



Tall trails: ants resolve an asymmetry of information and capacity in collective maintenance of infrastructure



Andrew I. Bruce^{a,*}, Tomer J. Czaczkes^b, Martin Burd^a

^a School of Biological Sciences, Monash University, Melbourne, Victoria, Australia

^b Biologie I, Universität Regensburg, Regensburg, Germany

ARTICLE INFO

Article history:

Received 12 September 2016

Initial acceptance 4 January 2017

Final acceptance 2 March 2017

MS. number: 16-00800R

Keywords:

behavioural regulation

construction

foraging trails

leaf-cutter ants

self-organization

Information asymmetry is common in many aspects of natural and economic systems. Collective self-organized behaviour in social insects may involve asymmetries in which an individual may possess information but only another individual is able to act on it. We examined this phenomenon on foraging trails of leaf-cutting ants (*Atta colombica*) to determine whether workers can resolve such an asymmetry. Cleared trails facilitate the transfer of resources and information but require constant maintenance to remove obstacles that arise in a dynamic environment. Overhead obstructions, which occur frequently along trails, present a specific asymmetry for collective behaviours. Returning foragers carrying leaf fragments above their heads may be hindered by such obstructions but must rely on unladen workers to remove them. Can leaf-cutting ants resolve this asymmetry? Do they do so in an indiscriminate or discriminate fashion? We created experimental overhead obstructions that hindered laden but not unladen ants. Clearing efforts by unladen workers were sensitive to the experience of their laden nest-mates; they intensified attacks on a low barrier that impeded traffic but not on an equivalent barrier too high to strike leaf fragments. By contrast, a low barrier in the absence of laden ants or an ineffective visual 'barrier' did not elicit increased clearance attempts. Our results demonstrate that leaf-cutting ants can overcome an information asymmetry challenge, in which one group possesses the information that another must act upon. This allows the ants to adaptively modulate their trail-clearing efforts.

© 2017 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Information asymmetry, an imbalance of information between two parties, is so common in human and natural systems that it is rarely thought about as a phenomenon in itself. Scouting, research and, most especially, communication are all means to redress information asymmetry. In a competitive system, such as the human economy, information asymmetry often produces an advantage that one party can exploit to the disadvantage of another (Aboody & Lev, 2000). However, asymmetry of information may disadvantage both parties (Balakrishnan & Koza, 1993; Doherty, 1999), which leads to attempts to resolve the asymmetry through the creation of institutions and traditions, such as regulation, contracts, third-party facilitators or the use of reputation (Balakrishnan & Koza, 1993; Healy & Palepu, 2001; Hobbs, 2004; Scott-Phillips, 2008). Similar dynamics of information asymmetry within a competitive system can also lead animals to resolve information asymmetry to the benefit of both parties, such as through stotting in Thomson's

gazelles, *Eudorcas thomsonii* (FitzGibbon & Fanshawe, 1988) or calling in frogs (Wagner, 1992). A more unusual dynamic in biology is information asymmetry within a cooperative framework. This can occur in social insects when an individual possesses information that the colony requires to make a correct decision, such as when an ant colony is looking for a new home (Franks, Mallon, Bray, Hamilton, & Mischler, 2003), or bees are foraging for food (Biesmeijer & Seeley, 2005). In leaf-cutting ants, which construct a transport infrastructure of cleared trails, information asymmetry can arise between workers that perceive the need for creation and maintenance of the trails and those capable of effecting the work. Here we examine this asymmetry and its resolution.

Trails play a primary role in an ant colony's activity and communication. The cleared foraging trail networks of leaf-cutting ants (*Acromyrmex* spp. and *Atta* spp.: Attini, Formicidae) are particularly sophisticated and multifunctional: they facilitate the transfer of leaf resources (Bruce & Burd, 2012; Burd & Howard, 2005; Hölldobler & Wilson, 1990; Moreira, Forti, Andrade, Boaretto, & Lopes, 2004), recruits and defenders (Jaffe & Howse, 1979; Powell & Clark, 2004) and information (Bollazzi & Roces, 2011; Farji-Brener et al., 2010) through a colony's territory to its

* Correspondence: A. I. Bruce, Michaelispassage 7, Hamburg, Hamburg, 20459, Germany.

E-mail address: andrew.iain.bruce@gmail.com (A. I. Bruce).

nest. Individual trails can reach 300 m in length, and trail systems several thousand metres, requiring a substantial investment of worker time to clear debris (Howard, 2001). Smooth transport on trails is important because even seemingly minor obstructions may cause congestion that could impose disproportionately large costs on the colony.

Leaf-cutting ant colonies do not invest indiscriminately in trail clearance (Shepherd, 1982). Too much investment in the maintenance workforce could potentially make trail clearance energetically unprofitable (Bochynek, Meyer, & Burd, 2017). For example, colonies of *Atta cephalotes* and *Atta colombica* modulate the geometry of their trail networks to balance the travel time experienced by returning laden foragers against the costs of trail maintenance (Farji-Brener et al., 2015). A geometry that allows reduced travel time prevails in exposed habitats where desiccation is a danger, while a geometry that minimizes the effort needed for trail clearance is a higher priority under a forest canopy where desiccation is unlikely but leaf litter is copious.

