Ants estimate area using Buffon's needle

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We show for the first time, to our knowledge, that ants can measure the size of potential nest sites. Nest size assessment is by individual scouts. Such scouts always make more than one visit to a potential nest before initiating an emigration of their nest mates and they deploy individual-specific trails within the potential new nest on their first visit. We test three alternative hypotheses for the way in which scouts might measure nests. Experiments indicated that individual scouts use the intersection frequency between their own paths to assess nest areas. These results are consistent with ants using a 'Buffon's needle algorithm' to assess nest areas.

Keywords: ants; colony emigration; individual-specific pheromones; *Leptothorax*; nest sites; rules of thumb

1. INTRODUCTION

Social insect colonies are groups of autonomous individuals which appear, on certain occasions, to reach such complete accord that it has long become popular to see the colony as analogous to a single organism or super-organism (Wheeler 1928; Seeley 1989, 1995; Wilson & Sober 1989; Hölldobler & Wilson 1990). How the behaviour of individual workers translates into collective decisions by the whole or large parts of a colony is now a major area of interest in the study of social insects (Franks 1989; Beckers *et al*. 1993; Bourke & Franks 1995; Seeley 1995; Bonabeau *et al*. 1997; Detrain & Deneubourg 1997; Pratt 1998; Detrain *et al*. 1999). However, relatively little work has been done on the information gathering which provides the options for these decision-making processes (but see Seeley 1977; Lumsden & Hölldobler 1983; Beckers *et al*. 1990, 1992; Franks *et al*. 1991).

In this paper we are concerned with the assessment of potential new nest sites by individual ant workers prior to the emigration of their colony from an old nest to a new nest site. Nest-site selection by honeybee scouts attempting to find suitable hive sites for their swarming colonies has been the subject of a number of classic studies (Lindauer 1955, 1961; Seeley 1977). However, we are unaware of any analogous work on nest-site assessment by members of ant colonies.

Leptothorax albipennis ant colonies inhabit minute flat crevices in rocks and scouts assess potential new nest sites when their old nest is destroyed. The scale and geometry of natural nest sites of *L. albipennis* can be closely approximated in the laboratory by nest sites made of microscope slides (Franks *et al*. 1992; Franks & Deneubourg 1997) (figure 1). Such nests are flat and their floor area is related to the number of ants they can accommodate (Franks *et al*. 1992). We used such microscope slide nests with nest cavities of different sizes, shapes and configurations in order to examine preferences. Furthermore, because scouts are visible at all times in such nests, the details of their behaviour can be accurately recorded. The simplicity of these nests also means that nests can be relatively easily manipulated during the assessment process and in this way the rule of thumb which scouts use to measure potential nest areas can be elucidated.

2. METHODS

Colonies of *L. albipennis* were collected from areas near the Dorset coast (Partridge *et al*. 1997) and cultured in the laboratory using the methods described in Sendova-Franks & Franks (1995a). In nest-choice experiments individual colonies within their nests were transferred to a large (220 mm × 220 mm), square Petri dish, the sides of which were covered with Fluon[1] to prevent the ants escaping. New nests, of the types described in figure 1 and table 1, were positioned equidistantly (entrance to entrance) from the old nest. An emigration was then initiated by removing the uppermost glass slide from the old nest (Sendova-Franks & Franks 1995b). The relative positions of the different potential nests were randomized in the different replicates to eliminate possible directional biases. A nest was considered chosen when all of the adult ants (except a few foragers) and all of the brood were present within a nest. Nest choices were, therefore, unequivocal.

During experiments in which the behaviour of individual scouts was analysed, all of the workers in each colony were individually and uniquely marked with paint (Sendova-Franks & Franks 1993). The behaviour of scouts during visits to potential new nest sites was videotaped. The path of individual ants was digitized by viewing the videotapes on the VDU of a computer equipped with suitable software.

3. RESULTS AND DISCUSSION

Given choices, colonies with a single queen, brood and 50–100 workers will emigrate into nests of a certain 'standard size' and will reliably reject nests both of half standard size and of five-eighths standard size (table 1, experiments A and B). This shows that these ants can measure areas. How do they do this?

