



The cavity-dwelling ant *Leptothorax curvispinosus* uses nest geometry to discriminate between potential homes

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(Received 18 August 2000; initial acceptance 19 October 2000;
final acceptance 17 April 2001; MS. number: 6669R)

Nest site selection is a frequent context for decision making in ants, but little is known of the criteria used to make a choice. We tested the nest site preferences of *Leptothorax curvispinosus*, both by measuring hollow acorn nests occupied in nature, and by inducing laboratory colonies to choose between artificial nests of different design. Three criteria were examined. (1) Entrance size: the ants preferred small entrance holes, presumably for their greater defensibility and crypsis. Natural nest entrances were small, and 52% of them were reduced still further by the addition of rims of soil and leaf litter. In choice tests, colonies selected nest entrances near the median size of rimmed natural holes, rejecting those near the larger end of the distribution of raw natural holes. (2) Cavity volume: acorn cavity volume was weakly correlated with the size of the occupying colony. In choice tests, colonies rejected cavities near the median size of natural nests, preferring instead larger cavities near the upper end of the natural size distribution. This may reflect active size matching of colonies to nests, because the colonies used in the choice test were bigger than those from the natural nest sample. Alternatively, all colonies may prefer big nests, but face limited availability of large cavities in nature. (3) Cavity shape: colonies preferred shapes roughly similar to that of an acorn interior, rejecting thin crevices in favour of compact, high-ceilinged cavities.

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Behavioural ecologists commonly interpret the ultimate causes of behaviour in terms of decision making, with animals expected to adopt the fitness-maximizing course of action in any given situation (Krebs & Kacelnik 1991). However, the proximate mechanisms underlying particular decisions are generally not well understood. This is particularly true for nest site selection, because it is difficult to identify the factors that influence an animal's choice. Descriptions of nest sites are abundant for several taxa, and many studies have inferred preferences by comparing the sites used for nesting with others sampled at random (e.g. Christian 1980; Wilson 1998; Clark & Shutler 1999). Less common are experimental analyses of proximate cues affecting an animal's choice (Partridge 1974; Seeley & Morse 1978; Buhot-Averseng 1981; Duncan & Kite 1989; Ottoni & Ades 1991). Without such studies, the association of a particular environmental feature with the presence of nests does not necessarily imply a direct influence on behaviour. Irrelevant features may simply be correlated with genuine cues. Furthermore, associations may arise even in the absence

of active choice, if nests situated in less favourable sites fail more often and thus are unavailable for counting.

Among ants, the high frequency of colony emigration makes nest site choice a crucial problem (Smallwood 1982; Hölldobler & Wilson 1990). Effective decision making is especially important to those species inhabiting fragile, preformed cavities, such as hollow twigs or seed husks. Unlike ants that build their own nests, cavity dwellers face restricted opportunities for nest improvement. If the cavity is damaged or its capacities are outstripped by colony growth, the ants must find a better nest, rather than repairing or enlarging the old one. These constraints make cavity dwellers a promising subject in which to determine how emigrating colonies evaluate prospective sites. We initiated such a study by examining the nest site preferences of *Leptothorax curvispinosus*.

The small colonies of *L. curvispinosus* (fewer than 500 workers) typically live in hollow acorns or other nuts, with entrances provided by the exit holes of seed-eating insects (Headley 1943; Creighton 1950). Leptothoracines are frequent and adept emigrants (Möglich 1978; Yamaguchi 1992; Foitzik & Heinze 1998), and colony movements can easily be induced in the laboratory. Several studies have addressed the roles of division of labour and recruitment behaviour in organizing emigrations (Möglich 1978; Sendova-Franks & Franks 1995),

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and the process by which the colony restores its spatial and social structure in the new nest (Sendova-Franks & Franks 1994; Backen et al. 2000). Nest site preferences have been examined directly in only one species: colonies of *Leptothorax albipennis*, which typically live in thin rock crevices, discriminate between artificial nests on the basis of area and reject those that are too small (Mallon & Franks 2000). There is also indirect evidence that *Leptothorax longispinosus* prefers relatively small cavities (Herbers & Banschbach 1995).

