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Energetics of locomotion and load carriage in the nectar feeding ant, *Camponotus rufipes*

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Abstract. To investigate if there is an energetic constraint influencing a nectar feeding ant's decision to come back to the nest with partial loads, the energetic costs of running and carrying a load in the ant *Camponotus rufipes* are measured. Metabolic rates of individuals are measured in a running tube respirometer while they are unladen and laden at 25 °C. Workers voluntarily collect a load of 6 µL of a 30% sucrose solution (mass = 6.8 mg), which results in an internal load of about 50% of the ant mass and is close to a full load for ants within this size range. The gross cost of unladen running is 264 J kg⁻¹ m⁻¹, while that of laden running is 225 J kg⁻¹ m⁻¹. The mass used to calculate the cost of laden running includes body mass of ant and load carried. Load carriage cost in *C. rufipes* foragers is calculated to be about 60% as much as body carriage per unit mass. Internal load carriage in *C. rufipes* is energetically cheaper compared with external carriage in other ant species. Such low carriage costs make it unlikely that the collection of partial crop loads in *C. rufipes* foragers is based on a minimization of foraging costs, as suggested for honeybees.

Key words. Central place foraging, cost of transport, loading, metabolism, partial crop-filling, running speed.

Introduction

Most species of ants are 'central place foragers', and display a variety of foraging strategies (see review by Traniello, 1989). These range from individual to collective foraging behaviour, and from external to internal load carriage. Foragers are responsible for the energy intake of the entire colony and therefore its survival and fitness. The cost of foraging includes the locomotion cost of foragers from the nest to the food source, the cost of carrying loads back to the nest and the handling cost, such as those arising from positioning an object in the mandibles and maintaining stability during subsequent locomotion (which can be insignificant for nectar collectors). All those facts may explain the fascination for work on ant energetics, which yields a larger number of studies on ant locomotion than with other small insects.

From the pioneer work of Nielsen *et al.* (1982) to the more recent field-data validation of laboratory measurements on ant locomotion (Lighton & Duncan, 2002), different techniques have been used to measure energetic costs of locomotion. Basically, the metabolic rate of locomotion can be measured with an ant running in: (1) the 'running tube', which allows single workers to spontaneously run at a voluntary speed inside a glass-tube, or (2) the 'treadmill', where an ant is forced to run at a fixed speed. Minimum cost of transport is defined as the slope of the relation between running speed and metabolic rate. Measurements on the treadmill, where the ant is artificially stimulated to run, have the disadvantage of elevating the intercept of the minimum cost of transport curve when speed is 0 above the standard metabolic rate, making comparative studies difficult. Lighton & Feener (1989) show that it is not the case with the running tube (the interception of the minimum cost of transport at 0 speed did not differ from the standard metabolic rate). This finding has been corroborated in other studies with different ant species (Duncan & Crewe, 1993; Lighton *et al.*, 1993; Duncan & Lighton, 1994; Duncan, 1995, 1999), as well as other insects such as flies (Berrigan & Lighton, 1993, 1994), mites (Lighton & Duncan, 1995) and wasps (Duncan & Lighton, 1997).

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Usually, the cost of carrying a load has been evaluated using different laden and unladen individuals (exception: Nielsen, 2001) and artificial loads, except for a few studies, e.g. (Bartholomew *et al.*, 1988; Duncan & Lighton, 1994; Fewell *et al.*, 1996; Duncan, 1999). The second study was the only one that measured the cost of internal load carriage of a natural load, i.e. ingested honey water. Duncan & Lighton (1994) found in the honey pot ant, *Myrmecocystus mendax*, equivalent costs per unit mass of internal load carriage and body mass carriage. These results suggest that internal load carriage does not appear to save costs compared with external load carriage (Duncan & Lighton, 1994).

