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RESEARCH ARTICLE

Ergonomics of load transport in the seed harvesting ant *Messor barbarus*: morphology influences transportation method and efficiency

Abel Bernadou*, Antoine Felden[‡], Mathieu Moreau, Pierre Moretto and Vincent Fourcassie[§]

ABSTRACT

We studied in the field the load transport behavior of workers of the polymorphic Mediterranean seed harvester ant *Messor barbarus*. Individual ants used two different methods to transport food items: carrying and dragging. The probability of dragging instead of carrying varied significantly with both the mass of the item transported and its linear dimension. Moreover, the values of item mass and length at which dragging began to occur increased with increasing size of the workers. However, larger ants began dragging at decreasing values of the relative mass represented by the items transported, which reflects different biomechanical constraints resulting from allometric relationships between the different parts of their body. Transport rate was significantly higher in large ants but varied in the same way for workers of different sizes with the relative mass of the item transported. Nevertheless, although large ants were individually more efficient than small ants in transporting food items, the relative transport rate, defined as the ratio of transport rate to the mass of the ant, was higher for small ants than for large ants. Colonies should thus have a greater benefit in investing in small ants than in large ants for the transport of food items. This may explain why the proportion of large ants is so small on the foraging columns of *M. barbarus* and why large ants are most often employed in colonies for tasks other than transporting food items.

KEY WORDS: Morphology, Biomechanics, Polymorphism, Foraging

INTRODUCTION

The transport of heavy loads over long distances rarely occurs naturally in animals. Ants are a notable exception to this rule, and their ability to transport loads several times their own mass over distances equivalent to several thousands of times their size has always been an object of amazement and fascination for naturalists. Thanks to specific morphological and anatomical features, such as the efficient and dynamic control of tarsal pad adhesion (Federle et al., 2001; Federle and Endlein, 2004), and the extreme resistance of their neck joints (Moll et al., 2013; Nguyen et al., 2014), ants are able to lift, hold and carry extremely heavy loads with their mouthparts. For example, individual workers of the species *Azteca andreae* are able to hold loads weighing up to

5700 times their own mass while clinging on a leaf margin (Dejean et al., 2010). External load transport is particularly important in the ant species whose diet depends on the retrieval of solid material, i.e. leaf-cutting ants, seed-harvesting ants and predatory ants. In these species, foraging workers can routinely transport loads that are more than 10 times their own mass (Sudd, 1965). Load transport is also occasionally used in many other ant species for the transport of brood or nestmates, for the transport of nest material (Aleksiev et al., 2007) or for removing obstacles along foraging trails (Howard, 2001).

Ants use a variety of different methods to carry heavy loads. For example, army ants carry their brood and prey below their bodies (Franks, 1986), harvesting ants generally carry seeds in a frontward position, and leaf-cutting ants carry leaf fragments above their bodies, in an upward to backward position (Moll et al., 2010). When the load reaches a certain weight, ants switch from carrying to dragging (Sudd, 1960, 1965) or proceed to cooperative transport (Gelblum et al., 2015; reviewed by Czaczkes and Ratnieks, 2013; McCreery and Breed, 2014). The carrying method and carrying limits of each species are probably partly imposed by biomechanical constraints linked to the morphology (e.g. leg lengths relative to body size: Zollkofer, 1994; Moll et al., 2013) and/or the anatomy of the workers (e.g. neck joint muscles: Keller et al., 2014).

Interestingly, most species of ants whose diet depends on the collection of solid material are characterized by a high polymorphism of the worker caste (Hölldobler and Wilson, 1990). This polymorphism is generally assumed to benefit the colonies because it allows them to have access to a wider range of food resources (seed-harvesting ants: Davidson, 1978; Retana and Cerdá, 1994; Cerdá and Retana, 1994; Arnan et al., 2011; army-ants: Powell and Franks, 2005; leaf-cutting ants: Wetterer, 1994; Clark, 2006). In general, there is a relatively strong relationship between the size of the workers and the mass of the loads they carry ('size-matching': Davidson, 1978), although in leaf-cutting ants (Röschard and Roces, 2003) and seed-harvesting ants (Reyes and Fernandez-Haeger, 1999; Arnan et al., 2011; Bernadou et al., 2011) this is more the result of a progressive adjustment in a sequence of transfer among workers along foraging trails than an active choice of the loads by the workers. Polymorphism can also enhance foraging efficiency by lowering the costs of load retrieval (Oster and Wilson, 1978; Traniello, 1989). For example, in *Eciton burchelli* colonies, even if workers of the submajor subcaste constitute only 3% of the colony, they represent 25% of all prey carriers (Franks, 1986; see also Powell and Franks, 2005), presumably because, due to their particular morphology, they are more cost effective than other workers in carrying prey (Franks, 1986). The same is true for leaf-cutting ants, in which the transport of leaf fragments is overwhelmingly achieved by medium-sized workers (Hölldobler and Wilson, 2010).