We examined three features of nest geometry important to nest function. Cavity volume must be large enough to house all of a colony's members, but too large a cavity may impede the regulation of temperature, humidity, or other nest conditions. Cavity shape may also affect environmental regulation, as well as indirectly influencing the colony's social organization, through its effect on the spatial distribution of ants and brood within the nest (Sendova-Franks & Franks 1995). Entrance hole size must allow passage of the largest colony members, but smaller holes will probably be less conspicuous to enemies and more easily defended. *Leptothorax curvispinosus* face threats from conspecific territorial aggression, slave-making ants and other predators for whom the concentrated brood and workers make an attractive resource (Alloway 1980).

To discover the nest designs used by ants, we measured the volumes and entrance sizes of naturally occupied acorn nests. To determine the degree to which commonly used designs reflect active choice by the ants, we performed preference tests in the laboratory with nests differing in cavity shape, volume and entrance size.

METHODS

Collection and Measurement of Nests and Colonies

We collected 41 colonies of *L. curvispinosus* in deciduous woodlands at Middlesex Fells Reservation and Rock Meadow Preserve near Boston, Massachusetts, U.S.A. between 2 and 18 October 1997. We found colonies by searching the leaf litter for acorns with visible entrance holes. In the laboratory, we opened the acorns with a sharp knife; when an occupied acorn was found, the ants were gently knocked out and induced to move into 1-ml plastic centrifuge tubes. We weighed the occupied tubes on a Mettler MT5 balance to the nearest 0.01 mg and the colony weight was taken as the difference between this weight and that of the empty tube. The colonies were then moved into observation nests (Fig. 1) where we could roughly count the numbers of adults and brood items. Colonies were weighed within 5 days of collection, and censused within 10 days.

To measure cavity volume, we first glued the empty acorn nests back together and then filled them with fine sand. The difference between the filled and empty weights of each acorn was divided by the density of the sand (1.728 g/ml) to give an estimate of volume.

We estimated entrance size as the area of an ellipse approximately matching the shape of the entrance hole; that is, $\pi(a/2)(b/2)$, where a is the longest diameter of the

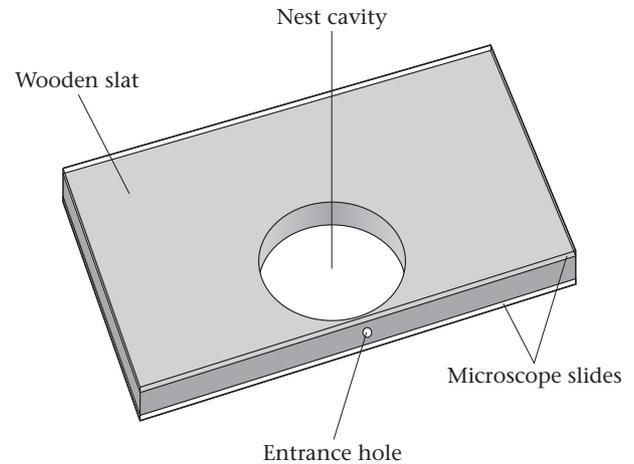


Figure 1. Artificial nest used in preference tests. The volume of the cavity was varied by altering its diameter and its shape was varied independently of its volume by altering both the cavity diameter and the thickness of the wooden slat. The size of the entrance hole was varied by altering its diameter.

hole and b the diameter orthogonal to this. Diameters were measured under a dissecting microscope equipped with an ocular micrometer. Because the original hole was often lined by a rim of soil and leaf litter, we measured the entrances both with this lining intact, and after removing it. Entrance holes and volumes could not be measured for some nests that were damaged during extraction of the ants. After the experiments, the colonies were maintained in culture for use in other projects.

Statistical analyses are described in the Results. Data that were not normally distributed (according to the Anderson–Darling test) were analysed with appropriate nonparametric methods. All tests are two tailed.

Preference Tests

We gave emigrating colonies a choice between nests differing in entrance size, cavity volume, or cavity shape. For volume and entrance size, each choice was between the median and extreme values of the distributions found in natural nests. For cavity shape, the choice was between a thin, flat crevice and a compact, roughly spherical form more closely approximating the shape of natural acorn nests.

