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The selection of building material for wall construction by ants

ANTONY S. ALEKSIEV*, ANA B. SENDOVA-FRANKS† & NIGEL R. FRANKS*
*School of Biological Sciences, University of Bristol
†School of Mathematical Sciences, University of the West of England, Bristol

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Building by ants often involves excavation, but *Temnothorax albipennis* colonies build walls in preformed cavities. To do this they need to choose and retrieve building material. Thus, building in *T. albipennis* can be analysed, in part, from the perspective of a foraging strategy. We gave ant colonies a choice between large and small sand grains that were available at three different distances. From theoretical considerations, we expected ant colonies to maximize the amount of material collected per unit time and therefore to choose large grains exclusively. Instead, they always chose grains of both sizes. Such partial preferences can be explained in terms of the mechanical benefits of constructing walls as a mixture of two grain sizes. Barricades composed of two grain sizes can be more resilient than walls made from a single grain size, as estimated in terms of angles of maximum stability and packing densities. Thus, foraging decisions need to be analysed in the broader context of how collected material is utilized. Here partial foraging preferences can have direct benefits: different choices by different foragers and even individual 'error' proneness might contribute to the collective good.

Keywords: ant colony; building material; foraging strategy; nest building; partial preferences; *Temnothorax albipennis*

Currently, there is a great deal of interest in how groups of organisms achieve collective decisions (Spencer et al. 1998; Glimcher 2002; Nicolis et al. 2003; Fantino 2004; Conradt & Roper 2005). Building behaviour is also fascinating because animals use it to extend their phenotypes (Dawkins 1999; Hansell 2005). These two fields combine when a society is doing the building and its members must forage for, and choose, building materials.

A major issue in the study of animal decision making is the nonexclusivity of choice (Luce 1959; Stephens & Krebs 1986). Empirical research shows that animals often have partial preferences (McNamara & Houston 1987). In a choice between two alternatives, which differ in profitability, both options are often taken. The conventional theory on foraging for food predicts, however, that preference should be given exclusively to the more profitable option (Stephens & Krebs 1986; Stephens et al. 1986; Zeiler 1987). Theoretically, partial preferences may arise from the application of different assumptions or different constraints to foraging. Foraging models consider either the maximization of energy gains or the minimization of time spent on food acquisition. Time, prey distribution, encounter rate and prey discrimination are among the most important constraints in the derivation of, and deviations from, an optimal foraging strategy (Houston & McNamara 1999; Langen 1999).

Conventionally, in most models, the distribution of prey and hence prey encounters are random, and the forager is always perfectly informed of the value of different prey; it thereby chooses exclusively the most profitable ones (Pulliam 1974). When prey distributions are clumped (Lucas 1983) or different prey are encountered simultaneously (Waddington 1982), the optimum strategy can be to take the less profitable items on some encounters. A lack of experience can also result in partial preferences (Kaiser et al. 1993; Richter & Waddington 1993; Dukas & Visscher 1994; Hertwig et al. 2004; Warburton & Thomson 2006). When the detection probabilities of different prey items depend on previous choices, it might be optimal to forage nonexclusively (Bernays & Funk 1999). The assumption that animals make perfect

Correspondence: N. R. Franks, School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, U.K. (email: nigel.franks@bristol.ac.uk). A. B. Sendova-Franks is at the School of Mathematical Sciences, CEMS, University of the West of England, Bristol, Frenchay Campus, Coldharbour Lane, Bristol BS16 1QY, U.K.

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choices idealizes their cognitive capacities and underrates the stochastic nature of their environment. Memory failures or inaccuracies in estimating time costs will result in suboptimal choices (Hirvonen et al. 1999; Ishii 2005). Therefore, learning and experience can be an integral part of decision making. Empirical studies have shown an inverse relation between the rate of discrimination learning and the variability of choices in the environment (Getty 1985; Johnson et al. 1994).

In the model for the analysis of partial preferences developed by McNamara & Houston (1987) the performance of an optimal action depends on the cost, in terms of future reproductive success, of the nonperformance of that action. This model suggests that deviations from the optimal policy can be expected when the cost of such deviations, that is, the cost of making errors, is small. Other models have explored further the behavioural mechanisms leading to partial preferences in foraging (Belisle & Cresswell 1997; Berec 2000; Berec & Krivan 2000).