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In this study we report the results of field experiments aiming at investigating the transport of loads by workers of the Mediterranean seed harvesting ant *Messor barbarus* Linnaeus 1767. This species is an important seed predator in Mediterranean ecosystems (Detrain et al., 2000; Azcárate and Peco, 2003; Azcárate et al., 2005). Workers collect seeds in their environment and transport them to their nest along well-defined physical trunk trails (Lopez et al., 1994) (Fig. S1A). *Messor barbarus* shows the larger range of body size among the *Messor* genus, and its worker caste is characterized by a continuous polymorphism (Heredia and Detrain, 2000; Plowes et al., 2013). Using calibrated pieces of alimentary pasta as food items, we first examined whether the rules used by *M. barbarus* workers to decide which method to use to transport an item – carry or drag – differ between workers of different sizes. We then investigated whether the locomotory rate of different sized workers is impacted in the same way by the load they transport and the transport method they use. Finally, we investigated the performance of ants of different sizes in transporting items to their nest, at both the individual and colony levels. Because the rules used by individual ants to transport an item are likely to depend on their morphology, we conducted in complement to this study a series of morphological measurements on a sample of *M. barbarus* workers. This allowed us to characterize their polymorphism and, through a 3D reconstruction of their body, determine the position of their center of mass. We discuss our results in light of colonies' investment in the production of different sized workers.

MATERIALS AND METHODS

Studied colonies and field site

We worked on six colonies located on the campus of the Universitat Autònoma de Barcelona, Spain (41°30'00N, 2°06'49E). One foraging trail was chosen for each colony. The minimum distance between two colonies was 20 m. The experiments were carried out during two consecutive summers (2007 and 2008) and ants were observed during the two peaks of activity of *M. barbarus* in summer, i.e. early morning and late afternoon (Cros et al., 1997). The temperature during the experiments ranged between 17.9 and 48.1°C.

Experimental protocol and data collected

To control as much as possible the loads offered to the ants, we used pieces of alimentary pasta instead of seeds. Pieces of pasta are readily accepted by *M. barbarus* workers when placed on their foraging trails and, contrary to seeds of different plant species, they present the advantage of having the same appeal to the ants. We used dried pasta of the same brand and of the three different diameters commercially available (0.91, 1.45 and 1.86 mm). The mandible gap of *M. barbarus* workers ranges between 0.80 and 2.80 mm (Oliveras et al., 2005). Therefore, even the pasta of the largest diameter can be seized by some foraging workers. The pieces of pasta varied in mass (range: 2.8–128.8 mg) and length (range: 3.08–29.27 mm) and were classified in 12 categories according to their mass and diameter (Table S1). All six colonies were tested with five items of each category.

An experiment began by placing a single piece of alimentary pasta at 1.5–2.0 m from the nest entrance, on a foraging trail supporting a sustained traffic of ants. As soon as an ant seized the pasta it was followed on its way back to the nest for a distance of 1 m and its travel time was noted. We interrupted and gave up the tracking when an ant abandoned its item before traveling a length of 1 m or when the item was seized by one or several other ants and began to be transported collectively. We also noted the transport

method used by the ant (carrying or dragging), as well as the temperature indicated by a thermometer (accuracy: $\pm 0.1^\circ\text{C}$) placed directly on the ground, on the edge of the physical trail. The ant was then gently picked up with forceps and placed in a numbered vial, along with the piece of pasta it was transporting. The vial was then placed in crushed ice to avoid tissue desiccation. Both the ant and its load were weighed in the laboratory at the end of the day with a precision balance (± 0.1 mg). The mass of the pasta piece was expressed in units of ant body mass, using the formula $1 + (\text{load mass}/\text{ant body mass})$, hereafter called load ratio (Bartholomew et al., 1988). We used ant mass as a continuous variable in most of our analyses. Nevertheless, we had to use size categories for two of our analyses. We thus defined three size classes: small ants (fresh body mass < 5 mg), medium-sized ants (5–10 mg) and large ants (> 10 mg) (Fig. S1B).

Morphometric measures

To characterize the polymorphism of the worker caste in *M. barbarus*, morphological and mass measurements were made on a sample of 57 workers, covering approximately 95% of the size range of the workers we tested in the field (range of body mass of the workers in our sample: 1.65–37.56 mg; range of body mass of the workers tested in the field: 1.30–38.90 mg). After killing ants by freezing them at -20°C , we measured the linear dimensions of various body parts of the ants (head, thorax, abdomen, legs) using a binocular microscope equipped with a graduated ocular coupled with a stage micrometer. We then separated these different body parts with micro-dissection tools and weighed them separately to the nearest 0.01 mg using a microbalance (Mettler ME30, Switzerland). Following Molet et al. (2014), to investigate the growth rules between the different parts of the workers, we first transformed our measures of masses to a linear dimension using a cube root transformation. We then log-transformed our data and, using standardized major axis regression (smatr package in R; Warton et al., 2012), performed regressions on pairs of transformed variables to reveal the growth rules between the different body parts of the ants. The slope of the regression line corresponds to the allometry coefficient (growth rate), which describes how much the body part in y increases when the body part in x increases. It can be tested against unity (which represents the case in which body shape does not change with size, i.e. isometry) with a one-sample test implemented as a simple function in the package smatr.

From a biomechanical point of view, the locomotory performances of an animal can be accounted for by classical mechanics and depend on the forces that apply at the center of mass of its body. The calculation of the position of the center of mass of ants of different sizes should thus allow us to reveal potential inter-individual differences in biomechanical properties due to allometric growth between the different parts of their bodies. To determine the position of the center of mass of different sized ants, we used a 3D reconstruction of their body. In a first stage, we built 3D models from two orthogonal views (ventral and sagittal) of free-walking ants, following the intersecting silhouettes procedure of Baumgart (1975). The projections of each body part (head, thorax and gaster) were manually determined from the two views and processed in R 2.13.1 (R Foundation for Statistical Computing, Vienna, Austria) to construct a 3D test function representative of the ant. In a second stage, we calculated the positions of the geometrical center of each body part by adaptive 3D integration (sp package in R, Pebesma and Bivand, 2005; cubature package in R, <http://CRAN.R-project.org/package=cubature>). Finally, we used the positions of the geometrical center of each body part as well as their masses to

determine the position of the center of mass of the whole body. The relative position of the center of mass, expressed in proportion to the ants' thorax length, was then regressed against thorax length to investigate the shift of the center of mass as a function of the size of the ants.