We tested colonies in opaque Plexiglas arenas (75 × 29 cm and 13 cm high) under even lighting in a climate-controlled chamber (25 °C, 60% relative humidity, 12:12 h light:dark schedule). We placed a colony in its artificial nest against the centre of one long wall of each arena and two uninhabited nests, identical in design except for the parameter under test, against the short walls of the arena, equidistant from the colony. Each nest consisted of a circular chamber cut out of a rectangular segment of basswood, sandwiched between two glass slides (50 × 76 mm). A round entrance hole was drilled through one wall of the chamber (Fig. 1). A sheet of red acetate film was placed on the roof of each

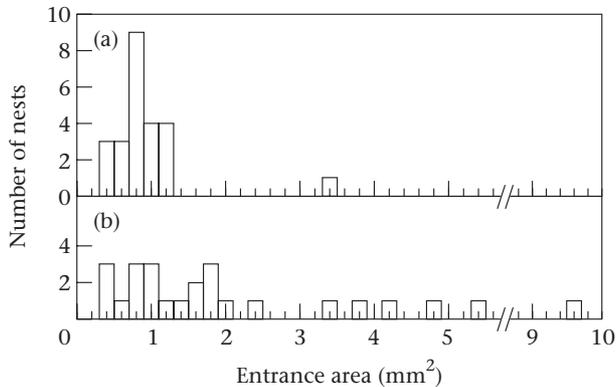


Figure 2. Distribution of entrance sizes in naturally occupied acorn nests. (a) Intact entrances, $N=25$. (b) Entrances with their soil and leaf litter rims removed, $N=13$.

uninhabited nest to darken its interior and enhance its attractiveness to the ants.

Once the colony had acclimated to the arena for 1–2 h, we induced it to emigrate by removing the top slide of the old nest. On the following day, we noted the nest into which the ants had moved. We repeated each test with 16–30 colonies, drawn from 30 of those collected for nest measurements, as well as another 16 collected in July 1996 at Beaver Brook Reservation and in June–August 1997 at Rock Meadow Preserve. All colonies were used in more than one test. There is no evidence that testing experience influences a colony's subsequent preferences but we minimized any possible effects by interposing long intervals (5 days to 2 months) between tests. Within each test, the majority of colonies had identical prior experience, and our results did not change when we excluded the minority of colonies with different histories.

Each emigration ended with one of three outcomes: (1) the colony moved into one of the nest designs; (2) the colony moved into the other nest design; (3) the colony split and moved into both nest designs. These outcomes were scored as 0, 1 and 0.5, respectively. To determine whether the colonies preferred one design over the other, we compared the sum of these scores over all colonies to the distribution expected under the null hypothesis of no preference: that is, a binomial distribution with a mean of $0.5 \times n$, where n is the number of colonies tested. For noninteger sums, P values were derived from an incomplete beta function, a continuous approximation of the binomial distribution (Press et al. 1992). All tests were carried out between August and December 1997.

RESULTS

Natural Nests

Occupied acorns appeared old and discoloured, but all had intact walls with a single small, inconspicuous and roughly circular entrance hole. Of the 25 holes measured, 13 were lined with soil and leaf litter. Figure 2 shows the distribution of hole sizes with and without these rims. The mean area of raw holes was $2.16 \pm 2.08 \text{ mm}^2$, $N=25$, but the same sample, when measured with the 13 rimmed holes still intact, had a significantly lower mean area

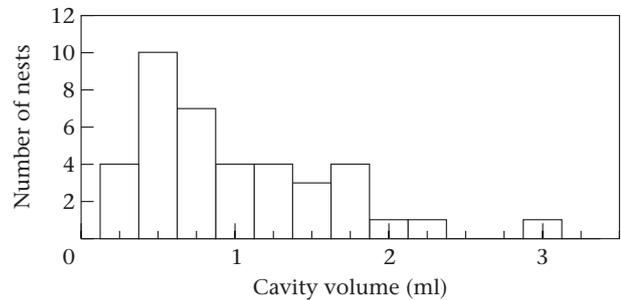


Figure 3. Distribution of cavity volumes of naturally occupied acorn nests.