The traffic of leaf-cutting ant trails comprises laden ants returning to the nest with a leaf fragment, and unladen ants that may be either inbound or outbound. Information on whether a trail is sufficiently cleared to allow an adequate flow will reside largely with the laden ants themselves, as their own progress is the measure of trail condition. However, since laden ants are occupied with their burden, they do not have the capacity to clear obstructions. Instead, unladen ants clear foraging trails (Howard, 2001). How, then, do leaf-cutting ants make investment decisions regarding their infrastructure? The challenge is that one component of the traffic stream must adequately prepare the trail for the benefit of another group. If laden and unladen ants are impeded by the same obstacles, it may be enough for unladen ants to clear any obstacle that they encounter. In some cases, however, particular trail conditions that affect laden ants will have no consequence for the locomotion of their unladen nestmates. For those situations, a more sophisticated organization of investment in trail maintenance would be necessary to facilitate optimal trail flow.

The vertical clearance of a trail is one such special case that will affect laden and unladen leaf-cutting ants differently. Leaf-cutting

ants transport leaf-fragments above their heads (Fig. 1); therefore overhead obstacles such as grass, leaves and small sticks can delay the movement of laden workers (Lewis, Pollard, & Dibley, 1974). Thus, the removal of trail debris to a sufficient height is a particularly important feature of trail infrastructure investment. But overhead obstacles that do not obstruct the trail surface may allow an unladen worker to pass without impediment, even as a laden nestmate is hindered. In most cases of trail construction, as in other self-organized activities (Camazine et al., 2001), ants respond to cues concerning the need for a given task that they directly experience. Laden ants rarely put down their loads to attack obstructions except in unusual circumstances when traffic is nearly completely blocked (A. I. Bruce, personal observation). How, then, is information about the need for clearing aligned with the capacity to clear in this case? The response of unladen ants to overhead obstructions can reveal whether they are simply clearing obstacles that block their own progress, with coincidental benefit to laden foragers, or whether they manage to resolve the asymmetry between information and capacity.

At present, the mechanisms that regulate trail clearance and the adaptive principles they serve are not fully understood, as there have been few investigations into the regulation of trail height. Dussutour, Deneubourg, Beshers, and Fourcassié (2009) examined how a laboratory colony of *A. colombica* responded to an obstruction 1 cm above the trail surface that delayed the progress of leaf-laden ants. They found that workers cut smaller leaf fragments to readily fit under the obstruction and they compensated for the smaller loads by increasing the number of ants engaged in retrieving leaf fragments. This work did not explore an alternative strategy that is normally available to leaf-cutting ants: in a natural situation, ants can remove obstructions rather than reduce the size of leaf fragments (Fig. 1).

Here we test several hypothetical mechanisms that would allow unladen ants to clear a trail or tunnel to a height appropriate for laden ants. First, it may be that anything on or above the trail that is in the path of an unladen ant will serve as stimulus for attack and removal, whether or not it is delaying laden ants. Alternatively, ants may be responding to visual cues that the trail height is too low and use their individual judgement to assess the situation and clear the

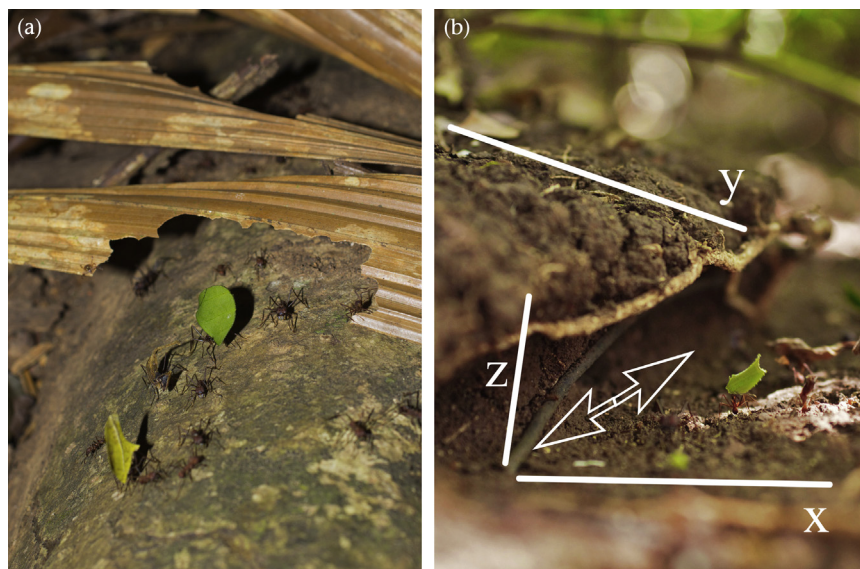


Figure 1. (a) *Atta colombica* transport leaf fragments back to the nest along a fallen branch. A long leaf crossing the trail has been cut so as to allow the smooth transportation of leaf fragments by laden ants. (b) *Atta colombica* transport leaf fragments along a trail that has been levelled (x) from the slope of the hill (y) and heightened (z). White arrows indicate direction of bidirectional trail flow.

trail to an appropriate height. Finally, it is also possible that delays in the progress of their laden colony-mates stimulate the clearing ants to seek out, attack and remove obstructions. We erected artificial overhead obstructions on natural foraging trails of leaf-cutting ants to test these possibilities.

