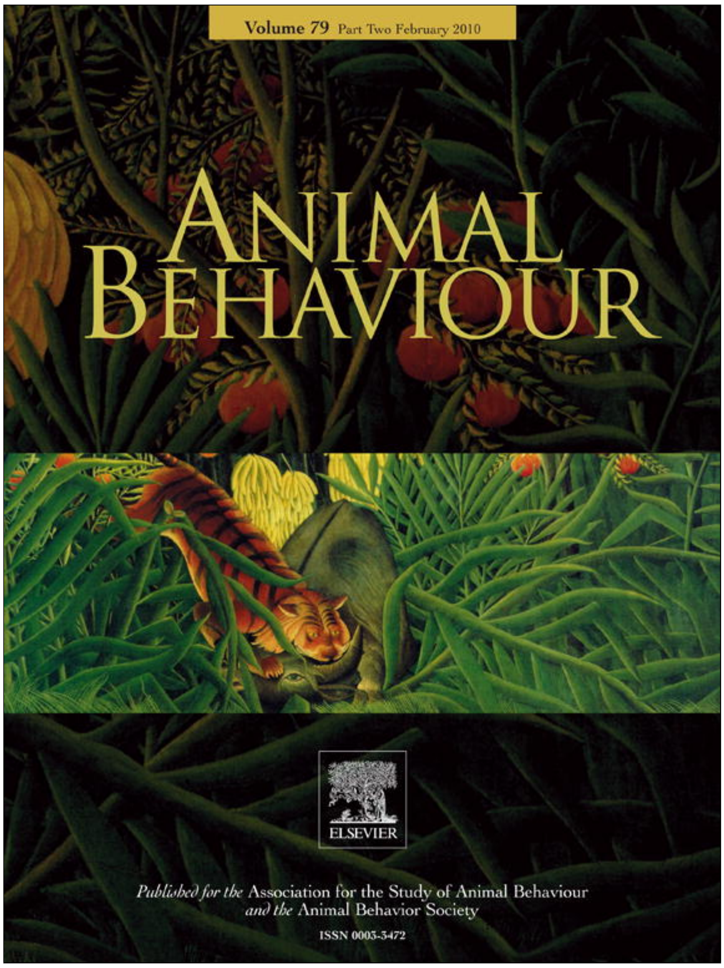
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Information transfer in head-on encounters between leaf-cutting ant workers: food, trail condition or orientation cues?

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Living in large societies involves costs associated with high density of individuals, but being near others includes the benefit of access to conspecifics' information. High densities of workers in ant colonies impose traffic congestion costs on foraging trails. It has been postulated that crowding also increases foraging efficiency by facilitating information transfer between workers in head-on encounters. However, this hypothesis remains untested. Here we assessed, in 24 field nests of the leaf-cutting ant *Atta cephalotes*, whether head-on encounters between workers facilitate information transfer about trail condition, orientation and food. Several experimental manipulations failed to fit predictions of certain types of communication. (1) Trail disturbance (and thus potential need for information transfer) did not affect the rate of head-on encounters, (2) head-on encounters did not decrease the time required for laden ants to properly orient when entering a trail, and (3) ants that had been experimentally disoriented did not increase the number of head-on encounters when they returned to the trail. Nevertheless, one experiment strongly suggested information acquisition: (4) outbound ants were more likely to find and collect food after a head-on encounter with an ant carrying the same kind of food. These results do not support the hypotheses that workers exchange information about trail condition and orientation in head-on encounters, but suggest that workers acquire food information. The information transferred in head-on encounters could thus increase foraging efficiency under crowded conditions. The cost of the reduced speed due to worker collisions might be outweighed by the benefits of information acquisition, and could explain why leaf-cutting ants do not form distinct lanes of outbound and returning workers. Our results reinforce the key role of information use in the adaptive behaviour of animals and in the maintenance of group living.

