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Soldier-based defences dynamically track resource availability and quality in ants

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Specialized defence traits and strategies are crucial in surviving enemy attacks and in resource acquisition. In numerous social insect lineages, soldiers function as specialized defence traits of the colony, but associated defence strategies are poorly known. The turtle ant *Cephalotes rohweri* is an obligate cavity-nesting ant with highly specialized soldiers. To maximize growth and reproduction, colonies must use their limited availability of soldiers to defend multiple cavities. Using laboratory experiments informed by field data, we addressed how soldier 'deployment' across cavities adjusts to changes in cavity availability and quality. From initial field-like conditions, soldier deployment to newly available cavities was rapid, stabilized quickly, and at least doubled the number of cavities defended by each colony. New cavities were defended by fewer soldiers than original cavities still in use. Nevertheless, when new cavities differed in size, an important quality metric, large cavities were used more often and defended by more soldiers than small cavities. Despite these dynamic responses, total soldier deployment to new cavities was limited to an approximately constant proportion (0.4) of overall soldier availability across colonies and resource contexts. Moreover, there was a significant positive relationship between total soldier deployment to new cavities (greater for larger colonies) and both the number of newly defended cavities and their average level of defence. These results demonstrate that colony-wide soldier deployment is dynamic, predictable and context sensitive but ultimately constrained by the availability of soldiers in the colony. Furthermore, the consistently lower number of soldiers in new cavities, which always limits the potential losses to enemies, is concordant with a 'conservative bet-hedging' life history strategy. Broadly, our findings show that a specialized soldier caste can be associated with a far more sophisticated defence strategy than previously recognized. This provides a more complete perspective on the evolution of soldier-based defences in insect societies.

Specialized defence traits can be key axes of adaptive evolution, because they play a crucial role in surviving enemy attacks and in securing resources (e.g. insects: Gentry & Dyer 2002; vertebrates: Vamosi & Schluter 2004; Marchinko 2009; plants: Agrawal 2007). For any organism, specialized defence traits yield fitness gains through the combination of functional characteristics and associated defence strategies. In some social insects, soldier morphotypes, or 'castes', function as specialized defence traits of colonies that have attained a level of functional integration and conflict resolution comparable to unitary organisms (Pepper & Herron 2008; Powell 2008; Hou et al. 2010; Strassmann & Queller 2010). In these cases, the colony is the adaptive unit, and selection for colony defence can drive the morphology and behaviour of soldiers to such extremes that they can no longer feed themselves (reviewed in: Hölldobler & Wilson 1990; Dornhaus & Powell 2010). While the basic functional morphology of soldiers is well understood, the defence strategies with which they are associated are not (Dornhaus & Powell 2010).

Soldier defence strategies are defined here as the processes that determine the number of soldiers that meet a given threat. They are critical for fitness because threats faced by a colony can be distributed unpredictably in space and time (Oster & Wilson 1978). Studies of soldier defence strategies are thus needed to fill a significant gap in our understanding of adaptive evolution in derived social organisms. Moreover, the problem of having to meet distributed threats effectively with a limited supply of specialized defence traits has intriguing parallels with animal immune defences (reviewed in: Jean 2001; Schmid-Hempel 2005, 2011) and plant defences (reviewed in: Kaspari & Byrne 1995; Agrawal 2011). Deepened understanding of soldier-based defences in derived social taxa may therefore facilitate comparisons of the evolution of defence across levels of biological organization.

Soldiers have evolved in at least six major social insect lineages (ants: Dornhaus & Powell 2010; aphids: Stern 1994; polyembryonic wasps: Cruz 1981; stingless bees: Grüter et al. 2012; termites:

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Thorne et al. 2003; thrips: McLeish & Chapman 2007). Moreover, they have evolved many times independently in ants, including in some of the most diverse and ecologically important genera (Baroni Urbani 1998; Dornhaus & Powell 2010). Ant soldiers typically develop from totipotent eggs, with the developmental pathways turned on in the larval stage by worker-controlled feeding regimes (Wheeler 1991). Once mature, the specialized soldier morphology is always coupled with specialized behavioural responses to threats (reviewed in Dornhaus & Powell 2010). Soldier defence strategies thus have two main components that may be adaptive: availability and deployment. Availability is defined here as the total number of soldiers in the colony at any given moment, which is the net balance between soldier production and death rates. Deployment is defined as how the available soldiers are dynamically used in space and time.

