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Tomb evaders: house-hunting hygiene in ants

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House-hunting ants avoid otherwise excellent potential nest sites that contain dead ants which may pose risks from poor hygiene. This discovery adds another category to the exceptionally long list of nest site attributes that ants evaluate. It further indicates the importance of disease as a selection pressure on social insects.

Keywords: decision making; disease; pathogen; social insects; *Temnothorax albipennis*

1. INTRODUCTION

House-hunting by complete social insect colonies provides an opportunity to study links between individual and collective decision-making (Franks *et al.* 2002). This is important beyond social insects because, for example, our own brains can be considered as societies of neurons, and similar processes might apply (Schall 1999, 2001; Shadlen & Newsome 2001; Fewell 2003; Heekeren *et al.* 2004). This is not as incredible as it might at first appear. For example, in house-hunting ant colonies, a classic speed–accuracy trade-off has been demonstrated (Franks *et al.* 2003*a*) and such trade-offs occur in the decision-making systems of innumerable organisms from solitarily foraging bumble bees (Chittka *et al.* 2003) to humans (Edwards 1965). One of the reasons for a speed–accuracy trade-off is the compromise needed between gathering more information to make a well-informed decision and the time that this takes. Thus, speed–accuracy trade-offs are all the more likely if diverse information on a variety of very different attributes is required (Franks *et al.* 2003*a*,*b*).

Two house-hunting social insect systems have been investigated in-depth to date: first, new hive selection by swarms of honeybees (Seeley & Buhrman 1999, 2001); second, new nest site selection by colonies of *Temnothorax* (formerly *Leptothorax*) *albipennis* (Franks *et al.* 2003*a*,*b*). In both cases, individual scouts gather and evaluate diverse qualitative and quantitative information on potential nest sites. For example, honeybees assess, among other factors: the volume of the cavity, the size of the entrance, the height of the entrance above the ground, the height of the entrance above the floor of the cavity, and the compass bearing of the entrance (Seeley & Morse 1978; Seeley 1982; Visscher *et al.* 1985). *Temnothorax albipennis* workers assess the floor area of a cavity, its darkness, the amount of headroom it offers and the width of the entrance (Franks *et al.* 2003*a*). As first shown for the ants, quorum sensing is used to collate individual assessments and form them into a collective decision (Pratt *et al.* 2002). Recent work strongly suggests a similar phenomenon in honeybees (Seeley & Visscher 2004).

One intriguing potential difference between these systems is associated with the costs and benefits of nest site re-usage. An obvious disadvantage of using a previously occupied nest site is that it may be a source of disease due to lingering pathogens. Hygiene is important to many social insects. For example, when waste, including dead ants, accumulates in leaf cutter ant colonies, there is an increase in ant mortality (Bot *et al.* 2001), and undertaking behaviour is well documented in other ants (Theraulaz *et al.* 2002) and honeybees (Frumhoff & Baker 1988; Robinson & Page 1988; Trumbo *et al.* 1997; Julian & Cahan 1999). Nevertheless, honeybees are known to prefer new nest sites with honeycomb present (Seeley 1982; Visscher *et al.* 1985). In this case, the benefits of utilizing such a valuable resource might outweigh the costs associated with the risk of pathogen transmission. Here, we test *T. albipennis* ant colonies to determine whether they avoid potentially good nest sites in which there are dead conspecifics. If they do, this would add an entirely new category of criterion to the long list of house selection attributes that these ants evaluate. In addition, it would further indicate the importance of disease as a major selection pressure on social insect populations that affects both individual and colony-level behaviours (Schmid-Hempel 1998; Hart & Ratnieks 2001, 2002; Hart *et al.* 2002).

2. METHODS

Individual *T. albipennis* colonies were presented with a choice between two potential new nest sites. All the nests were constructed from cardboard, 76×51 mm and 2 mm thick, sandwiched between two microscope slides of the same length and breadth. The nest cavity was 32×24 mm with a nest entrance 3 mm wide and 5 mm long. We induced colonies to leave their old nest by removing the top slide, exposing the ants and brood. The old nest was destroyed in a large Petri dish, of dimensions 220×220×22 mm, containing the two symetrically arranged potential new nest sites, each 10 cm from the old nest.

Are dead foreign conspecific workers sufficiently repulsive to influence nest site choices? In experiment 1, 15 emigrating colonies had to choose, on two separate occasions, between a nest containing dead ant material from foreign colonies and a nest containing carborundum grains. Carborundum grains were used to control for the avoidance of fragmentary material in potential nest sites (which would occupy space or need to be removed). Grade 16 carborundum is approximately equal in volume to an intact worker and grade 36 to that of a head, thorax or abdomen. Piles of dead ants consisting of an intact worker corpse, a head, a thorax and an abdomen, or piles of carborundum grain equivalents, were made at each of five points around the cavity perimeter (figure 1*a*,*b*) before the nest top slide was added. The dead ants used in all 15 emigrations originated from the same foreign conspecific colony. In all the experiments involving dead ants, workers were killed by freezing, stored in a deep freeze for 1.5 h, and then thawed out for 48–72 h prior to use.