Camponotus rufipes workers feed on arthropods and collect nectar from extrafloral sources (Jaffé & Sánchez, 1984). A previous study found that foraging times of *C. rufipes* are strongly affected by the richness of the food source (Schilman & Roces, 2003). *Camponotus rufipes* foragers trained to collect sugar solution from an artificial patch with different flow rates stop collecting nectar and come back to nest with partial crop loads (Schilman & Roces, 2003). It is evident that coming back to nest with a partially filled crop saves time, but it is not known if there are any energetic constraints influencing the workers' decision to stop feeding. It is possible that carrying a large load will be highly costly, so that workers return to the nest with partial crop loads.

In this study, the energy costs of internal load carriage and locomotion are measured in the nectar-feeding ant *C. rufipes* in order to determine whether partial crop filling in *Camponotus* ants minimizes transport costs during foraging. Here, the metabolic cost of locomotion and load carriage in the same foragers of the ant *C. rufipes* are measured. Measuring the same individuals, unladen and laden, eliminates inter-individual differences for calculation of load carriage efficiency. The costs of carrying an internal food load (i.e. sugar solution) in *C. rufipes* are compared with previously published data on the honey pot ant, *M. mendax* (Duncan & Lighton, 1994).

Materials and methods

Insects

Only one colony was used to control for potential inter-colony differences in running energetics due to factors such as nutritional state, colony age and size, etc. Thus, the number of workers, rather than the number of colonies, was used as sample size for statistical analysis. A colony of *C. rufipes* consisting of one queen, approximately 600 workers and brood was used for the study. The founding queen was collected in November 1994 in Misiones, Argentina. The colony was reared in a plaster nest and kept in an open-top Plexiglas container (37 × 57 × 27 cm), with fluon-coated walls to prevent escape. The colony was maintained at 25 °C, 50% relative humidity (RH) and LD 12 : 12 h regime (lights-on: 07.30 hours).

Social insects collect and store food, when available, for times of necessity. Ant colonies of *C. rufipes* differ from honey bee colonies in that they store the nectar they collected inside their own bodies, i.e. in worker's crops. This implies that the foraging behaviour of individuals may be affected by their level of starvation or by their crop loading. In order to avoid changes in foraging behaviour, the physiological state of the colony was standardized following Schilman & Roces (2003). The colony was fed sugar solution *ad libitum* overnight (all workers showed fully expanded gasters after feeding). It was then provided access, *ad libitum*, to cockroaches and water, but was deprived of sugar solution for 3–7 days prior to measurements. This period of time does not significantly modify their feeding behaviour (unpublished data). Under the same conditions, *C. rufipes* colonies were observed to survive at least 14 days of sugar deprivation (unpublished data), indicating that a period of 3–7 days is not a severe starvation because of the presence of crop reserves.

Respirometry measurements

A high-resolution respirometry system TR-2 (Sable System International, Las Vegas, Nevada; resolution 0.01 p.p.m. CO₂) was used as described in Lighton (1990). This system allows CO₂- and H₂O-free air to be drawn through a glass tube (84 cm long × 1.8 cm diameter; approximately 214 cm³), in which an ant can move freely, at a flow rate of 300 mL min⁻¹ standardized to temperature and pressure, and controlled by a mass-flow controller. The CO₂ produced by the ant was measured by an IR-CO₂ analyser (Li-Cor; Lincoln, Nevada) and the data were stored in a computer (Fig. 1). The running tube used and its advantages are described by Lighton & Feener (1989). They found that the use of treadmills has the disadvantage of elevating the intercept of the minimum cost of transport curve, when speed is 0, above the standard metabolic rate, whereas a running tube does not affect locomotion energetics. This was recently validated by *in situ* field measurements (Lighton & Duncan, 2002). This method takes advantage of the stereotypical escape behaviour many insects exhibit when confined in a closed end tube. They often spend long periods of time running or walking from one end of the tube to the other. During runs, the speed of the ant was measured by tracing the ant's path manually and noting the travel time.

Each recording consisted of a variable number of data points taken at 1.5-s intervals. To determine CO₂ emission rates, data acquisition and analysis system DATACAN V software was used (Sable System International).

Prior to and after each ant's metabolic recording, CO₂ levels in the empty running-glass tube were recorded as a baseline. During analysis, the start- and end-baselines were subtracted assuming a linear drift and the CO₂ values corrected. All measurements were performed at controlled room temperature of 25 ± 0.5 °C.