METHODS

The experiment was performed on Barro Colorado Island (BCI) and mainland Panama during 10 March – 3 April 2014, between 0845 and 1830 hours with colonies of *A. colombica*. Because of local field conditions at the time, especially a decline in the density of *A. colombica* colonies on BCI, collecting a broad sample population was not possible. One large colony with multiple trails was the subject of most replicates ($N = 23$). Additionally, a colony from the mainland was sampled once and a second colony was sampled twice. We initially analysed the colonies separately (see Appendix), but upon finding that the pattern of responses was concordant among colonies, we then pooled the data from all the colonies for the main analysis presented here. Individual trails were sampled multiple times but never more than once in a day and never from exactly the same location. We collected data in a manner designed to maximize the independence of trials within the prevailing constraints. First, as the experiment investigated transient responses that were highly localized to a time and place on a particular trail, replicates at different times and trails were unlikely to influence each other. Indeed, for trail maintenance to be adaptive, it would need to be responsive at small spatial and temporal scales, increasing the likelihood of independence. Additionally, the colony from which most data were gathered was very large with very long trails and it is therefore likely that different individual ants experienced the experiment from trial to trial. Finally, *Atta* queens are multiply mated and so there is likely to be genetic variability within the group of sampled workers, reducing nonindependence due to colony-level effects. None the less, we recognize that replication on additional colonies would help to further explore the issues raised in this study.

The intention of the experiment was to impede laden ants while allowing unladen ants free passage. We created an overhead hindrance of a 1 mm diameter metal wire stretched across the trail. In different treatments the wire either did or did not hinder laden ants depending on the height at which it was placed, but it never hindered unladen ants, even when they were quite large (Fig. 2). Poles of 1 mm diameter wire were placed 3 cm apart across the width of the trail to provide ants access to the overhead wire. Ants attacked both the overhead wire and the poles, but were unable to cut or clear it. Thus, it provided a constant stimulus for the duration of the trial. Once the experimental wire was in place for each treatment, a 5 min delay allowed any disturbance of the ant traffic to pass before data recording. Video recordings were taken for half an hour for each replicate and the number of clearing attacks by ants on the apparatus were counted. We defined clearing attacks as occurring when ants opened their mandibles and made contact with any piece of wire or lunged at it. Only one attack was counted per ant, and the overall rate of attack in half an hour provided the response variable of the experiment. We also measured the total traffic flow (number of ants passing a point on the trail per unit time) and trail width, which were entered as covariates in the statistical analyses (see below). Four treatment levels were applied to each trail as follows.

(1) The ‘no-obstruction’ treatment functioned as the control (Fig. 2a). The wire was high enough (2 cm) that laden ants could pass underneath without hindrance.

(2) The ‘obstruction’ treatment was intended to hinder the passage of laden ants without stopping them entirely, while being sufficiently high that nonladen ants would not directly encounter it (Fig. 2b). The wire was 0.9–1.2 mm above the ground, conforming with the contours of the trail floor as much as possible. The obstruction treatment achieved the desired effect: laden ants in the obstruction treatment transited the apparatus on average 30.72% slower (see Results) than in the no-obstruction treatment, while unladen ants were not significantly affected. Despite the delay to

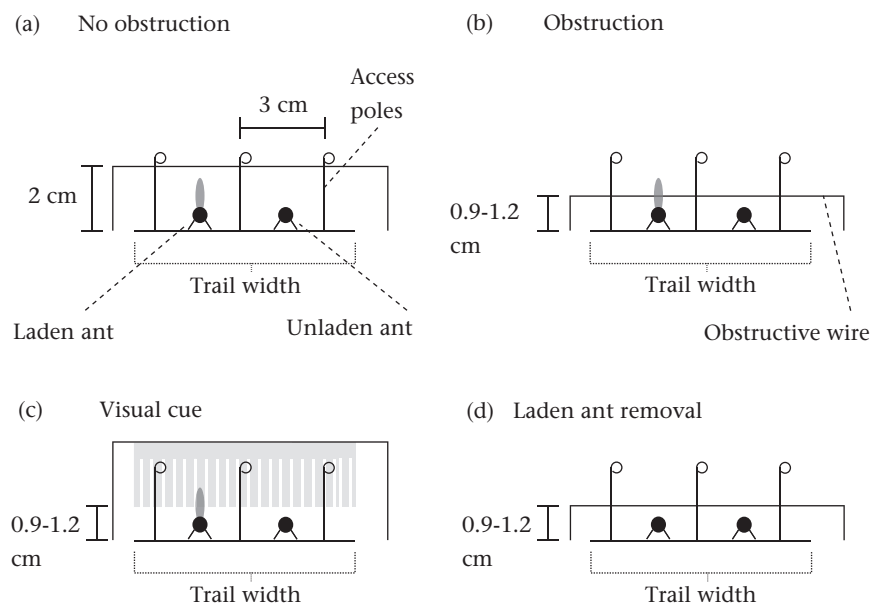


Figure 2. (a) No-obstruction treatment: the cross wire was high enough to allow laden ants to pass underneath without hindrance. (b) Obstruction treatment: the cross wire was low enough that laden ants were hindered by its presence, but unladen ants were not. (c) Visual cue treatment: light plastic strips hung down to the same height as an obstruction in the obstruction treatment, but laden ants were able to pass through without hindrance. (d) Laden ant removal treatment: laden ants were removed from the trail.

them, laden ants did not participate in trail clearance, nor did caches of dropped leaf fragments form at the site.

