



How a few help all: living pothole plugs speed prey delivery in the army ant *Eciton burchellii*

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We investigated an extreme behavioural specialization in the army ant *Eciton burchellii*. The spectacular group raids of these ants, which can contain up to 200 000 workers, always remain connected to the nest by a 'principal trail' of forager traffic. Remarkably, some workers use their bodies to plug potholes in the natural surfaces that the principal trail travels over, to provide a partly living surface for their nest-mates to use. We found that this highly specialized behaviour results in a clear net benefit to the colony. Our experiments show that foragers do not discriminate against surfaces that force all individuals to run as slowly as the smallest workers, but that this prompts some ants to plug neighbouring low-quality surfaces. Individuals size-match to the hole they plug and cooperate to plug larger holes. The resulting modified surface allows prey-laden foragers to attain maximum speed. Overall, this results in a strong positive relationship between ant size and speed and an increase in the mean speed of prey-laden traffic. Moreover, calculations suggest that under a range of realistic scenarios, plugging behaviour results in a clear increase in daily prey intake. Broadly, our study provides rare quantitative evidence that extreme specialization by a minority can significantly improve the performance of a majority, and benefit the group as a whole. It also suggests, however, that these benefits are a consequence of the unusual and derived foraging strategy of *E. burchellii*. This highlights the importance of considering ecology and evolutionary history in the study of social organization in animal societies.

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Individual specialization underpins the complex social organization within eusocial insect societies (reviewed in: Oster & Wilson 1978; Hölldobler & Wilson 1990; Bourke & Franks 1995). This specialization is most evident in the sophisticated and diverse patterns of division of labour among workers, which results from different individuals specializing on different subsets of colony-related tasks (reviewed in: Hölldobler & Wilson 1990; Bourke & Franks 1995). The mechanisms that generate these organizational patterns within the work force have been studied in depth (reviewed in: Beshers & Fewell 2001), but why particular specializations have evolved, and why they often differ

considerably between species have received far less attention, particularly from empiricists (see reviews in: Hölldobler & Wilson 1990; Bourke & Franks 1995). Theory predicts that a particular pattern of specialization will evolve only if it yields a net benefit to colony efficiency (Oster & Wilson 1978). Yet the cost–benefit trade-off of a particular specialization almost certainly varies with ecology, and may be further affected by phylogenetically constrained aspects of a species' basic biology. Empirical studies that address the quantitative benefits of specialization within the work force whilst also taking into account the ecology and evolutionary history of focal species are scarce (but see Foster 1990; Matsuura 2002; Perry et al. 2004 for morphological specialization). However, studies of this kind promise new general insights into the evolution of social organization. First, they promise a better understanding of how and why individual specialization affects the behaviour of others and the efficiency of the group as a whole. Second, they can help elucidate the importance

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of ecology and basic biology in the evolution of particular specializations and, thus, why they have evolved in some taxa and not in others.

Ants arguably display the most diverse patterns of colony organization among eusocial insect taxa, providing a rich choice of specialized behaviours to study. Broadly, the subset of tasks that ant workers specialize on is either correlated with their age category ('temporal polyethism'; see Franks et al. 1997; Robson & Beshers 1997; Traniello & Rosengaus 1997; Beshers & Fewell 2001 for discussion and review) or based on their size and shape ('size polyethism'; reviewed in: Hölldobler & Wilson 1990), or both. Yet on closer inspection, individuals often show flexible task switching within and among their specialized task subset, and these patterns can vary considerably among individuals, colonies and species (reviewed in: Bourke & Franks 1995; Gordon 1996). This means that quantifying and understanding the benefits of any particular pattern of specialization and comparing these complex patterns among species is extremely challenging. In many species, however, there are some members of the work force that specialize on a particular task for hours without switching, or with unusually high frequency throughout their lives (e.g. Dejean & Lachaud 1991; Sendova-Franks & Franks 1994, 1995; Julian & Cahan 1999; Hart & Ratnieks 2002; Powell & Franks 2005; Vieira-Neto et al. 2006). Empirical studies of the benefits of this kind of extreme specialization should be more tractable than studies of more complex patterns of specialization, but they may still offer general insights. Indeed, they may yield particularly useful insights if the focal specialization can be manipulated in the field, to provide a natural ecological setting, and it is not seen in closely related species, providing a phylogenetic context for interpreting results.

Our focus here is on an extreme specialization found in the army ant *Eciton burchellii* (spelling follows Bolton 1995), where some workers use their bodies to fill potholes in natural surfaces, creating a new, partly living substrate for their nestmates to travel over.

Eciton burchellii colonies can contain up to 700 000 workers that vary considerably in size and shape (Franks 1985; Powell & Franks 2006), and in addition to being obligate group predators, they are nomadic, cycling between well-defined nomadic and stationary phases (Schneirla 1971; Teles da Silva 1977; Franks & Fletcher 1983). A diurnal raid is conducted every day in the 15-day nomadic phase and on about half of the days in the 20-day stationary phase, and each raid contains about one-third of the work force (Willis 1967; Franks & Fletcher 1983). The raid structure is generated via self-organizing processes (Franks et al. 1991), and prey is captured at the raid front or 'swarm', which is a continuous carpet of foragers that can be over 10 m wide (Schneirla 1971). As the swarm advances it leaves in its wake a network of forager trails that consolidate into a 'principal trail' that always stays connected to the nest. This trail provides an established route for inbound ants to deliver prey and outbound ants to return to the swarm, and it can stretch over 100 m by the time the raid ends at dusk (Schneirla 1971). The traffic on the principal trail can be up to 12 ants wide, and it can also fluctuate considerably, from 3 to 12 ants in width