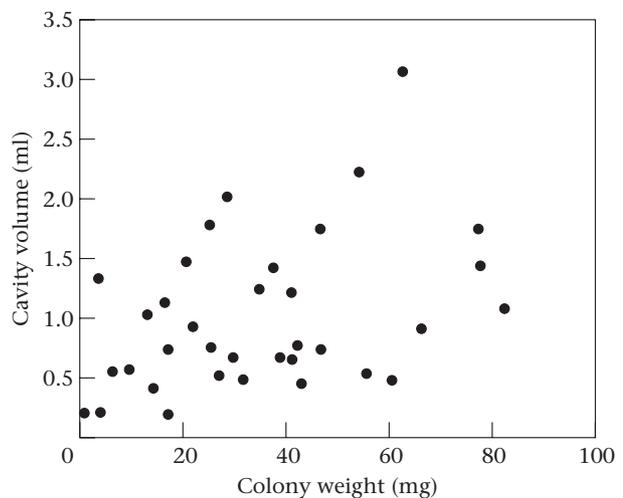


Figure 4. Correlation between cavity volumes of acorn nests and weights of the colonies inhabiting them (Spearman rank correlation: $r_s=0.35$, $N=35$, $P<0.05$).

of $0.95 \pm 0.59 \text{ mm}^2$, $N=24$ (Mann–Whitney: $U=461.5$, $P<0.01$). (The sample size for intact holes was lower because one rim was damaged before the hole could be measured.) Rims also reduced the variation in size; raw holes had a coefficient of variation of 0.96, compared to 0.62 with the rims intact.

Acorn interiors were generally well hollowed, but often contained remains of the nut. Figure 3 shows the considerable variation in cavity volume ($\bar{X} \pm \text{SD} = 0.98 \pm 0.64 \text{ ml}$, $N=39$). Colony weight was also variable ($\bar{X} \pm \text{SD} = 41.2 \pm 26.8 \text{ mg}$, $N=37$) and was weakly but significantly correlated with volume (Fig. 4). Weight gives a more reliable measure of colony size than the population count, because it incorporates variation in brood size and avoids the difficulty of accurately counting live ants in observation nests. None the less, there was a strong correlation between colony weight and the total count of adults and brood ($r_{34}=0.91$, $P<0.001$).

Preference Tests

Colonies strongly preferred smaller entrances (0.93 mm^2) to larger ones (4.4 mm^2 ; Fig. 5a). The preferred value was near the median of natural, rimmed entrances (0.86 mm^2), while the rejected value was at the

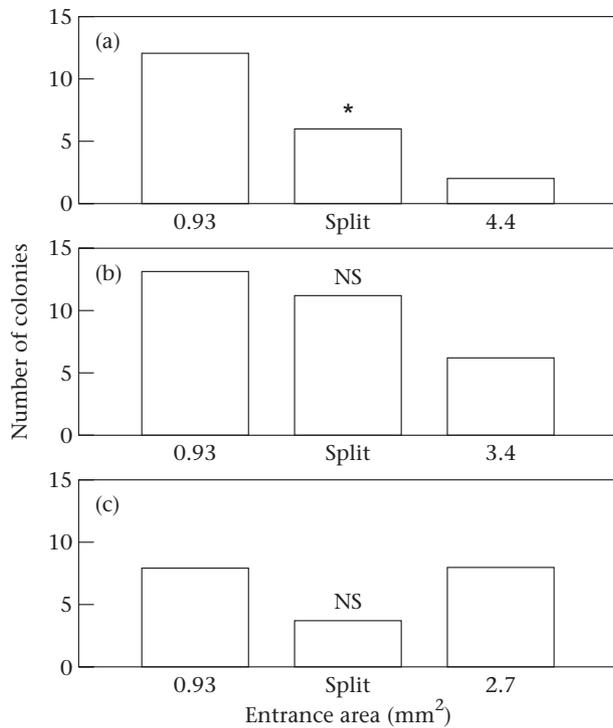


Figure 5. Outcomes of emigrations in which colonies chose between nests differing in entrance size. The number of colonies moving into each nest type, or splitting and moving into both nests, is shown. The number of colonies tested was 20 in (a) and (c) and 30 in (b). All nests had a volume of 1.93 ml (3.8 mm high and 25.4 mm in diameter). * $P < 0.05$, binomial test.