Statistical analysis

We first examined whether ants of different size classes had limited transport capacities by comparing the distribution of the load ratio of the pieces of pasta offered with that of the pieces of pasta actually picked up and transported by ants using a Kolmogorov–Smirnov test. The load ratio for the pieces of pasta offered was calculated for the mean mass of the ants of each size class. We then used a generalized linear mixed model (GLMM) (Bolker et al., 2009) to test the relationship between the mass of the ants and the mass and the length of the items transported when ants were carrying or dragging an item. Ant mass, transportation method and their interaction were entered as explanatory variables in the initial model. Variation between colonies (and hence foraging trails, which could differ in the type of substrate they offered) was accounted for using colony as a random effect. We then examined the differences in diameter of the items transported by the different size classes of workers when they were carrying or dragging an item. The distributions of items of different diameters in the different size classes were compared with a χ^2 test for contingency tables. A separate test was run for items that were carried and items that were dragged.

To examine the conditions in which ants dragged or carried an item, we used a binomial GLMM (Zuur et al., 2009). The model was fitted by the Laplace approximation (lmer function of the lme4 R package; <http://CRAN.R-project.org/package=lme4>). The response variable was the probability of dragging an item. We ran a first model to test whether this probability depended on worker size (taking mass as a proxy of their size) and item mass, and a second model to test whether it depended on worker size and load ratio. For each model we included the interaction between worker size and the other variable. Including this interaction term in the models allowed us to test whether the rules used by ants of different sizes to decide when to carry or drag an item are the same. Variation between colonies (and hence foraging trails) in the decision rules regarding the transportation method was accounted for using colony as a random effect in the statistical models.

As is the case for all invertebrates, the locomotory rate of ants is known to be highly dependent on ambient temperature (Hurlbert et al., 2008): it generally increases with increasing temperatures. To examine the effect of load ratio on the travel time of loaded ants of different sizes using different transport methods, we thus first regressed travel time on temperature. We then used a GLMM (Zuur et al., 2009) with travel time corrected for the effect of temperature (by subtracting the effect of temperature on the values of travel time) as the response variable and worker mass, load ratio and the transportation method (drag/carry) as explanatory variables; colony was introduced in the model as a random effect.

For each ant followed, a measure of transport rate was computed as the product of the mass of the item transported by the speed of the ant (Rudolph and Loudon, 1986), assessed from its travel time (corrected for the effect of temperature). Transport rate is thus expressed in mg cm s^{-1} . We then used a generalized additive mixed model (GAMM) (Zuur et al., 2009) in which load ratio and ant mass were entered as smooth terms to examine how transport rate was affected by both load ratio and ant mass. The model was fitted with the gam function of the R package mgcv (Wood, 2006).

Finally, we calculated the relative transport rate, defined as the ratio of transport rate to the mass of the ant. Relative transport rate gives a measure of the benefit in prey biomass returned to the colony per unit of biomass invested in foragers (Cerdá and Retana, 1997; Cerdá et al., 2009). It is expressed in $\text{mg cm s}^{-1} \text{mg}^{-1}$ of worker. To examine the variation in relative transport rate between different worker sizes for the two transportation methods used by ants, we ran a GLMM with relative transport rate as the response variable and worker mass, transportation method and their interaction as explanatory variables. Colony was introduced in the model as a random effect.

For all statistical models we started with a full model that contained all explanatory variables and then used a stepwise backward simplification procedure to find the minimum adequate model; the successive models were simplified by dropping the least significant term and then refitting the model and comparing the change in likelihood between the new and old model with a likelihood ratio test. Following the recommendation of Pinheiro and Bates (2000), intermediate models were fitted with the maximum likelihood (ML) method, whereas the final model was fitted with the restricted maximum likelihood (REML) method. To ensure the normality and homoscedasticity of the model residuals, the variables ant mass, travel time, load ratio, item length, transport rate and relative transport rate were \log_{10} transformed when used in the models. The variance explained by the models was assessed by the value of the R^2 for GLM and by the marginal and conditional R^2 for GLMM (Nakagawa and Schielzeth, 2013). The marginal R^2 describes the proportion of variance explained by the fixed factors alone, while the conditional R^2 describes the proportion of variance explained by both the fixed and random factors.

All statistical analyses were performed in R 2.13.1. All means in the Results section are given $\pm 95\%$ confidence intervals (CI).

RESULTS

Morphometrics

Among all relationships between pairs of measures corresponding to the different body parts of the workers, the most striking one is that between head mass and thorax length: head mass increased significantly faster than thorax length for workers of increasing sizes (allometric coefficient = 1.363, 95% CI = 1.305–1.424, $R^2 = 0.974$; Fig. 1A). Moreover, the fact that the points in Fig. 1A are well aligned shows that this relationship is monophasic. The polymorphism of *M. barbarus* workers is thus characterized by a continuous monophasic allometry (Hölldobler and Wilson, 1990) between head mass and thorax length. As a consequence, the center of mass of large ants is significantly shifted forward compared with that of small ants (ANOVA: $F_{1,55} = 76.5$, $P < 0.001$, $R^2 = 0.574$; Fig. 1B).

