

The ‘truck-driver’ effect in leaf-cutting ants: how individual load influences the walking speed of nest-mates

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Abstract. The foraging behaviour of social insects is highly flexible because it depends on the interplay between individual and collective decisions. In ants that use foraging trails, high ant flow may entail traffic problems if different workers vary widely in their walking speed. Slow ants carrying extra-large loads in the leaf-cutting ant *Atta cephalotes* L. (Hymenoptera: Formicidae) are characterized as ‘highly-laden’ ants, and their effect on delaying other laden ants is analyzed. Highly-laden ants carry loads that are 100% larger and show a 50% greater load-carrying capacity (i.e. load size/body size) than ‘ordinary-laden’ ants. Field manipulations reveal that these slow ants carrying extra-large loads can reduce the walking speed of the laden ants behind them by up to 50%. Moreover, the percentage of highly-laden ants decreases at high ant flow. Because the delaying effect of highly-laden ants on nest-mates is enhanced at high traffic levels, these results suggest that load size might be adjusted to reduce the negative effect on the rate of foraging input to the colony. Several causes have been proposed to explain why leaf-cutting ants cut and carry leaf fragments of sizes below their individual capacities. The avoidance of delay in laden nest-mates is suggested as another novel factor related to traffic flow that also might affect load size selection. The results of the present study illustrate how leaf-cutting ants are able to reduce their individual carrying performance to maximize the overall colony performance.

Key words. Ant behaviour, ant traffic, *Atta cephalotes*, Costa Rica, foraging trails, traffic speed.

Introduction

Foraging behaviours are expected to be under selection to optimize the net profit of individuals (Stephens & Krebs, 1986). However, in social insects, behaviours that enhance the performance of individuals do not necessarily maximize the performance of the colony as a whole (Burd &

Howard, 2008). For example, worker honey bees can transport food below their individual carrying performance, returning earlier to the nest for further recruitment, which could result in higher overall gains for the colony (Nuñez, 1982). Collective nest building by social wasps is more successful when workers carry material for nest construction below their load capacity because the handling of material at the nest is more efficient and wasps can make more foraging trips per unit of time (Jeanne, 1999). As these examples illustrate, foraging by workers of social insects is a complex process in which individual and social aspects interact to determine food intake for the colony and, ultimately, colony fitness (Roces & Hölldobler,

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1994). Therefore, to understand the overall foraging success in social insects, it is necessary to analyze both the performance of individuals as well as the performance of nest-mates (Roces & Nuñez, 1993).

Leaf-cutting ants (*Atta* and *Acromyrmex*) (Hymenoptera: Formicidae) are good model organisms for studying this interplay between individual and social aspects of foraging because workers can, through their behaviour, determine the leaf fragment size to be cut and carried to the colony (Roces & Hölldobler, 1994). Leaf-cutting ants maintain trunk trails free of debris to direct foragers through the forest litter to their host plants as well as to facilitate the transport of leaf fragments to their subterranean nest, where the tissue is used to cultivate fungal gardens to feed the colony's larvae (Weber, 1972; Howard, 2001). There are several studies investigating the individual criteria used by workers to determine the size of leaf fragments that they cut and carry (Roces & Nuñez, 1993; Van Breda & Stradling, 1994; Burd, 2000a, b; Dussutour *et al.*, 2009a; Roces & Bollazzi, 2009). Earlier studies suggest that polymorphic foragers often harvest leaf pieces that correspond in size to their body dimensions (Cherrett, 1972; Rudolph & Loudon, 1986; Wetterer, 1990; Burd, 1995). This could result, to some extent, from the method of leaf cutting: workers anchor themselves on the leaf edges by their hind legs and pivot around their body when cutting. The load size would consequently be determined by a fixed reach that depends on the body size of the leaf-cutting ant (Weber, 1972). However, further studies report an absence of size-matching, suggesting that workers may vary the size of the fragments that they cut and transport to improve the colony performance rather than their own load-carrying capacity (Burd & Howard, 2005a, b; Dussutour *et al.*, 2009a, b).