(3) The 'visual cue' treatment was intended to provide a strong visual stimulus to the ants while not significantly hindering the progress of laden ants. This was achieved by hanging thin white plastic strips (Fig. 2c) from the horizontal wire, so that they fell to the same height as the laden ant obstruction. However, in contrast to the solid wire of the laden ant obstruction, laden ants could easily brush through the hanging strips. There was no significant effect on speed compared with the no-obstruction treatment (see Results).

(4) The 'laden ant removal treatment' was used to test whether the presence of laden ants was necessary for the clearance of trail height or whether an indirect effect such as experience could be responsible. For this treatment, we attempted to remove all the returning laden ants from the trail. The wire obstruction was set at 0.9–1.2 mm cm above the trail (i.e. at the same height as in the laden ant obstruction treatment; Fig. 2d). Two wire mesh barriers upstream of the experimental apparatus temporarily obstructed both laden and unladen ants, but had a much greater effect on laden ants, allowing any laden escapees to be removed by hand. It was common for laden ants to drop leaf fragments while being obstructed and often these ants would continue inbound along the trail, leaving their leaf fragment behind. While the vast majority of the laden ants were prevented from traversing the experiment, a small number did slip through. These were mostly carrying very small pieces of plant material.

The treatments were applied in random order, except for the laden ant removal treatment, which was always applied last because this treatment involved significant trail disruption and, had it been run before the other replicates, could have affected traffic movement for subsequent replicates. Furthermore, this ordering would reveal an 'experience effect'. In this scenario, leaf-laden ants might pass through an obstruction, drop their load either upon arrival at the fungus garden or before, then return along the cleared trail and encounter the obstruction that they had previously passed through. The previous encounter with the obstruction as a laden ant might then trigger the ant, now unladen, to clear the obstacle. If there were an 'experience effect' that elevated attack rate when laden ants passed through the experiment and returned, we would expect to see its strongest presence in the treatment that was always applied last (i.e. the laden ant removal treatment). The other treatments had only mild and immediate effects on the traffic flow.

In addition to the number of attacks on the wire barrier, we also recorded the speed at which ants transited from one side of the apparatus to the other across a fixed distance, usually 10 cm, but on one occasion it was 6 cm, another 7 cm, and another 9 cm. For each treatment, we recorded transit times for two randomly selected ants from each of the following classes of ant: outbound and unladen, inbound and unladen, and inbound and laden. For the laden ant removal treatment, we did not record transit times for the 'inbound and laden' class as there were few to no laden ants on the trail. Flow was obtained by randomly choosing one random minute per treatment and counting all ants that passed an imaginary centre line.

Statistical Analysis

We used an ANOVA followed by a post hoc Tukey's test to compare the mean speed during transit of laden and unladen ants among the four treatment levels (with the exception that there were no laden ants in the laden ant removal treatment). The purpose of this test was to verify the efficacy of the experimental obstruction.

We used an ANCOVA to compare the effect of the four treatment levels on the rate of clearing attacks on the obstruction, with traffic flow and trail width as covariates. Homogeneity of slopes among all four treatments was checked and found to be consistent with the assumptions of ANCOVA. Flow was a relevant covariate because more ants passing the experimental apparatus may produce a larger number of clearance attacks. Trail width is a surrogate that captures characteristics of usage not captured by flow, such as whether the trail was a main or peripheral trail.

We calculated a Tukey–Kramer multiple comparison test for ANCOVA for post hoc analysis of treatment differences in the clearance attack rate (Huitema, 2001). Statistical analyses were performed with R (R Development Core Team, 2012) and SYSTAT 10 (Systat Inc., Chicago, IL, U.S.A.).

Ethical Note

This work was performed with permission of the Smithsonian Tropical Research Institute and the Ministry of the Environment of the Panamanian government. The field manipulations were analogous to leaf-falls or branch-falls that leaf-cutting ant colonies regularly experience, and individual ants were not harmed. Trail foraging rapidly returned to normal following the experiment.

RESULTS

The mean (\pm SD) speed of laden ants during transit of the experimental apparatus was significantly slower for the obstruction treatment (2.03 ± 0.97 cm/s, $N = 50$) than for the no-obstruction (2.93 ± 1.05 cm/s, $N = 52$) or visual cue (2.87 ± 0.89 cm/s, $N = 52$) treatments, while the transit speeds in the latter two treatments did not differ significantly from each other (ANOVA: $F_{2,151} = 6.734$, $P < 0.001$, with Tukey's post hoc tests to confirm pairwise differences at an overall significance level of 0.05). None of the experimental placements interfered with the locomotion of inbound and outbound unladen ants, which maintained statistically indistinguishable mean speeds among treatments (ANOVA: $F_{3,406} = 1.404$, $P = 0.241$): obstruction (3.18 ± 1.37 cm/s, $N = 100$), no obstruction (3.39 ± 1.38 cm/s, $N = 112$), visual cue (3.21 ± 1.20 cm/s, $N = 102$), laden ant removal (3.52 ± 1.29 cm/s, $N = 96$).