(Rettenmeyer 1963). Yet, despite the heavy and variable trail traffic, a strong positive relationship between ant size and speed is maintained throughout the day (Powell & Franks 2005), and the speeds attained are greater than those seen in ants outside the subfamily Ecitoninae (Hurlbert et al., in press). The consistently high and size-related speed attained by *E. burchellii* foragers is even more remarkable given that the principal trail is not stable from day to day, because colonies never immediately raid the same area twice (Franks & Fletcher 1983). Instead, the principal trail is established anew each day over the mixture of decaying leaves, twigs and branches on the forest floor. The ants find a reasonably smooth composite surface over which to run, but these makeshift highways contain many gaps and potholes along their length, until, that is, some individuals use their bodies to fill them.

The ant structures that form along the principal trails of *E. burchellii* can contain one to many tens of individuals and can increase in size and number during colony emigrations. However, similar structures are rare or absent in the raids of other *Eciton*, even though all congeners share the same basic biology (Schneirla 1971). The simplest and most common of these structures are what we define here as 'plugs', which are composed of one or more ants that all retain contact with the substrate. Plugs are usually present on almost every metre of principal trail throughout the day and can reach high densities in areas with rough leaf litter (Schneirla 1971; S. Powell, personal observation). We sought to answer the following key questions with respect to plugging behaviour. How do plugs form? When do plugs form? How do plugs affect the behavioural performance of other foragers? And, how do plugs benefit the foraging efficiency of *E. burchellii* colonies? To answer these questions, we conducted a series of field-based experiments and an analytical study that explored the net benefits of this specialized behaviour at the colony level.

MATERIALS AND METHODS

Focal Species, Study Site and Experimental Apparatus

The focal species was *Eciton burchellii foreli*, and all data were collected on Barro Colorado Island (BCI), Panama. All studies were conducted with experimental apparatus that allowed the type of surface used by foragers to be manipulated (Fig. 1a). In each case, the experimental apparatus was inserted into the principal trail and the forager traffic redirected over it, such that the apparatus replaced the natural surfaces previously used by the ants at that location. Once traffic returned to normal, the initial surface was replaced by the appropriate experimental surface(s) for the study, causing only limited disturbance. The experimental apparatus was necessary because natural surfaces could not be manipulated to a suitable degree, and even small manipulations caused massive disturbance to the forager traffic. Six types of replaceable surfaces were used in the experiments (Fig. 1b) and their dimensions replicated those of natural surfaces (e.g. fallen twigs and branches, and exposed roots) routinely used by

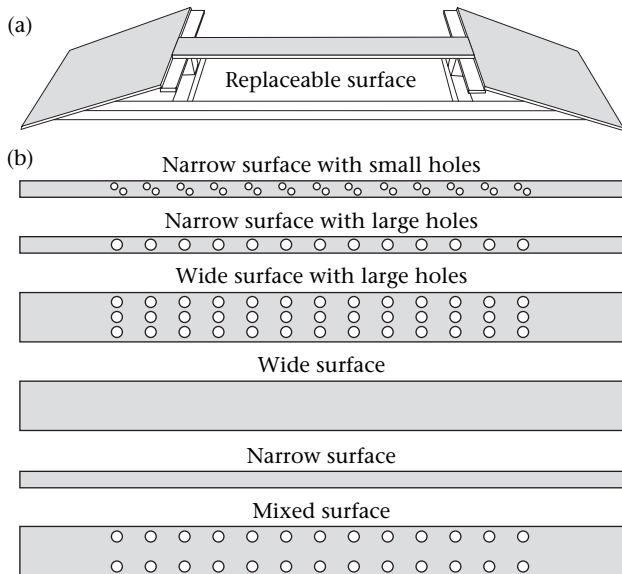


Figure 1. (a) Experimental apparatus with a central replaceable surface and (b) the six types of replaceable surfaces used in experimental studies. All replaceable surfaces were 440 mm long. Wide surfaces were 36 mm wide, and narrow surfaces were 12 mm wide. Holes were drilled in four of the six surfaces in the numbers and arrangements shown. All holes had a diameter of 10 mm, except for those in the 'narrow surface with small holes', which had a diameter of 6 mm. The mixed surface was composed of a central 'narrow surface' bordered on each side by a 'narrow surface with large holes'. Forager traffic ran over the grey surfaces. The inclination of the ramps was 20°.

E. burchellii when establishing a principal trail. Some surfaces had holes drilled through them (either large or small) to mimic insect boreholes and other imperfections that *E. burchellii* workers plug on natural surfaces. For the dimensions of each of the six experimental surfaces, as well as hole size (if present), hole number and hole arrangement, see Fig. 1. Data were collected between 0800 and 1200 hours local time.

Plug Formation and Structure

The behaviours performed by individuals when forming a plug and when exiting a hole were first described from field observations and high magnification video footage. For three colonies, observations were made on natural holes found along the principal trail. For an additional two colonies, holes on the experimental apparatus were observed and filmed. For these two colonies, plugs were repeatedly removed with forceps so that the plug-forming process was repeated. Plugs on the experimental apparatus were also observed and filmed as the forager traffic moving over them was interrupted, prompting the ants to exit the hole they were plugging.