There are many reasons why transporting leaf fragments below an individual's load-carrying capacity might improve the colony performance. A reduced leaf fragment can: (i) increase the speed of workers, generating an earlier return to the colony for further recruitment (Roces & Nuñez, 1993; Roces & Hölldobler, 1994); (ii) avoid bottlenecks at the nest entrances (Van Breda & Stradling, 1994); (iii) facilitate the underground processing and distribution of leaf fragments among garden chambers (Burd & Howard, 2005a, b, 2008); (iv) reduce interference among workers at the cutting sites on the leaf margin (Burd, 1996); and (v) improve the carrying of leaf fragments in foraging trails that have physical obstacles (Dussutour *et al.*, 2009b). Thus, current evidence indicates that the foraging of leaf-cutting ants is not merely based on rate or efficiency maximization at the individual level (Roces & Nuñez, 1993).

The transport of leaf fragments below the individual load capacity has another potential explanation that is based on colony effects. Ants carrying larger loads not only reduce their own locomotion speed, but also they might decrease the walking speed of the laden ants behind them, affecting the rate at which laden ants deliver food into the colony. Leaf-cutting ants of the genus *Atta* on foraging trails present an attractive analogy to vehicles on highways. Resembling a mixture of different vehicle models from the same car company but with a range of size and speeds, *Atta* foragers are highly polymorphic and

vary widely in the locomotion speeds that they attain (Burd, 2000b). Furthermore, walking speed is related to the size of carrying load. Some laden ants carry extra-large leaf fragments and thus walk slower than the majority of laden workers. These ants (hereafter termed 'highly-laden' ants) might partially block traffic flow by forcing portions of traffic streams to adopt their slow speed (Burd *et al.*, 2002), such as trucks might delay the cars behind them on a highway. However, as far as we are aware, the effect of these highly-laden, slow ants on the speed of other laden workers (metaphorically speaking, the 'truck-driver' effect) has not been experimentally tested and quantified. Moreover, this effect might be particularly relevant at high ant traffic flows. If a large number of laden ants are forced to adopt the slow speed of highly-laden ants, the rate at which substrate is delivered to the nest could be highly reduced.

In the present study, the effect of highly-laden ants on the speed of other laden ants in field nests of the leaf-cutting ant *Atta cephalotes* L. (Hymenoptera: Formicidae) is examined. First, highly-laden ants carrying extra-large leaf fragments that demonstrate an evident slow speed and 'ordinary' laden ants are sampled to characterize their loads, body sizes and load capacity. Second, the load carried by workers in foraging trails is manipulated to determine whether highly-laden ants delay the walking speed of nest-mates. Finally, the relationship between the proportion of highly-laden ants and ant flow is determined.

Materials and methods

This study was conducted at La Selva Biological Station of the Organization for Tropical Studies (10°26'N, 83°59'W) in the Atlantic slope of Costa Rica, between January and February 2010. The area is a lowland wet forest that receives a mean annual rainfall of 4000 mm. A full site description is provided in McDade *et al.* (1994). Colonies of leaf-cutting ants *A. cephalotes* are common in La Selva (Farji-Brener, 2001). A total of 14 *A. cephalotes* nests located in primary and secondary forests were used for the present study. All colonies were large and well established, with diameters of the nest ground surface in the range 7–10 m, and showed diurnal foraging on several dicotyledonous plants that were not identified. Ant flow on the studied foraging trails in the sampling period varied in the range 0.2–1.5 ants/100 cm² s⁻¹.

To characterize ants based on their loads, 60 laden ants and their loads were collected (30 were considered highly-laden and remaining 30 were considered ordinary-laden ants) from ten foraging trails of four *A. cephalotes* colonies. Highly-laden ants were characterized as workers carrying extra-large loads, with a very slow speed and limited walking stability. The way to identify highly-laden ants was previously discussed and field-tested among seven sampling persons aiming to standardize the selection criteria. Control ants were randomly selected ordinary-laden ants. Both highly-laden and ordinary-laden (control) ants were sampled simultaneously on foraging trails. Both types of laden ants were intercepted a few metres from the nest entrances and lifted from the trail with a forceps.

