



# Avoidance of conspecific colonies during nest choice by ants

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Conspecific ant colonies are often overdispersed, i.e. they are further apart than they would be if they were distributed randomly. This overdispersion might be driven by competition for food resources or nest sites and may result from established colonies preventing incipient colonies from settling too close to them. We investigated another possible mechanism for overdispersion: active nest choice by emigrating colonies. Colonies may be influenced by the presence of conspecifics when they are emigrating from a nest that has become uninhabitable. In the laboratory, we presented *Temnothorax albipennis* ant colonies with a choice of three new nests, which were equidistant from their old nest site. The new nests were identical except that one was near to an established conspecific colony. The emigrating colonies significantly preferred the new nest site that was furthest from the resident colony. This selection was not just the result of access to the other nests being blocked by aggression from the resident colony; emigrating colonies thus made active choices. Odour cues may influence nest selection: odours left around nest sites by foreign colonies deterred nest occupancy. There was more aggression near the resident colony, but this appeared to be caused by the greater density of resident ants there rather than those ants being more aggressive per capita. We also observed a relatively high proportion of fusions between colonies. Possible reasons for this are considered together with their implications.

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The behaviours that cause animals to increase their spacing from one another can be important in the establishment of territories (Davies & Houston 1984), which in turn can lead to density-dependent population regulation (Lewis & Murray 1993; Gordon 1996; White et al. 1996; López-Sepulcre & Kokko 2005). The mechanisms of territory establishment are thus central to understanding the regulation of population density in many species. Acoustic or visual signals are often used by individuals to maintain territories (Krebs et al. 1978), and studies of such communication have been successfully carried out on animals as diverse as fiddler crabs, *Uca pugilator* (Pope 2000), frogs (Bee 2003; Murphy & Floyd 2005), birds (Nelson 2000; Molles & Vehrencamp 2001; Wilson &

Vehrencamp 2001; Brumm & Todt 2004), lions, *Panthera leo* (Grinnell & McComb 1996, 2001) and chimpanzees, *Pan troglodytes* (Wilson et al. 2001, 2002). The proximate and ultimate causes of territoriality remain a lively area of research (Stamps & Krishnan 1999; Maher & Lott 2000; Lamanna & Eason 2003; Pereira et al. 2003; Morell & Kokko 2005). Even when focal species have been studied long term, such as in the case of the Eurasian badger, *Meles meles*, it may be hard to determine which resources, for example suitable sett sites or the abundance of forage, determine where territories are formed (Blackwell & Macdonald 2000; Doncaster 2001; Johnson et al. 2001; Macdonald et al. 2004).

Density dependence and territoriality have also been extensively studied in ants (Hölldobler & Wilson 1990). Conspecific ant colonies, within suitable habitat, are frequently overdispersed (Levings & Traniello 1981). That is, they are often further apart than they would be if they were distributed at random. This could occur because established colonies kill or expel colony-founding queens that try to establish nests within their territory (Levings &

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Franks 1982), or because large colonies can outcompete smaller ones (Gordon & Kulig 1996). In addition, for one species of *Temnothorax* ants nest sites have been shown to be a limiting resource (Foitzik & Heinze 1998), so the distribution of nest sites may constrain the distribution of colonies. We propose a fourth mechanism: established colonies may tend to choose new nests that are a good distance from their rivals when they have to emigrate because their nest is no longer habitable.

We used colonies of the ant *Temnothorax albipennis* to determine whether the proximity of conspecific neighbours might influence nest choice under controlled conditions in the laboratory. Nest choice by *T. albipennis* has been studied intensively and extensively and it is an almost ideal model system to determine the integration of individual and collective decision making. The workers are small and the largest colonies have fewer than 500 workers. In the field they live in narrow fissures in rocks, and several colonies can be found within the same square metre of suitable habitat. So the scale of their nest emigrations and colony density can be approximated in large arenas in the laboratory (Franks et al. 2002).

When forced to emigrate by the destruction of their old nest, a subset of the colony's workforce scout for potential new nest sites. Scouts finding a suitable nest sometimes recruit others by tandem running, but when they find a sufficient number, i.e. a quorum, of their nestmates in the new nest they switch to carrying their nestmates (both adults and brood; Pratt et al. 2002). Such carrying is much faster than tandem running (Franks et al. 2002), and the emigration is usually quickly completed after transport by carrying has started.