Using the experimental apparatus, plugs were then collected from large (10-mm diameter) and small (6-mm diameter) holes to determine experimentally if the size and number of ants changes with hole size. For each of four colonies, 30 plugs were collected from a narrow surface with large holes, and 30 were collected from a narrow

surface with small holes (Fig. 1b). The surface with small holes was used first for two colonies and used second for the other two colonies, to control for order effects. The paths were wiped down with alcohol and washed with mild detergent and water before use with a new colony. Plugs were collected in multiple passes from one end of a surface to the other, because holes were quickly re-plugged. The right back-leg length (trochanter to last tarsal segment) of each ant was measured to the nearest 0.13 mm, using a dissecting microscope fitted with an ocular micrometer. Back-leg length was chosen as the focal morphological measure for ant size because it is the most relevant to the behaviour (leg length determines the size of hole that can be spanned), and it has a very tight scaling relationship with overall size measured by dry weight (Powell & Franks 2006). The relationship between ant size and hole size was assessed with analysis of variance (ANOVA), with back-leg length of the ants as the dependent variable, and hole size and colony as factors. These data sets did not deviate significantly from the assumptions of ANOVA. The relationship between hole size and number of ants was assessed with log-likelihood ratio tests.

Plugs and Surface Choice

Paired surface-choice experiments were used to address why trail traffic uses surfaces that prompt plugging behaviour. Each of three colonies was given 20 paired choices between a wide surface and a wide surface with large holes, and 20 choices between a narrow surface and a wide surface (Fig. 1b). The first pairing combination provided surfaces with the same dimensions that differed in the presence or absence of holes, while the second combination provided surfaces with the same smooth texture but different dimensions. These two choice pairings were used to address the relative importance of the presence of holes and surface width during the process of surface choice. For each choice trial, the paired surfaces were placed 3 cm apart on the experimental apparatus, on either side of the existing ant trail, which was central (i.e. the centre of the ant trail was 1.5 cm from each of the two paths). This positioning prevented biases associated with the distance from the pheromone of the existing trail on the ramps, and the two surfaces used in each trial were new. 'Pioneers' explored both new surfaces, and the surface across which the first continuous traffic passed was recorded as 'crossed first'. After 5 min, the use of the surfaces by the re-established trail traffic was assessed, with the 'chosen' surface type recorded if only one surface was in use and 'split' recorded if both surfaces had continuous traffic. Within each set of 20 pairings, the left/right positioning was balanced, with the order randomized. Log-likelihood ratio tests were used to first test for biases associated with left/right positioning, and then to test for preferences for different surface types.

Plugs and the Performance of Prey-laden Foragers

Surface type was manipulated experimentally to address how the speed of prey-laden foragers was affected by the

presence of plugs. For each of three colonies, 50 laden foragers were timed over a wide surface, a narrow surface and a mixed surface (Fig. 1b). The wide surface offered the ants ideal properties, the narrow surface offered a smooth but width-limited surface, and the mixed surface offered the same initial properties as the narrow surface but with the opportunity to expand the usable width by plugging the bordering holed surfaces. Sampling bias was avoided by selecting the next forager to pass a predetermined point after the previous sample had been collected. The right back-leg of each timed individual was measured later. Differences in transport speed were assessed with analysis of covariance (ANCOVA), with transport speed as the dependent variable, back-leg length as the covariate, and surface type and colony as factors. These data sets did not deviate significantly from the assumptions of ANCOVA, and the assumption of homogeneity of slopes was tested before running a main factor model.

The Net Benefit of Plugs for the Colony

Eciton burchellii has a well-defined and relatively short period each day to collect prey, before the colony moves to a new location. Daily net gain in the dry weight of prey (G , in mg) was therefore used to explore the benefit of plugs to the colony, and it was calculated as follows:

$$G = I_p - I_n \quad (1)$$

where I_p is the daily intake of prey dry weight with plugging behaviour and I_n is the daily intake of prey dry weight without plugging behaviour. Daily intake without plugging (I_n) was defined as follows:

$$I_n = S_n f N M T \quad (2)$$

where S_n is the mean speed of prey-laden foragers when plugs are not present (m/s), N is the number of ants in the raid, f is the mean fraction of the ants in the raid

that carry prey on a given metre of trail, fN is thus the density of prey-laden ants per metre of principal trail (ants/m), M is the mean dry weight of a prey item transported by each ant (mg/ant), T is the mean duration of a day's raid (s). The daily intake of prey dry weight with plugging behaviour (I_p) was defined as follows:

$$I_p = S_p f (N - P) M T \quad (3)$$

Equation (3) can be rearranged as follows:

$$I_p = S_p f N M T - S_p f P M T \quad (4)$$

where S_p is the mean speed of prey-laden foragers when plugs are present and P is the number of ants forming plugs; thus, fP is the mean density of prey-laden ants per metre of trail that would result from the liberation of ants that formed plugs. $S_p f T = K$, where K is the daily opportunity cost per plug ant, measured in lost prey items. Opportunity cost is therefore defined here as the potential prey items resulting from foraging activities that are lost when the alternative action of plugging is performed. Mean and maximum estimates of K can be calculated from existing data on daily prey intake and mean raid duration (Franks 1983) and the number of ants in the raid (N ; see Table 1 for details), so the second part of equation (4) is equal to PMK . With these modifications to equations (4) and (2), equation (1) can be expanded as follows:

$$G = (S_p f N M T - PMK) - (S_n f N M T) \quad (5)$$

RESULTS

Plug Formation and Structure

These results address the behaviours performed by individuals when forming a plug and exiting a hole, and the relationship between hole size and the size and number of ants that plug them. Figure 2 describes the relatively simple

Table 1. The calculated daily net gain in prey that results from plugging behaviour in *E. burchellii*, with different opportunity cost scenarios and numbers of ants involved in plugging

