The accuracy of Buffon's needle: a rule of thumb used by ants to estimate area

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Colonies of the ant *Leptothorax albipennis* naturally inhabit flat rock crevices. Scouts can determine, before initiating an emigration, if a nest has sufficient area to house their colony. They do so with a rule of thumb: the Buffon's needle algorithm. Based on a derivation from the classical statistical geometry of Comte George de Buffon in the 18th century, it can be shown that it is possible to estimate the area of a plane from the frequency of intersections between two sets of randomly scattered lines of known lengths. Our earlier work has shown that individual ants use this Buffon's needle algorithm by laying individual-specific trail pheromones on a first visit to a potential nest site and by assessing the frequency at which they intersect that path on a second visit. Nest area would be inversely proportional to the intersection frequency. The simplest procedure would be for individual ants to keep their first-visit path-length constant regardless of the size of the nest they are visiting. Here we show, for the first time, that this is the case. We also determine the potential quality of information that individual ants might have at their disposal from their own path-laying and path-crossing activities. Hence, we can determine the potential accuracy of nest area estimation by individual ants. Our findings suggest that ants using the Buffon's needle rule of thumb might obtain remarkably accurate assessments of nest area. *Key words:* ants, Buffon's needle algorithm, *Leptothorax albipennis,* nest measurement, pheromones. *[Behav Ecol 12:655–658 (2001)]*

The ability of animals to make decisions about where to live is crucial to their fitness (Lack, 1968; Seeley, 1985; von Frisch, 1974). Many animals have the ability to discriminate among nesting sites or among territories on the basis of quality. Rendell and Verbeek (1996) showed that the nest cavity choice of the tree swallow is influenced by the amount of debris remaining from previous inhabitants, as this affects both the size of the cavity and the number of ectoparasites. For cliff swallows, the time it would take to build a nest at a new site is the most important factor in site selection (Gauthier and Thomas, 1993). Honeybees have been shown to discriminate between potential nest cavities based on many different variables, including volume of the nest cavity, presence or absence of comb, and height above the ground (Seeley, 1977).

Although Seeley (1977) proposed that volume estimation was related to how long honeybees walked around the nest, none of the other reports proposed a mechanism by which the individual could assess the quality of the site or the quantity of resources. Few studies have attempted to elucidate such a mechanism (although see Schmidt and Smith, 1986, for their elegant study of host egg measurement by the parasitoid wasp, *Trichogramma minutum*).

Leptothorax albipennis is a small (approximately 3 mm long) monomorphic myrmicine ant. It lives in small colonies with fewer than 500 workers and a single queen. *L. albipennis* colonies in Britain nest in crevices in rocks (Partridge et al., 1997). These crevices can be replicated in the laboratory in geometry and size by artificial nests made from microscope slides (Sendova-Franks and Franks, 1993). Mallon and Franks (2000) demonstrated that the workers of this species are ca-

pable of measuring the floor area of artificial nests and rejecting those that are too small. They provided evidence that individual ants make measurements of the area of the new nest using a method which they termed the "Buffon's needle algorithm."

Buffon's needle is a classic exercise in geometrical probability named after the eighteenth-century mathematician Georges Louis Leclerc Comte de Buffon (Kendall and Moran, 1963). An equation ($\hat{A} = 2SL/\pi N$) can be derived from Buffon's analysis which relates the area of a plane ($\hat{A}$) to the lengths of two sets of random lines (S and L) and the number of intersections (N) between them (see Mallon and Franks, 2000, for a detailed explanation).

Mallon and Franks (2000) showed that upon entering a nest each scout ant lays an individual-specific trail pheromone inside the nest. She then leaves the nest, reenters it, and estimates her frequency of intersection with her previous trail. This intersection frequency is inversely proportional to the area of the nest. Mallon and Franks (2000) reduced this intersection frequency (between first- and second-visit paths) by presenting ants with nests in which there was a floor-sheet that had holes over half its area and by taking away this sheet between first and second visits. Removal of this sheet should have removed approximately half the trails laid on first visits and should also have reduced trail intersections on second visits by a factor of about 2. This caused colonies to accept nests that they would have otherwise rejected as too small.