The access and use of information is essential for animals from both a behavioural and evolutionary perspective. Because adaptive behaviour depends on accurate estimation of significant ecological factors, the best informed individual will be better able to adjust its behaviour to meet the demands of a changing environment (Dall et al. 2005). Particularly, information sharing is a key benefit derived from group living. To best exploit potential opportunities and avoid dangers, individuals are able to monitor and use the discoveries of others to modify their own behaviour. Animals can thus enhance their fitness by obtaining information from conspecifics about food, predators, navigation and other relevant selective pressures (Dukas 1998). Several group decisions in foraging are affected by the behaviour of conspecifics. For example, certain bird assemblages are considered as information centers for food finding (Ward & Zahavi 1973). Individuals may obtain information on food location simply by watching the behaviour of successful foragers rather than searching for food by themselves (Barta & Giraldeau 2001). Information transfer in bird flocks can also be used to escape predators and permit decisions about when and whether to scan for predators (Fernández-Juricic & Kacelnik 2004). Directional

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information can also be transferred through individuals within groups, such as in birds or fishes, to make decisions about where to move (Sumpter 2006; Sumpter et al. 2008). Evolutionarily, information transfer about food may have contributed to the evolution of male sociality in bats (Safi & Kerth 2007), colonial life in birds (Brown 1987) and sociality in insects (Hölldobler & Wilson 1990; Bonabeau et al. 1997; Franks et al. 2002). Thus, information use is important in the ecology and evolution of adaptive behaviour and group living (Safi & Kerth 2007).

Living in societies entails both costs and benefits. Living in large societies involves costs related to high density of individuals, but being near others also involves the benefit of access to information provided by conspecifics. For example, high density of ants in colonies imposes costs associated with factors such as waste management, spread of disease agents (Schmid-Hempel 1998) and traffic congestion on foraging trails. The high density of foraging workers on a trail often causes traffic congestion and, consequently, decreases worker speed and thus reduces the overall ant flow of the colony (Burd 1996). Leaf-cutting ants of the genus *Atta* provide a good opportunity to explore these traffic costs because they form colonies with more than 10^6 workers occupying a single nest (Fowler et al. 1986), and they use an extensive system of foraging trails where ant flow can be extremely high (Burd et al. 2002; Kost et al. 2005). The fact that leaf-cutting ants endure the costs of living in large colonies implies that behaviours reducing these costs should be positively selected. Work to date has emphasized the behavioural strategies to avoid diseases (see Fernández-Marín et al. 2006 and references therein). Conversely, it is less known how leaf-cutting ants reduce the cost of traffic congestions on foraging trails.

Leaf-cutting ants construct persistent foraging trails (up to 300 m long) free of debris to direct foragers through the forest litter to their host plants and to facilitate the transport of leaf fragments to the nest to feed their fungus gardens (Howard 2001; Kost et al. 2005). These trails promote the flow of food and information by minimizing travelling times between the nest and resources (Rockwood & Hubbell 1987; Burd et al. 2002). However, trail traffic in opposite directions can reach very high volume. Hence, traffic congestion can occur and the overall flow of workers on the trails can dwindle (Burd & Aranwela 2003; Dussutour et al. 2004). To avoid overcrowding, some ant species establish new trails (Dussutour et al. 2004), segregate outbound and returning streams spatially (Couzin & Franks 2003), or desynchronize the flow of outbound and nestbound ants (Dussutour et al. 2005, 2009a, b). In nature, leaf-cutting ants do not seem to posses any of these regulatory mechanisms to prevent or reduce overcrowding. Consequently, the rate of head-on encounters between workers moving in opposite directions under crowded conditions is usually high (Dussutour et al. 2007). These encounters impede the flow of foragers, reducing the net speed by an average of 20% relative to free-flow velocities (Burd & Aranwela 2003). The decrease in ant speed over the whole length of the trail may considerably reduce the overall foraging efficiency of the colony (Burd et al. 2002; Burd & Aranwela 2003). Which behaviours might reduce this cost? It has been postulated that in head-on encounters, workers acquire information about the vegetation being harvested (Roces & Nuñez 1993; Roces 1994; Burd & Aranwela 2003). However, this hypothesis and alternative explanations, such as information of the state of the trail or directional cues, remain untested.