The assessment of new nest sites is by individual scouts (see figure 2). Experiments involving individually marked workers showed that scouts will typically only initiate the recruitment of nest-mates when they have made more than one visit to a suitable nest site (13 out of 18 ants made repeat visits before recruiting). The median time that a scout spends within a nest cavity assessing a
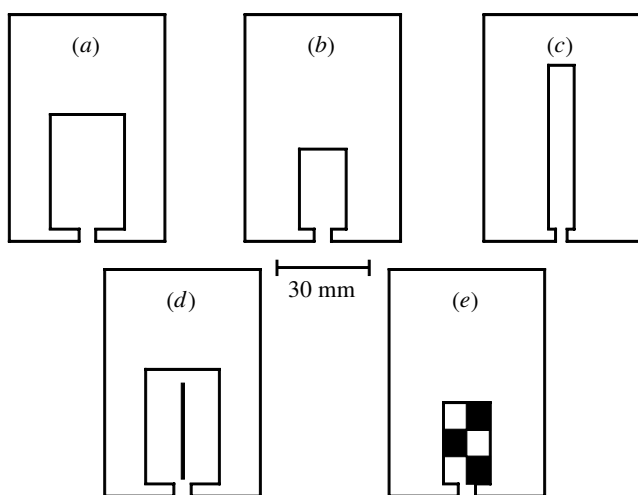
Figure 1. Nest designs: (*a*) standard-size nest, (*b*) half-size nest, (*c*) half-size nest with same internal perimeter as a standard-size nest, (*d*) standard-size, partial barrier nest—the black line is a cardboard wall from floor to roof which could be circumnavigated only at its ends, and (*e*) half-size, magic carpet nest—the shaded areas represent the holes in the upper carpet (see the text). All the nests were constructed from 0.8 mm cardboard, from which rectangular cavities had been cut, sandwiched between microscope slides.
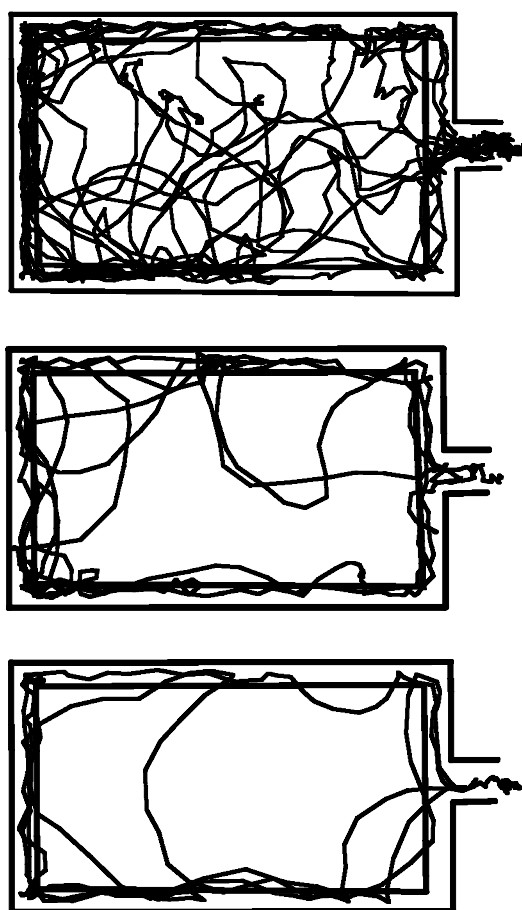

Figure 2. The path of a single scout (thin black line) on each of its three successive visits to the same potential nest site. The ant appears to spend a considerable part of its visit near the internal perimeter of the new nest. Nevertheless, in general, the number of intersections between second and first visit paths in the central region of the nest (within the inner box) and the edge region of the nest (between the two boxes) is similar (see the text). The first visit path in the central region of the nest line is reasonably uniformly distributed. This should ensure that the Buffon's needle algorithm gives a reasonably accurate estimation of the nest area.

potential nest is 110 s per visit (interquartile range 140 s and $n = 115$) (data pooled from visits by scouts to standard-size nests during five separate experiments involving five colonies).

We tested three alternative hypotheses about the method which individual scouts use to assess nest area. They may (i) measure the length of the internal perimeter of the nest as a loose correlate of nest area, (ii) use a 'mean, free-path-length algorithm' or (iii) employ 'Buffon's needle algorithm'.

The ants do not use the length of the internal perimeter of the nest as a surrogate index of nest area. Given a choice between a standard-size nest and a half-size nest with the same internal perimeter length (figure 1*c*), the ants choose the larger nest (table 1, experiment C). Scouts spend a good proportion of their visits exploring the perimeter of a potential nest site (figure 2). This may reflect a need to check that the wall is not breached in too many places and may help scouts return to the nest entrance.

