ANIMAL BEHAVIOUR, 2007, **74**, 567–575
doi:10.1016/j.anbehav.2006.12.023

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ScienceDirect

Nest 'moulting' in the ant *Temnothorax albipennis*

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(Received 27 July 2006; initial acceptance 22 September 2006; final acceptance 2 December 2006; published online 22 August 2007; MS. number: 9063)

We showed how super-organisms, here ant colonies, modify their home according to their increasing or decreasing space requirements. The ontogeny of wall building by colonies of the ant *Temnothorax albipennis* involves discontinuous rebuilding events that are reminiscent of moulting in insects. Here for the first time we manipulated worker density by changing nest cavity size instead of worker number, thus avoiding accidentally shifting the balance of workers with different propensities for building tasks. Our results suggest for the first time that history influences wall building in ants when worker density decreases (e.g. with colony diminution) as well as when it increases (e.g. with colony growth) as shown by earlier work. Furthermore, we found that ants used a greater number of the larger building blocks (big sand grains) both after cavity expansion and, more surprisingly, also after cavity contraction. The pattern of nest 'moulting' we experimentally manipulated and analysed should provide insights into possible trade-offs between the various functions and structural properties of the nest that these animals may have to optimize.

Keywords: ant; building; growth; moulting; *Temnothorax albipennis*

Individual animals, and animal groups, typically spend much of their lives growing, in size or in number; but groups may also decline. Such individuals or groups often seek relative security in size-matched homes either built by themselves or naturally available in their environment (Hansell 2005). Supply and demand in such a property market (Chaise et al. 1988; Weissberg et al. 1991) might select for house remodelling, extensions, upgrades or downsizing as the animal or the group grows or shrinks (Chaise et al. 1988; Weissberg et al. 1991).

Growth is an inherent feature of organisms. Some organisms, like arthropods, can grow their body, or certain body parts only discontinuously by moulting (Hutchinson et al. 1997). The strategic implications of discontinuous growth may involve a constant rate of size increase between moults as predicted by Dyar's Rule (Dyar 1890). Conversely, investment principles suggest that growth rate at each moult can vary and is flexibly optimised as a function of feeding rate and body size (Hutchinson et al. 1997).

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External structures like a nest may also grow with the organism or organisms they accommodate. The nest can be rebuilt so as to fit the expanding needs of the growing organism. Alternatively, if the animal or group is using a preformed cavity, it may need to move into another, more spacious one. The replacement of a cavity that has been outgrown by its occupant will depend on available choice in the environment. It comes, however, at a cost; that of searching for and emigrating to a new home under increased predation risk. A typical example of relocation to a new home when the old one becomes too tight is the change of shells by hermit crabs (Turra & Leite 2003, 2004; Rotjan et al. 2004). Not only can such hermit crabs change their shells but a shell may also mould its occupant morphologically so that the crab may need to remain faithful to a particular type of shell when it moves (Elwood et al. 1979).

Size adjustment of a structure that requires rebuilding incurs costs not only of the reconstruction work but also those associated with risks in an incomplete home (Hansell 2005). Rebuilding can occur continuously or as episodic 'moults' (Franks & Deneubourg 1997).

Nest rebuilding usually progresses towards nest expansion although in some cases animals reduce the space they occupy by building a smaller, tightly fitting structure inside the main nest. For instance, overwintering rodents

0003–3472/07/$30.00/0

snuggle into a miniature nest inside their burrow to increase insulation against cold (Merritt 1986).

Group builders like social insects often construct nests that are impressive both in size and complexity (Camazine et al. 2001). They too modify their nests as the colony grows. These animals may build arboreal, epigeal or subterranean nests and can also inhabit and build in preformed cavities. The size of the nest correlates positively with the population size of the colony (Deneubourg & Franks 1995; Tschinkel 2004). Smaller colonies tend to take longer to complete the same amount of building work than larger colonies (Jeanne 1986).

The adjustment of nest size to the size of the colony may be an adaptation for the regulation of colony activities like efficient brood care (Jeanne 1996; Jeanne & Bouwma 2002) or an antipredatory adaptation (as in social mites, Mori & Saito 2004). The type of building material used for the nest may also reflect different predation pressures and behavioural adaptations to different predators and predation techniques. For example, wasps building fragile paper nests and those building mud nests differ in collective aggression towards intruders after nest disturbance (O'Donnell & Jeanne 2002).