The rate of clearing attacks on barriers for all colonies was linearly related to traffic flow ($F_{1,97} = 7.24$, $P = 0.0084$) and trail width ($F_{1,97} = 60.36$, $P < 0.001$). Statistically controlling for these effects, we found that the attack rate on experimental barriers differed significantly between treatments (ANCOVA: $F_{3,97} = 9.53$, $P < 0.001$). There was a significantly higher rate of clearing attacks in the obstruction treatment than in any other treatment (Tukey test:

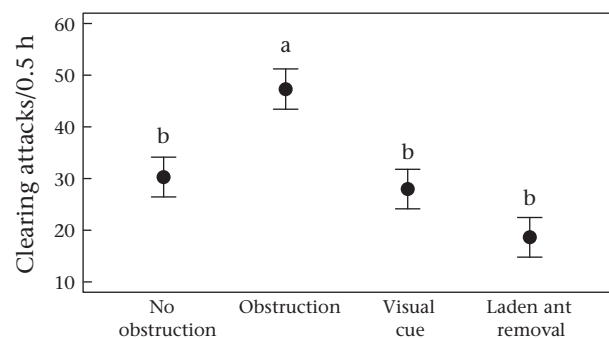


Figure 3. Adjusted mean and standard error of clearing attacks over half an hour for all colonies and all treatments with a post hoc Tukey–Kramer test ($N = 26$).

$P < 0.05$), but no significant differences between the remaining treatments (Fig. 3). The overall ANCOVA model had an adjusted R^2 of 0.51. The significantly higher rate of attack in the obstruction treatment remained true in the analysis of the BCI colony alone, and in addition the attack rate was significantly lower in the laden ant removal treatment than in the no-obstruction treatment (see Appendix).

DISCUSSION

The results demonstrate that unladen ants attempt to remove an overhead obstruction at a significantly higher rate when their laden colony-mates are slowed by an obstruction (Fig. 3). Unladen ants were not simply responding at a fixed rate to any potential barrier on or above the trail regardless of whether laden ants were affected, as shown by the significantly higher rate of clearing attacks for the obstruction treatment compared to the no-obstruction treatment (Fig. 3). Secondly, ants are not stimulated to clear overhead obstacles purely by the visual cues of an obstruction at a low height. If they were, then the visual cue apparatus would have been attacked at the same rate as the obstruction in the laden ant obstruction treatment, but it was not (Fig. 3). Finally, unladen ants attempted to clear overhead obstructions because of the immediate effect of obstructions on their laden nestmates and likely not because of previously experiencing the apparatus as laden ants or any other indirect effect. This is demonstrated by the significantly lower rate of clearing attacks in the laden ant removal treatment than in the obstruction treatment, despite the presence of identical barriers at identical heights (Fig. 3). It would be economically efficient, of course, for unladen workers to refrain from height clearance if there were no laden ants using a trail.

Ant trails function as conduits for communication that facilitate foraging. Information is normally thought to flow downstream or upstream along foraging trails (Farji-Brener et al., 2010; Traniello & Robson, 1995; Wilson, 1962), but trail obstructions are local problems that require a localized signal and response for their efficient resolution. We have shown that information about overhead obstructions is acquired locally by unladen *A. colombica* workers, even though they do not experience it as an obstruction. Their response depends on a functional impairment experienced by their nestmates. A graded response that matches the degree of impairment would allow a colony to manage efficiently its investment in transport infrastructure, matching investment to colony-level goals rather than to individual experience. This modulation of function is part of how leaf-cutting ant trails reach the level of sophistication that they do.

What could be the stimulus that triggers the clearing of trail height in leaf-cutting ants? When laden ants are delayed by some obstacle, the momentary congestion may also slow the transit speed of unladen ants. The reduction in their own speed could then stimulate some unladen ants to switch from traversing the trail to clearing any immediate obstacles and possibly to search for obstacles further afield. However, we found no significant difference in mean speed during transit for unladen ants amongst any of the treatments. Therefore, this explanation does not appear likely.

Alternatively, unladen ants could be sensitive to encounter rates, which have been shown to be important in the regulation of other ant colony functions in previous work (Czaczkes, Franz, Witte, & Heinze, 2015; Czaczkes, Grüter, & Ratnieks, 2013; Deneubourg, Lioni, & Detrain, 2002; Depickère, Fresneau, & Deneubourg, 2004, 2008; Gordon, Paul, & Thorpe, 1993; Jeanson, Deneubourg, Grimal, & Theraulaz, 2004). It is possible that unladen workers increase their clearing attacks when they experience a high

encounter rate with either laden or unladen nestmates at the traffic jam. Under this scenario, the hindering of laden ants causes their speed to reduce and their density to increase, thus increasing the rate at which unladen workers encounter them at the site of disturbance (Dussutour et al., 2009). Furthermore, if an obstacle reduces the returning traffic flow between itself and the nest, it would increase the contrast between encounter rates that outbound ants experience when they come upon the obstacle. Under this mechanism, investment in the removal of obstructions could be made proportional to the degree of delay imposed on laden foragers.