All ants and their loads were individually bagged and both load size and dorsal ant size were measured (in mm²) in the laboratory using an area meter (LI-COR[®] model 3100C; Li-Cor Biosciences, Lincoln, Nebraska). Ant size, load size and the relative load-carrying capacity of the ant (i.e. load size/body size) were compared between highly-laden and control ants using Student's *t*-tests ($\alpha = 0.05$).

To determine the effect of highly-laden ants on the walking speed of laden nest-mates, two experiments were performed on foraging trails: (i) removal of highly-laden ants and (ii) 'creation' of highly-laden ants (Fig. 1). The sections of the trail chosen in all the experiments had smooth soil bases and were free of major obstacles. First, both the speeds of a laden ant walking behind (i.e. at 1–3 cm) and a highly-laden ant ('treated' ant) were determined, as well as the speed of a nearby laden ant as a control (i.e. a laden ant without a laden ant ahead). Walking speed was measured as the time spent walking along a 20-cm length of a trunk trail. Both ants were similar in size and carried leaf fragments of similar dimensions without minute workers on the leaves (i.e. without 'hitchhikers'). Highly-laden ants were identified according to the characteristics described above rather than by looking at their potential effects on other ants. A few seconds later, the highly-laden ant was lifted and removed from the trail using forceps by picking up the leaf fragment that she was carrying, with minimal disruption to the rest of the traffic flow. To control for the potential effect of the manipulation itself, the same hand-movement was made 10 cm in front of the control laden ant. After a few seconds (approximately 5 s), the walking speeds of the 'treated' ant and the control ant were measured again. This experiment was replicated 70 times in different sections

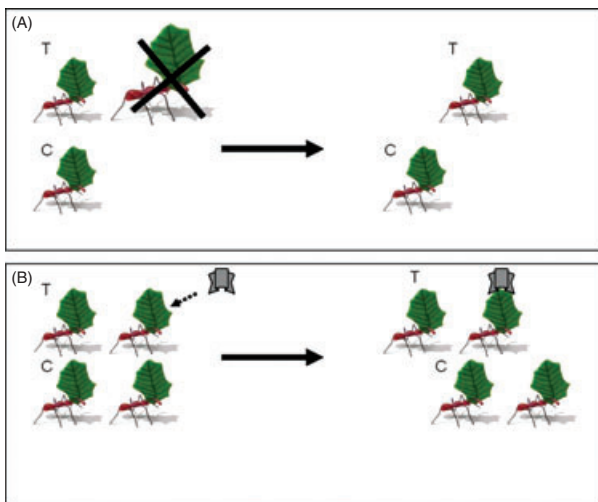


Fig. 1. Schematic representation of field manipulations to demonstrate whether *Atta cephalotes* ants carrying extra-large loads (highly-laden ants) slow down laden nest-mates. (A) Walking speeds were measured in treated (T) and control (C) laden ants before and after the removal of a highly-laden ant. (B) Walking speeds were measured in treated (T) and control (C) laden ants before and after an ordinary-laden ant was transformed into a highly-laden ant by adding a piece of aluminium foil on its load.

of 18 foraging trails from six nests. Data were analyzed with a repeated-measure analysis of variance (ANOVA: $\alpha = 0.05$). The ant position relative to the highly-laden ant (i.e. behind or not) was considered as a fixed factor. Sequence (before and after the removal of the highly-laden ant) was the repeated measure. The response variable was examined for normality and heterogeneity of variance and log-transformed when necessary. If highly-laden ants retard the walking speed of the laden ants behind them, only the 'treated' ant (i.e. the ant behind the highly-laden ant) should increase its velocity after the highly-laden ant removal. In ANOVA terms, a significant interaction between sequence and treatment was expected.

