



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

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(Received 30 May 2006; initial acceptance 6 September 2006;
final acceptance 15 November 2006; published online 7 May 2007; MS. number: A10456R)

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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Keywords: ant structures; army ant; colony organization; cooperation; division of labour; *Eciton burchellii*; foraging strategies; group raiding; habitat ecology; task specialization

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

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