Finally, there may be some form of direct communication from laden ants to unladen ants indicating their obstruction. For example, the laden ants may be releasing a pheromone when they are obstructed that alerts unladen ants to a problem and triggers an increase in their clearing rate. Direct communication through antennation or other tactile contact may also transfer such information. Further studies will be required to test these hypotheses.

Dussutour et al. (2009) showed that laboratory colonies of leaf-cutting ants would adapt to an overhead obstruction by reducing leaf fragment size and increasing the number of workers on a foraging trail. This response would allow a colony to maintain its rate of leaf tissue harvesting despite the overhead trail obstruction. However, one might expect that investment in cleared trail height would be more profitable than adjusting fragment size to the constraints of the trail; a small number of ants can clear a trail for a very large number of nestmates, whereas reduction in fragment size imposes an inefficiency on each forager individually. Leaf fragment sizes are normally highly tuned for efficient carriage (Burd, 2000; Burd & Howard, 2005; Lewis, Martin, & Czaczkes, 2008; Röschar & Roces, 2002; Rudolph & Loudon, 1986), and imposing height restrictions would impede this process. Therefore, a small investment in trail construction work is likely to have a very large payoff in foraging efficiency. This effect is also likely to be present in tunnels, explaining why foraging tunnels are both wide and high enough to allow unrestricted flow of leaf-carrying ants (Burd & Howard, 2005; Moreira, Forti, Andrade, et al., 2004). Indeed, we suggest that the system of clearing trail height is likely to be the same as that for tunnels. There is a similarity of physical characteristics between trail overhangs and tunnels (Fig. 1), especially foraging tunnels, which can be both high and wide (Moreira, Forti, Boaretto et al., 2004). Furthermore, trail height investment does not appear to require visual stimulus, which would not be available in deep, lightless tunnels. It may be that trail construction is an extension of tunnel-digging behaviour laid out over two dimensions instead of three.

Investigations into information asymmetry have long been part of economics (Akerlof, 1970; Spence, 1973; Stiglitz & Weiss, 1981). In humans, an asymmetry of information is often presented as an opportunity for one party to exploit another (Akerlof, 1970; Dawson, Watson, & Boudreau, 2010; Leland, 1979; Mocan, 2006). The struggle in coordinating collective behaviour in human groups lies in aligning competing interests, but, once aligned, the communication and cognitive tools available to coordinate individuals are sophisticated and plentiful. By contrast, the eusocial nature of ants means that their interests are already aligned, but communication and cognition systems are comparatively limited. In leaf-cutting ants, we see a self-organized system using local information to resolve a mismatch between a group with information but no capacity to solve a problem (laden ants), and another group with capacity but no information (unladen ants). The resolution of this imbalance helps to create a smoothly functioning system despite difficult terrain.

Acknowledgments

This work was supported by Monash University Dean's Scholarship to A.I.B. Thanks go to the Smithsonian Institute for providing access to Barro Colorado Island. T.J.C. was funded by an Alexander von Humboldt postdoctoral fellowship and a DFG Emmy Noether group leader grant (grant number CZ 237/1-1).