A scout using the mean, free-path-length algorithm would use the average distance it walks between collisions with the walls in the new nest to estimate the area of the nest. The greater the average distance the greater the nest area. An experiment in which a thin partial barrier was placed down the centre of an otherwise standard-size nest (figure 1*d*) showed that the ants are not using this method. The ants chose similar numbers of such partial barrier nests in which their mean, free-path length would be small- and standard-size nests (table 1, experiment D).

Two centuries ago, Comte George de Buffon proposed a method for estimating π empirically. A needle of length B dropped randomly onto a plane inscribed with parallel straight lines I units apart (where $B < I$) has a probability $p = 2B/I\pi$ of intersecting a line (Kendall & Moran 1963). Based on such reasoning, it can be shown (Newman 1966; Franks 1982) that the estimated area of a plane ($\hat{A}$) is inversely proportional to the number of intersections (N) between two sets of lines, of total lengths S and L, randomly scattered on to it: thus $\hat{A} = 2SL/\pi N$. This formula establishes that the number of intersections between two sets of lines could be used as a relatively simple rule of thumb to estimate area.

Scouts using such a Buffon's needle algorithm will assess nest area as inversely proportional to the number of intersections they make between a first set of pheromone-marked paths and a second set of census paths. Hence, use of the Buffon's needle algorithm might explain why scouts make more than one visit to a potential nest site. The Buffon's needle algorithm requires the deployment of two distinct sets of paths. Conceivably, an ant could remain within the new nest site between the deployment of its first and second paths but some transitional break between these activities is necessary. Departure from the nest would not only provide such a break but may also allow the ant to check the route between the old and the new nest. Scout ants often return to the old nest between

Table 1. *Nest-choice experiments*

(The table records the number of colonies which chose each type of nest. In experiment A choices of standard-size and two times standard-size nests were pooled because we were concerned with the rejection of half-size nests. The frequencies were analysed with either one-tailed (indicated by an asterisk) or two-tailed (indicated by a double asterisk) binomial tests. n.s., not significant.)

experiment	nest choice			p
A	twice standard size	standard size	half size	
chosen	7	8	1	—
	above threshold size	below threshold size		
chosen	15	1		$< 0.0010^{**}$
B	standard size	five-eighths standard size		
chosen	15	0		$< 0.0001^{**}$
C	standard size	half size with standard-size internal perimeter		
chosen	10	3		$< 0.0500^{*}$
D	standard	size standard size with partial barrier		
chosen	6	9		$> 0.3000^{*\text{n.s.}}$
E	standard size	magic carpet half size		
chosen	12	8		$> 0.8000^{*\text{n.s.}}$

visits to the new one (E. B. Mallon and N. R. Franks, unpublished observations).

However, the Buffon's needle algorithm can only work if the first visit path was marked with an individual-specific trail pheromone which could be detected on the second visit. The trail pheromones would need to be individual specific because several scouts can simultaneously discover a potential nest site and if they deployed the same trail pheromones in the new nest site the number of second visit intersections would depend heavily not just on the nest area but on the number of scouts involved. Hence, private trail signals are required.

Closely related species of *Leptothorax* to *L. albipennis* are known to use individual-specific trail pheromones for orientation outside their nests (Maschwitz *et al.* 1986; Aron *et al.* 1988). We present here, to the authors' knowledge, the first evidence that *L. albipennis* ants deploy individual-specific trail pheromones within new nest sites. Typically, scouts spend less time within the potential nest cavity during subsequent visits (figure 3). Experiments in which potential nest sites were substituted between a scout's first and subsequent visits showed that she only reduced the length of her scouting periods if she had herself made an earlier visit to the nest site. Visits by other nest-mates or by conspecific ants from other colonies had no influence. We recorded the duration of visits by individually marked workers to a standard-size nest and to a substitute nest of the same size. After the ant left the nest following its first visit, the nest was either (i) substituted by one visited by a worker from a different colony or (ii) substituted by one visited by a nest-mate. In (i) and (ii) the individual worker spent as long in the replacement nest as expected on a first visit (Wilcoxon signed-ranks test for paired comparisons, (i) $z = -1.224$, $n = 14$ and $p = 0.221$, and (ii) $z = -0.336$, $n = 16$ and $p = 0.737$). These experiments indicated that scouts deploy

individual-specific trail pheromones during their first visit to a nest site and that they respond to these on their second visit. This is the first time individual-specific trail pheromones have been shown to be used inside nest cavities.