Characteristics of the ants tested and of the items transported

Fig. S2 shows the distribution of the masses of the ants tested. The mean mass and number of individuals of different size classes was: 3.42 ± 0.19 ($N = 96$), 6.95 ± 0.29 ($N = 79$) and 16.98 ± 1.57 mg ($N = 64$) for small, medium and large ants, respectively. Fig. S3 shows the relationship between the mass and the length of the items for the 12 categories of alimentary pasta offered to the ants. For large and medium-sized workers, the distribution of load ratios of the pieces of pasta that were actually transported by ants, i.e. the ratio of the sum of ant body mass and load mass to ant body mass (Bartholomew et al., 1988), was not different from that of the pieces of pasta that were offered (Fig. S4). For small ants, however, the mean load ratio of the items transported was significantly

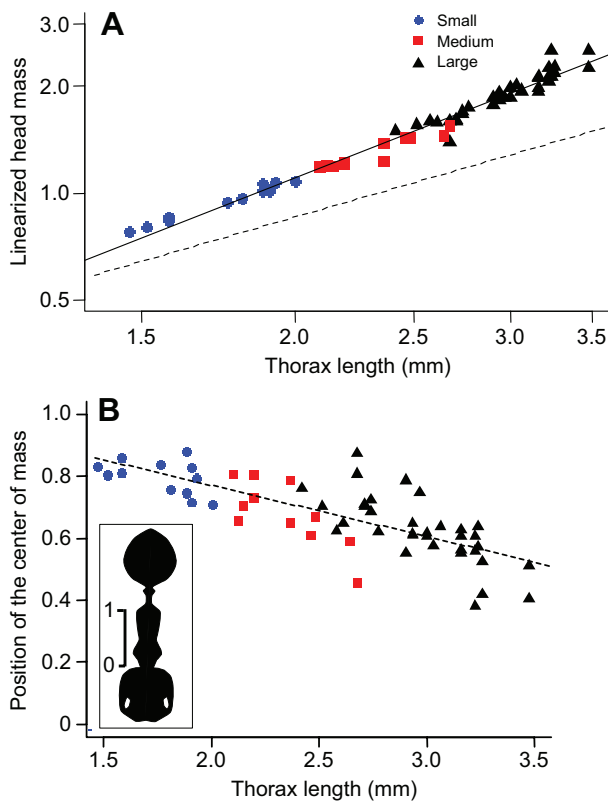


Fig. 1. Morphometrics of *Messor barbarus* workers. (A) Relationship between the head mass of the workers and their thorax length. Head mass was linearized using the cube root of the values. Head mass increased significantly faster than thorax length. Equation of the regression line: $\log(\text{head mass}^{1/3}) = -0.368 + 1.363 \log(\text{thorax length})$. The dashed line has a slope of 1 and would correspond to an isometric growth between head mass and thorax length. $N=57$ ants. (B) Relationship between the position of the center of mass of the ants and their thorax length. The position of the center of mass is expressed in proportion to the ant thorax length (see inset). Equation of the regression line: position of the center of mass $= 1.101 - 0.166 \times \text{thorax length}$. $N=57$ ants.

smaller than that of the items offered (9.47 ± 0.91 versus 5.41 ± 0.78 , for the items offered and those collected, respectively).

Transportation method

Ants used two different methods to transport the pieces of pasta that were offered: carrying or dragging. When carrying an item, ants began by seizing the item in their mandibles, then lifting it from the ground and maintaining it in a more or less upright position while walking (Fig. S1B). In contrast, when dragging an item, ants moved towards the nest entrance walking backwards while at the same time maintaining their load in their mandibles and dragging it on the

ground. The probability of dragging an item depended significantly on its mass (GLMM: $z=6.676$, $P<0.001$, $R^2_{\text{marg}}=0.805$, $R^2_{\text{cond}}=0.816$; Fig. 2A), as well as on its load ratio (GLMM: $z=6.780$, $P<0.001$, $R^2_{\text{marg}}=0.769$, $R^2_{\text{cond}}=0.783$; Fig. 2B). As expected, small ants began to drag at smaller values of item mass compared with large ants (GLMM: $z=-5.604$, $P<0.001$; Fig. 2A). More surprisingly, however, they began to drag at larger values of load ratio (GLMM: $z=2.609$, $P=0.009$; Fig. 2B).

There was a significant relationship between the size of the ants and the mass of the items transported (GLMM: $F_{1,231}=125.807$, $P<0.001$, $R^2_{\text{marg}}=0.581$, $R^2_{\text{cond}}=0.581$; Fig. 3A). This relationship was independent of the transportation method used by ants. However, the mass of dragged items was 3.5 times larger than that of the carried items (GLMM: $F_{1,231}=204.136$, $P<0.001$). Ants of different size classes carried items of significantly different diameters ($\chi^2=39.39$, d.f.=4, $P<0.001$; Fig. 3B): the larger the ants, the higher the percentage of items of the largest diameter that were carried. However, the distributions of items of different diameters that were dragged did not significantly differ between size classes ($\chi^2=4.66$, d.f.=2, $P=0.09$ after pooling the pasta of the two smallest diameters to comply with the conditions of application of the χ^2 ; Fig. 3B).

