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SHORT COMMUNICATION

Large ants do not carry their fair share: maximal load-carrying performance of leaf-cutter ants (*Atta cephalotes*)

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ABSTRACT

Although ants are lauded for their strength, little is known about the limits of their load-carrying abilities. We determined the maximal load-carrying capacity of leaf-cutter ants by incrementally adding mass to the leaves they carried. Maximal load-carrying ability scaled isometrically with body size, indicating that larger ants had the capacity to lift the same proportion of their body mass as smaller ants (8.78 times body mass). However, larger ants were captured carrying leaf fragments that represented a lower proportion of their body mass compared with their smaller counterparts. Therefore, when selecting leaves, larger ants retained a higher proportion of their load-carrying capacity in reserve. This suggests that either larger ants require greater power reserves to overcome challenges they encounter along the trail or leaf-cutter ants do not select loads that maximize the overall leaf transport rate of the colony.

KEY WORDS: Leaf-cutter ants, Biomechanics, Force generation, Power reserves, Scaling

INTRODUCTION

Humans have long been fascinated by the strength of ants. The Roman naturalist Pliny the Elder wrote, ‘If anybody compared the loads that ants carry with the size of their bodies, he would confess that no creatures have proportionally greater strength’ (Pliny, 77AD). In much more recent literature, the comic book character Ant-Man has the ability to retain his human strength even when he shrinks to the size of an ant (Lee et al., 1958). In spite of our temporally widespread fascination, little is actually known about the true maximal load-carrying ability of ants, of any species. Many studies have skirted the edges of this question, examining parameters and behaviors such as mandibular strength (Gronenberg et al., 1997), stiffness of the neck (Nguyen et al., 2014), prey-dragging performance (Sudd, 1965) and cooperative transport of large items (Czaczkes and Ratnieks, 2014). Several studies found that ants switched between carrying and dragging prey items that exceeded a certain weight threshold (i.e. *Myrmica rubra*: 2–4.5 times body mass; Sudd, 1965). However, the choice between transportation modes represents a voluntary decision based on energetic efficiency as well as the shape and perceived resistance of the item (Bernadou et al., 2016; Sudd, 1965). Still, ‘how much weight can ants carry?’ remains an open question.

Maximal load-carrying ability is more than just a philosophical metric and it has important implications for foraging ecology. The tradeoff between walking speed and load size has been studied in ants of many species: as load increases, walking speed decreases (Burd, 2000; Zollikofer, 1994). Additionally, when ants walk up inclines, their energy expenditure increases (Holt and Askew, 2012). These patterns reflect the physical relationship:

$$\text{Power} = \text{force} \cdot \text{velocity}, \tag{1}$$

which demonstrates how the power required to move an object is influenced by the competing needs for force production and velocity. When the load is moved upwards, additional force is required to displace the object against gravity. In other words, the power an ant can generate can be applied to carry heavier loads (force), increase vertical displacement (also force), increase walking speed (velocity), or a combination of the three. But power output is finite, and if an ant selects a load that is too heavy, then it may not be able to walk at its preferred speed or have enough power to overcome challenges, such as inclines (Holt and Askew, 2012; Lewis et al., 2008), obstructions (Bruce et al., 2017), rain (Farji-Brener et al., 2018) or wind (Alma et al., 2016). Instead, if an ant selects a submaximal load, it maintains power reserves that can be tapped into, if needed. Measuring maximum power output is not straightforward because of issues of motivation. However, under conditions of near-maximal loading, most of an ant’s power is invested in generating force, and velocity is minimized as a result (Eqn 1). Therefore, testing maximal load-carrying ability minimizes velocity and is a simpler proxy for estimating maximum power-generating capabilities. Meanwhile, measuring self-selected loads lends insight into how much power the ant chooses to maintain in reserve.

There are probably few species of ants that are more strongly impacted by the tradeoffs between load size, travel velocity and power reserves than leaf-cutters. Denizens of neotropical forests, leaf-cutter ants make their living by sending out streams of workers to foraging sites where they cut leaves into fragments and transport them back to large colonies, to feed their fungal gardens (Cherrett, 1968). The workers travel in their thousands along well-maintained trails, sometimes over 500 m long (Urbas et al., 2007). Collectively, they harvest a staggering amount of leaf matter (up to 14% of the forest; Urbas et al., 2007), performing valuable ecosystem services that include transporting nutrients and creating disruptions in the canopy (Corrêa et al., 2010). Obtaining enough leaf matter to sustain a colony requires a high rate of leaf-matter transport. However, based on the tradeoffs between walking speed and leaf fragment size alone, leaf-cutter ants do not carry loads that maximize the overall transport rate of the colony (Rudolph and Loudon, 1986). It is possible that individual leaf-cutter ants select smaller loads in order to maintain power reserves that can be used to overcome obstacles along the trail, but this remains to be tested. Leaf-cutter ant workers are highly polymorphic and the larger ants