There is evidence that individual scouts recognize and respond to intersections between their second visit path and their first visit path. Scouts briefly but significantly slowed down during their second visit when they intersected their first visit path. Videotape images of the behaviour of ants on their first and second visits were digitized and analysed and the locations of the intersections between second visit and first visit paths were recorded. The speeds of the ants during second visits were calculated every 0.2 s. The speeds at intersections were noted when an ant was within one antenna's length (= 5 pixels) of its first visit path. Ants may also move at different speeds in the centre of the nest or close to a wall. Hence, we analysed the ants' intersection and non-intersection speeds in two regions: (i) central (any point greater than 30 pixels, i.e. slightly greater than one body length, from a wall), and (ii) edge (points less than 30 pixels from a wall). Nine ants were examined; of these six showed significant changes of speed at intersections and all six slowed down (median non-intersection speed in the central region $5.80 \, \text{mm s}^{-1}$ and interquartile range $10.44 \, \text{mm s}^{-1}$, median intersection speed in the central region $3.79 \, \text{mm s}^{-1}$ and interquartile range $9.52 \, \text{mm s}^{-1}$, median non-intersection speed in the edge region $4.53 \, \text{mm s}^{-1}$ and interquartile range $7.97 \, \text{mm s}^{-1}$, and median intersection speed in the edge region $3.04 \, \text{mm s}^{-1}$ and interquartile range $6.02 \, \text{mm s}^{-1}$). These data were analysed using a two-way ANOVA design for ranks by the Scheirer–Ray–Hare extension of the Kruskal–Wallis test (H range 5.1–29.9, d.f. = 1 and p range < 0.05–< 0.001) (Sokal & Rohlf 1995).
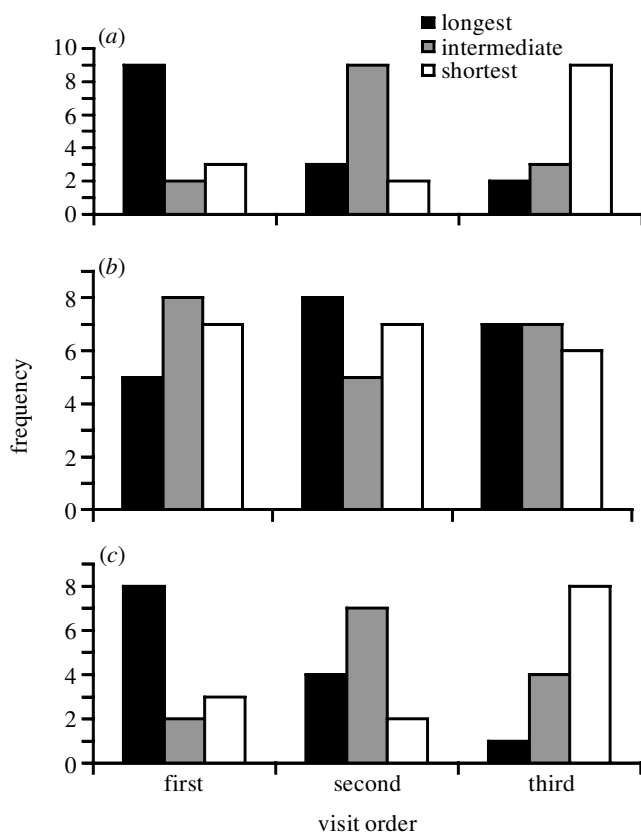
Figure 3. (*a*) The duration of assessment visits by individually marked workers to standard-size nests were recorded for their first, second and third visits to the same nest. The visits of individuals were ranked: longest (black bars), intermediate (shaded bars) and shortest (white bars) in duration. Visits became progressively shorter (Friedman's two-way analysis of ranks $\chi^2_{r2} = 6.14$ and $p < 0.05$). (*b*) If the nest was replaced by an identical new clean nest after each visit the ant spent the same amount of time on each visit ($\chi^2_{r2} = 0.3$ and n.s.). (*c*) As a control for physical disturbance in the nest-substitution experiments, the original nest was moved and then placed back in position. Here, as in figure 2*a*, the ants spent less time on each subsequent visit ($\chi^2_{r2} = 6.00$ and $p < 0.05$).

Buffon's needle algorithm requires that the trail pheromone is relatively long lived. Individual-specific trail pheromones are likely to be more persistent than mass recruitment pheromones which can be reinforced quickly by nest-mates. For example, individual-specific pheromones deployed during foraging must last long enough for an individual ant to get to the end of its journey and for it to be able to retrace its steps. For *L. albipennis*, we believe that their foraging distances are likely to exceed their emigration distances. Therefore, individual-specific pheromones which are sufficiently long lived for foraging should be sufficiently long lived for nest assessment. Highly persistent ground-marking pheromones have been demonstrated in other contexts (Hölldobler & Wilson 1977, 1986). In fact, the median intervisit duration is only 145 s (interquartile range of 461 s, $n = 89$).