In this study, we used 24 field nests to experimentally determine whether there is information transfer between workers of the leaf-cutting ant *Atta cephalotes* through head-on encounters that is related to trail condition, orientation and/or food. If information is transferred from laden to unladen workers concerning (1) trail conditions, (2) orientation cues and (3) food, we predicted that (a) the number of head-on encounters between outbound and returning ants (and thus potential need for information transfer) would increase after a trail disturbance, (b) the time loss per ant to properly orient themselves would be lower for ants experiencing a high rate of head-on encounters than those experiencing a low rate of encounters and (c) head-on encounters between laden and unladen ants would increase the probability that unladen ants would find food sources (Table 1).

GENERAL METHODS

We conducted this study at the La Selva Biological Station of the Organization for Tropical Studies (10°26′N, 83°59′W) in the Atlantic lowlands of Costa Rica, between January and February 2009. The area is a lowland wet forest that receives a mean annual rainfall of 4000 mm (see McDade et al. 1994 for a full description). Research was conducted under scientific permit no. 206 (SINAC), in accordance with the current laws and animal welfare protocols of the Republic of Costa Rica. Colonies of leaf-cutting ants *Atta cephalotes* are common in La Selva (Farji-Brener 2001). We worked with 24 large nests of *A. cephalotes* located in different successional stages of forest. To test the three hypotheses described above, we measured head-on encounters between ants (adjusted by ant traffic), and other response variables according to the nature of the experiment (see below). To control for ant traffic, we divided the number of head-on encounters by the total number of ants crossing a 30 × 10 cm section of trail during 30 s in each case. Means ± 1 SE are reported.

GENERAL RESULTS

Head-on encounters between returning and outbound workers were very frequent on the trails of the leaf-cutting ant *Atta cephalotes*. Overall, workers experienced a mean of 8 ± 2 head-on encounters on a 30 cm section of the trail ($N = 178$ ants), with a range of 2–27 encounters depending on traffic flow. Traffic flow

Table 1
Hypotheses, rationale and expected results tested in this work about the kind of information transfer between leaf-cutting ant workers in head-on encounters

Hypotheses	Rationale	Predictions
Trail condition	Information about changes in trail topography is important for rapid, accurate locomotion in a given area, and thus for the ant flow	Head-on encounters between outbound and returning ants increase after trail disturbance
Orientation cues	Faster and proper orientation reduce delays in the foraging process	(a) Laden ants that frequently experience head-on encounters should properly orient themselves more quickly when entering into a main trail than laden ants that experience few encounters (b) Laden ants experimentally displaced from the trail should experience higher rates of head-on encounters when they return to the trail than they did before displacement
Food location	Information about food increases the foraging rate	Head-on encounters between unladed and laden ants increase the probability that unladed ants reach a food source

varied between 5 and 47 ants per 30 s within a 10 cm of trail length. During encounters, workers usually touched each other with their antennae; the outbound forager also often touched the food carried by returning workers with her antennae. However, some encounters (∼30%) were collisions without any visual evidence of antennation.

EXPERIMENT 1: HEAD-ON ENCOUNTERS ALLOW INFORMATION TRANSFER ABOUT TRAIL CONDITION

Rationale

If information on the location of relevant topographic features is necessary for rapid, accurate locomotion in a given area (Stamps 1995), then transfer of this information might increase the foraging rate of a colony. In tropical forests, when previously cleared trunk trails of leaf-cutting ants are temporarily obstructed by fallen debris (Farji-Brener et al. 2007; Evison et al. 2008), ants quickly cut and remove the obstacles from the trail (Howard 2001). Both fallen debris and aggregations of ants working to clear the trail can delay the flow of foraging workers. Because familiarity with an area enhances fitness (Stamps 1995), knowing the presence and/or the location of upcoming trail obstructions may allow ants to avoid them more easily or to choose an alternative track within the trail before encountering the obstacle. These behaviours can save time and thus improve the speed of workers. Hence, ants might transfer information about the condition of the preceding trail section and/or about the progress of clearing work through head-on encounters.