Fig. 1. Experimental design used to measure the metabolic rate of a running unladen and laden forager. Water- and CO_2 -free air is drawn through the running tube at a flow rate of 300 mL min^{-1} at 25°C . The CO_2 produced by the ant was measured by an IR- CO_2 analyser and the data were stored in the computer for further analysis.

Experimental procedure

The metabolic activity of each ant was measured running with and without a load. Single *C. rufipes* ants were trained to collect sugar solution from an artificial food source (Schilman & Roces, 2003). Each worker was allowed to consume $6 \mu\text{L}$ of a 30% sucrose (Sigma-Aldrich; Deisenhofen, Germany) solution (6.8 mg, about 50% of the ants body mass). This quantity was chosen because it represents the average amount of sugar solution collected from an *ad libitum* source by *C. rufipes* ants of similar size (Schilman & Roces, 2003). Moreover, as the ant always collected all the solution provided, this quantity does not represent more than the maximal crop load, thus ensuring that the same load was carried for all ants measured. Following two or three foraging cycles where the ant returned to the nest, unloaded the food via trophallaxis and returned to the food, the loaded ant was allowed to

voluntarily enter the running tube (respirometric chamber). The tube was then closed and the CO_2 production by the walking ant was measured for 5–8 min. To calculate velocity, the distance walked (workers transected the tube four to eight times) was divided by the time elapsed. The glass tube was then opened and the ant allowed to return to the nest to unload the sugar solution via trophallaxis with nestmates. On subsequent visits to the food source, the metabolic rate of the worker was measured as the ant returned through the glass tube. Each ant was measured between one and three times loaded and one or two times unloaded. In all cases the ant inside the tube walked in an almost straight line and changed direction at the end of the tube without a significant pause. After the last measurement, the individual was weighed to the nearest 0.1 mg using an analytical balance (Ohaus Model AS60; Karlsruhe, Germany) and discarded. Water loss is unlikely to influence any change in mass because trials were short and workers were able to feed on sugar water. In all experiments, care was taken to limit disturbance to the ants.

Data analyses and statistics

Thirteen ants with a total of 32 metabolic recordings were used for the analysis. Repeated recordings on a single worker were averaged to avoid pseudoreplication (Hurlbert, 1984). Ants are highly tracheated insects, and have full aerobic respiration at normal running speeds (Lighton *et al.*, 1987, 1993). Therefore, CO_2 emission rate was converted to energy units (Joules) assuming (as is reasonable with carbohydrate-fed ants) the dissipative catabolism of glucose.

Laden vs. unladen data were compared using a paired-sample Student's *t*-test. In addition, a two-sample Student's *t*-test was used to compare our results with previous published data. A one-sample Student's *t*-test was used to compare the present results with expected values (Zar, 1984).

Camponotus rufipes is a polymorphic species (Hölldobler & Wilson, 1990). To eliminate the influence of worker-size variation, the same workers were measured with and without a load. This allows for the comparison of the metabolic rates from different treatments without considering size effects on metabolic rates. In addition, medium size workers (*c.* 14 mg) were selected to investigate a homogenous size group of ants.

Results

Data are presented in Table 1. As the same ant foragers were measured loaded and unloaded, the average ant mass is the same for both measures (Table 1). Using the allometric equation metabolic rate (MR) = $973\text{M}^{0.856}$, where M is the ant mass in g (Lighton *et al.*, 2001), the catabolic flux rate predicted on the basis of body mass in inactive insects or Standard Metabolic Rate (SMR) was $24.62 \pm 0.73 \mu\text{W}$

Table 1. Values are mean $\pm$ SD of ant masses, running speeds, and metabolic costs of laden and unladen workers of the ant *C. rufipes*.