Examples of soldier availability responding to environmental change are rare in ants (but see Passera et al. 1996; McGlynn & Owen 2002), and this process is always bound by egg-to-adult development times of one to a few months (e.g. 1 month in *Eciton*: Schneirla 1971; 3 months in *Cephalotes*: Creighton 1963; Wilson 1976a). Changes in soldier availability are thus likely to lag behind the rate of change of important environmental contingencies. For instance, more soldiers may be needed to defend a burst of new resources on a timescale of days, and threats from resource competitors can escalate in minutes. Indeed, the likely discrepancy between the rate of change in environmental threats and soldier availability is thought to explain why many social insects have stable, nonplastic soldier production rates (Oster & Wilson 1978). Put simply, if threats change faster than a colony can change soldier availability, selection should favour a stable production rate that provides an adequate number of soldiers for a range of threats. Moreover, stable soldier production at levels that could cover all conceivable threats is likely to be prohibitively expensive in terms of resources needed to produce them and the opportunity cost of reduced worker production (Oster & Wilson 1978). All considered, it is clear that soldier availability and the underlying production rates lack flexibility in ants, even if the degree to which they are adaptive remains an open question (Schmid-Hempel 1992; Dornhaus et al. 2012).

With soldier availability fixed over the timescale of one to a few months, natural selection should shape the evolution of dynamic soldier deployment. More specifically, the number of soldiers deployed to certain locations, and how colony-wide deployment patterns adjust to changing demands for defence, are likely to have significant fitness consequences. This may be particularly true in the acquisition of new resources for future growth, and under elevated enemy threat. For instance, soldiers are deployed rapidly to newly available nesting cavities in wild *Cephalotes persimilis* colonies, which obligately use multiple cavities (Powell 2009). But how is this deployment to new locations balanced against defence of existing locations? Similarly, ant soldiers are known to be deployed rapidly to escalated threat at a specific location (e.g. Wilson 1976b; Powell & Clark 2004), but does this come at the cost of increased vulnerability elsewhere? Studies that address how soldiers defend specific locations are a critical component of understanding colony defence. However, they do not provide a complete picture of the colony-wide, potentially adaptive strategies that are being used. Studies that address colony-wide dynamics of organization are exceptionally rare and, to our knowledge, there are no studies on the colony-wide dynamics of soldier deployment.

Ants in the genus *Cephalotes*, known commonly as ‘turtle ants’, represent an ideal group for advancing our understanding of the colony-wide dynamics of soldier deployment. First, most species have a highly specialized and morphologically discrete soldier caste (de Andrade & Baroni Urbani 1999; Fig. 1) with well-understood functional morphology: soldiers have heavily armoured heads that they use to physically block nest entrances of arboreal nesting cavities (Creighton & Gregg 1954; Powell 2008; Fig. 1, inset). *Cephalotes* do not make the cavities they inhabit. Instead, they use abandoned tunnels of wood-boring beetles (Creighton 1963), and typically show strong preferences for particular cavity properties (Powell 2008, 2009). Second, colonies obligately expand into additional cavities as they grow (Powell 2008, 2009). Each new cavity provides additional shelter for adults and brood, as space in existing cavities becomes limited. Third, cavity acquisition and defence is dangerous, because nesting cavities are a limited and aggressively contested resource used by most arboreal ants (e.g. Carroll 1979; Philpott & Foster 2005; Powell 2009; Powell et al. 2011). Cavity availability is probably influenced by seasonal shifts in production by beetles, cavity decay rates, competitor abundance and predation rates on occupied cavities. These contingencies suggest that selection for dynamic deployment strategies may be particularly strong in this group. Finally, recent studies have demonstrated that soldiers are critical in cavity defence, and that growth and reproductive output are strongly related to the number of cavities a colony defends (Powell 2008, 2009). Moreover, the number of soldiers per cavity reflects the level of defence, because soldiers cooperate in blocking larger entrances and in forming additional lines of defence behind the front-most individual (Powell 2008, 2009, unpublished data; present study). The number of cavities that a colony secures through the process of soldier

Figure 1. Worker and soldier (right) of the turtle ant *Cephalotes rohweri*. Note the highly specialized and armoured head-disc (dorsal surface) of the soldier. The inset shows how a soldier uses its specialized head-disc to block the entrance of a nesting cavity in the wild (worker and soldier photo, Alex Wild; blocking photo, Scott Powell).