



The effect of prior experience on nest site evaluation by the ant *Temnothorax curvispinosus*

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Animals are expected to follow decision-making strategies that balance the benefits of choosing the best option with the costs of finding and assessing candidates. Because costs and benefits will vary across time and space, an animal may profit by adjusting its tactics according to recent experience. In particular, animals should be less selective when experience indicates that the average quality of options is low. We tested this prediction in the context of nest site selection by the ant *Temnothorax curvispinosus*. Colonies received prolonged exposure either to a good or to a poor nest and then were tested for their readiness to accept a mediocre nest. Previous studies have shown that colonies move more rapidly into nests that they rate more highly, as a result of faster recruitment initiation by individual ants. Hence, if exposure to a low-quality nest makes colonies more willing to accept a mediocre one, we predicted speedier moves into the mediocre nest after the poor treatment than after the good treatment. Our results showed a clear effect of treatment, but contrary to our prediction, ants moved more rapidly after living in a good nest than after living in a poor nest. We discuss three effects that may explain these results: (1) quality-dependent changes in colony condition, (2) quality-dependent changes in colony size and (3) differences in the urgency of emigration perceived by ants in the two nest types. Our finding illustrates that animal collectives, like individuals, use recent experience to tune their decision strategies.

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Animals gain fitness benefits from choosing the best among a set of options, whether mates, food sources or nest sites. However, they must balance these benefits with the costs of finding and assessing candidates. Because these costs and benefits will vary across time and space, an animal may gain from learning the values for these in its current context and adjusting its decision tactics accordingly (Luttbegg 1996; Wiegmann et al. 1996; Collins et al. 2006). Theory predicts that as costs rise animals should lower their selectivity, the effort they are willing to expend

to attain a preferred option (Real 1990; Jennions & Petrie 1997; Baker & Rao 2004; Stamps et al. 2005). Many studies have confirmed this prediction for females who encounter males one at a time and must choose whether to mate with a current suitor or to continue searching for a better one: females are less likely to search under increasing predation risk or energetic costs, or as the approaching end of the breeding season raises the risk of failing to mate at all (Bakker & Milinski 1991; Milinski & Bakker 1992; Godin & Briggs 1995; Jennions & Petrie 1997; Luttbegg et al. 2001; Borg et al. 2006). Selectivity is also expected to depend on the quality distribution of options in the chooser's environment (Real 1990; Wiegmann et al. 1996). A female is more likely to gain by rejecting a mediocre option in favour of further search when high-quality candidates are abundant than when good candidates are

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rare. Studies in a variety of taxa suggest that females can use their recent experience to estimate average male quality and tune their selectivity accordingly (Bakker & Milinski 1991; Collins 1995; Reid & Stamps 1997; Wagner et al. 2001; Dukas 2005). In particular, females show less interest in intermediate-quality males after exposure to high-quality males than after exposure to low-quality males.

Most work in this field has concerned mate choice, but the same issues apply to habitat selection. The choice of a place to live has important fitness consequences, and animals evaluate habitat on the basis of many features, including vegetation type, foraging quality, predation risk, parasite presence and conspecific density (Clobert et al. 2001; Fontaine & Martin 2006; Parejo et al. 2007). Natal experience influences habitat choice in a broad array of taxa, but the adaptive significance of these effects is generally unclear (Davis & Stamps 2004). In theory, experience could influence selectivity by giving animals information that aids them in choosing the best search strategy (Stamps & Davis 2006). One source of information is simply the effect of natal habitat on the animal's own state: individuals dispersing from high-quality habitats might be in better condition and thus more selective because they can better sustain a prolonged search. Another kind of information concerns the quality distribution of habitats in the animal's environment. Experience with high-quality habitat may yield a higher estimate of expected encounter rates with good habitats than experience with low-quality habitat. As a result, animals from good habitats would be more likely to continue searching rather than settling for a mediocre option. This argument should apply not only to natal experience, but also to any later experience of habitat quality that gives an animal reliable information about the prevalence of good places to settle.

In this study we tested the hypothesis that colonies of the ant *Temnothorax curvispinosus* adjust their evaluation of nest site quality on the basis of prior experience. Ant colonies and other animal groups make highly coordinated collective decisions (Conradt & Roper 2005), and recent work has begun to show how learning can affect this process (Djipto-Lordon & Dejean 1999; Langridge et al. 2004, 2008). The genus *Temnothorax* is especially suited to such an analysis, because its nesting criteria and decision-making tactics have been particularly well studied. Colonies typically live in preformed cavities such as hollow nuts or rock crevices. In the laboratory they can be housed in simple artificial cavities, and nest site preferences can be studied by destroying a colony's nest, presenting it two intact nests of different design, and observing which nest it moves into. This approach has shown that colonies assess several site features, including cavity volume, cavity height, entrance size, interior illumination, proximity of conspecific nests and presence of dead conspecifics (Mallon & Franks 2000; Mallon et al. 2001; Pratt & Pierce 2001; Franks et al. 2003b, 2005, 2007a; Pratt 2005b).