On their second visit, scouts could be assessing the frequency of the intersections they make with their own individual-specific trail which they deployed on their first visit. The median number of intersections per scout between second visit paths and first visit paths in the central and edge regions of the nest were 178 and 172,
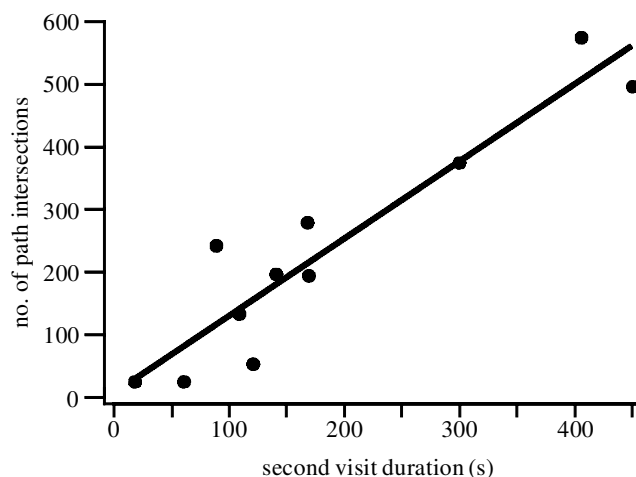

Figure 4. The number of intersections between second visit paths and first visit paths as a function of the duration of the second visit by 11 scouts to nests of standard size. The relationship is best described by number of intersections ($\mathcal{N}$) = $7.4 + 1.23$. (Second visit duration, in seconds). ($r^2 = 0.873$ and $p < 0.001$.)

respectively ($n = 11$ scouts). First visit and subsequent visit paths appear to sample the whole area of the nest fairly evenly (figure 2). Figure 4 shows the relationship between the length of an ant's second visit and the number of intersections it makes during that visit with its first visit path. The relationship is strong and linear. This suggests that the paths are distributed to facilitate unbiased surveying. In other words, the distribution of the first set of lines (L) and the second set of lines (S) is a sufficient approximation to randomness. The median distances scouts walk on first, second and third visits are 726, 498 and 404 mm, respectively ($n = 11$ scouts). For many ants (31%) two visits appears to be not only a necessary condition but also a sufficient condition for estimation of a nest's area. For this reason and to simplify the analysis, we focused on the behaviour of ants on their second visit compared to their first visit. Scouts may only deploy individual-specific trails on their first visit: all subsequent visits might be for assessment. For example, during their third visit, five out of 11 ants slowed down when crossing the trail they had personally deployed on their first visit (H range 9.68–17.44, d.f. = 1 and p range < 0.01–< 0.001). The average speed of scouts overall is markedly less on the first visit (median 3.36 mm s^{-1}, interquartile range 6.33 mm s^{-1} and $n = 8681$) than during subsequent visits (median 4.06 mm s^{-1}, interquartile range 6.93 mm s^{-1} and $n = 9834$ for second and third visits combined: Mann–Whitney U-test, $p < 0.0001$) (the data for the second and third visits were combined because they were not significantly different from one another, $p > 0.05$). This may be indicative of trail laying only on the first visit. If ants laid trails on more than one visit, the complexity of estimating a nest's area from the intersection rate would be greatly increased. Multiple visits may increase the accuracy of nest-area assessment through repeated measurement of the intersection frequencies.

The Buffon's needle equation for estimating area is $\hat{A} = 2SL/\pi\mathcal{N}$. Hence, an ant might estimate area $\hat{A}$ as inversely proportional to the number of intersections ($\mathcal{N}$) it makes between its first visit path (length L) and its
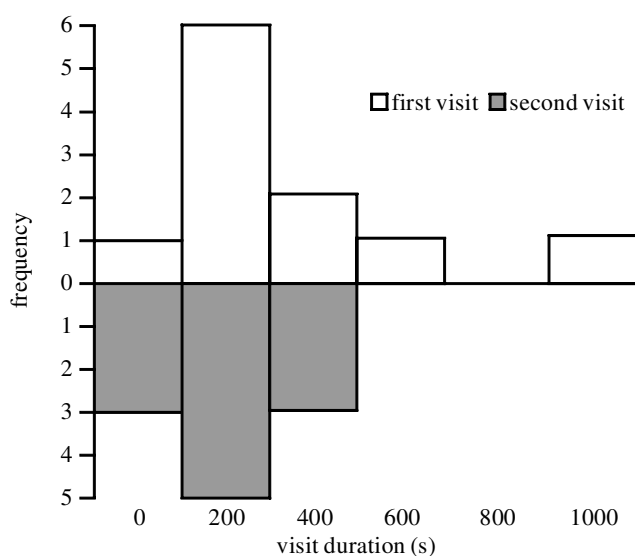
Figure 5. Histogram of the first (white) and second (shaded) visit durations (s) of 11 scouts to nests of standard size.