In the second manipulation, artificially highly-laden ants were made by adding a piece of aluminium foil (1 cm²) to their load on a randomly selected laden ant. This technique has been successfully used to retard the walking speed of laden leaf-cutting ants (Burd, 2000b). The walking speeds of two randomly selected laden ants were measured as described above. Both ants were similar in size, carried leaf fragments of similar dimensions without minute workers on the leaves (i.e. without 'hitchhikers') and had laden ants ahead at comparable distances (approximately 5 cm). One of these two ants was randomly selected as the 'treated' ant and the load weight mass of the laden ant ahead was altered by attaching a piece of aluminium foil (approximately 10 mg) to its leaf fragment (Fig. 1). In this manner, an ordinary-laden ant was transformed into a highly-laden ant. After allowing the ant to adjust to the new load for a few seconds (approximately 10 s), the walking speeds of the 'treated' ant (i.e. the ant behind the transformed highly-laden ant) and the control ant were measured. This experiment was replicated 50 times but, because of the intrinsic difficulty of this manipulation, only 12 of the experiments were successful. These 12 trials were performed in different sections of six foraging trails from three nests. Data were analyzed with a repeated-measure ANOVA: position (behind or not to the laden ant transformed into a highly-laden ant) was considered as a fixed factor and sequence (before and after the addition of weight) as the repeated measure. The response variable was examined for normality and heterogeneity of variance and log-transformed when necessary. If highly-laden ants retard the walking speed of the laden ants behind them, only the 'treated' ants should decrease their walking speed after the addition of an extra weight to the ant ahead. In ANOVA terms, a significant interaction between sequence and treatment was expected. The response variable was walking speed (cm s⁻¹) in all cases. Therefore, the experiments involved a double-control because the speeds of both 'control' and 'treated' ants were measured before and after the manipulation.

To analyze the relationship between the number of highly-laden ants and the ant flow, the number of laden ants and highly-laden ants was measured in 57 sampling periods of 20 s in 15-cm sections at different foraging trails from nine nests ($n = 57$). Sampling was performed at different times of the day to allow the greatest possible variance in traffic flow. All the ants measured were foragers (i.e. not involved in trail clearing). Highly-laden ants were identified according to the characteristics described above. Traffic flow was estimated in each case

as the number of ants/100 cm² s⁻¹. The relationship between the percentage of highly-laden ants and ant flow was analyzed with exponential regression. All analyses were performed using STATISTICA software (StatSoft Inc., Tulsa, Oklahoma).

Results

Ants characterized as highly-laden were bigger and carried larger loads than ordinary-laden ants. Furthermore, they showed higher load-carrying capacity (i.e. carried larger loads per unit of body size). The mean \pm SD size of the carried leaf fragment by highly-laden ants was 0.68 ± 0.13 cm² versus 0.43 ± 0.34 cm² for the control (ordinary-laden) ants ($t_{1,28} = 6.8$, $P < 0.001$). The mean \pm SD body size of highly-laden ants was 0.07 ± 0.03 cm² versus 0.05 ± 0.02 cm² for the control ants ($t_{1,28} = 2.4$, $P = 0.02$). The mean \pm SD load-carrying capacity (i.e. load size/body size) was 22.7 ± 6 for highly-laden ants versus 14.6 ± 2 for control ants ($t_{1,28} = 3.3$, $P < 0.01$; Fig. 2).

The field experiments revealed that highly-laden ants affected the walking speed of the laden workers behind them (Fig. 3). In the first experiment, only ants behind a highly-laden ant increased their walking speed after highly-laden ants were removed from the trail (sequence \times treatment: $F_{1,138} = 8.6$,