Travel time

The travel time of laden ants over a distance of 1 m decreased significantly with increasing temperature [GLM: $F_{1,237}=22.23$, $P<0.001$, $\log_{10}(\text{travel time}) = 2.512 - 0.015 \text{ temperature}$, $R^2=0.082$]. Travel time corrected for the effect of temperature depended significantly on the method used to transport an item (GLMM: $F_{1,229}=335.221$, $P<0.001$, $R^2_{\text{marg}}=0.676$, $R^2_{\text{cond}}=0.711$) and increased significantly with increasing values of the load ratio of the item transported (GLMM: $F_{1,229}=171.003$, $P<0.001$) and with decreasing size of the workers (GLMM: $F_{1,229}=9.945$, $P=0.002$; Fig. 4). Moreover, there was a significant interaction between load ratio and transportation method (GLMM: $F_{1,229}=11.090$, $P=0.001$). The lines of equal travel time on Fig. 4 were less distant for ants that carried (Fig. 4A) than for ants that dragged an item (Fig. 4B), showing that the travel time increased much more rapidly with increasing load ratio for carried items than for dragged items.

Transport rate

Transport rate, defined as the product of ant speed by the mass of the load they transport (Rudolph and Loudon, 1986) increased significantly with increasing sizes of the workers (GAMM: d.f.=6.833, $F=8.799$, $P<0.001$) and varied significantly with the load ratio of the items they transported (GAMM: d.f.=4.195, $F=3.936$, $P=0.002$; Fig. 5). The GAMM shows that there was no significant interaction between load ratio and the size of the workers (GAMM: d.f.=2.984, $F=0.139$, $P=0.167$; Fig. 5). Thus, transport rate varies in

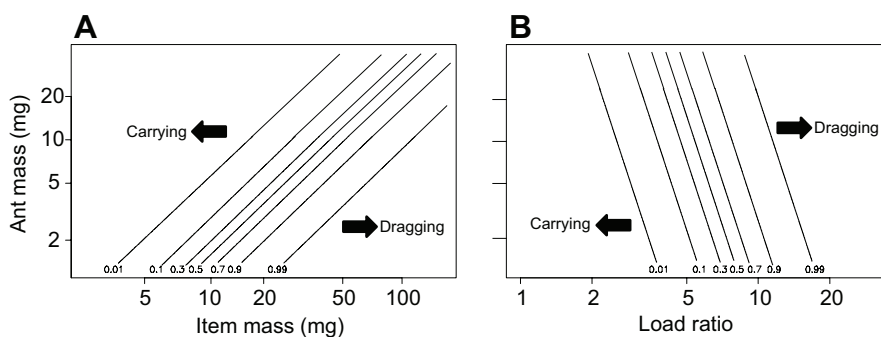


Fig. 2. Transportation method. (A) Probability of dragging an item as a function of the mass of the item transported and of the mass of the ant. $N=181$ ants. The lines of equal probability are given by a binomial generalized linear mixed model. (B) Probability of dragging an item as a function of the load ratio of the item and the mass of the ant. $N=58$ ants.

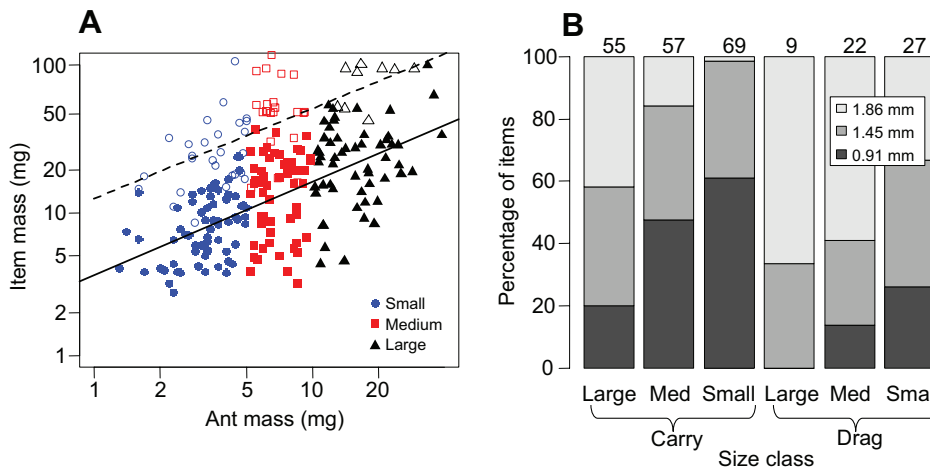


Fig. 3. Relationship between ant size and item characteristics. (A) Relationship between the mass of the items transported and the mass of the workers. The lines give the relationship predicted by a general linear mixed model (GLMM). Equation of the regression lines: $\log(\text{item mass}) = 0.564 + 0.568 \log(\text{ant mass})$ for ants that carry ($N=181$) and $\log(\text{item mass}) = 1.101 + 0.568 \log(\text{ant mass})$ for ants that drag ($N=57$) an item. Filled symbols and solid line correspond to ants that carry an item, open symbols and dashed line correspond to those that drag an item. (B) Distribution of the diameters of the items transported by ants of different size classes. The sample sizes are indicated above each bar. med, medium-sized ants.

the same way for ants of different sizes. The model explains 60.2% of the variance in transport rate. The relationship between ant mass and transport rate was nonlinear: it increased for values of load ratio up to 3.5 [$\log(0.5)$], decreased for values up to 6.31 [$\log(0.8)$], and increased slightly again for ants that dragged an item. Dragging thus allows ants to maintain a high level of transport rate, even when the transported items have a very high load ratio.