What is the potential accuracy of this rule of thumb? The simplest way this algorithm could give an estimate of area would be if each scout ant lays the same length of trail on her first visit to a new nest, no matter what size the nest (see Discussion). Here we detail experiments to test this prediction and also present experiments to quantify the accuracy of the Buffon's needle algorithm.

METHODS

Collection and marking of colonies

Colonies of *Leptothorax albipennis* (Curtis) were collected from Portland Bill, England, in March 1999. They were cul-

tured in the laboratory by housing each colony in a nest made by sandwiching a piece of cardboard between two glass microscope slides (Sendova-Franks and Franks, 1993). The standard nesting cavity within the cardboard was $35 \times 25 \times 0.8$ mm. The single entrance to the cavity measured $2 \times 2 \times 0.8$ mm. Each nest was placed in a petri dish, $100 \times 100 \times 17$ mm, the walls of which were covered with Fluon to prevent the ants from escaping.

In each of three colonies, we marked every worker with a unique combination of four different colors of paint spots (from a palette of six possible colors): one spot on the head, one on the thorax, and two on the gaster.

Emigration

We induced the colonies to emigrate to new nests of standard (25×35 mm) and double-standard (35×50 mm) floor area. The old and new nests were placed 10 cm apart (entrance to entrance) in a large (220×220 mm) petri dish with Fluon-coated sides. The emigration was triggered by removing the upper glass slide from the old nest so that the cavity was exposed. The experiment was recorded using a Panasonic NV-SX30B S-VHS camera, trained on the new nest, recording directly onto a Panasonic TL700 time-lapse VCR in real time. The color resolution of the camera did not permit sufficiently accurate recognition of individuals from the videotape. Hence, we determined the identity of the ants entering and leaving the nest by direct observation during each experiment and recorded this information on the audio channel of the tape. Using this setup, it was possible to record exactly when each ant entered and left the nest. The filming stopped when most ants entering the nest were involved in recruiting or transporting activities, usually within 1–2 h of the beginning of the emigration. Each colony emigrated four times, twice to a standard nest and twice to a double standard-sized nest.

Measurement of visit distance

We recorded both first and second visits for 10 ants to both standard- and double-sized nests. The paths of these visits were traced onto acetate sheets directly from the monitor by advancing the videotape at 1-s intervals and marking the position of the gaster (for first visits) or head (for second visits). For first visits we recorded gaster position, as it would indicate approximately the position of trail laying (for myrmicine ants most of the trail-laying pheromones are produced by their hind regions; Hölldobler and Wilson, 1990). The head position during second visits would indicate roughly where the ant was intersecting its first-visit path with its antennae. Each point was connected to the next by a straight line and the distance measured with a map measurer. We recorded the total distance covered for each visit in millimeters. We estimated the number of intersections made between the paths of first and second visits to the same nest by overlaying the acetate sheets from the two visits and counting the number of intersections between the two lines.

RESULTS

The distribution of distances traveled for each first visit of scouts from one of the colonies was normalized by the square-root transformation. There was no significant difference between the distance an ant traveled inside the nest on her first visit to a standard-sized nest (raw data median: 486 mm, square-root-transformed data: mean $\pm$ SD $= 21.64 \pm 3.83$) and the distance traveled on her first visit to a double standard-sized nest (600 mm, 25.57 ± 8.43; paired t test: $t = 1.79$, $n = 9$).
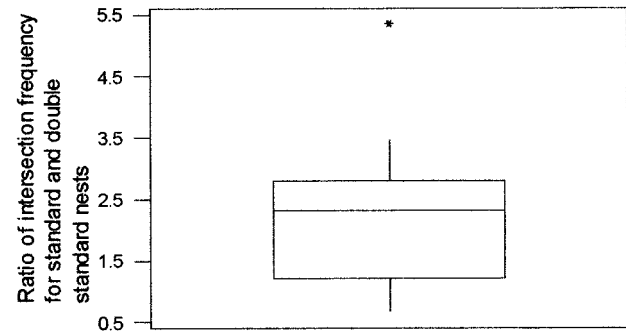