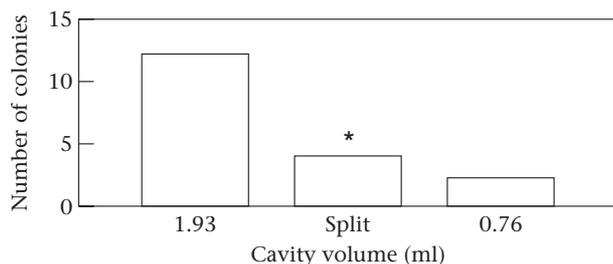


Figure 6. Outcomes of emigrations in which colonies chose between nests differing in cavity volume. The number of colonies moving into each nest type, or splitting and moving into both nests, is shown. $N = 18$ colonies tested. All nests had an entrance area of 3 mm². Both cavities had heights of 3.8 mm, but diameters of 16 and 25.4 mm, respectively. * $P < 0.05$, binomial test.

high end of the distribution of raw entrances (Fig. 2b). Colonies showed a statistically nonsignificant trend towards the smaller holes when choosing between 0.93 and 3.4 mm² (Fig. 5b), and no apparent preference between 0.93 and 2.7 mm² (Fig. 5c).

Ants consistently selected larger cavities (1.93 versus 0.76 ml; Fig. 6). In contrast to entrance size, the rejected volume was near the median of natural nest values (0.74 ml) and the preferred one near the maximum (Fig. 3). The test colonies were censused 8 days after the experiment and their populations compared to those of the colonies from the measured natural nests. The two

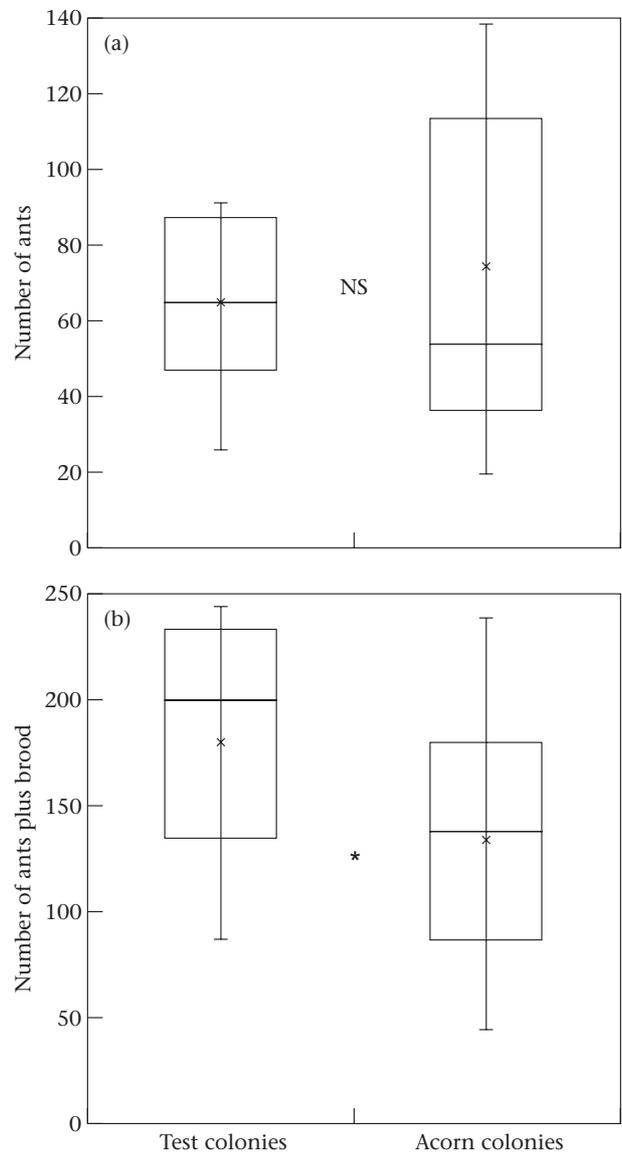


Figure 7. Populations of colonies used in the preference test for cavity volume, compared with populations of colonies living in the measured acorn nests. (a) Numbers of adult ants (t test: $t_{53} = 0.71$, $P = 0.48$). (b) Total population of ants and brood (t test: $t_{53} = 2.09$, $P < 0.05$). Each bar extends from the first to the third quartiles and is crossed by a horizontal line at the median; the mean is indicated by a cross; vertical lines indicate the 10th and 90th percentiles.

groups had similar numbers of adults, but the total population of adults and brood was significantly larger in the test colonies (Fig. 7).