Daily opportunity cost per plug ant (prey items; K)	Number of ants forming plugs (P)	Proportion of foragers forming plugs (P/N)	Total daily net gain in prey (dry weight, mg; G)	% Daily net gain in prey
0.24 (mean)	1500	0.01	18 083	31
1 (maximum)	1500	0.01	15 643	27
0.24 (mean)	7500	0.05	15 001	26
1 (maximum)	7500	0.05	2803	5
0.24 (mean)	15 000	0.10	11 149	19
1 (maximum)	15 000	0.10	-13 247	-23
0.24 (mean)	30 000	0.20	3445	6
1 (maximum)	30 000	0.20	-45 347	-79

Results of calculations are presented as total daily net gain in prey and percentage daily net gain in prey (italicized columns). Calculations based on equation (5) (see Methods) with the following constants: $S_p = 7.7$ cm/s; $S_n = 5.8$ cm/s; $fN = 16.1$ ants/m, calculated from Q/S_p ($Q = 1.24$ items/s in natural colonies; Franks 1983); $M = 2.14$ mg (Franks 1983); $T = 8$ h (Franks 1983); $N = 150\,000$ ants (the estimated raid population of a mean colony size of 450 000 ants; Franks 1985; S. Powell, unpublished data). Two values were used for K . Mean K was calculated from the mean number of items retrieved per individual in an average-size raid ($K = QT/N = 0.24$ items/ant), whereas the maximum opportunity cost assumed that each ant specializing in plugging would otherwise contribute a whole prey item ($K = 1$). % Daily net gain in prey = $(G/I_n)100$.

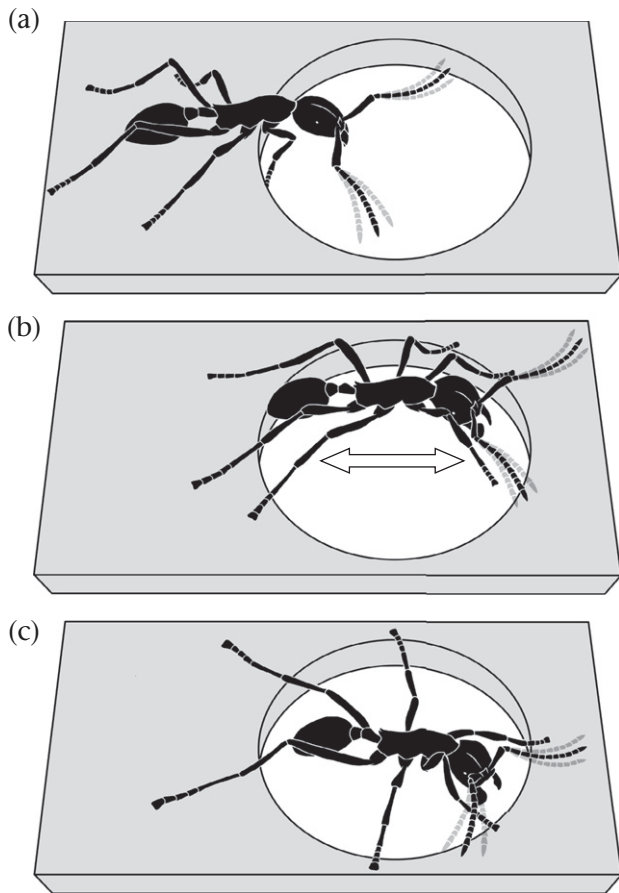


Figure 2. The behaviours performed by individuals when forming a plug and when exiting a hole to re-enter the forager traffic. (a) An unladen ant arriving at a hole first detected its dimensions. (b) The ant then crossed the hole by crawling around the edge, and if other ants travelled over it during this process, it began to spread its legs, while rocking back and forth to detect its fit to the hole. (c) If the ant was an appropriate fit, it then became motionless, except for rapid antennal movement. Ants that were too big to fit into a hole continued without adopting the final motionless posture, and ants that were too small to cross waited until others had plugged the hole or they found an alternative route. Plugs were formed in open holes in less than 30 s, and remained as long as traffic continued to pass over them. When the traffic was interrupted, so that foragers were no longer running over the plugs, the rapid antennal movement of the ant(s) forming the plugs increased, and the ants exited the hole if no traffic was detected for approximately 5 s.

behaviours performed by individuals when forming plugs and when exiting a hole to re-enter the trail traffic. The same behaviours were performed when a plug with more than one ant was formed, except that after the first individual had adopted a static posture, the remaining ants fitted into the space that remained (see Fig. 3c for typical arrangement of a plug with two individuals).

Figure 4 shows that workers matched themselves to the size of the hole that they plugged. The difference between the number of ants in large holes (10-mm diameter) and small holes (6-mm diameter) was highly significant (log-likelihood ratio tests: colony 1: $G_2 = 19.07$, $N = 60$, $P < 0.0001$; colony 2: $G_2 = 13.13$, $N = 60$, $P = 0.0014$; colony 3: $G_2 = 15.52$, $N = 60$, $P = 0.0004$; colony 4:

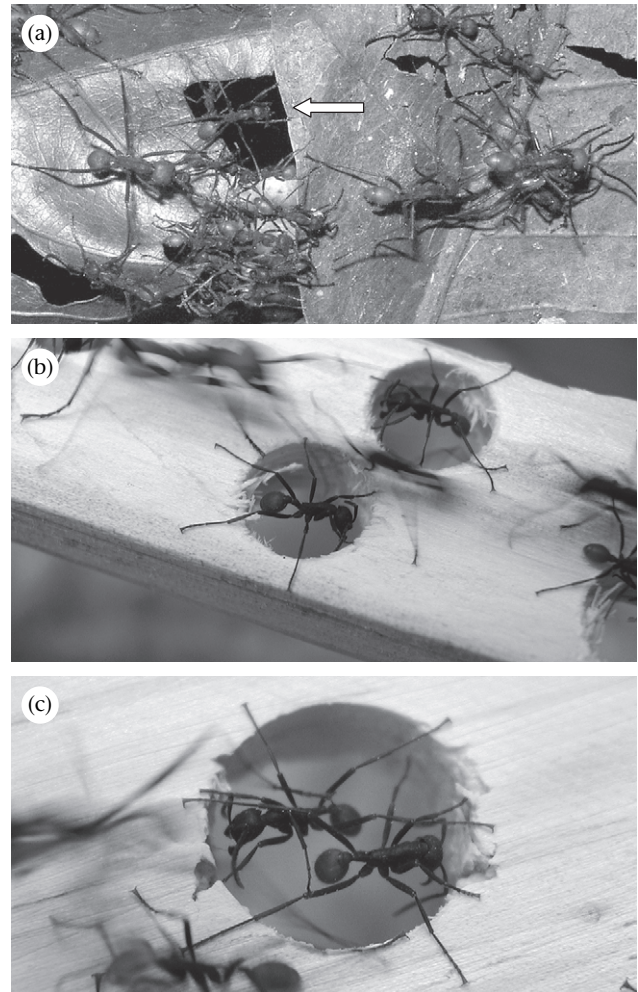


Figure 3. Plugs in the army ant *E. burchellii*. (a) Natural plugs formed in gaps in the leaf litter (arrow indicates most obvious plug). (b) Plugs with single members formed in small holes on the experimental apparatus. (c) A plug with two members in a typical configuration, also in a small hole on the experimental apparatus. In all examples, the individuals forming the plugs remained motionless while forger traffic streamed over them.

$G_2 = 44.06$, $N = 60$, $P < 0.0001$). Plugs composed of two individuals were more common in large holes than in small holes, and plugs with three individuals occurred only in large holes. This finding indicates that in addition to individuals 'size matching' to the size of the hole, they also cooperated to plug bigger holes. Figure 3 shows a plug in a natural hole and typical plugs with one and two individuals on the experimental apparatus.

Plugs and Surface Choice

These data address the preferences of *E. burchellii* for different types of surfaces and, therefore, why the trail traffic uses surfaces that prompt plugging behaviour. Preliminary analyses established that there were no biases associated with the randomized left/right positioning of surface pairings. In the preference tests for surfaces with and without holes, pioneers crossed the wide surface without holes before they crossed the wide surface with holes in all but one

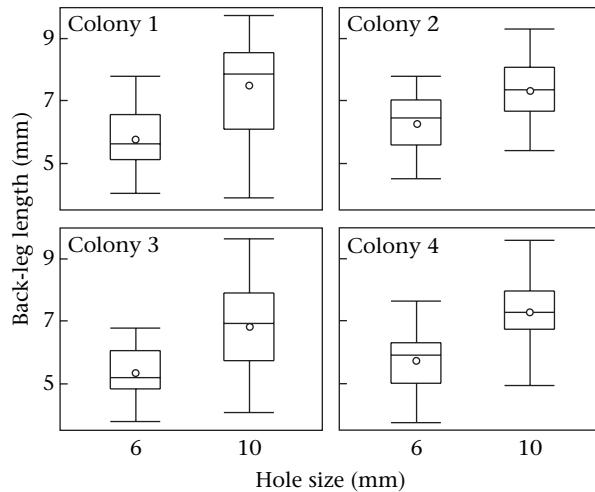


Figure 4. The relationship between hole size and ant size for *E. burchellii* plugs. Hole size had a highly significant effect on the size of ants (represented by back-leg length) that formed plugs (ANOVA: hole size: $F_{1,357} = 135.2$, $P < 0.0001$, $\eta^2 = 27\%$; colony: $F_{3,357} = 6.5$, $P = 0.0003$, $\eta^2 = 5\%$). The ants that plugged the experimental holes did not encompass the full size range of workers in *E. burchellii* (complete range for back-leg length = 3.6–14.6 mm) and never included members of the submajor caste or the major caste found in this species (Powell & Franks 2006). In each box plot, the box encompasses the interquartile range, a line is drawn at the median, a circle represents the mean, and whiskers extend to the minimum and maximum values (nearest value within 1.5 times the interquartile range with no outliers).

of the trials (likelihood ratio tests: no colony differences: $G_2 = 2.2$, $N = 60$, $P = 0.3$; 'crossed first' test with combined data: $G_1 = 73.0$, $N = 60$, $P < 0.0001$), and the general traffic also collectively chose the wide surface without holes rather than the wide surface with holes in all but one of the trials (likelihood ratio tests: no colony differences: $G_2 = 2.2$, $N = 60$, $P = 0.3$; 'surface choice' test with combined data: $G_1 = 73.0$, $N = 60$, $P < 0.0001$). Thus, ants showed a strong preference for smooth surfaces, suggesting that surfaces that require extensive plugging are not chosen if an alternative is available.