Relative transport rate

Relative transport rate, defined as the ratio of transport rate to the mass of the ants (Cerdá et al., 2009), decreased significantly with increasing sizes of the workers (GLMM: $F_{1,231}=16.280$, $P<0.001$, $R^2_{\text{marg}}=0.066$, $R^2_{\text{cond}}=0.155$) but did not vary significantly with the method used by ants to transport an item (GLMM: $F_{1,231}=0.326$, $P=0.568$; Fig. 6).

DISCUSSION

In this study, we investigated the ergonomics of load transport in the Mediterranean seed harvester ant *M. barbarus* when traveling on foraging trails. Depending on the dimension and mass of the item transported, ants used two different methods of transport: carrying or dragging. Workers of different sizes switched from one method to the other for different relative masses represented by the items, which probably reflects different biomechanical constraints resulting from differences in their morphology. Although dragging had a higher impact than carrying on ant locomotory rate, switching from one transportation method to the other allowed ants to maintain a high transport rate. When measured at the individual level, transport rate

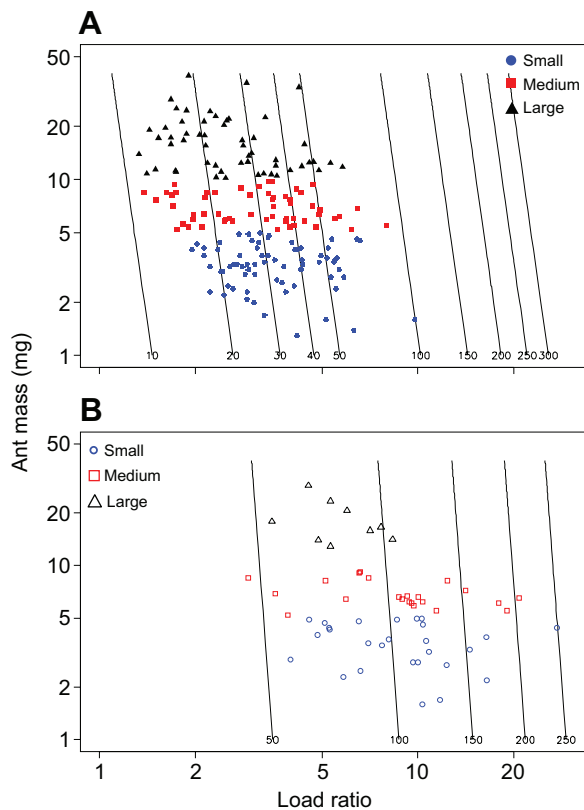


Fig. 4. Travel time. (A) Relationship between the travel time of the ants that dragged an item, their mass, and the load ratio of the item transported. $N=181$ ants. (B) Relationship between the travel time of the ants that carried an item, their mass, and the load ratio of the item transported. $N=58$ ants. The travel time (s) was measured for a distance of 1 m and was corrected for the effect of temperature. The lines of equal travel time are given by a generalized linear mixed model.

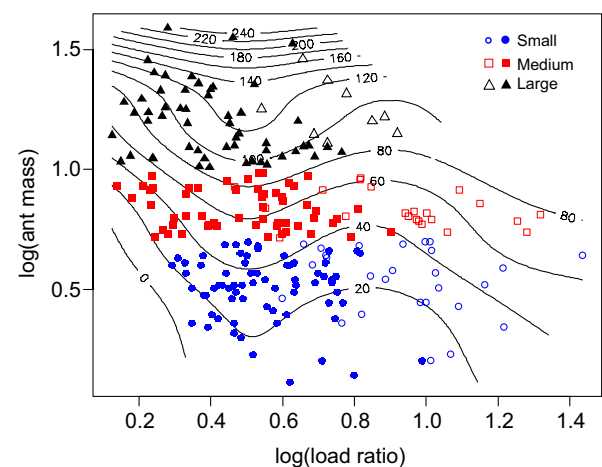


Fig. 5. Relationship between transport rate, ant mass and the load ratio of the item transported. Transport rate (mg cm s^{-1}) is calculated as the product of an ant's speed (corrected for the effect of temperature) by the mass of the item it transports [either by carrying (filled symbols) or by dragging (open symbols)]. The lines show the values of equal transport rate predicted by a generalized additive mixed model. The model explains 60.2% of the variance in transport rate. $N=181$ individuals for ants that carry and $N=58$ individuals for ants that drag.