When ants excavate nests their work may be episodic, but in general the amount of excavation scales with worker numbers (Buhl et al. 2004). So population density may remain fairly similar as the colony grows (Mikheyev & Tschinkel 2004). In addition rebuilding typically shares many attributes of initial building (Rasse & Deneubourg 2001).

A similar positive correlation between nest size and colony size has been observed in an ant species that builds above ground, namely *Temnothorax albipennis* (Franks et al. 1992; Franks & Deneubourg 1997). This species occupies, in nature, preformed cavities in rock where a colony often encircles itself with a dry-stone wall. The selection of material for the wall trades foraging efficiency for the mechanistic efficiency of the construction (Aleksiev et al. 2007a).

When *T. albipennis* colonies build de novo in association with an emigration to a new nest site, the average area per worker inside the perimeter wall of the nest is constant at 5 mm^2 so that per capita area is independent of the size of the colony (Franks et al. 1992). *Temnothorax* colonies preferentially choose cavities of 2000 mm^2 that provide an optimal accommodation for the growing colony, since the biggest colonies typically have about 400 workers (Franks et al. 2006). Other work suggests that these colonies also prefer the solid walls of the cavity to the ones they can build themselves (Franks et al. 2006).

Franks & Deneubourg (1997) also examined the possible effects of rapid colony growth on nest rebuilding in *T. albipennis*. Their method was to partition colonies and then to allow only one part of them to build before returning the other fraction. The amount of increase in the size of the wall depended on the amount of increase in colony size after the colony was reunited. Smaller increases in colony size did not bring about wall rebuilding. Theoretical considerations and certain data suggest that the growth in the size of the wall can show hysteresis, with changes in the nest size lagging behind changes in the colony size (Franks & Deneubourg 1997).

The experimental work presented here uses a different approach to study the dynamics of wall 'moulting' in *T. albipennis*. We manipulated the size of the nest cavity instead of colony size. For an interesting parallel see the work by Gravel et al. (2004) who provided hermit crabs with artificial nests. The manipulation of cavity size subjected *Temnothorax* colonies to different spatial constraints. It also provided the opportunity to examine the dynamics of rebuilding in both expanding and contracting cavities. Finally, changing the size of the nest cavity meant that colony densities could be manipulated without taking away or adding workers and thereby risking a possible disturbance in the organization of task performance in the colony.

To manipulate the size of the nest cavity we designed a special type of nest with a piston-like device in one of its three solid walls. We increased or decreased cavity size by pulling the piston out or pushing the piston in, respectively. We examined the strategies *T. albipennis* colonies use to adjust the size of the nest to the size of the colony by considering the amount of building and rebuilding work they carried out across the wide nest entrance (or missing fourth wall). We quantified their work as the area occupied by this fourth wall built or rebuilt by the ants themselves.

Earlier work (Aleksiev et al. 2007a) has shown that these ants, when given the option, will build a wall with both large and small grains. Such mixed walls may have beneficial properties. We, therefore, also looked at the changing grain composition of walls during rebuilding events.

METHODS

The Piston Nest

The piston nest was designed on the basis of the standard nest for wall building in *Temnothorax* colonies used in experiments by Aleksiev et al. (2007a). This standard nest consisted of three fixed walls, giving ants the opportunity to build the missing fourth wall out of sand grains (Fig. 1). The new element in the piston nest was that the fixed short wall, opposite the missing one, was replaced by the piston (Fig. 1).

The piston, a rectangular 75×30 mm and 1 mm piece of cardboard, could be pulled out or pushed in the cavity thereby increasing or decreasing cavity size. The size of the piston-nest cavity was 70×30 mm and 1 mm, that is, the same as that of a standard nest, although, inserting the piston increased the width up to 32 mm. This was the 100% cavity size and it was achieved by inserting the piston 5 mm into the nest. We achieved cavity sizes of 50% or 25% by inserting the piston 35 or 52 mm into the nest, respectively (Fig. 1).

Experimental Design

The piston-nest experiment was carried out between 4 April and 30 May 2005 with 30 queen-right *T. albipennis* colonies of medium size collected on 5 March 2005 from