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tend to cut and carry larger fragments (Burd, 2000). However, the ants do not always carry the fragments they cut, and there are many opportunities for leaf fragment exchange along the trail (Hubbell et al., 1980). Unlike most other ant species, leaf-cutters carry their loads above their heads and rarely resort to dragging their loads (Sudd, 1965). These qualities make leaf-cutter ants the ideal study system for investigating maximal load-carrying performance and its effects on individual foraging efficiency, and so we asked the following questions: (1) what is the maximal load-carrying capacity of leaf-cutter ants, and how does it scale with body size?; and (2) when selecting leaves to transport back to the colony, how much of their maximal load-carrying capacity do leaf-cutter ants keep in reserve?

MATERIALS AND METHODS

Between June and August of 2018 we measured the maximal load-carrying capacity of 90 leaf-cutter ants, *Atta cephalotes* (Linnaeus 1758), from nine colonies at the La Selva Biological Station in Costa Rica. Trials were conducted at ambient temperatures between 17.5 and 25°C. We haphazardly selected ants that were carrying leaf fragments back to their colony and placed them on a white piece of paper near the foraging trail. Once on the paper, the ants began searching for the trail but did not appear otherwise affected by their new environment. We then incrementally increased the weight of the leaf fragments by adding color-coded stickers created from strips of athletic tape weighing approximately 5, 10 or 20 mg. After each sticker was added, the ant was given multiple opportunities to readjust the position of the weighted leaf fragment. If the ant successfully lifted the weighted leaf fragment off the ground and was able to walk (complete a full cycle of the tripod gait), we added additional stickers. If the ant failed to lift the leaf fragment overhead, we ended the trial and collected the ant, the leaf fragment and the stickers. Over the course of the trial, we decreased the size of the additional stickers used, in an attempt to keep the failure-causing mass as small as possible (~5 mg for ants weighing <5 mg; <1 times body mass for larger ants). Trials where the ants dropped their weighted leaf fragments without attempting to lift them occurred frequently and were not included in the final dataset. Immediately after a round of trials, we returned to the lab to weigh the ant, the leaf fragment and the mass of the stickers added before failure. Data analysis was performed using the Python programming language and the Scipy toolkit.

A subset of 15 trials were filmed using a single dorsal camera (Xiaomi Yi Lite, 120 frames s^{-1}). We digitized the steps of the single ant for which all of the legs were clearly visible over the course of four footfall cycles. Using Matlab and DLTdv5 (Hedrick, 2008), we measured the position of the tarsi as they made contact with the ground, while the ant walked unladen or carrying a maximal load.

RESULTS AND DISCUSSION

We measured the maximal load-carrying performance of 90 leaf-cutter ants ranging in size from 1.2 to 36.8 mg (mean±s.d. 9.3±5.8 mg; Table S1). Although there were larger ants on the trail, they rarely carried leaf fragments and were quick to abandon their loads when disturbed. As they approached their maximal load-carrying ability, the ants' walking patterns changed: the alternating tripod gait was distorted (as per Zollikofer, 1994), the walking pace slowed (as per Burd, 2000), and the steps became more staggered and irregular (an example is shown in Fig. 1). A heavily laden ant would often have to stop mid-stride to rest its tarsus in an intermediate position before resuming the swing phase to complete the tripod position (Fig. 1, dotted lines).