When preferences for surface width were assessed, a wide surface was no more likely to be crossed first by pioneers than a narrow surface (log-likelihood ratio tests: no colony differences: $G_2 = 0.9$, $N = 60$, $P = 0.6$; 'crossed first' test with combined data: $G_1 = 0.27$, $N = 60$, $P = 0.61$), and one width was not chosen significantly more than the other (likelihood ratio tests: no colony differences: $G_2 = 0.9$, $N = 60$, $P = 0.6$; 'surface choice' test with combined data: $G_1 = 0.27$, $N = 60$, $P = 0.61$). In all trials, the surface that was crossed first was the one that was subsequently chosen. Thus, for smooth surfaces, width did not influence surface choice, and the traffic was always established on the first smooth surface that was crossed successfully.

Plugs and the Performance of Prey-laden Foragers

These data address how the presence and absence of plugs affect the speed attained by prey-laden foragers.

Surface width did not influence surface choice when the surface was smooth (previous section). However, the narrow surface significantly reduced the speeds attained by prey-laden foragers, compared to the ideal wide surface (ANCOVA: surface type effect: $F_{1,293} = 338.2$, $P < 0.0001$, $\eta^2 = 54\%$; colony effect: $F_{2,293} = 59.9$, $P < 0.0001$, $\eta^2 = 29\%$; Fig. 5). While the narrow surface had properties that would be chosen in nature (previous section), the fact that it was raised clear of other surfaces artificially prevented it from being modified with plugs. As such, it represented a scenario that is rarely encountered with natural narrow surfaces on the forest floor. In contrast, the mixed surface represented a common situation; it provided the same narrow smooth surface, but with bordering low-quality surfaces that could be used once the holes in them had been plugged.

When the ants were made to run over the mixed surface, plugs formed rapidly in the holes, effectively expanding its useable width. With these plugs in place, laden foragers attained significantly faster speeds over the mixed surface than over the narrow surface that prevented plugging (ANCOVA: surface type effect: $F_{1,294} = 300.2$, $P < 0.0001$, $\eta^2 = 51\%$; colony effect: $F_{2,294} = 78.6$, $P < 0.0001$, $\eta^2 = 35\%$; Fig. 5). Moreover, the speeds attained by laden foragers over the plugged mixed surface were only marginally slower than those attained over the ideal wide surface, with differences between colonies explaining more of the variance than surface type (ANCOVA: surface type effect: $F_{1,294} = 6.7$, $P = 0.01$,

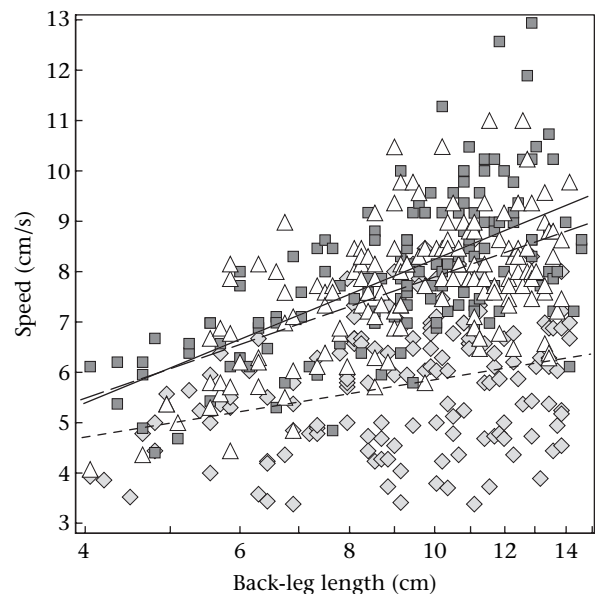


Figure 5. The relationship between the size of prey-laden *E. burchellii* foragers and running speed over three experimental surfaces (■: wide surface; △: mixed surface; ◇: narrow surface). The linear least-squared regression fit is plotted for each surface, and the line equations were as follows: wide surface (solid line): speed = $1.0798014 + 3.1030893 \ln(\text{leg length})$, $R^2 = 0.40$, $P < 0.0001$; mixed surface (dashed line): speed = $1.824828 + 2.6204421 \ln(\text{leg length})$, $R^2 = 0.33$, $P < 0.0001$; narrow surface (dotted line): speed = $2.907206 + 1.2871071 \ln(\text{leg length})$, $R^2 = 0.09$, $P = 0.0002$.

$\eta^2 = 2\%$; colony effect: $F_{2,294} = 22.5$, $P < 0.0001$, $\eta^2 = 13\%$; Fig. 5). Thus, plugging of bordering, low-quality surfaces by a few individuals allowed laden foragers to attain near maximum performance over what would have otherwise been a speed-limiting narrow surface.

Under normal conditions, larger ants can attain their maximum speed because they overtake their smaller, slower nestmates. This results in a strong relationship between ant size and speed (Fig. 5, wide surface and mixed surface; Powell & Franks 2005). However, when the ants used the narrow surface that could not be expanded with plugs, the relationship between ant size and speed became very weak, with larger individuals slowed to almost the same speed as the smallest ants (Fig. 5). This result indicates that when surface width is limited, all prey-laden foragers travel at approximately the same speed, without overtaking.