Are dead nest-mates as repulsive as dead foreign conspecifics? To answer this, experiment 2 replicated experiment 1 but used dead nest-mates instead of dead foreign conspecific workers. In experiment 2, 20 emigrating colonies had to choose between a nest containing carborundum, and a nest containing whole corpses

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Table 1. Nest choices of colonies in the three experiments.

	nests containing:					
	dead ants					
experiment	nest-mate	non-nest-mate	carborundum	empty	split colonies	*n*
1a	—	4	10	—	1	15
1b	—	0	15	—	0	15
2	0	—	20	—	0	20
3	—	—	10	6	4	20

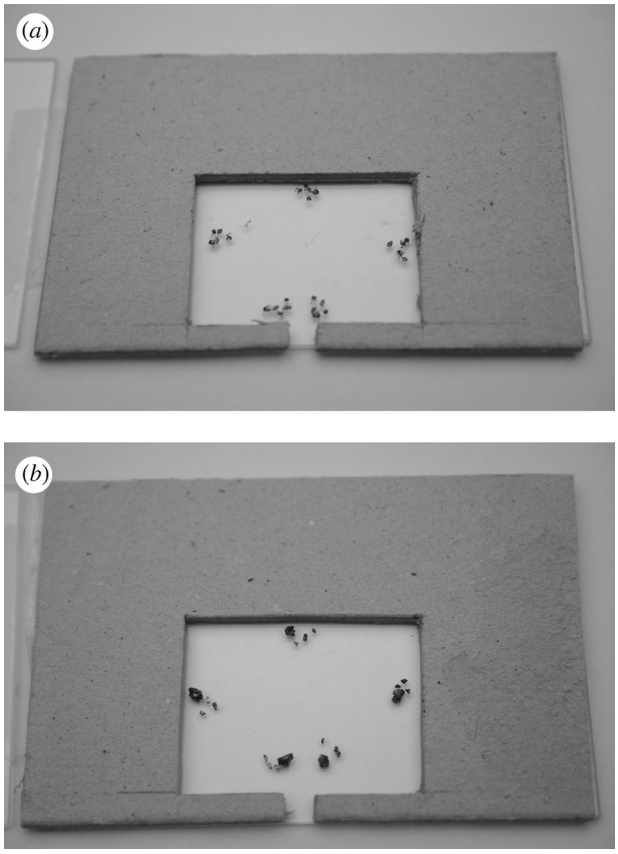

Figure 1. This figure shows the pattern of (*a*) dead ants and (*b*) carborundum grains in potential nest sites.

and body parts of individual workers previously taken at random from their own colony.

Are dead ants repulsive and/or is carborundum attractive? The ants might exhibit a preference for nests containing carborundum grit because such grit might be useful, for example, to reduce the width of the nest entrance for better defence (Franks *et al.* 1992). Experiment 3 is thus a further control. In experiment 3, 20 emigrating colonies had to choose between a nest containing carborundum and an empty nest. As above, apart from the nest contents, all new nests were identical. All other aspects of the three choice experiments 1, 2 and 3 are identical to those in Franks *et al.* (2003*b*).

3. RESULTS

In experiment 1, 10 of the 15 colonies chose carborundum nests twice, and none chose dead ant nests twice. This is a significant choice of carborundum over dead ants (Wilcoxon statistic 55, $n=15$, $p=0.006$). If colonies were choosing at random we would expect them to choose both types of nest at the same frequency. Thus each colony might be expected to choose the nest with carborundum grains once in its two trials and the nest with dead ants once in its two trials. We therefore tested for preferences by asking how many times colonies choose carborundum nests twice against the random expectation of one such choice. In experiment 1, only one colony split, i.e. brood was present in both nests 48 h after the start of the experiment (table 1).

In experiment 2, all 20 colonies choose the nests with carborundum grit rather than their own dead nest-mates and no colonies split (two-tailed cumulative binomial test, $p<0.0001$; table 1).

In experiment 3, 10 colonies chose the carborundum nest, 6 choose the empty nests and 4 split, indicating that the ants did not have a preference for either nest type (two-tailed cumulative binomial test of 10 versus 6, $p=0.4544$). Furthermore, splitting by some colonies is indicative of the nests being treated as if they are of similar quality (Franks *et al.* 2003*b*; table 1). Experiment 3 therefore suggests that the presence of carborundum grains does not make nests more attractive.

4. DISCUSSION

The results of experiments 1 and 2 suggest that house-hunting ant colonies avoid otherwise ideal nest sites if they contain dead conspecific workers irrespective of their origin (i.e. whether they were nest-mates or non-nest-mates). Our controls clearly showed that it was the presence of dead ants, rather than material *per se*, that made nest sites unattractive. Furthermore, carborundum grit, a potential building material (Franks *et al.* 1992), was not attractive to the ants. Franks *et al.* (in preparation) have shown that this species avoids non-nest-mate conspecific odours, but we have shown that all dead conspecific ants are repulsive. This indicates hygiene as the selection pressure that has favoured such behaviour, rather than foreign dead ants being a cue to the possible presence nearby of living conspecific competitors.

An intriguing comparative test would be to see if honeybees reject cavities, with and without honey comb, in which there are dead bees. The latter might indicate that the previous inhabitants suffered deadly diseases.

Our results add a whole new qualitative category, hygiene awareness, to the nest evaluations of house-hunting ant colonies. Until now, it had been assumed that ant colonies sometimes emigrated to avoid pests and diseases at their old nest site (Hart 2002). We have shown for the first time that ants evaluate

hygiene issues before moving to a new nest site. Earlier work has shown that *T. albipennis* colonies use a weighted additive decision-making strategy, one of the most thorough and time-consuming strategies of all, to evaluate the physical properties of nest sites (Franks *et al*. 2003*b*). It will now be interesting to determine whether such evaluations are completely abandoned when the ants find dead conspecifics in potential nest sites. In other words, is tomb evasion an over-riding criterion for abandoning nest-site evaluation? Irrespective of the ranking of hygiene considerations in the nest-choice criteria of these ants, our findings show, for the first time, that disease risk and hygiene issues must be added to the long list of attributes that the ants take into account. This further supports the notion that parasites and pathogens are a major selective force on social insect ecology and behaviour.

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