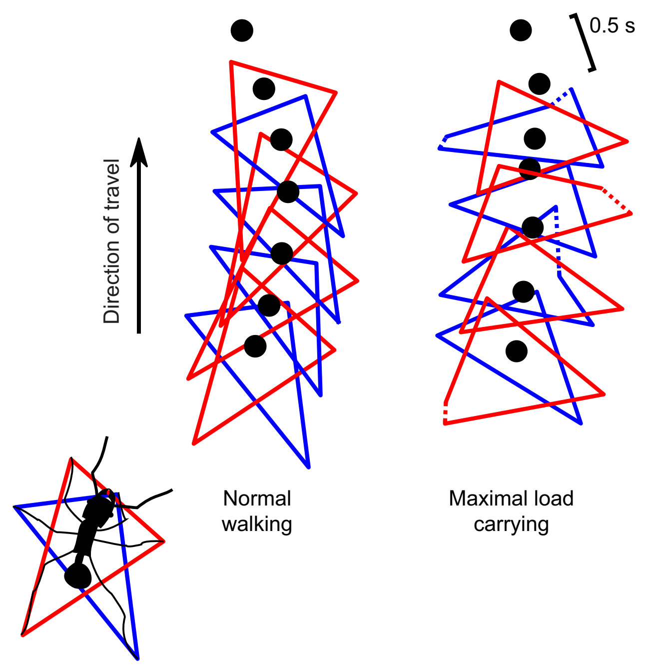

Fig. 1. A leaf-cutter ant distorts its normal walking gait to carry a heavy load. Inset: the red triangles represent the position of the left fore-leg, the right mid-leg and the left hind-leg as they made contact with the ground while the other legs swung forward; the blue triangles represent the right fore-leg, the left mid-leg and the right hind-leg during their stance phase. The black circles represent the position of the thorax, digitized every 0.5 s. Left: walking normally, the ant used an alternating tripod gait. Right: while carrying a maximal load, the ant used a similar gait, but the legs were more spread out, the tripods were not spaced regularly, the movement of the thorax was less consistent, and the ant often paused to rest its legs on the ground halfway through the swing phase (dotted lines).

Maximal load-carrying ability scaled isometrically with body mass, with the slope of the log–log regression equal to 1.04 (R^2=0.83; not significantly different from 1.00, P=0.45; Fig. 2A). Leaf-cutter ants were able to carry a maximum of 8.78±0.26 times (mean±s.e.m.) their body mass, and the results of the scaling analysis suggests that this remains constant as body mass increases. This number is close to the theoretically predicted maximum load-carrying ability of *A. cephalotes* (6.9 times body mass, but see caveats; Burd, 2000). In contrast, when we captured the ants, they were carrying leaf fragments that exhibited negative allometry with respect to body mass, with the slope of the log–log regression equal to 0.61. However, there was a lot of variation in fragment size (R^2=0.32). This slope suggests that larger ants carried leaf fragments that were a lower proportion of their body mass compared with their smaller counterparts. The reserve lifting capacity, the difference between the weight of the leaf fragment and the maximal load-carrying capacity, demonstrated positive allometry with respect to body mass (Fig. 2B), with a slope of 1.27 (R^2=0.76).

Although ants are lauded for their ability to lift heavy weights, the maximal load-carrying capacity of ants has never been studied. This knowledge gap is particularly surprising given that widely varying estimates of maximal lifting performance abound in the popular press. Many factors contribute to the ability of an ant to carry heavy objects: mandibular strength is required for grip (Gronenberg et al., 1997), neck muscles are used for lifting (Moll et al., 2010; Nguyen et al., 2014), and the legs must be able to support the additional weight through the step cycle (Zollikofer, 1994). When our leaf-cutter ants were presented with a load that was too heavy to carry,

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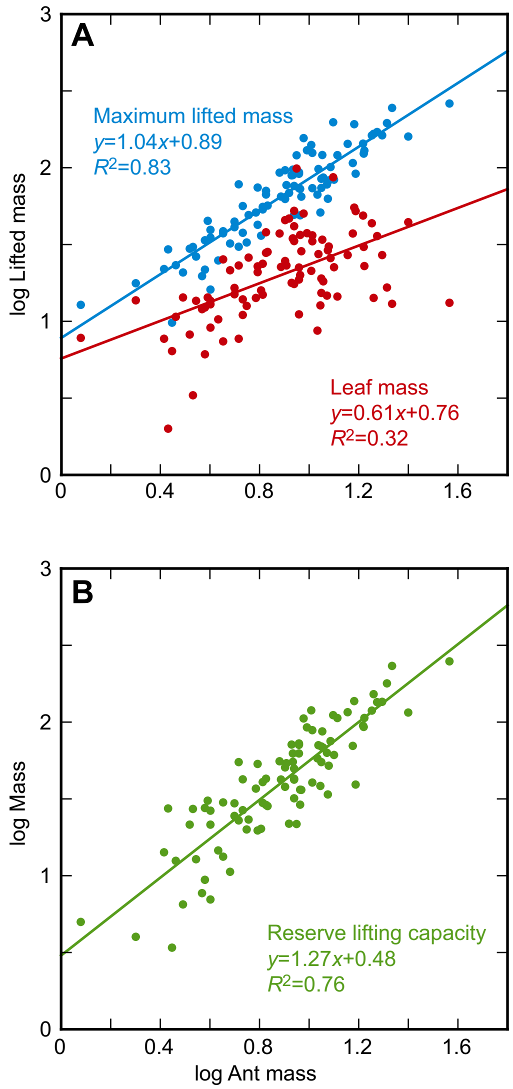

Fig. 2. Load-carrying performance of leaf-cutter ants. (A) Maximal load-carrying ability of leaf-cutter ants scales isometrically with body mass (mg; blue), suggesting that larger individuals have the capacity to lift the same proportion of their weight as their smaller counterparts (8.78 times body mass). However, larger ants were found carrying leaf fragments that represented a lower proportion of their body mass (red). (B) This means that larger leaf-cutter ants maintained a higher proportion of their load-carrying capacity in reserve when selecting leaves to carry back to their colony (green).