These ants have been shown to use a large set of criteria to select new nest sites, such as floor area (Mallon & Franks 2000), cavity height, width and abundance of nest entrances (Franks et al. 2003, 2006a) and whether or not there are dead conspecifics in the nest chambers (Franks et al. 2005). They also show a speed–accuracy trade-off, choosing nests more quickly but with more errors in harsh rather than benign conditions (Franks et al. 2003; Dornhaus et al. 2004). In harsh conditions, they may dispense with tandem running and recruit only by carrying (Franks et al. 2003). We determined whether their choices of new nest sites are influenced by the presence of foreign conspecific colonies.

Emigrating away from an established conspecific colony could be advantageous for a number of reasons: avoidance of aggression; avoidance of competition for foraging space and resources; and to reduce the risk of brood being stolen during an emigration. Transporting young to a site containing conspecifics can be dangerous and it may be that ants, like certain frogs (Murphy 2003), seek to reduce this risk. Increasing the distance between themselves and other conspecific colonies may also reduce the risk of parasite transfer and disease transmission between colonies and the likelihood of attracting predators.

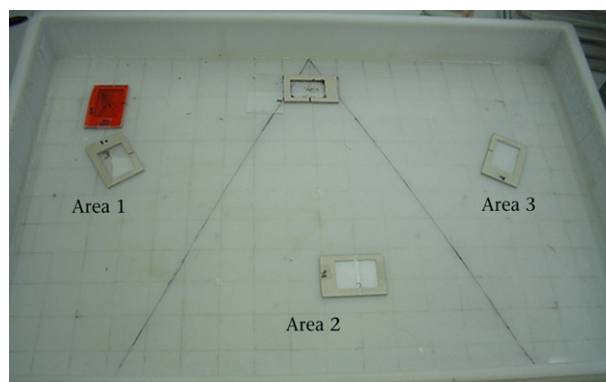
We investigated the influence of conspecific neighbours on colony nest choice in emigrations in two experiments. In the first experiment, we allowed a colony to emigrate in the presence of a conspecific resident colony. By recording nest choices and the amount of aggression between

workers of the two colonies, we could determine whether colonies make active choices for nests away from resident colonies. Second, we investigated a mechanism by which the ants may determine their proximity to neighbouring colonies by recording nest choices in colony emigrations to nests that were surrounded by odours of conspecific colonies versus control nests, but in the absence of any potentially hostile ants.

## METHODS

All of the *T. albipennis* colonies used in our experiments were collected from a coastal site in Dorset, U.K. All were collected on 2 October 2004, except for some of the colonies used in the odour preference experiment, which were collected in late September 2003. We collected 116 colonies in October 2004; details of the size of these are given in Franks et al. (2006b). The colonies used here were taken from the middle of the size range of this larger collection, to facilitate rough matching by size of resident and test colonies. The median size of the colonies used here was approximately 93 workers (interquartile range 61.5–118). The sizes of the colonies used in the odour experiment were similar (median 92 workers, 70–122). Colonies were housed in nests formed by sandwiching cardboard between two microscope slides (50 × 76 mm). Each standard nest had a cavity of internal area 35 × 49 mm and height 1.2 mm with an entrance 2 mm wide. These were kept in petri dishes with lids and Fluon-coated walls to prevent the ants escaping. Water and food were always available except during emigration experiments. Colonies were given fresh dilute honey solution and *Drosophila* flies once a week.

To determine how the presence of a second colony influenced nest choice during emigration, we divided an arena (734 × 472 mm) into three equal areas and placed a 'resident' and a 'test' colony, as well as three empty nests, into it (Fig. 1). The resident ant colony was housed



**Figure 1.** The positions of nests in the emigration experiment. The superior nest housing the resident colony was situated in Area 1 next to Nest 1 and had a red filter. The old nest of the emigrating colony was situated top-centre equidistant (250 mm) from Nest 1, Nest 2 and Nest 3 (situated in Areas 1, 2 and 3, respectively). Nest 2 was aligned slightly to the left or to the right, depending on which side the resident nest was on, so that it was always the same distance from the resident colony.

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