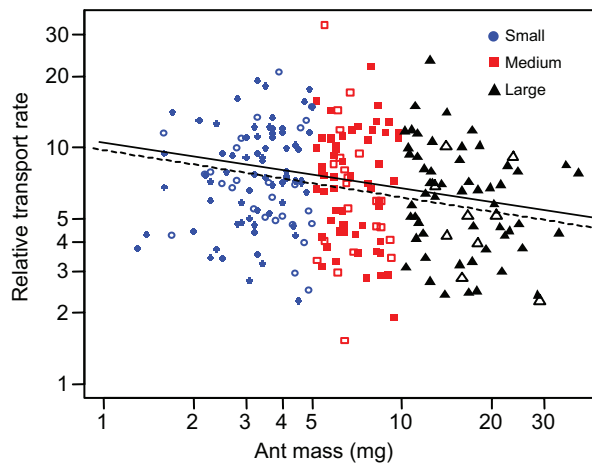


Fig. 6. Relationship between relative transport rate and worker mass. Relative transport rate ($\text{mg cm s}^{-1} \text{mg}^{-1}$ of worker) is defined for a given ant as the ratio of transport rate (corrected for the effect of temperature) to the mass of the ant. Equation of the regression line: $\log(\text{relative transport rate}) = 0.990 - 0.200 \log(\text{ant mass})$. Filled symbols and solid lines: carried items; open symbols and dashed lines: dragged items. The lines give the relationship predicted by a generalized linear mixed model.

was higher for large ants than for small ants. At the colony level, however, when the cost of worker production for the colony is taken into consideration (Shik, 2010), transport rate became significantly higher for small ants, which suggests that colonies would be better off investing in the production of small ants than large ants for the transport of food items.

Except for small workers, the distribution of load ratios of the items collected did not differ significantly from that of the items offered. The maximal mass of the items offered to small ants probably exceeds the maximal mass of the items they are able to transport. *Messor barbarus* workers show low selectivity in their choice of food items (Bernadou et al., 2011). Therefore, small workers may seize items just below the maximal mass of the items they are able to transport, transport them a short distance, and either drop and abandon them on the foraging trails or transfer them to larger ants (Reyes and Fernandez-Haeger, 1999; Arnan et al., 2011).

Our results show that *M. barbarus* workers use two different methods to transport an item: carrying and dragging. The use of these two transportation methods has been described in other ant species (*Pheidole crassinoda*: Sudd, 1960; *Myrmica rubra* and *Formica lugubris*: Sudd, 1965; *Cataglyphis fortis*: Zollikofer, 1994; *Aphaenogaster senilis*: Cerdá et al., 2009). The use of one or the other transportation method is probably not a deliberate choice of the ants but rather is likely to be imposed by biomechanical constraints. On encountering a large food item, ants first attempt to lift it from the ground and carry it in an upright position (Sudd, 1960, 1965; Czaczkes and Ratnieks, 2013). If, in doing so, the position of their center of mass is shifted forward so that it falls outside the polygon formed by the legs in contact with the soil (Moll et al., 2013), they shift to a dragging strategy, unless, as in some ant species (e.g. *Oecophylla smaragdina*: Federle et al., 2001), they are able to avoid falling forward because they are equipped with specialized adhesive organs that allow them to cling to the substrate. The transportation method that ants eventually use depends therefore on the difficulty they experience in maintaining their balance.

The values of item mass and item length at which dragging began to occur increased with increasing sizes of the workers. Moreover,

our results show that large ants began to drag items at smaller values of load ratio compared with small ants. This can be explained by the allometric relationship in *M. barbarus* workers between the size of their head and that of their body (Fig. 1A), i.e. large ants have proportionally larger heads than small ants. The center of mass of large ants is therefore shifted forward compared with that of small ants (Fig. 1B), making them more prone to lose their balance when lifting loads of comparable load ratios.

Independent of the transport method that is used, our results show a significant relationship between the size of the ants and the mass of the item they transport, i.e. *M. barbarus*, like many other ant species transporting food items externally, show size-matching. Moreover, the diameters of the items carried depended directly on ant size: the larger the ants, the higher the percentage of items of the largest diameter they carry. Major ants can probably grip items of large diameters more easily in their mandibles because of (1) their larger mandible gap, which allows them to wrap their mandibles around the pieces of pasta of large diameter, and (2) their powerful mandibular muscles, which allows them to apply stronger pressure and therefore to grip large items more firmly. In comparison, small and medium-sized workers can only pinch the items of large diameters with the tips of their mandibles. These ants may therefore experience some difficulties in maintaining items of large diameters in an upright position. This may be even more difficult for long items. In fact, because ants seize the pieces of pasta close to their lower end, they may be unable to counteract the moment of forces applied by long items on the tips of their mandibles. The item may thus rotate around their mandible tips until its other extremity touches the ground. Ants should then switch to dragging the item. This probably explains why in our experiments small ants dragged rather than carried pasta of large diameter (Fig. S5). The ability to wrap a pasta piece with the mandibles instead of just pinching it probably helps a lot in keeping it in an upright position. In fact, large ants were able to carry pasta items over 12 mm in length regardless of their diameter (see Fig. S1B for an illustration), whereas small and medium-sized ants could do so only for pasta with a diameter of less than 1 mm (Fig. S5).

The travel time of the ants depended significantly on both the method used to transport an item and the load ratio of the item transported. A reduction in speed in foraging ants transporting external loads has been reported in several ant genera (*Eciton*: Bartholomew et al., 1988; *Atta*: Rudolph and Loudon, 1986; Burd, 2000; Röscher and Roces, 2002; Moll et al., 2013; Rhytidoponera: Nielsen, 2001; *Dorymyrmex*: Torres-Contreras and Vasquez, 2004; *Messor*: Bernadou et al., 2011). In ants carrying external food items in their mandibles, the load is located on the anterior part of the body, resulting in a forward shift of the center of mass of the whole system composed of the ant and the load it carries. Consequently, laden workers resort to a range of kinematic adjustments in order to preserve their stability and to avoid falling over (Zollikofer, 1994; Moll et al., 2010, 2013). Zollikofer (1994) observed, for example, that the geometry of the leg tripod supporting the body is somewhat distorted in laden ants compared with unladen ants and that both the mean stride length and mean stride frequency are reduced. The number of legs in contact with the ground can also increase in order to maintain stability (Moll et al., 2013). All these adjustments result in a reduction of the average speed of load-carrying ants. An additional result we found was also that the speed of the ants decreased much more rapidly with increasing load ratio when the item was carried than when it was dragged. This is most likely due to the frictional forces between the item being dragged and the substrate. In load-dragging ants, frictional forces probably largely