The Net Benefit of Plugs for the Colony

This analysis addresses how the improved performance of prey-laden foragers, resulting from the formation of plugs, benefits the colony as a whole. Under natural conditions, plugs and other less common ant structures distributed along the principal trail result in a strong positive relationship between the size of prey-laden foragers and the speed that they attain (Powell & Franks 2005; Fig. 5). With this relationship established, our unbiased samples showed that the mean \pm SD speeds of prey-laden foragers over the wide and mixed surfaces were 8.0 ± 1.5 cm/s and 7.7 ± 1.3 cm/s, respectively. For the purposes of the net benefit calculations (based on equation (3)) the slower, more conservative mean speed of 7.7 cm/s was used as the mean speed of prey-laden foragers when plugs were present (S_p). In contrast, our experiments showed that when plugs were not allowed to form, the strong positive relationship between ant size and speed broke down, and all foragers ran at approximately the same speed as the slowest ants (Fig. 5). Accordingly, our unbiased samples from the narrow surface showed that when this occurs, the mean speed of prey-laden foragers drops to 5.8 ± 1.3 cm/s, which is approximately the speed attained by the smallest ants under normal conditions (Powell & Franks 2005; Fig. 5). Given the liberal distribution of plugs along natural principal trails, the lack of plugging behaviour would probably result in a similar collapse of the relationship between ant size and speed throughout the principal trail, all else being equal. For our calculations we therefore used 5.8 cm/s as the mean speed of prey-laden foragers when plugs were not present on the principal trail (S_n).

Our calculations (based on equation (5), see Methods) suggest that the colony accumulates a clear net gain in daily prey intake from plugs, even when the opportunity cost per plug ant (K) is unrealistically high and a nontrivial proportion of the work force specializes in the behaviour (Table 1, maximum opportunity cost, with 5% of the foragers forming plugs). When we used a more realistic opportunity cost in the analysis, plugs still yielded a net gain when a relatively large proportion of the work force

specialized in plugging behaviour (Table 1, mean opportunity cost, 20% of foragers forming plugs).

DISCUSSION

Here we have shown that plugging behaviour in the army ant *E. burchellii* results in a significant improvement in the performance of prey-laden foragers, and that this results in a net benefit for the colony. The foraging ecology of *E. burchellii* is such that in the wake of each day's swarm, a new principal trail back to the nest must be established over the decaying organic material found on the forest floor. Our experiments show that foragers do not discriminate against surfaces that force all individuals to run as slowly as the smallest workers. However, under these conditions some workers plug potholes in bordering, low-quality substrate, both size matching to the hole and cooperating to plug larger holes. The new, partly living surface then allows prey-laden foragers to attain maximum speed, producing a strong positive relationship between ant size and speed, and an overall increase in the mean speed of prey-laden traffic. Our calculations suggest that this increase in forager speed results in a clear net gain in daily prey intake for the colony.

These results strongly suggest that plugging increases foraging efficiency, but to explain the evolution of this specialized behaviour we ultimately need to address how an increase in daily prey intake improves colony fitness. In short, greater daily prey intake in *E. burchellii* is likely to result in faster reproduction. Army ants reproduce by fission at a certain colony size, and *Eciton* colonies grow by producing a synchronized cohort of workers every 35 days, with a daily raid and emigration when the larvae are developing (Schneirla 1971). This strict cycle results in a fixed daily foraging period, and the size of each cohort is almost certainly limited by the amount of fresh prey that can be delivered each day before the colony has to move (Franks 1985; Powell & Franks 2006). The increase in the daily prey intake, resulting from plugging behaviour, should therefore translate into more workers per cycle, and a shorter time to reach fission size.

Broadly, then, our findings provide rare quantitative evidence that extreme specialization by a minority can significantly improve the performance of a majority, and yield a clear net gain in an important resource for the colony. Our study, however, also indicates that the net benefits that are accrued from this specialized behaviour are a consequence of the unusual and derived foraging ecology of this species. This finding stresses the importance of considering ecology and evolutionary history in the study of social organization in eusocial insects, which we will now discuss in more detail.

Focusing first on the behaviours involved in forming plugs, the size matching between ant and hole may make an important contribution to the benefits of this behaviour. Size matching between ant and prey has been reported for a number of species (e.g. Robson & Traniello 1998; Franks et al. 1999; Roschard & Roces 2003; Powell & Franks 2005) and it ensures that the intake of resources is maximized, but why might selection have favoured size

matching in plugs? There are two possibilities that seem likely. First, ants that are too small or too big may create a substandard substrate for others to run over, resulting in slower speeds attained by prey-laden foragers. Second, because bigger ants transport heavier prey items, both individually and as team leaders (Franks 1986; Franks et al. 2001; Powell & Franks 2005), the opportunity cost of plugging would be inflated if individuals were unnecessarily large for the hole they filled. The net gains accrued by the colony from plugging may, therefore, be increased with effective size matching. Given the apparent benefits of effective, size-matched plugs in *E. burchellii*, it is interesting to focus next on the broader issue of why plugging is not common in other ants. With respect to other *Eciton* species, it appears likely that the routine use of plugs evolved in *E. burchellii* because this species experiences unique problems within the confines of the *Eciton* lifestyle.