References

- Aboody, D., & Lev, B. (2000). Information asymmetry, R&D, and insider gains. *Journal of Finance*, 55(6), 2747–2766.
- Akerlof, G. A. (1970). The market for 'lemons': Quality uncertainty and the market mechanism. *Quarterly Journal of Economics*, 84(3), 488–500.
- Balakrishnan, S., & Koza, M. P. (1993). Information asymmetry, adverse selection and joint-ventures: Theory and evidence. *Journal of Economic Behavior & Organization*, 20(1), 99–117.
- Biesmeijer, J. C., & Seeley, T. D. (2005). The use of waggle dance information by honey bees throughout their foraging careers. *Behavioral Ecology and Sociobiology*, 59(1), 133–142. <http://dx.doi.org/10.1007/s00265-005-0019-6>.
- Bochynek, T., Meyer, B., & Burd, M. (2017). Energetics of trail clearing in the leaf-cutter ant *Atta cephalotes*. *Behavioral Ecology and Sociobiology*, 71(1), 1–10. <http://dx.doi.org/10.1007/s00265-016-2237-5>.
- Bollazzi, M., & Rocas, F. (2011). Information needs at the beginning of foraging: Grass-cutting ants trade off load size for a faster return to the nest. *PLoS One*, 6(3), e17667.
- Bruce, A. I., & Burd, M. (2012). Allometric scaling of foraging rate with trail dimensions in leaf-cutting ants. *Proceedings of the Royal Society B: Biological Sciences*, 279(1737), 2442–2447.
- Burd, M. (2000). Body size effects on locomotion and load carriage in the highly polymorphic leaf-cutting ants *Atta colombica* and *Atta cephalotes*. *Behavioral Ecology*, 11(2), 125–131.
- Burd, M., & Howard, J. J. (2005). Global optimization from suboptimal parts: Foraging sensu lato by leaf-cutting ants. *Behavioural Ecology and Sociobiology*, 59(2), 234–242.
- Camazine, S., Deneubourg, J. L., Franks, N. R., Sneyd, J., Theraulaz, G., & Bonabeau, E. (2001). *Self-organization in biological systems*. Princeton, NJ: Princeton University Press.
- Czaczkes, T. J., Franz, S., Witte, V., & Heinze, J. (2015). Perception of collective path use affects path selection in ants. *Animal Behaviour*, 99, 15–24.
- Czaczkes, T. J., Grüter, C., & Ratnieks, F. L. W. (2013). Negative feedback in ants: Crowding results in less trail pheromone deposition. *Journal of Royal Society, Interface*, 10, 20121009. <http://dx.doi.org/10.1098/rsif.2012.1009>.
- Dawson, G. S., Watson, R. T., & Boudreau, M. (2010). Information asymmetry in information systems consulting: Towards a theory of relationship constraints. *Journal of Management Information Systems*, 27(3), 143–178.
- Deneubourg, J. L., Lioni, A., & Detrain, C. (2002). Dynamics of aggregation and emergence of cooperation. *Biological Bulletin*, 202(3), 262–267.
- Depickère, S., Fresneau, D., & Deneubourg, J. L. (2004). A basis for spatial and social patterns in ant species: Dynamics and mechanisms of aggregation. *Journal of Insect Behavior*, 17(1), 81–97.
- Depickère, S., Fresneau, D., & Deneubourg, J. L. (2008). Effect of social and environmental factors on ant aggregation: A general response? *Journal of Insect Physiology*, 54(9), 1349–1355.
- Doherty, A. M. (1999). Explaining international retailers' market entry mode strategy: Internalization theory, agency theory and the importance of information asymmetry. *International Review of Retail, Distribution and Consumer Research*, 9(4), 379–402.
- Dussutour, A., Deneubourg, J. L., Beshers, S. N., & Fourcassié, V. (2009). Individual and collective problem-solving in a foraging context in the leaf-cutting ant *Atta colombica*. *Animal Cognition*, 12(1), 21–30.
- Farji-Brener, A. G., Amador-Vargas, S., Chinchilla, F., Escobar, S., Cabrera, S., Herrera, M., et al. (2010). Information transfer in head-on encounters between leaf-cutting ant workers: Food, trail condition or orientation cues? *Animal Behaviour*, 79, 343–349.
- Farji-Brener, A. G., Chinchilla, F., Umaña, M. N., Oscasio-Torres, M., Chauta-Mellizo, A., Acosta-Rojas, D., et al. (2015). Branching angles reflect a tradeoff between reducing trail maintenance costs or travel distances in leaf-cutting ants. *Ecology*, 96(2), 510.
- FitzGibbon, C. D., & Fanshawe, J. H. (1988). Stotting in Thomson's gazelles: An honest signal of condition. *Behavioral Ecology and Sociobiology*, 23(2), 69–74.
- Franks, N. R., Mallon, E. B., Bray, H. E., Hamilton, M. J., & Mischler, T. C. (2003). Strategies for choosing between alternatives with different attributes: Exemplified by house-hunting ants. *Animal Behaviour*, 65, 215–223.
- Gordon, D. M., Paul, R. E., & Thorpe, K. (1993). What is the function of encounter patterns in ant colonies? *Animal Behaviour*, 45, 1083–1100.
- Healy, P. M., & Palepu, K. G. (2001). Information asymmetry, corporate disclosure, and the capital markets: A review of the empirical disclosure literature. *Journal of Accounting and Economics*, 31(1), 405–440.
- Hobbs, J. E. (2004). Information asymmetry and the role of traceability systems. *Agribusiness*, 20(4), 397–415.
- Hölldobler, B., & Wilson, E. O. (1990). *The ants*. Cambridge, MA: Belknap Press.
- Howard, J. J. (2001). Costs of trail construction and maintenance in the leaf-cutting ant *Atta colombica*. *Behavioral Ecology and Sociobiology*, 49(5), 348–356.
- Huitema, B. E. (2001). *The analysis of covariance and alternatives: Statistical methods for experiments, quasi-experiments, and single-case studies*. Hoboken, NJ: Wiley.
- Jaffe, K., & Howse, P. E. (1979). The mass recruitment system of the leaf cutting ant, *Atta cephalotes*. *Animal Behaviour*, 27, 930–939.
- Jeanson, R., Deneubourg, J. L., Grimal, A., & Theraulaz, G. (2004). Modulation of individual behavior and collective decision-making during aggregation site selection by the ant *Messor barbarus*. *Behavioral Ecology and Sociobiology*, 55(4), 388–394.
- Leland, H. E. (1979). Quacks, lemons and licensing: A theory of minimum quality standards. *Journal of Political Economy*, 87(6), 1328–1346.
- Lewis, O. T., Martin, M., & Czaczkes, T. J. (2008). Effects of trail gradient on leaf tissue transport and load size selection in leaf-cutter ants. *Behavioral Ecology*, 19(4), 805–809.
- Lewis, T., Pollard, G. V., & Dibley, G. C. (1974). Rhythmic foraging in the leaf-cutting ant *Atta cephalotes* (L.) (Formicidae: Attini). *Journal of Animal Ecology*, 43(1), 129–141.
- Mocan, N. (2006). Can consumers detect lemons? An empirical analysis of information asymmetry in the market for child care. *Journal of Population Economics*, 20(4), 743–780.
- Moreira, A. A., Forti, L. C., Andrade, A. P. P., Boaretto, M. A. C., & Lopes, J. (2004a). Nest architecture of *Atta laevigata* (F. Smith, 1858) (Hymenoptera: Formicidae). *Studies on Neotropical Fauna and Environment*, 39(2), 109–116.
- Moreira, A. A., Forti, L. C., Boaretto, M. A. C., Andrade, A. P. P., Lopes, J. F. S., & Ramos, V. M. (2004b). External and internal structure of *Atta bisphaerica* Förl (Hymenoptera: Formicidae) nests. *Journal of Applied Entomology*, 128(3), 204–211.
- Powell, S., & Clark, E. (2004). Combat between large derived societies: A subterranean army ant established as a predator of mature leaf-cutting ant colonies. *Insectes Sociaux*, 51(4), 342–351.
- R Development Core Team. (2012). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Röschard, J., & Rocas, F. (2002). The effect of load length, width and mass on transport rate in the grass-cutting ant *Atta vollenweideri*. *Oecologia*, 131(2), 319–324.
- Rudolph, S. G., & Loudon, C. (1986). Load size selection by foraging leaf-cutter ants (*Atta cephalotes*). *Ecological Entomology*, 11(4), 401–410.
- Scott-Phillips, T. C. (2008). On the correct application of animal signalling theory to human communication. *Proceedings of the International Conference on the Evolution of Language*, 7, 275–282.
- Shepherd, J. D. (1982). Trunk trails and the searching strategy of a leaf-cutter ant, *Atta colombica*. *Behavioral Ecology and Sociobiology*, 11(2), 77–84.
- Spence, M. (1973). Job market signaling. *Quarterly Journal of Economics*, 87(3), 355–374.
- Stiglitz, J. E., & Weiss, A. (1981). Credit rationing in markets with imperfect information. *American Economic Review*, 71(3), 393–410.
- Traniello, J. F. A., & Robson, S. K. (1995). Trail and territorial communication in social insects. In R. T. Cardé, & W. J. Bell (Eds.), *The chemical ecology of insects* (Vol. 2, pp. 241–286). New York, NY: Chapman & Hall.
- Wagner, W. E. (1992). Deceptive or honest signalling of fighting ability? A test of alternative hypotheses for the function of changes in call dominant frequency by male cricket frogs. *Animal Behaviour*, 44, 449–462.
- Wilson, E. O. (1962). Chemical communication among workers of the fire ant *Solenopsis saevissima* (Fr. Smith) 1. The organization of mass-foraging. *Animal Behaviour*, 10, 134–147.