outweigh the forces because of the mass of the item transported. Because locomotory rate decreased more slowly for increasing load ratio for ants that dragged compared with ants that carried an item (Fig. 4), the effect of these frictional forces on locomotion should actually be less important than the effect of the forces represented by the mass of the item being carried in the ants' mandibles.

Transport rate, measured as the product of ant speed by load mass, initially increased with increasing load ratio, leveled off for loads representing more than twice the mass of the workers, and decreased thereafter (Fig. 6). This pattern matches that observed in other ant species carrying food items externally (*Atta cephalotes*: Rudolph and Loudon, 1986; Burd, 2001; *Formica schaufussii*: Traniello and Beshers, 1991). Transport rate initially increases for small load ratios because workers are not hindered by the item they transport and can maintain a high locomotory rate. However, as load ratio continues to increase, ants move more slowly to maintain their stability (see above) and, as a consequence, transport rate levels off and begins to decline. In principle, if ants were using only the carrying method, a continuous decline in transport rate would be expected for items with a high load ratio (Burd, 2001), up to a point where ants would either be unable to lift the item from the ground altogether, or would abandon their load after traveling a few centimeters. However, switching from carrying to dragging allows ants to maintain their transport rate at a high level and even to slightly increase it for items with a very high load ratio. Because large seeds have generally higher energetic contents, this would allow ants to increase the rate of energetic return to the colony in natural conditions. Nevertheless, at the individual level, dragging may also have a higher cost than carrying because it reduces dramatically the walking speed of the workers and thus increases the time they can be exposed to predation (Cerdá et al., 2013), pathogens (Bocher et al., 2007) or desiccation (Feener and Lighton, 1991; Lighton et al., 1994).

We found that transport rate was significantly higher in large ants than in small ants but that it varied in the same manner with increasing load ratio for workers of different sizes. This latter result stands in contrast to that of Burd (2001), who showed that in the leaf-cutting ant *Atta cephalotes*, increasing values of load ratio have different effects on leaf transport rate for workers of different size classes. This discrepancy may be explained by the difference in the type of polymorphism between the two species studied: whereas the polymorphism of *M. barbarus* is characterized by a continuous monophasic allometry pattern (present study), that of *A. cephalotes* is characterized by a more complex allometry pattern (Wilson, 1953; Wetterer, 1991). The transport of heavy loads may thus hinder workers' displacement differently because of the different mechanical constraints acting on their bodies.

Although larger ants were more efficient in transporting food items, the relative transport rate, defined as the ratio of transport rate to the mass of the ant, was higher for small ants than for large ants. The question therefore arises as to why *Messor* colonies produce large workers if they are less efficient per unit of biomass for transporting loads. In fact, given that the mass of one large ant represents on average the mass of five small or two medium-sized workers, colonies should receive a greater benefit in terms of the transport of food items by investing in five small or two medium-sized workers rather than in one large worker. There are at least two answers to this question. First, the presence of major workers allows a better match of the size distribution of the food resources and to widen the niche breadth of the colonies (Rissing and Pollock, 1984; Retana and Cerdá, 1994). Second, major ants are probably employed for tasks other than food transport, e.g. patrolling along

foraging trails, removing obstacles off the trails or milling seeds inside the nest. With their overdeveloped mandibular muscles, major workers are also particularly adapted to cut spikelets or plant stems, two energetically demanding activities (Roces and Lighton, 1995). All this may explain their weak participation in foraging columns (Heredia and Detrain, 2005).

We have shown in this study that *M. barbarus* has evolved two methods for transporting food items – carrying and dragging. The use of these two methods allows foraging workers, whatever their size, to maintain at the individual level a high efficiency in the transport of food items over a wide range of sizes. Along with cooperative transport (Reyes and Fernández Haeger, 1999) and the adaptability of foraging trails (Reyes, 1986; Lopez et al., 1994; Doblas-Miranda and Reyes-López, 2008), these two transportation methods contribute to the efficient exploitation by *M. barbarus* of the abundant, yet patchy and ephemeral food resources available in Mediterranean environments. At the colony level, however, our study shows that large workers are less efficient in transporting food items than small and medium-sized workers. Major workers are thus probably better employed for tasks other than carrying food items. Further studies are required to investigate their exact role within *M. barbarus* colonies.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

A.B. and V.F. conceived, designed and conducted field experiments and interpreted their results; V.F., P.M. and A.F. conceived the morphological study of the ants and A.F. performed the morphological measurements and analyses; M.M. developed the R script to determine the position of the center of mass of the ants; V.F. and A.B. did the statistical analyses of the data; V.F. and A.B. wrote the paper and A.F. and P.M. made essential contributions to the text.

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Data availability

Morphometric and transportation datasets are available from the Zenodo repository <http://dx.doi.org/10.5281/zenodo.60347>

Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.141556.supplemental>

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