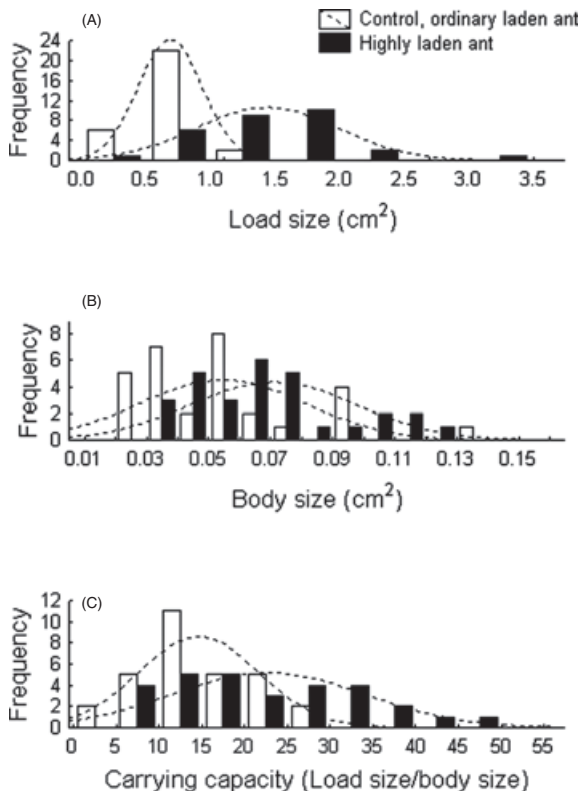


Fig. 2. Frequency distribution of control (ordinary-laden) (white bars, $n = 30$) and highly-laden (black bars, $n = 30$). (A) *Atta cephalotes* ants in terms of load size, (B) body size and (C) load-carrying capacity (load size/body size). Dashed lines represent normal curves.

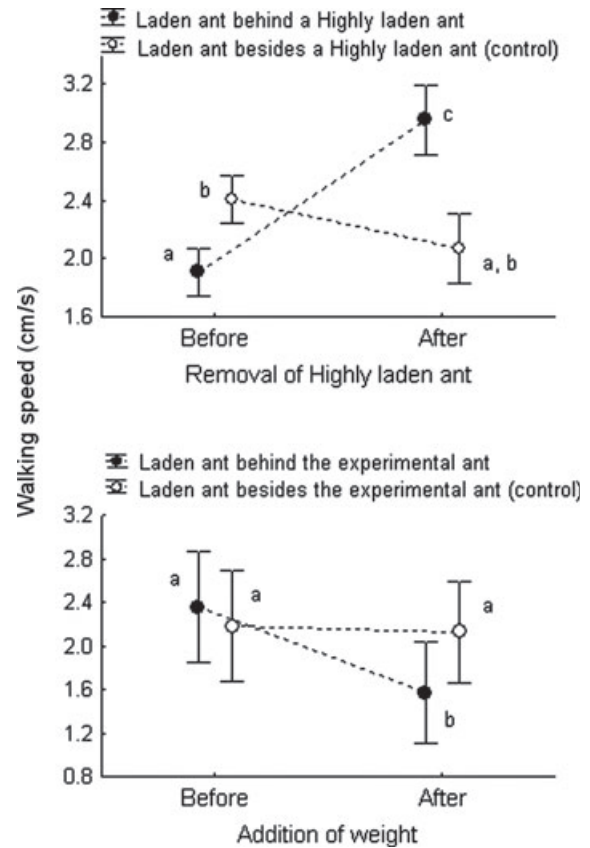


Fig. 3. Walking speed in treated and control laden *Atta cephalotes* ants. Different letters denotes statistically significant differences ($P < 0.05$, analysis of variance, Tukey's post-hoc comparisons). Vertical bars denote 0.95 confidence intervals. Dashed lines are shown to better visualize the existence of a statistically significant interaction.

$P < 0.001$). Although control ants showed a small, nonsignificant increase in their mean walking speed after highly-laden ants were removed (i.e. increased from 2.1 to 2.4 cm s⁻¹), ants directly behind highly-laden ants significantly increased their mean velocity from 1.9 to 2.9 cm s⁻¹ when highly-laden ants were removed (Fig. 3). Accordingly, when a laden ant was transformed into a highly-laden ant by adding a piece of aluminium foil on its load, only the laden ant behind significantly decreased its mean walking speed (from 2.4 to 1.6 cm s⁻¹) compared with an adjacent, control laden ant (2.3 to 2.3 cm s⁻¹) (sequence \times treatment $F_{1,22} = 4.4$, $P = 0.04$; Fig. 3). This decreased walking speed (1.6 cm s⁻¹) was similar to the mean velocity of laden ants found walking behind a highly-laden ant in the first experiment (1.9 cm s⁻¹; see above).