	Laden	Unladen
Temperature ($^{\circ}\text{C}$)	25	25
<i>n</i>	13	13
Individual ant mass (mg)	13.7 ± 1.7	13.7 ± 1.7
SMR (μW)	24.6 ± 2.6	24.6 ± 2.6
Speed (cm s^{-1})	3.4 ± 0.5	3.5 ± 0.4
MR ($\mu\text{L CO}_2 \text{ ant}^{-1}$)	26.3 ± 3.4	21.3 ± 2.3
GCOT _{body mass} ($\text{J kg}^{-1} \text{ m}^{-1}$)	340.2 ± 49.4	264.0 ± 39.6
GCOT _{total mass} ($\text{J kg}^{-1} \text{ m}^{-1}$)	225.9 ± 28.0	264.0 ± 39.6
NCOT _{body mass} ($\text{J kg}^{-1} \text{ m}^{-1}$)	285.8 ± 47.3	212.3 ± 34.5
NCOT _{total mass} ($\text{J kg}^{-1} \text{ m}^{-1}$)	189.6 ± 26.8	212.3 ± 34.5
LR	1.5	1

SMR, standard metabolic rate (calculated from allometric equation $\text{SMR} = 973M^{0.856}$, where *M* is ant mass in g; Lighton *et al.*, 2001). MR, metabolic rate. GCOT, gross cost of transport. NCOT, net cost of transport ($\text{NCOT} = (\text{MR}_{\text{running}} - \text{SMR})/\text{speed}$; Bartholomew *et al.*, 1988). LR, load ratio ($\text{LR} = (\text{load mass} + \text{body mass})/(\text{body mass})$). GCOT and NCOT values are expressed per unit of body mass and per unit of total mass (Total mass = body + load mass).

(Table 1). The MR or Gross Cost of Transport (GCOT) of unladen and laden workers was about five and six times their SMR, respectively (Table 1).

Workers loaded with a mass of 6.8 mg (6 μL of a 30% sucrose solution), which represents a Load Ratio (LR) of 1.50 (i.e. about 50% of the ant mass), had higher MR or GCOT than the same unloaded workers ($t_{12} = 5.572$, $P < 0.0001$, Paired-sample Student's *t*-test; Table 1). However, when the GCOT was calculated taking into account the total mass (total mass = ant mass + load mass), GCOT was lower for laden foragers ($t_{12} = 3.323$, $P < 0.0061$, Paired-sample Student's *t*-test; Table 1). This indicates a lower cost of transport per unit of load carriage than per unit body mass. Similar results were obtained when the Net Cost of Transport ($\text{NCOT} = \text{GCOT} - \text{SMR}$), instead of GCOT, was compared (Table 1, statistics not shown). Both laden and unladen foragers ran at similar speed ($t_{12} = 0.715$, NS, Paired-sample Student's *t*-test; Table 1). To evaluate the Cost of Load Carriage (CLC), we calculated the ratio of laden vs. unladen NCOT, and then divided it by the LR. A value of 1 indicates that transport costs per unit carriage are equal to the transport costs of body mass, whereas a value of 0 indicates no cost of load carriage. The CLC estimated in this way was 0.61 ± 0.03 , which is significantly different from 1 ($t_{12} = 11.936$, $P < 0.0001$, One-sample Student's *t*-test).

Discussion

The cost of locomotion measured for *C. rufipes* is lower than predicted using Full's equation (Full, 1989; 68% of the predicted value, see below), as found in other studies (Lighton & Duncan, 1995, 2002; Duncan, 1999). The

present measurements of running costs for an unladen ant (GCOT) were $264.04 \pm 10.98 \text{ J kg}^{-1} \text{ m}^{-1}$ (Table 1), whereas the calculated value with the allometric Eq. (1):

$$E_{\text{metab.}} = 10.8M^{-0.32} \quad (1)$$

where *M* is body mass in kg (Full, 1989), gives a value of $390.44 \pm 4.34 \text{ J kg}^{-1} \text{ m}^{-1}$. This value is significantly higher ($t_{24} = 10.7$, $P < 0.001$, two-sample Student's *t*-test). However, using a more recent allometric Eq. (2):

$$\text{MCOT} = 30.9M^{-0.312} \quad (2)$$

where *M* is body mass in g (Lighton & Duncan, 1995), The calculated value is $118.34 \pm 1.28 \text{ J kg}^{-1} \text{ m}^{-1}$, which is about 50% lower than the present measurement. Similar relationships between the measured and predicted values with Eqs (1) and (2) are found by Duncan (1999) for the ponerine ant *Pachycondyla berthoudi*.