All *Eciton* species live in colonies with many tens of thousands of workers, raid and emigrate on the surface, and have similar cyclic patterns of nomadism. However, the densely populated 'swarm raids' of *E. burchellii* and the strength of the associated trail traffic are exceptional within the genus (Rettenmeyer 1963; Schneirla 1971). For instance, the trail traffic of *E. burchellii* is usually twice the width of trail traffic in *Eciton hamatum*, even though colonies of these species can be the same size (Rettenmeyer 1963; Schneirla 1971). The difference in trail traffic results from *E. burchellii* colonies conducting a single raid, whereas *E. hamatum* colonies split their foragers between as many as three simultaneous raids that go in opposite directions (Schneirla 1971). Accordingly, an *E. burchellii* raid delivers a mean of 1.24 items/s (Franks 1983), while each *E. hamatum* trail delivers a mean of only 0.31 items/s (calculations based on reanalysis of prey data in Powell & Franks 2006). Thus, although both species run on similar natural surfaces and can have the same colony size, the foraging strategy of *E. burchellii* ensures that the density of trail traffic is two to three times higher. Moreover, swarm raiding is thought to have evolved multiple times within the army ants (Brady & Ward 2005), and there is little doubt that the presence of this strategy in *E. burchellii* represents one of the independent origins. Overall, these comparisons suggest that *E. burchellii* has an unusual and derived foraging strategy, and that this results in traffic density that pushes or exceeds the limit that can be accommodated on the natural surfaces used by all *Eciton* species. Our study shows that plugging behaviour provides a cost-effective solution to this unique problem within the *Eciton* genus. However, the traffic density on *E. burchellii* trails is not uncommon outside the genus *Eciton*. Why, then, has plugging behaviour not evolved convergently in taxa that have similarly high traffic density? The answer here appears to be that other solutions are more likely to evolve in the absence of the combined constraints associated with the high-speed, surface-active and nomadic lifestyle shared by *Eciton* species.

A number of species that experience high traffic flow construct and maintain smooth paths or 'trunk trails' that can persist for months or years. Examples, include *Atta* leaf-cutting ants, *Pogonomyrmex* seed harvesting ants (reviewed in: Traniello 1989), and subterranean trunk trails

in the Old World army ant *Dorylus laevigatus* (Berghoff et al. 2002). Moreover, trunk trail construction appears to have evolved a number of times independently, because many of the taxa that construct them are distantly related (Moreau et al. 2006). Stable trunk trails provide an ideal surface for forager traffic to travel to and from persistent patches of rich resources, and although they are time-consuming to construct, the initial costs may be small compared to the long-term benefits (Howard 2001). However, the prey of *E. burchellii* is either highly mobile or easily depleted (Franks & Bossert 1983), and the characteristic *Eciton* nomadic cycle means that colonies move on to a new area long before a trunk trail could be constructed. The potential importance of these characteristics in precluding the evolution of trunk trail construction in *E. burchellii* is perhaps best explored by a comparison with the Old World army ant *D. laevigatus*, which uses subterranean trunk trails (Berghoff et al. 2002). Both species are members of the monophyletic army ant group and are therefore nomadic group-predators (Brady 2003). However, *D. laevigatus* has an irregular nomadic pattern, often staying in one location for months at a time, and preys on some large stable food sources, like termite mounds, that can be exploited over several weeks or months (Berghoff et al. 2002). Thus, even in army ants, trunk trails appear to be viable solutions for managing strong traffic flow, as long as the foraging ecology of the species provides enough time for their construction and use, and they lead to a stable resource.

Flexible forager behaviour can also help to overcome the problem of high traffic flow. For instance, in natural trail traffic of *Atta cephalotes*, forager speed is a decreasing function of the density of ants on the trail, and maximum traffic flow is achieved when density is relatively high and foragers are constrained to run below maximum speeds (Burd et al. 2002). This is very different to the consistent positive relationship between forager size and speed in *E. burchellii*, which is maintained despite changes in traffic density throughout the day (Powell & Franks 2005; Hurlbert et al., in press; present study). Again, fundamental differences in ecology help to explain the differences in behaviour. *Atta* colonies can forage day and night to resource patches that can be stable for days or weeks, giving them fine control over harvesting and delivery rates and therefore trail traffic (Burd 1996; Burd & Howard 2005). In contrast, *E. burchellii* colonies forage for only about 8 h in a 100-m transect, and prey is patchily distributed and easily depleted, creating large fluctuations in trail traffic and prey retrieval rates (Rettenmeyer 1963; Schneirla 1971; Franks 1983). It is already known that lane-formation in *E. burchellii* traffic reduces collisions between inbound and outbound ants, and improves overall traffic flow (Couzin & Franks 2003). Our results indicate that selection has also favoured an unusual behavioural specialization that helps to maximize the speed of prey-laden foragers and increase the intake of prey within the fixed foraging period of this species. Clearly, the need for speed is paramount for *E. burchellii*, whereas reduced forager speed does not necessarily decrease the intake of resources in ants like *A. cephalotes*, which have a more sessile central-place foraging strategy.

Another flexible forager behaviour seen in other ants is the dynamic redirection of traffic to an alternative surface when traffic flow is impeded on the current surface, as demonstrated in laboratory-based experiments with *Lasius niger* (Dussutour et al. 2004). In nature, the alternative to the natural surfaces that *E. burchellii* foragers are using at any given time are other natural surfaces found on the forest floor. Quickly finding alternative surfaces with suitable width in the decaying organic material is not likely to be easy, particularly given that they must reconnect with the principal trail at some point. Even if good alternatives can be found, a significant amount of exploration time would most likely be required, potentially disrupting forager speed and, therefore, the rate at which prey is delivered to the nest. Traffic redirection may also disrupt the return rate of individuals to the swarm, which would probably have a negative impact on prey harvesting rates because the swarm's effectiveness is dependent on its strength in numbers (Schneirla 1971). Thus, instead of redirecting traffic, plugs allow *E. burchellii* to dynamically modify the existing surfaces with much the same results; the maximization of resources returned to the nest. Thus, while the ecology of some ants appears to have selected for flexible use of other readily available surfaces, the ecology of *E. burchellii* has selected for a remarkable specialization that maximizes forager performance on existing surfaces. Broadly, these findings indicate that unique ecology can select for unique patterns of behavioural specialization, even when the general problem that the specialization solves is common.

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