The proportion of highly-laden ants at foraging trails partially depended on ant flow. The percentage of workers carrying extra-large leaf fragments on foraging trails sharply decreased with a traffic flow greater than 0.3 ants/100 cm² s⁻¹. Highly-laden ants were very frequent at very low traffic flow, intermediate (40%) at traffic flow in the range 0.2–0.4 ants/100 cm² s⁻¹ and comprised approximately

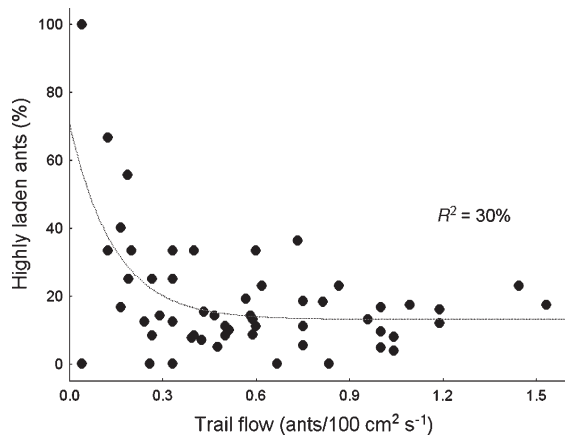


Fig. 4. Percentage of highly-laden *Atta cephalotes* ants according to the ant flow at foraging trails. Logistic regression: $P < 0.006$, $R^2 = 0.30$; $n = 57$ sampling periods of 20 s.

10% of the foragers force at high traffic flow ($R^2 = 0.30$, $P = 0.006$, exponential regression; Fig. 4).

Discussion

Similar to one-way human highways, high-flow foraging trails entail traffic problems if different moving units vary widely in their locomotion speed (Burd, 2000b; Burd *et al.*, 2002). In the present study, slow-moving, extra-large load carriers are characterized as highly-laden ants, and the experiments demonstrate that their presence in foraging trails decreases the walking speed of other laden nest-mates. Furthermore, a negative relationship is found between the proportion of highly-laden ants and ordinary-laden ant flow in foraging trails, suggesting that the individual behaviour of carrying extra-large loads may be adjusted to reduce its negative effect at the colony level.

Ants characterized *a priori* as highly-laden differ significantly in the size of their loads and their body dimensions compared with the randomly selected, ordinary-laden ants. Highly-laden ants are 25% bigger and carry loads that are 100% larger than the majority of loads carried by other laden workers. Data from other studies support our characterization of highly-laden ants. Although the mean sizes of leaf pieces carried by ordinary-laden (control) ants in the present study are approximately the same as those carried by *Atta* workers in other studies (0.50–0.97 cm²; Wetterer, 1994; Burd, 2000a; Wirth *et al.*, 2003), the load sizes carried by highly-laden ants in the present study are among the largest loads reported in *Atta* workers (1.5–2.5 cm²; Burd & Howard, 2008). Perhaps more intriguingly, highly-laden ants carry loads that are 50% larger (standardized for ant size) than loads carried by other worker ants. In other words, highly-laden ants differ more from ordinary-laden ants with respect to the size of their loads than the size of their bodies. This suggests that the ‘extra load carrying’ behaviour of this species depends on factors other than the body size of an individual ant.

Ants carrying extra-large loads are often slower than other workers and therefore retard the walking speed of the laden ants behind them. The experiments of the present study show that these highly-laden ants could reduce the walking speed of other laden ants by 0.8–1 cm s⁻¹. This means that a laden worker could increase its walking speed by 50% if the laden worker in front was not a highly-laden ant. We consider that our field manipulations are a good representation of what happens in nature: the running speed values of our ‘control’ and ‘treated’ laden ants are similar to those found in other studies under normal traffic conditions and natural bottleneck situations in foraging trails, respectively (Roces & Nuñez, 1993; Burd *et al.*, 2002; Burd & Aranwela, 2003; Farji-Brener *et al.*, 2007; Dussutour *et al.*, 2009a, b). Treated ants run significantly faster than nearby, equally-laden ants, probably because the absence of highly-laden ants ahead stimulates a short-term acceleration in their walking speed. Accordingly, laden ants attempt to overtake the highly-laden ant in front of them, although the traffic flow often frustrates their movements. Therefore, the presence of highly-laden ants on foraging trails potentially represents an important delay in the rate of food input into the colony and thus intra-colonial fitness.