Methods

To determine whether information about trail condition is transferred during head-on encounters between returning laden and outbound unladen workers, we performed the following experiment. During the peak of foraging activity, we recorded the number of head-on encounters between outbound and returning workers during 25 s on a 30 cm section of a main trail 5–7 m away from the nest entrance. Then we partially blocked the trail with a fallen leaf. One minute later, we assessed again the number of head-on encounters between outbound and returning workers in two sectors located 20 cm away from the obstacle (in opposite directions). The partial obstruction of a trail was expected to stimulate the potential need for information transfer if information concerning trail condition is being transferred. We performed 26 trials on different trails of 14 nests. We compared the number of head-on encounters before and after placing the obstacle using a paired *t* test. We predicted that the number of head-on encounters between workers would be greater after placement of the obstacle.

Results and Discussion

The fallen leaf experimentally placed on the trail always generated a bottleneck. The obstacle per se and the aggregation of workers clearing the trail clearly decreased movements of the workers along the trail. However, the mean number of head-on encounters on a 30 cm section of the trail did not differ significantly before and after we had experimentally blocked a part of the trail (8.4 ± 2.7 versus 8.1 ± 2.5, respectively; $t = 0.9$, $N = 26$, $P = 0.4$).

The ability to anticipate unpredictable obstacles along trails (e.g. fallen debris) is beneficial for ant species with a long trail system and high rate of trail disturbance, as in tropical leafcutters. Accordingly, we predicted that head-on encounters would contribute to information transfer about trail status (i.e. the existence of transient obstacles and/or of overcrowding conditions). However, our results did not support this hypothesis. The number of head-on encounters between workers did not change after we experimentally obstructed a part of a trail, suggesting no potential need for information transfer under the existence of a novel obstacle on the trail. Either our experimental obstruction was too small to effectively reduce traffic flow, and thus, too trivial to inform, or workers can effectively elude the trail obstruction by following pheromone trails (Hart & Jackson 2006; Evison et al. 2008). Additionally, clearing of trail debris is often performed by minim workers and their small sizes offer no impediment to the progress of media and major workers walking on the trail (Burd & Aranwela 2003).

EXPERIMENT 2: HEAD-ON ENCOUNTERS PROVIDE DIRECTIONAL CUES

Rationale

The mere fact of an encounter, even in the absence of antennation, has a function because it indicates the number and density of ants, and induces task allocation (Gordon & Mehdiabadi 1999; Gordon 2002), but it also may provide cues about direction. For example, laden *Pheidologeton diversus* workers on a foraging trail used the flow of other laden workers to orient themselves towards the nest, a mechanism that maintained correct flow through the confluence of trails (Moffet 1987). While walking in a network of trails, leaf-cutting ants face a succession of bifurcations, and at each bifurcation they have to choose the proper direction they will take next. Additionally, leaf-cutting ants often explore the forest floor outside of the trails and need to return and properly orient themselves on the trail system (Farji-Brener & Sierra 1998). Since leaf-cutting ants show no evidence of using polarity in their trail pheromones for orientation (Vilela et al. 1987; Wetterer et al. 1992), contacts between laden and unladen workers may enable ants to choose the appropriate direction between nest and food, particularly when they enter a trail from the ground or when workers arrive at a main trail through a trail junction.

Methods

To determine whether information regarding direction is transferred through head-on encounters between workers, we performed two field experiments. First, we randomly selected a returning laden ant with a leaf fragment, and recorded the number of head-on encounters it experienced for 40 s. Then, we lifted the ant from the trail for 20 s and released it 10 cm away from the trail (hereafter 'treated ant'). Ants hold tightly to the leaf they are carrying, even in the air, so we used forceps to lift the leaf fragment and thereby lifted the ant; thus, we did not directly manipulate the ants. When the treated ant entered the trail again, we recorded the number of head-on encounters that it experienced for the next 40 s. As a control, simultaneously and on the same trail section, we recorded the number of head-on encounters experienced by another laden ant, which we lifted and immediately released at its original position (hereafter, 'control ant'). Treated and control ants were similar in size, carried leaf fragments of similar dimensions, and were not marked. We sampled 64 ants from 20 trails of 10 nests. The number of head-on encounters (adjusted for ant traffic as explained above) was analysed using repeated measures ANOVA. Treatment (treated and control ants) was considered as a fixed factor, time (before and after the lift) was the repeated measure and the pair (treated and control ants) was the block (random) factor. If head-on encounters provide orientation cues, we predicted that treated ants would increase the rate of head-on encounters after they were experimentally lost, while control ants would not (in ANOVA terms, we expected a significant interaction between treatment and time).

