica*; Lighton *et al.* 1987, and 0.86 in *Eciton hamatum*; Bartholomew *et al.* 1988). In those investigations, MCOT when laden could not be determined. As a result, the null hypothesis that load and body carriage costs are equivalent per unit mass (yielding 1.0 as the result of the above calculations) could not be rejected on statistical grounds, although the below-unity results were suggestive. When the same analytical method was used in the present investigation, the large standard deviations of the NCOT values also precluded rejection of the null hypothesis.

Analysis of the effect of LR on MCOT may be a more sensitive approach. However, our findings concerning the cost of load carriage must be viewed against the background of the usual practice of measuring MCOT, which is to use pooled data sets. By using analysis of covariance, we have shown that the usual assumption of homogeneity of intercepts between individuals is invalid in the case of *P. rugosus*, and it is therefore not legitimate (at least in this case) to pool the data in the usual way.

Had we simply pooled our data, MCOT determined by regressing AMR against (speed  $\times$  load ratio) would have been  $147.4 \text{ J kg}^{-1} \text{ m}^{-1}$  in the case of unladen ants and  $173.5 \text{ J kg}^{-1} \text{ m}^{-1}$  in the case of laden ants (mean LR=1.51). As explained in the Materials and methods, data analyzed in this way will share a common MCOT if the cost of load and body carriage are equivalent per unit mass. These two slopes suggest that, contrary to this, load carriage costs significantly more than body carriage ( $P < 0.001$ ; see Results). However, the slopes of the two regressions are invalid because they result from the statistically invalid pooling of data with heterogeneous intercepts.

In contrast, the unladen and laden data sets are each homogeneous with respect to slope if subjected to ANCOVA, and their two resulting common slopes ( $158.0 \text{ J kg}^{-1} \text{ m}^{-1}$  for

unladen ants and  $136.6 \text{ J kg}^{-1} \text{ m}^{-1}$  for laden ants) are significantly different from each other.

Using the approaches outlined above, it is now possible to calculate a ‘coefficient of load carriage cost’ (CLCC). First, it is helpful to contrast two hypotheses with respect to load carriage costs:

$H_0$ ; the cost of load carriage is zero. In this case, laden MCOT (measured as described above) would decrease relative to unladen MCOT by the factor  $\text{LR}^{-1}$  or in the present case, to  $104.6 \text{ J kg}^{-1} \text{ m}^{-1}$ .

$H_1$ ; the cost of load carriage is equal to the cost of body carriage per unit mass. In such a case, laden MCOT would be equal to unladen MCOT.

If we define the ‘coefficient of load carriage cost’ as 1.0 if the cost of body and load carriage are equivalent and as 0 if load carriage is free, then the CLCC can be expressed as:

$$\text{CLCC} = [\text{MCOT}_l - (\text{MCOT}_u \times \text{LR}_m^{-1})][\text{MCOT}_u - (\text{MCOT}_u \times \text{LR}_m^{-1})]^{-1}, \quad (5)$$

where CLCC is the fractional cost of load carriage (ranging from 0 to 1, or more than 1 if load carriage is more expensive than body carriage per unit mass),  $\text{LR}_m$  is the mean load ratio (which cannot equal 1 because CLCC then becomes undefined), and  $\text{MCOT}_u$  and  $\text{MCOT}_l$  are the unladen and laden minimum costs of transport, respectively. These are determined by regressing MR (or AMR if temperature varies and must be compensated for) against the product of running speed and load ratio. If CLCC equals 0, the load is carried at no cost; if CLCC equals 1, then load carriage costs and somatic mass carriage costs are equivalent. Defined in this way, CLCC for *P. rugosus* is 0.60. In other words, under the conditions of our experiments, load carriage costs *P. rugosus* approximately 60% as much as body carriage per unit mass. Broadly comparable findings in the harvester ant *Messor capitatus* (Nielsen and Baroni-Urbani, 1990), and even more dramatic findings in crabs (Herreid and Full, 1986) and Kikuyu women (Maloiy *et al.* 1986), both of whom appear to have no measurable cost of load carriage under certain experimental conditions, suggest that low-cost load carriage is not unprecedented.

The origin or cause of this efficient load carriage capability is problematic. Nevertheless, the fact that it occurs in other species emphasizes that the phenomenon is real. Its occurrence in crabs may, in part, be due to a shift in catabolic processes from aerobic to anaerobic pathways, but this is not a likely explanation in insects. Aerobic scopes in excess of 50 are routinely reported for flying insects, and even the relatively sedate mode of pedestrian locomotion may yield factorial increases over SMR of 10–64 (Bartholomew *et al.* 1985). Our data yield a mean aerobic factorial increase over SMR of approximately 3, equivalent in mammals to undemanding pedestrian locomotion and well within the aerobic range of any mobile adult insect. This low factorial increase reflects the relatively low speeds at which our ants ran voluntarily. Ants forced to run at higher speeds may yield factorial increases of up to 8 (Lighton *et al.* 1987), still well within the reasonable aerobic range for insects. Two explanations for ants’ high load-carriage efficiency remain. Load carriage may be intrinsically more efficient in ants than in other organisms, or ants may be optimized for load carriage and may function less efficiently in

the absence of a load. Kinematic analysis of ant locomotion is necessary for further progress in this area, more detailed discussion of which is beyond the scope of this paper.

In any event, it is now possible to derive a simple equation that will allow an approximation of *P. rugosus* energy transactions in the field:

$$MR = SMR_T + (MCOT \times V) + \{MCOT \times V \times [(LR - 1) \times CLCC]\}, \quad (6)$$

where MR is metabolic rate in  $Wkg^{-1}$ ,  $SMR_T$  is standard metabolic rate in  $Wkg^{-1}$  at ant body temperature  $T$ , MCOT is minimum cost of transport in  $Jkg^{-1}m^{-1}$  when unladen ( $158Jkg^{-1}m^{-1}$  for *P. rugosus*),  $V$  is running speed, LR is load ratio, and CLCC is the coefficient of load carriage cost, defined in equation 5 above.

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