Figure 1
A boxplot showing the distribution of ratios of intersection frequencies experienced by each ant as it visits standard nests and intersection frequencies experienced by each ant as it visits double-standard nests. The solid line inside the box represents the median of the data. The bottom and top of the box represent, respectively, the 1st quartile and 3rd quartile of the data. The vertical lines extending from the box represent the data inside a range of 1.5 times the interquartile range from the box. An outlier is represented by an asterisk.

For the data pooled from the three colonies, there was also no significant difference between the visit duration (seconds; square-root transformed to normalize) of an ant on its first visit to a standard-sized nest (raw data median: 222 s, square-root-transformed data: mean $\pm$ SD $= 15.801 \pm 4.460$) and on its first visit to the double standard-sized nest (182 s, 13.765 ± 4.482; paired t test: $t = 1.65$, $n = 23$).

The intersection frequency (intersections per millimeter) data, calculated for one colony, was also normalized by the square-root transformation. There was a significant difference between the intersection frequencies of an ant when it visited the standard nest (mean $\pm$ SD $= 0.7193 \pm 0.2004$) and the double-standard nest (0.5205 ± 0.1660; paired t test: $t = 2.96$, $n = 9$, $p = .016$; Figure 1).

We observed that when an enters a nest containing several other ants, she spends time making antennal contact with and grooming these ants. This might cause considerable variation in visit duration. For example, ants that enter the new nest early in the emigration may spend less time in the nest because there are fewer ants to groom. To test whether this was the case, a correlation was performed of the duration of first visits of ants of the colony against the average nest population of the new nest at the time of their visits. There was no significant correlation between average population and visit duration (Spearman rank correlation: $r_s = .168$, $n = 59$, $p = .203$; Figure 2).

Assuming these 10 ants were using Buffon's needle algorithm (see equation 2 in Discussion), we calculated the nest area they would have perceived on the basis of their own trail laying and intersection frequencies. Figure 3 compares the mean perceived area for each type of nest against its true value.

DISCUSSION

We have shown that ants surveying a new nest cover a similar distance on their first visit to a nest regardless of the size of the nest cavity. They also spend the same amount of time in a nest on their first visit regardless of the size of the nest. First-visit durations are not correlated with the number of nest mates that are in the new nest at the time of the visit. The frequency at which an ant intersects its previous path is significantly greater when the ant scouts a standard-sized nest compared to a double-sized nest. Fur-
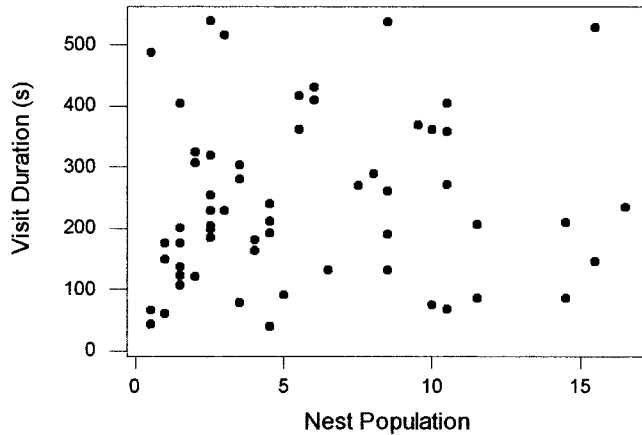
Figure 2
Visit duration (seconds) versus nest population at the time of the visit.