In a second measure, we selected a trail section that included a bifurcation, and we followed individual laden ants (focals) that naturally moved onto the main trail through the junction during 10 s. We recorded the number of head-on encounters between focal ants and other workers, and the time that it took the focal ants to become properly oriented (i.e. towards the nest, as for a laden ant). We recorded 30 ants from five trail sections from 10 nests. The number of head-on encounters (adjusted for ant traffic as explained above) was correlated with the time needed to choose the correct direction using a nonparametric Spearman correlation. If head-on encounters provide orientation cues, we predicted that an increase in the number of head-on encounters should reduce the time needed to choose the correct direction.

Results and Discussion

Experimentally lost ants did not participate in more head-on encounters when they returned to the trail than did control ants. The mean number of head-on encounters did not differ significantly between treated and control ants (1.25 ± 0.5 versus 1.3 ± 0.6; treatment effect: $F_{1,93} = 0.28$, $P = 0.60$) or before and after treated ants were experimentally lost (1.3 ± 0.5 versus 1.2 ± 0.6; time effect: $F_{1,93} = 0.14$, $P = 0.71$). Accordingly, both control and treated ants showed similar mean numbers of head-on encounters on a 30 cm section of the trail before and after treated ants were experimentally lost (treatment $\times$ time: $F_{1,93} = 0.95$, $P = 0.33$). In addition, the time spent by a laden ant to properly orient towards the nest when she entered a trail through a junction was not correlated with the number of experienced head-on encounters (Spearman rank correlation: $r_S = 0.10$, $N = 30$ ants, $P = 0.60$). In several cases, a laden ant properly oriented herself within a few seconds of entering the main trail without encountering any other ants (Fig. 1). Moreover, the time required to properly orient was similar between laden ants that did and did not experience head-on encounters (11.1 ± 1 s versus 11.7 ± 2 s; $t = 0.36$, $N = 30$, $P = 0.72$).

A proper navigation is essential for leafcutters because they have a large and complex system of nest trails (Kost et al. 2005).

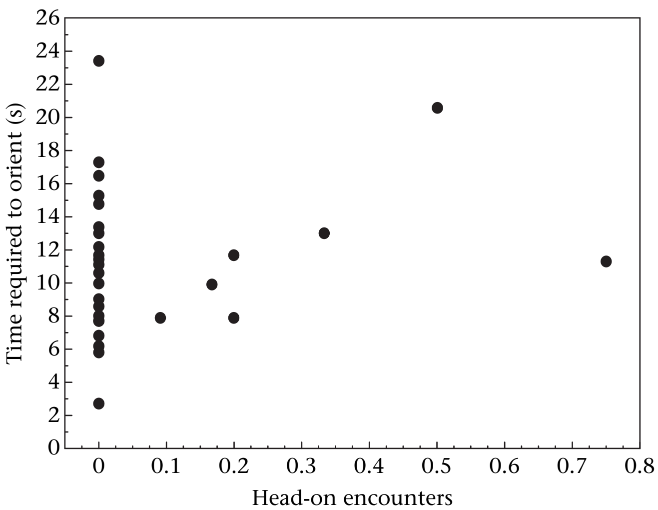

Figure 1. Time spent (in seconds) by a laden ant to properly orient towards the nest when she entered a trail through a junction, based on the number of experienced head-on encounters ($r_S = 0.10$, $N = 30$ ants, $P = 0.60$). Number of head-on encounters was adjusted by ant traffic (see text for details).