Both laden and unladen foragers ran at similar speeds (Table 1). This contrasts to the reduction in running speeds for laden ants found in other studies (e.g. Lighton *et al.*, 1987, 1993; Bartholomew *et al.*, 1988). However, similar results have been observed for *M. mendax* in a running tube respirometer (Duncan & Lighton, 1994), as well as in the field (Duncan & Lighton, 1994) and for *Messor pergandei* (Rissing, 1982; Lighton & Duncan, 2002). In fact, Lighton & Duncan (2002) have shown that the effect of load on running speed is in the opposite direction, i.e. laden ants run faster, although not significantly so. In general, running speed in ants is expected to depend not only on the load carried, but also on the physiological condition that is influenced by the quality of the food being carried (Roces, 1993).

Although caution is required with these comparisons, as GCOT and NCOT values are speed-dependent, the GCOT value is in agreement with the values found for workers of the related species, *Camponotus herculeanus*, $299 \text{ J kg}^{-1} \text{ m}^{-1}$ (Nielsen *et al.*, 1982), and for the ant *Messor capitatus*, $363 \text{ J kg}^{-1} \text{ m}^{-1}$ (Nielsen & Baroni-Urbani, 1990). For unladen workers of *Pogonomyrmex rugosus*, Lighton *et al.* (1993) show a NCOT value of $231 \text{ J kg}^{-1} \text{ m}^{-1}$, which does not significant differ from our NCOT value found for *C. rufipes* ($t_{36} = 0.79$, $P = < 0.43$, two-sample Student's *t*-test), whereas for laden workers their value is $306.8 \text{ J kg}^{-1} \text{ m}^{-1}$ that also did not differ from *C. rufipes* ($t_{30} = 0.46$, $P = 0.65$, two-sample Student's *t*-test). Net cost of transport in *C. rufipes* was also similar to that of laden workers of *Pachycondyla berthoudi* $248 \text{ J kg}^{-1} \text{ m}^{-1}$ ($t_{31} = 1.41$, $P = 0.17$, two-sample Student's *t*-test) (Duncan, 1999). However, the NCOT for unladen workers of the same species was $144 \text{ J kg}^{-1} \text{ m}^{-1}$, significantly lower than *C. rufipes* ($t_{43} = 3.91$, $P < 0.001$, two-sample Student's *t*-test) (Duncan, 1999). The mean cost of locomotion or NCOT for an unladen *Rhytidoponera aurata* worker was $166 \text{ J kg}^{-1} \text{ m}^{-1}$, also significantly lower than *C. rufipes* ($t_{26} = 3.20$, $P < 0.005$, two-sample Student's *t*-test) (Nielsen, 2001). When we compare *C. rufipes* with the honey pot ant, *M. mendax*, again the NCOT was similar, both unladen ($\text{NCOT} = 203 \text{ J kg}^{-1} \text{ m}^{-1}$, $t_{27} = 0.43$, $P = 0.67$, two-sample Student's *t*-test) and laden ($\text{NCOT} = 253 \text{ J kg}^{-1} \text{ m}^{-1}$,

$t_{21} = 1.135$, $P = 0.27$, two-sample Student's t -test) (Duncan & Lighton, 1994). All the comparisons mentioned above have in common that they are energetic measurements of voluntary locomotion in ants. However, they arise from a wide variety of ant species, which carry their loads internally or externally, and with both natural and artificial loads. In spite of these differences, all ants had similar and very low carrying costs, suggesting that natural selection has favoured very efficient load carriage in ants.