some individuals continued to carry the fragment even though it was dragging on the ground, while others repeatedly tried and failed to lift the fragment overhead. A few ants were able to lift the weighted fragment but then began shaking violently. Once they abandoned the object and rested for some time, they were able to begin walking normally. Ten individuals repeatedly tried to carry the weighted fragment before setting it down and cutting it into smaller segments. We did not include ants that abandoned their leaf fragments without attempting to carry them. In spite of these differing mechanisms of failure, there was a strong isometric relationship between body size and maximum load carried (Fig. 2A; R^2=0.83), which suggests that our assay measured near-maximal levels of performance. This result suggests that maximum load-carrying capacity is directly related to muscle power output and thus scales with muscle volume. Leaf-cutter ants were able to lift an average of 8.78 times their body mass, irrespective of their size. This number is close to the predicted maximum load-lifting capacity of *A. cephalotes* (Burd, 2000), but smaller than many of the widely proposed estimates of maximum lifting performance across the family.

Leaf-cutter ants are known for their ability to carry heavy loads over long distances, and the relationship between load size and walking speed has been well documented (Burd, 2000; Rudolph and Loudon, 1986). As leaf fragments become heavier, walking pace slows (Burd, 2000) and as the loads near maximum capacity, the ants can only stagger through a few steps (Fig. 1). This suggests that carrying very heavy loads is not a sound strategy for foraging. However, maximal load-carrying capacity has other important implications for foraging ecology. We found that larger ants carried leaf fragments that represented a smaller proportion of their body mass, compared with smaller ants (scaling coefficient=0.61). Yet, larger ants had the capacity to lift the same proportion of their body weight as smaller ants (scaling coefficient=1.04). This means that larger leaf-cutter ants maintained a higher proportion of their load-carrying capacity in reserve, when selecting leaves to carry back to their colony (scaling coefficient=1.27). Reserve lifting capacity is a reflection of the excess mechanical power that an ant has available after it has selected a load to carry (Eqn 1): power that is not used for lifting can be applied to increase walking speed or to overcome obstacles along the trail (Holt and Askew, 2012; Lewis et al., 2008). The fact that smaller ants maintain lower power reserves when selecting leaf fragments to take to the colony means that they may have more difficulty negotiating physical obstacles in the terrain (Bruce et al., 2017), overcoming mass added by raindrops (Farji-Brener et al., 2018), dealing with gusts of wind (Alma et al., 2016) and maintaining an efficient velocity (Holt and Askew, 2012). Meanwhile, larger ants that have higher power reserves choose smaller leaf fragments than their ability suggests they should be able to carry efficiently and effectively.

There are a few plausible explanations for why leaf-cutter ants of different sizes maintain differential power reserves. One possibility is that larger ants consciously maintain higher power reserves to overcome the effect that scaling has on different types of challenges. Burd (2001) demonstrated that the relationship between load and velocity changes for different sized ants, likely as a result of allometric morphology. Whether challenges such as terrain obstacles, inclines, rain drops or gusts of wind disproportionately affect larger ants enough that they require higher power reserves to overcome remains to be tested. A second possibility is that the mechanism by which ants select leaf fragments does not maximize individual performance. Although larger ants generally carry larger leaf fragments, there is a lot of variation in the loads that ants carry (Burd, 2000; Rudolph and Loudon, 1986; Fig. 2A). Furthermore, ants will often trade leaves multiple times between the foraging site and the colony, suggesting that there is an element of stochasticity to load selection (Hubbell et al., 1980). If there is no physical mechanism or decision-making process behind the selection of leaf fragments, then haphazard events may result in non-optimal load carriage. This would have important implications for leaf-cutter ant ecology, suggesting that colonies may be taking a brute-force approach to foraging. At the individual level, ants may be carrying loads that are too big or too small for their body size, respectively hampering their ability to walk at a preferred speed and overcome obstacles, or diminishing the amount of leaf matter that they bring to the colony. If this is true, then the colony may be overcoming these individual inefficiencies solely with the sheer number of its workers. In this study, we demonstrate that different sized leaf-cutter ants carry loads that reflect differing proportions of their overall load-carrying capabilities. However,

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understanding the underlying reasons behind this pattern will require further investigation.

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Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: P.S.S.; Methodology: P.S.S., E.D.T.; Formal analysis: P.S.S., E.D.T.; Investigation: E.D.T.; Data curation: P.S.S., E.D.T.; Writing - original draft: P.S.S.; Writing - review & editing: E.D.T.; Supervision: P.S.S.

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