Although, in foraging studies, energy is the most commonly used currency for both costs and benefits (McNamara & Houston 1986), in some cases such as the foraging for seeds in desert ants (Johnson 1991; Lighton et al. 1993; Weier et al. 1995; Wehner et al. 2004), energy costs seem to be trivial. Currencies other than energy are also necessary for measuring the costs and benefits of foraging for items that cannot be used directly for food, such as the foliage foraged by leaf-cutter ants (Burd 1996, 2000; Burd & Howard 2005).

Building materials are an extreme example in which foraging does not provide direct energy benefits (McGinley 1984). While energy gain is a suitable benefit measure for food foraging, we need other currencies for measuring the benefit of foraging for building materials. Amount of material collected or measures for the quality of the built structure might both be appropriate.

The costs of foraging for building materials might largely involve time. The reason is that time spent foraging for building materials is likely to be time lost to foraging for food. In addition, foraging for food is often an everyday activity whereas foraging for building materials is likely to be far less frequent and may even be highly episodic, with intense bouts of building punctuated by much longer periods of stasis (Franks & Deneubourg 1997). Thus, in this study we considered costs in terms of time for retrieving different materials from different distances.

Nest building is a fitness-related activity and it occurs at different intervals and bout lengths in different species (Hansell 2005). It has both short- and long-term consequences for the survival and reproductive success of organisms. In mammals and birds, the building of a nest often occurs in anticipation of the need to accommodate new offspring or after the establishment of an individual range or territory. In social insects, nest building may occur in response to colony growth (Deneubourg & Franks 1995; Franks & Deneubourg 1997) or whenever the colony emigrates because it outgrows the old nest or the current nest is destroyed (Hölldobler & Wilson 1990). The colony may remain largely unprotected for the duration of the building, and foraging for building material is severely time constrained. While it is known that solitary mammals and birds often choose exclusively between different building materials (Hansell 2000), little research has focused so far on foraging for building material in either social insects or highly social vertebrates. Therefore, not much is known of the collective choices of materials for building (but see Jeanne 1996; Karsai & Balázsi 2002).

Temnothorax albipennis ant colonies are an ideal model for research into certain aspects of nest-building behaviour (Franks et al. 1992; Franks & Deneubourg 1997). This species forms small colonies (of up to 500 workers) that naturally dwell in rock crevices. There, the ants usually build a single circular wall around their colony. In the laboratory, *Temnothorax* colonies can be housed in nests consisting of a single chamber cut out of a thin piece of cardboard sandwiched between two microscope slides (Franks et al. 1992). When the cardboard cavity has one of its walls missing and building material is provided, the ants build a single wall to compensate for the missing one (personal observation). The building of a new wall after an emigration to a new nest site takes 24–48 h (Franks et al. 1992). Sand is an ideal experimental building material because walls built from sand grains can be quantified easily (Franks et al. 1992; Franks & Deneubourg 1997).

We considered choices of building materials by colonies (i.e. the outcome of the choices of all of the foragers involved) as a foraging problem where the resource is clumped. We gave colonies the opportunity to choose between two sizes of sand grain, big and small, placed in sand piles at three different distances from the nest. If the rate of building was all that mattered, the ants should choose exclusively the size of grain that gives the best return in terms of volume per unit time. However, if the quality of the built structure mattered most, then the ants might collect both grain sizes if a mixed wall was stronger and more compact. We examined two measures for the possible benefits of building a wall with a mix of grain sizes: the angle of maximum stability as a measure of wall strength and the packing density as a measure of wall compactness.

We asked four main questions. First, do ant colonies make an exclusive choice of either big or small grains in relation to foraging distance? Second, how does transport cost depend on distance and grain size? Third, what is the profitability of each of the two grain sizes in terms of the benefits of grain volume and the costs of foraging at different distances? Fourth, what are the benefits of building a mixed wall?

METHODS

We used plain dry sand as building material in all experiments. Sand grains were classified as big or small according to the following method. The sand was sieved through three mesh sizes: 300, 500 and 850 μm. The grains that did not pass through the 300-μm sieve but passed through the 500-μm sieve were classified as small. The grains that did not pass through the 500-μm sieve but passed through the 850-μm sieve were classified as big.