Appendix

Analysing colonies separately, the main colony ($N = 23$) had a rate of clearing attacks, when workers lunged at or contacted the wire or mock barrier with their mandibles and attempted to cut it, that was linearly related to traffic flow ($F_{1,85} = 7.06$, $P = 0.009$) and trail width ($F_{1,85} = 61.43$, $P < 0.001$). Statistically controlling for these effects, we found that the attack rate of experimental barriers differed significantly between treatments (ANCOVA: $F_{3,85} = 7.68$, $P < 0.001$). There was a significantly higher rate of clearing attacks in the obstruction treatment than in any other treatment (Tukey test: $P < 0.05$), and also a significant difference between the laden ant removal treatment and the no-obstruction and visual cue treatments (Fig. A1). The overall ANCOVA model had an adjusted R^2 of 0.53. While there were insufficient replicates to perform a similar statistical analysis for the remaining two colonies ($N = 3$), the visual appearance of the trends appeared much the same (Fig. A2). This gave us sufficient confidence to combine the two data sets and perform the final data analysis.

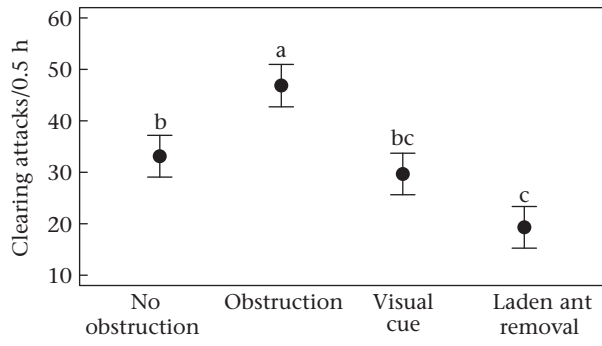


Figure A1. Adjusted mean and standard error of clearing attacks over half an hour for the main colony only with all treatments and a post hoc Tukey–Kramer test ($N = 23$).

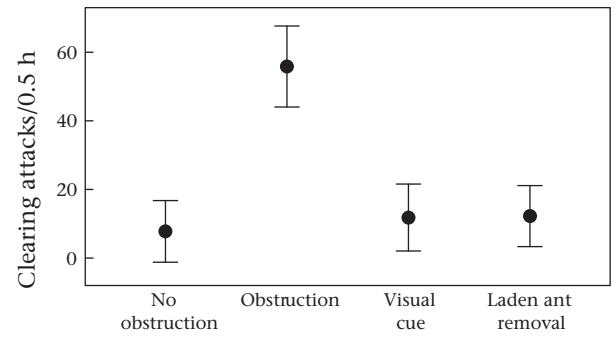


Figure A2. Adjusted mean and standard error of clearing attacks over half an hour for the two additional colonies with all treatments ($N = 3$).