second visit path (length S): 2 and π are constants and irrelevant here. This rule of thumb would be simplest if the ants keep L constant and estimate the intersection rate between their first and second paths. The duration and path length of the second visit could vary. This would influence the variance of the estimate, but not the mean intersection rate (see figure 4). The duration of first visits has a distinct peak at 200 s (see figure 5). Intriguingly, the duration of second visits also has a distinct peak at 200 s. This suggests that the ants are keeping both L and S fairly constant. Furthermore, in the clean nest-substitution experiment, each ant repeatedly spent approximately the same amount of time in each new nest it was offered. This explains the pattern of data presented in figure 3b.

All the findings documented above show that use of a Buffon's needle algorithm is plausible in terms of the behaviour of scouts. However, the key test is to manipulate the ants' trail intersection frequencies in such a way that the use of a Buffon's needle algorithm would lead them to make predictable but otherwise unexpected choices. These ants are using individual-specific trails so it is not possible for the experimenter to apply the trail pheromone directly to increase the trail intersection frequencies. However, it is possible to reduce the number of intersections. In the Buffon's needle algorithm the intersection frequency is inversely proportional to area. We presented emigrating colonies with a choice between standard-size nests and half-size nests. Both types of nest were carpeted with two layers of acetate sheet. The upper sheet in the half-size nest had rectangular holes in it over half the total floor area (figure 1e). Fifteen minutes after the start of each experiment, i.e. after half the median exploratory period, this upper sheet in the half-size nests was removed. By removing the 'magic carpet' at this time, approximately half of the trails laid in the small (half-size) nest should have been removed and the number of intersections between first visit and subsequent paths should have been similarly reduced. (As a control for disturbance the under-sheet in the full-size nest was removed at the same time.) In these experiments,

approximately half of the colonies chose the small nest, which would normally be rejected (table 1, experiment D). Given that the intersection frequency in the small nest was reduced by half, an ant using the Buffon's needle algorithm would then consider such a half-size nest to be full size. This result strongly suggests that scouts are using the Buffon's needle algorithm. We suggest that scouts may use the Buffon's needle algorithm by assessing the rate at which they cross their previous path. Such assessment is plausible since optimal foraging studies show that many insects can measure the rate at which they encounter stimuli (Stephens & Krebs 1986). Figure 4 strongly implies that the intersection rate between first and second visit paths is very nearly constant for these ants. The inverse of such an intersection rate should therefore provide a good estimate of nest area. The extremely high resolution in the choices between nests of different areas (table 1) may result not just from the behaviour of individual ants but also from many scouts being involved in independent decision-making processes. This 'voting' phenomenon is currently under investigation.

The employment of Buffon's needle algorithm by these ants is likely to be robust for two major reasons. First, it should be relatively insensitive to the shape of the area to be assessed and to the exact deployment of the census lines (as long as these lines are not concentrated within just one region). This is shown by the successful use of the Buffon's needle formula in estimating the length of plant roots (Newman 1966) and censusing animal populations (Franks 1982). Second, it can operate in an entirely dark nest.

Recent studies have revealed the sophisticated navigation and landmark recognition skills of individual ants and bees (Collett & Baron 1994; Wehner *et al.* 1996; Judd & Collett 1998). Our findings, that individual ants can make accurate assessments of nest areas based on a rule of thumb, show in a unique way how animals use robust algorithms to make well-informed quantitative decisions. Honeybee scouts are known to measure the size of potential nest cavities before advertising the value of a nest site to their swarm (Seeley 1977). The algorithm that honeybees use for such an assessment is not known, although they do spend much time walking the inside walls of nest cavities (Seeley 1977). Our work on ants opens up the possibility that honeybee scouts may also be using rules of thumb based in part on the Buffon's needle algorithm.

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