Figure 3
A boxplot showing the distribution of perceived areas calculated for each ant on its visit to both a standard and a double-standard nest. The points represent the respective true values of the area of the two nests. The solid line inside the box represents the median of the data. The bottom and top of the box represent, respectively, the 1st quartile and 3rd quartile of the data. The vertical lines extending from each box represent the data inside a range of 1.5 times the interquartile range from the box.

thermore, there is likely to be only a small amount of variation in the perceived area for different ants when they visit the same-size nest.

The area of a plane can be calculated from the following equation (see Introduction):

$$\hat{A} = 2SL/\pi N \qquad (1)$$

The frequency of intersection (I) of lines S (distance traveled inside the nest during the second visit) and L (distance traveled during first visit) is N (the number of intersections between first- and second-visit paths) divided by S, so equation 1 becomes

$$\hat{A} = 2L/\pi I. \qquad (2)$$

Dropping the constant $2/\pi$ from equation 2, we have

$$\hat{A} \sim L/I. \qquad (3)$$

The simplest use of this relationship as a rule of thumb would be for the ant to make her first-visit path distance (L) constant regardless of the size of the nest. This is indeed what the ants appear to do (see Results). Then expression 3 becomes

$$\hat{A} \sim 1/I \qquad (4)$$

(i.e., the area of a nest is inversely proportional to the intersection frequency). We have found that intersection frequency for a standard nest is just more than twice that of the intersection frequency for double-standard nests (median ratio = 2.31; see Figure 1).

The Buffon's needle algorithm shows that there can be a simple relationship between the intersection frequency of two sets of random lines and area. One remaining issue is the degree of accuracy of nest area estimation individual ants could achieve given their own particular pattern of trail laying and rate of path intersection. We can estimate this by putting the empirically calculated intersection frequencies of each of the 10 ants and their individual average first-visit lengths into equation 2. We are not, of course, suggesting that ants know about π or that they calculate distances in millimeters; rather, we are using this equation to calculate relative perceived areas to see how much variation there is in the estimation of nest area by individual ants. Such variation is relatively small (see Figure 3). Notice how close the perceived areas are to the nests' true values. However, this is not really important. What matters is that there is a close approximation to a 2:1 ratio for perceived areas for double-sized nests versus standard-sized nests (the calculated ratio
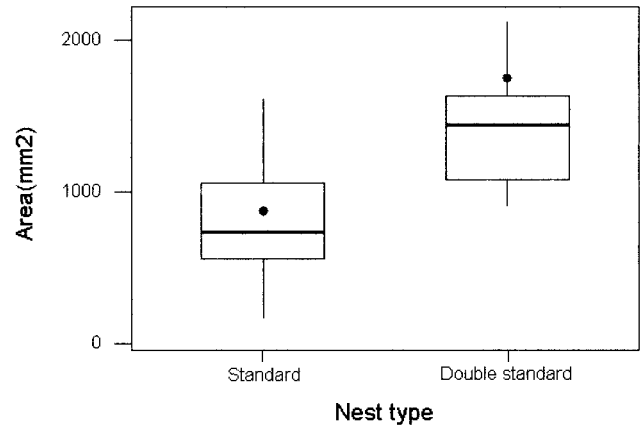
is 1.96:1). That is, ants using Buffon's needle algorithm would measure the double-standard nest as having twice the area of a standard-sized nest. For other cases in which the accuracy of the rules of thumb used by insects have been determined, see Cartwright and Collett (1983) and Müller and Wehner (1988).

Mallon and Franks (2000) introduced Buffon's needle algorithm as a possible method by which scout ants could measure nest area. The present study has provided further evidence that these ants are using such an algorithm. We also show the potential accuracy of this method by feeding the ants' own (potential) data into the algorithm. It may be the case that there is also collective decision making in this system in which the assessments of many different scouts are combined to add yet another level of robustness. This will be the subject of further work.

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