The transport of a large leaf fragment not only provides the benefit of a large food reward, but also entails the collective cost of slowing portions of the traffic stream. However, these benefits and costs may vary with different amounts of ant flow. Although the benefit of a highly-laden ant returning a large load to the nest remains constant with changes in ant flow, the overall reduction of walking speed caused by highly-laden ants on other laden ants increases at high traffic levels. Hence, a negative relationship between the proportion of highly-laden ants on foraging trails and ant flow is found. At very low traffic (approximately 0.1 ants/100 cm² s⁻¹), laden ants often carry extra-larger loads but, at elevated ant flow, the relative abundance of highly-laden ants drastically decreases. This correlative evidence suggests that the behaviour of carrying extra-large leaf fragments is partially modulated to avoid delays in the overall foraging rate of the colony. Ants are capable of modulating this behaviour through at least two steps. First, ants leaving the nest can estimate the future traffic level of laden ants because the number of outbound workers is a good estimate of the number and density of returning laden ants (Gordon, 2002). Second, ants may use this information to estimate the size of the fragment that they cut and/or carry to the nest. As discussed earlier above, fragment size is not a simple function of the ant’s legs acting as a pivot; ants are able to change their posture so that they can cut smaller leaf fragments (Van Breda & Stradling, 1994; Rocés & Bollazzi, 2009). Indeed, several studies report that leaf-cutting ants often cut leaf fragments smaller than the size they are able to cut (Roces & Hölldobler, 1994; Burd, 2000a, b; Burd & Howard, 2005a, b, 2008; Dussutour *et al.*, 2009b; Rocés & Bollazzi, 2009). Individual ants might estimate the future flow of laden ants returning to the nest and determine the size of the carried fragment to avoid delays in the overall colony foraging rate. Accordingly, whereas, at high ant flow, the majority of the sampled laden workers carry loads of sizes to optimize the net colony-wide processing rate (estimated as 50–90 mm²; Burd

& Howard, 2008), at very low ant flow, most of our sampled ants carry plant tissue of sizes considered to optimize their individual rate of tissue delivery to the nest (approximately 170 mm² for leaves with a typical density of 0.20 mg mm⁻²; Burd, 1996, 2000b; Burd & Howard, 2008). During high traffic conditions, the benefit of incorporating a big leaf fragment into the nest might be outweighed by the costs of delaying portions of the traffic stream.

The argument outlined above could be questionable. First, behaviours based on individual decisions may also explain the reduced number of highly-laden ants at high traffic levels. Carrying oversize loads might be problematic during high ant flow because it enhances the probability of collisions with other ants and load lost. Thus, ants may cut fragment size below their carrying capacity also to avoid the individual cost of transporting oversized loads during high ant flow. However, preliminary field observations suggest that highly-laden ants do not necessarily increase their rate of collisions at enhanced ant flow. Second, ants carrying leaf fragments of different sizes at different levels of ant flow are observed, although no systematic observations on ants cutting leaves are performed in the present study. Without such information, the argument for a causal link between the leaf-cutting ant behaviour and the ant flow is weakened because some other interactions might be responsible for the observed pattern. Although our correlative data support the idea that the behaviour of transporting larger loads depends on ant flow, a more rigorous experimental approach should be carried out to test this hypothesis.

There are several studies reporting investigations that aim to determine why ants cut and carry sizes of leaf fragments below their individual capacity (Roces & Bollazzi, 2009). As discussed earlier above, fragment size might be influenced by many factors, including the size of the worker ant, the energetic cost of cutting, the density of the leaf, the need to rapidly transfer foraging information to the colony, the distance and quality of the harvesting site, and the risk of potential exposure to natural enemies, as well as handling costs. In the present study, we describe and quantify a novel factor related to traffic flow that also might affect load size selection: the delay in laden nest-mates. Ants carrying extra-large size leaf fragments (i.e. highly-laden ants) clearly reduce the walking speed of other laden nest-mates, and this effect may drastically reduce the net foraging input to the colony at high ant flow. Therefore, ants might cut smaller leaf fragments than their individual capacity to avoid the potential delays on others laden nest-mates. The results of the present study, taken together with the findings of other recent studies (Burd & Howard, 2008; Dussutour *et al.*, 2009a), support the idea that leaf-cutting ants make choices not only as individuals, but also collectively, and demonstrate the high flexibility of the foraging behaviour exhibited by ants.

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