Unfortunately, the MCOT for *C. rufipes* could not be determined because the limited range of speeds did not allow us to assign a statistically meaningful slope to the CO₂ production–speed relation. Velocity was measured manually, in short running recordings and at one temperature. This allowed measurement of the same ant in consecutive trips to or from the food source without perturbing them, and so allows more accurate calculations of load carriage by eliminating inter-individual differences. As stated by Lighton *et al.* (1993): 'The most direct measure is the gross cost of transport (GCOT), obtained by dividing metabolic rate (MR, in J s⁻¹ kg⁻¹ = W kg⁻¹) by the speed in 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 present data allow for the calculation of the cost of carrying a load, based either on GCOT or on NCOT, without these two disadvantages, because: as measurements are made of laden and unladen GCOTs on the same foragers, the SMRs are exactly the same for both (Table 1), and laden and unladen foragers do not differ in running speed (see Table 1 and Results). These two points make the calculation of load transport from GCOT or NCOT measurements very robust. For example, using the laden and unladen values of NCOT (see Eq. (3)), a Cost of Load Carriage (CLC) of 0.87 for *Atta colombica* (Lighton *et al.*, 1987) and 0.86 *Eciton hamatum* (Bartholomew *et al.*, 1988) are found:

$$\text{CLC} = (\text{NCOT}_{\text{laden}}/\text{NCOT}_{\text{unladen}})/\text{LR} \quad (3)$$

In both cases, the huge variation makes these values not significantly different from 1 (1 means cost of carrying a load is the same as transporting their own body mass). Using the same formula to calculate CLC, *C. rufipes* has a value of 0.61, which is significantly different from 1 (see Results). In other words, *C. rufipes* spend 61% as much as body carriage per unit load mass. Calculating the CLC with GCOT values instead of NCOT ones, gives a result of 58% instead of 61%, which was also significantly different from 1 ($t_{12} = 12.91$, $P < 0.001$, one-sample Student's t -test).

The calculation of the energy necessary to carry 20 mg of load 1 m for *C. rufipes* is 3.21 ± 0.54 mJ, which is almost identical to the value found for other nectar collectors (e.g. *Myrmecocystus mendax*, 3.3 mJ, Duncan & Lighton, 1994). For comparisons with other ant species, see Duncan (1999; Table 3). It is important to mention that the biological significance of these comparisons is debatable as the LR will vary according to the body mass of the ant species. For example, whereas *C. rufipes* has a mean mass of 13.7 mg

(this study), *M. mendax* has a mean mass of 6.04 mg (Duncan & Lighton, 1994). Therefore, a 20 mg load will represent a LR of 2.5 and 4.3 for *C. rufipes* and *M. mendax*, respectively. The fact that the energy required to move 20 mg of load 1 m is similar for both ant species, together with the lower LR for *C. rufipes*, would indicate a higher relative cost of load carriage for *C. rufipes*. However, whereas in *M. mendax* the internal load carriage does not appear to offer savings compared with external load carriage (Duncan & Lighton, 1994), in *C. rufipes* it does.

It is interesting to note that handling costs, such as positioning an object in the mandibles, seem to be non-existent for nectar feeding insects. Other costs such as maintaining stability during subsequent locomotion, would vary and may be lower for internal than external carriers. An experiment that compares carrying costs of two natural loads, one external and one internal (e.g. nectar load and a larvae) of the same mass could determine the costs of different carrying methods. Moreover, further studies with different ant species carrying 'natural' and artificial loads will validate previous studies on the energetics of locomotion with artificial loads. This will also extrapolate laboratory results to ecological-energetic work in the field, as was done with measurements of unladen workers of *Messor pergandei* (Lighton & Duncan, 2002).

The measures presented here of relatively low transport costs for an almost full load of nectar suggest that returning to the nest with partial crop loads in ants (Schilman & Roces, 2003) is unlikely to be the consequence of an energetic constraint influencing the forager's decision to stop feeding. Schilman & Roces (2003) have shown that workers of *C. rufipes* come back to the nest, in some cases, with less than 20% of the maximal crop capacity. For *C. rufipes*, it seems unlikely that coming back to the nest with a partial crop load results from minimizing transport costs and thereby maximizing energy returns during foraging, as suggested for foraging honeybees visiting flowers (Schmid-Hempel *et al.*, 1985; but see Varjú & Núñez, 1991 and also Moffatt, 2000).

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