The ants chose a compact, high-ceilinged cavity over a flat, thin crevice of equal volume (Fig. 8). In the taller nests the workers and brood tended to gather in clusters several ants thick, but in the flat nests spread themselves into a thin monolayer.

DISCUSSION

Colonies of *L. curvispinosus* reliably preferred certain nest designs in laboratory tests, but these preferences did not

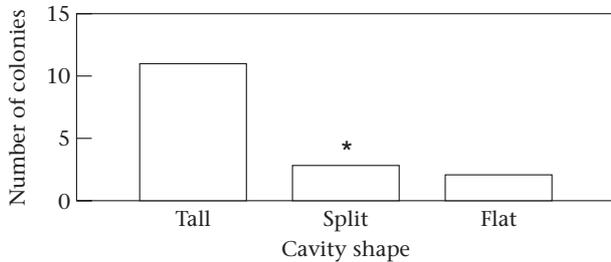


Figure 8. Outcomes of emigrations in which colonies chose between nests differing in cavity shape. The number of colonies moving into each nest type, or splitting and moving into both nests, is shown. $N=16$ colonies tested. All nests had an entrance area of 3 mm^2 and a volume of 0.76 ml but were either flat crevices (height: 1.5 mm ; diameter: 25.4 mm) or more compact cylinders (height: 16 mm ; diameter: 3.8 mm). $*P<0.05$, binomial test.

always mirror the design of their natural acorn nests. The ants consistently chose an entrance size near the median of natural entrances, rejecting larger alternatives. They also rejected crevice-shaped nests in favour of a more compact form that better approximated the interior of an acorn. However, they preferred cavity volumes significantly larger than most natural nest interiors. These choices are not mere artefacts of a biologically inappropriate array of choices; all of the entrance sizes and cavity volumes offered were among those found in natural nests.

Colonies may prize small entrance holes for their defensibility and crypsis. Honeybees, *Apis mellifera*, which also live in cavities, show a similar preference for relatively smaller nest entrances (Seeley & Morse 1978). The ants not only chose smaller holes in the first place, but they often reduced them further by adding rims of fine soil and leaf litter. Similar entrance reductions have been reported in colonies of *L. longispinosus* inhabiting artificial cavities (Herbers & Banschbach 1995). The entrance holes in acorns are generally drilled by curculionid beetles, and are not necessarily of an optimal size. Rims reduced both the mean and variance of hole area, suggesting that the ants aim for a smaller standard size. In the choice tests, colonies preferred entrances near the median of modified natural holes, rejecting those near the upper end of the size distribution of raw holes. This preference lacked precision, with only a non-significant trend towards the median size over the still-large 3.4-mm^2 holes, and no preference at all over 2.7-mm^2 holes. Because the ants can shrink the holes, their exact size before modification may be less important.

Volume preferences showed the opposite pattern, with the ants consistently rejecting cavities near the median natural size in favour of others at the high end of the natural distribution. This puzzling result might be explained by colonies actively choosing nests matched to their own size. The colonies from the natural nest sample were significantly smaller than those used in the choice tests, at least when brood as well as adults were counted. The more inclusive census is probably a better measure of

size because it takes into account all of the colony members that need to be accommodated in the nest. Smaller colonies might choose smaller cavities to improve their ability to regulate the nest environment. Ants have temperature and humidity optima that could be more difficult to maintain in a cavity that is too big relative to colony size. Relative nest size could also influence gas concentration gradients of potential use to the ants in coordinating colony spatial structure and behaviour (Cox & Blanchard 2000).

Size matching receives additional support from the correlation between colony weight and cavity volume in natural nests. Foitzik & Heinze (1998) reported a similar correlation between worker population and external nest volume in the closely related *L. nylanderii*, although cavity volume was not measured. Finally, indirect evidence suggests that *L. longispinosus*, which forms less populous colonies of similar-sized ants, prefers a cavity volume of only 0.4 ml to one of 1.3 ml (Herbers & Banschbach 1995).