Accordingly, we expected that head-on encounters transfer information about orientation. However, our results did not support this hypothesis. A higher rate of head-on encounters did not reduce the time required for a laden ant to properly orient herself when entering a trail, nor did lost ants increase the number of encounters when re-entering a trail, suggesting that head-on encounters were not used as orientation cues. Head-on encounters with unladen ants may provide only poor information about nest location, since there are numerous returning unladen ants walking in both directions along a trail (Evison et al. 2008). It is also probable that laden ants use other kinds of cues for proper orientation to the nest. For example, information inherent to the trail bifurcation can be used by foragers to determine trail polarity. In general, a large trail deviation would lead away from the nest, whereas a small trail deviation would lead to the nest (Jackson et al. 2004). In addition, leaf-cutting ants can use the earth's magnetic field as a reference to orient towards the nest (Riveros & Srygley 2008). Therefore, head-on encounters might play a minor role in trail orientation, and laden ants may use trail geometry, landmarks, or the earth's magnetic field to properly orient themselves. Alternatively, it is also possible that ants use encounters to orient themselves or to transfer information about trail obstructions, even if they do not increase the frequency of such encounters in response to changing conditions (as in our field experiments). Ants may regularly monitor these conditions and use the information as necessary. Therefore, more experiments comparing the behaviour of ants that do and do not experience head-on encounters are necessary to strongly discard the hypothesis that head-on encounters transfer information about orientation and trail status.

EXPERIMENT 3: HEAD-ON ENCOUNTERS ALLOW TRANSFER OF INFORMATION ABOUT FOOD

Rationale

The transfer of food information often increases foraging efficiency (Roces 1990, 1994; Howard et al. 1996). Therefore, if head-on encounters allow ants to acquire information about the vegetation being harvested by laden ants, then this behaviour could compensate for the negative effect of traffic congestions on the foraging efficiency of a colony. In agreement with this idea, Dussutour et al. (2007) found that crowding increased foraging efficiency (i.e. laden ant flow) in the leaf-cutting ant *Atta colombica* in a small laboratory colony when the width of the bridge between the nest and the ants' foraging area was reduced. These authors suggested that the high rate of head-on encounters on the narrow bridge could increase the communication between laden and unladen ants, which in turn, increases the overall foraging rate (Dussutour et al. 2007). However, this hypothesis remains untested. Previous studies on the adaptive nature of trail organization and on the role of head-on worker encounters in leaf-cutting ants have mostly been performed with only one nest under laboratory conditions, and have tested indirectly the existence of food information transfer (Burd et al. 2002; Burd & Aranwela 2003; Dussutour et al. 2007). Hence, there is no information about this phenomenon in natural conditions and whether there is variation in ant responses among colonies.

Methods

To determine whether information about food is transferred through head-on encounters between returning laden and outbound unladen workers, we performed the following field experiment. We placed a pile of corn flakes beside the main trail and 3 m away from the nest entrance. We used corn flakes as the food source because they are highly acceptable to leaf-cutting ants, and have been successfully used in several food preferences studies (see Farji-Brener 2001 and references therein). Usually, within a few minutes a worker discovered the pile, picked up one corn flake and returned to the nest. On the way to the nest, this ant experienced head-on encounters with unladen outbound workers. We followed the first outbound unladen ant that encountered the worker carrying the corn flake head-on (i.e. head-to-head contact), and recorded whether or not this ant discovered the corn-flake pile. As a control, we followed simultaneously another outbound unladen ant that had not contacted the ant with the corn flake, and recorded whether or not this ant discovered the corn-flake pile. All the followed ants were of similar size (medium workers). A discovery was considered successful when the ant picked up a corn flake and returned with it to the nest. The corn-flake carrier ants were removed from the trail before they could reach the nest entrance to avoid mass recruitment. Therefore, each ant was sampled only once. We followed 106 ants on 10 trails from five nests. We tested whether the probability of discovering and carrying a corn flake to the nest depended on a previous head-on encounter with a corn-flake-carrying ant using a chi-square test. If such encounters transferred food information, we predicted that ants that had experienced head-on encounters with corn-flake carriers would be more likely to find the corn-flake piles.