Alternatively colonies of *L. curvispinosus* may always take the largest cavity they can find (within the range of sizes examined), regardless of colony size. Such a strategy would avoid space limits on colony growth, and appears to be the policy of honeybees, where colony population has no influence on cavity size of preferred nest sites (Seeley 1977). If a cavity is too big for proper homeostasis, the ants can modify it to fit. *Leptothorax albipennis*, for example, builds walls within naturally occurring rock crevices to achieve a correspondence between nest area and colony size (Franks et al. 1992). The walled area can be enlarged as the colony grows, up to the limits imposed by the crevice size (Franks & Deneubourg 1997). Like *L. curvispinosus*, these ants prefer larger cavities, although it is not known how their laboratory preferences compare with the nests they occupy in nature (Mallon & Franks 2000). Both species may adopt a similar policy of modifying large cavities to achieve appropriate nest size along with flexibility for future growth.

If so, the ants may be constrained by the availability of desirably large nests. Other cavity-dwelling ants, including some leptothoracines, are known to be limited by nest site availability, with important effects on social structure (Herbers 1986, 1989; Foitzik & Heinze 1998; Herbers & Banschbach 1999). An added requirement for large nests would only strengthen this constraint. If cavity size limits colony growth, the observed weak correlation between colony weight and cavity volume could easily follow, even in the absence of active size matching by the ants. Small colonies may also be confined to the smallest nests because they are weak competitors. Colonies of *L. nylanderii* more frequently abandon small nests than large ones, suggesting that the former are inferior (Foitzik & Heinze 1998). Furthermore, the evidence presented above in favour of size matching is weakened by the considerable overlap in population size between the test colonies and acorn-dwelling colonies collected in the field. Many of those choosing the larger nest were close to the median size of colonies occupying the small acorn nests. None the less, our data cannot really determine whether colony

size affects nest size preference. Resolving the issue will require more choice tests with a larger range of colony sizes.

The ants were concerned with cavity shape as well as volume, preferring a compact, high-ceilinged form to a flat, crevice-like one. Cavity shape may influence nest homeostasis, but it could also indirectly influence the colony's social organization. The work an ant performs depends in part on what task demands she encounters, and this depends on how tasks and ants are distributed within the nest (Sendova-Franks & Franks 1995). In the interior of an acorn, *L. curvispinosus* colonies might contract into a roughly spherical cluster, as they appear to do when nesting in artificial nests with high ceilings. One effect of this shape, compared with the flatter distribution adopted within a crevice, would be to reduce the average distance between colony members. This could increase the relative size of the zone in which each ant acquires information about task demands, and thus speed the rate of learning about changes in colony state. Insofar as the spatial distribution of ants influences social organization, colonies that typically use flat or spherical nests may be better adapted to the corresponding colony distribution. If so, it would be interesting to find out if species that typically dwell in thin crevices, such as *L. albipennis*, *L. unifasciatus* and *L. rugatulus*, prefer flatter to more spherical cavities.

Given their preference for certain nest geometries, how do individual ants measure the relevant features of prospective sites? The mechanisms remain to be discovered, but the similar behaviours of other insects offer a few clues. In honeybees, the measurement of cavity volume depends on the lengths of random walks over the cavity walls (Seeley 1977). Seeley suggested that the bees compute volume by some kind of vector calculus, similar to the well-established path integration algorithms of navigating insects (Wehner et al. 1996). Alternatively, the ants might not assay volume per se, but instead combine independent measurements of cavity height and the surface area available for nesting. The latter approach could be adequate if the ants do not fill the available volume, as bees do with their sheets of honeycomb, but instead simply stand or lie on the inner walls of the cavity. Mallon & Franks (2000) described an intriguing pheromone-based algorithm that workers of *L. albipennis* may use to measure the floor area of crevices. A similar method might be used by *L. curvispinosus*. As for entrance size, ants could use their antennae or legs as callipers, as queen bees appear to do when measuring the cells of honeycomb (Koeniger 1970).

Once the ants have measured these features, the separate evaluations of many individuals visiting multiple sites must somehow be integrated into a colony-wide decision. Recent work had indicated how this integration is achieved in the related species *L. albipennis* (Mallon et al., in press). For *L. curvispinosus*, however, it remains to be discovered how either the individual or colony assessments are made. With some understanding of the ants' decision criteria, both issues can now be profitably addressed.

Acknowledgments

We thank Nigel Franks, Ana Sendova-Franks, Jay Denny, Eamonn Mallon and Kenro Kusumi for helpful comments on the manuscript.

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