Results and Discussion

The probability of finding a food source increased following a head-on encounter with a laden ant. While 21 of 53 ants that contacted a corn-flake carrier found the corn-flake pile, only 3 of 53 control ants found the food source ($\chi^2_1 = 15.2$, $P < 0.001$). In other words, 87.5% of the ants that found the corn-flake piles were ants that had previously contacted returning workers carrying a corn flake (Fig. 2).

The high percentage of ants that found food after an encounter with a corn-flake carrier ant strongly suggests that workers travelling in opposite directions acquire food information through head-on encounters. Earlier works suggested that head-on encounters in crowded trail conditions increase foraging efficiency in leaf-cutting ants (Roces 1994; Howard et al. 1996; Burd et al. 2002; Burd & Aranwela 2003; Dussutour et al. 2007, 2009b). However, these studies were often performed in laboratory conditions and used only one nest, and the responsible mechanism was untested. To our knowledge, this is the first field study that uses a large number of nests and demonstrates that head-on encounters can be responsible for the increase in foraging efficiency observed under crowded conditions. It has been postulated that multiple contacts with laden ants could increase the level of excitation of unladen ants and, consequently, their behavioural responses when reaching the foraging area. Thus, a higher rate of encounters with ants carrying leaf fragments should increase the probability of leaf cutting (Dussutour et al. 2007). Our results demonstrate that only one contact with a laden ant might be enough to stimulate an unladen ant to look for a food item and carry it to the nest. This mechanism could allow more rapid and flexible decisions and consequently permit colonies to rapidly exploit transient food sources such as seedlings, flowers, fallen fruits and seeds.

Returning laden foragers often lay a chemical trail with pheromones that may also stimulate recruited ants to collect and retrieve food back to the nest (Hölldobler & Wilson 1990). However, if trail pheromone had been the main recruitment signal in our experiment, then all outbound ants that contacted or moved across the path created by the laden ant should have reached the food source, independently of the existence of head-on encounters. However, outbound ants were more likely to find and transport food items following head-on encounters with laden ants. This finding suggests that the existence of trail pheromones per se do not explain the high percentage of food discovery. Even if outbound ants generally follow trail pheromones to a food source, our results strongly suggest that head-on encounters stimulate outbound foragers to follow this chemical track. We have demonstrated probable information transfer from laden to unladen workers. Our data do not allow us to evaluate whether laden workers actively signal to the unladen workers or whether unladen workers simply acquire information, a cue, associated with laden workers (e.g. the odour of a corn flake). Nor do they permit us to evaluate the possibility that laden workers receive information from unladen workers. Evaluation of these possibilities should be an important topic to investigate in the future.

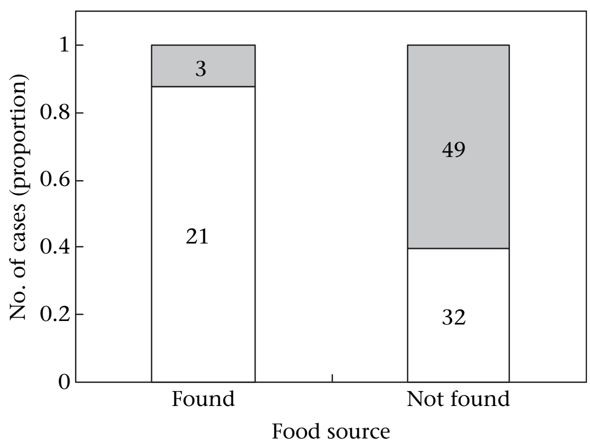

Figure 2. Number of cases in which an unladen ant found a corn-flake pile, picked up a corn flake and returned to (found) the nest in the presence (open bar) or absence (solid bar) of a head-on encounter with a corn-flake carrier ant (see text for explanation). $\chi^2_1 = 15.2$, $P < 0.001$. Sample sizes are given in bars.

GENERAL DISCUSSION

Head-on encounters between workers travelling in opposite directions were very frequent on *Atta cephalotes* trails. According to our results, a single forager can experience about 2600 collisions along a 100 m of trail at high traffic densities. These encounters may reduce the net speed of workers (Burd & Aranwela 2003; Dussutour et al. 2007), decrease the colony harvesting rate, and increase the exposure time of workers to parasites (Feener & Moss 1990). However, these costs might be outweighed by the benefits of information transfer (Burd & Aranwela 2003). Information transfer can usually be measured through its behavioural consequences. We have shown here that (1) trail disturbance (and thus the potential need for information transfer) did not affect the rate of head-on encounters, (2) head-on encounters did not decrease the time required for laden ants to properly orient when entering a trail, and (3) ants that had been experimentally disoriented did not increase the number of head-on encounters when they returned to the trail. These results do not support the hypotheses that workers transfer information about trail condition and orientation via head-on encounters. But, our results strongly support the hypothesis that head-on encounters allow information transfer about food, because outbound ants were more likely to find and collect food after a head-on encounter with a laden ant.

Our results and earlier works suggest that the mean traffic velocity would increase by around 20% in leaf-cutting ant foragers if they used lane segregation (Burd & Aranwela 2003). What factors may help account for the fact that leaf-cutting ants have not evolved segregated lanes of outbound and returning workers in their bidirectional traffic? Several explanations have been postulated: the loss of pheromone signals, the formation of clusters of slow ants that obstruct traffic flow, and the benefits of transferring a leaf to an unladen ant. Several leaf-cutting ant species deposit pheromones by touching their gasters to the ground, especially when carrying a high-quality resource (Roces 1990; Roces & Nuñez 1993; Lopes et al. 2004). If this chemical information was deposited only on a separated return lane, it might be more difficult to be detected by outbound ants. On the other hand, laden ants with larger leaf fragments usually are slower than workers carrying small leaf fragments and thus tend to group. This cluster of low-agility, laden workers might partially block traffic flow by forcing large portions of the traffic streams to adopt their slow speed (Burd et al. 2002; Dussutour et al. 2009a, b). Finally, unladen workers occasionally take leaf fragments from their laden nestmates, and these fragments are carried, on average, 60% faster following such transfers (Anderson & Jadin 2001). Leaf transfer between workers might be difficult to do if laden and unladen ants walk on segregated lanes. Here we confirm that information transfer about food is another advantage that might be lost if leaf-cutting ants organized their traffic along segregated foraging streams. Our results show that an unladen ant that undergoes a head-on encounter with a laden ant increases its probability of reaching food from 2% to 40%, suggesting a net increment of 38% in their foraging efficiency. Even without including the other proposed benefits of mixed-flow traffic, the cost of a decrease in speed due to head-on encounters might easily be outweighed by the benefits of information transfer.

In conclusion, our results reinforce the hypothesis that encounters between outbound and nestbound laden workers are important in transferring or acquiring food information (Roces 1990, 1994; Howard et al. 1996), demonstrating how crowding may increase foraging efficiency in leaf-cutting ants, as previously documented (Burd et al. 2002; Burd & Aranwela 2003; Dussutour et al. 2007, 2009a, b). Information transfer is also important in the foraging of several animal groups (Galef & Giraldeau 2005). For example, visual, olfactory or acoustic cues associated with successful foraging stimulate individuals to increase foraging in birds (Ward & Zahavi 1973; Brown 1987) bats (Wilkinson 1992; Safi & Kerth 2007), rats (Galef & Wigmore 1983), hamsters (Lupfer-Johnson et al. 2009), monkeys (Chauvin & Thierry 2005) and dogs (Heberlein & Turner 2009). In social insects, bumble bees (Dornhaus & Chittka 2001, 2004), stingless bees (Hrneir et al. 2000) and honeybees (von Frisch 1967) may be activated to forage when they contact successful foragers. During the first phases of foraging, the information transfer about a newly discovered food source motivates ants and bees to shorten their individual carrying performance and return earlier to the colony for further recruitment (Roces & Nuñez 1993). As discussed earlier, living in large societies implies costs but also benefits. Our results demonstrate that crowding may increase foraging efficiency, illustrating how organisms living in large societies can benefit, to some degree, from traffic congestion. Moreover, our results show how complex collective behaviour may emerge from simple interactions among individuals, reinforcing the key role of information transfer in the adaptive behaviour of animals and in the evolution of group living.

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