A colony's nest site choice relies on a subset of the colony's workers who scout for candidates, evaluate them, and recruit nestmates to promising finds (Pratt et al. 2002; Pratt 2005b). Because individual scouts generally lack the

opportunity to compare all available sites and choose the best one, the colony's decision instead emerges from a competition between recruitment efforts at different sites. A scout begins recruiting to a site only after a delay that depends inversely on site quality (Mallon et al. 2001; Pratt 2005b). The ants that she recruits in turn impose a similar delay before they join in the effort. If two sites of different quality are encountered, the disparity in recruitment latencies leads to faster accumulation of ants at the better site. This advantage is further amplified by a quorum rule under which scouts accelerate their recruitment once their site's population surpasses a threshold (Mallon et al. 2001; Pratt et al. 2002; Pratt 2005a, b).

Because the colony's choice emerges from interactions among its many workers, changes in decision-making strategy must be traced to changes in individual behaviour. The ants' method of encoding site quality suggests the possibility that individual workers tune their selectivity by lengthening or shortening their recruitment delays. In support of this idea, the urgency of emigration has a strong effect on recruitment latency: a scout from an intact but relatively poor nest imposes much longer latencies to a site of given quality than a scout from a nest that has just been destroyed (Pratt & Sumpter 2006). Prolonged latency is equivalent to postponing acceptance of an option in favour of more search because the scout herself or one of her many nestmates may find a better site while she hesitates. Greater search effort should be rewarded in less urgent conditions, when the ants can afford to be more selective about their new home. We hypothesized that ants might also benefit by adjusting their recruitment latencies according to the nest site quality they have recently experienced. If quality distribution varies among habitats, then a site quality near the middle of the distribution in one area may be among the best in another. Incorporating experience with recently encountered nest sites would allow colonies to avoid unnecessary delays when emigrating in poor neighbourhoods, as well as too-hasty moves to inferior nests in good neighbourhoods. Specifically, we predicted that ants with recent experience of poor nests would impose shorter recruitment delays to mediocre nests than ants that had recently experienced good nests.

METHODS

Nest Site Design

Nest sites consisted of a basswood slat (2.4 mm thick) sandwiched between two glass microscope slides (50 × 76 mm). A nest cavity was cut through the middle of the slat, and a round entrance hole drilled through the centre of the roof slide. The upper surface of the roof slide was painted blue to improve visual detection of workers and brood items during emigrations. Three nest designs were used: good nests had a large circular cavity (25 mm diameter) and a small entrance hole (1.6 mm diameter); mediocre nests had an identical cavity, but a larger entrance (4.8 mm diameter); poor nests had both a smaller cavity (17 mm diameter) and a still larger entrance (9.5 mm diameter).

Characterizations of site quality were based on earlier tests (Pratt & Pierce 2001; Pratt 2005b), but we confirmed the preference ranking by offering colonies choices between pairs of nest types and noting which nest they moved into. Separate tests were made for each of the three possible pairings: poor versus mediocre, mediocre versus good, and poor versus good. Each of 12 colonies was tested once with each pairing. The test colonies, and all others used in this study, were collected in Princeton, New Jersey, U.S.A. Testing methods closely followed those in Pratt (2005b), including controls for testing order and side bias. Emigrations were induced by removing the roof of the old nest. On the following day, the proportion of a colony's members in the nominally better site was noted. If colonies have no preference between the sites, then the mean proportion moving to the nominally better one should not be different from one-half. By testing proportions, rather than simply scoring each choice as one site or the other, we were able to include in the analysis a minority of colonies that split between sites. For each of the three pairings, a Wilcoxon signed-ranks test was used to detect a significant difference from the null expectation. The results confirmed the expected preferences for each pairing (Table 1).

Training and Emigrations

Each of 24 colonies was subjected to two treatments: in one treatment, colonies were housed in good nests for 8 weeks, and in the other, they were housed in poor nests for 8 weeks. We reasoned that ants might learn about the quality distribution of nests not only from the nest that they currently inhabit, but also by observing what is available when they emigrate. Colonies were therefore induced to emigrate at the end of weeks 2, 4 and 6 in each treatment, by removing the roof slide of their nest and providing nearby a single intact new nest, identical in design to their old nest. At the end of each treatment, colonies were similarly induced to emigrate to a mediocre nest. During this last emigration, a digital video camera trained on the entrance to the new nest recorded all entrances and exits. As described below, these video records were subsequently used to measure the ants' rating of the mediocre site. Throughout each treatment, colonies were kept in 20 cm square plastic assay dishes with Fluon-coated walls to prevent escape. Nests were centred against

one wall of the dish. During emigrations, the new nest was centred against the opposite wall. The emigration to the mediocre nest was induced by removing the wood perimeter as well as the roof slide. This ensured that the physical surroundings and degree of exposure were identical for colonies in each treatment while they evaluated and moved into the mediocre site. Treatments were offered in two sessions. To control for possible order effects, half of the colonies received the good treatment in the first session and the poor treatment in the second session, and half received the opposite order.

Measurement of Recruitment Rate

We measured the ants' judgment of the mediocre nest as the growth rate of the cumulative number of transports, over the course of the emigration. This measure is based on the assumption that each ant should start recruitment sooner when the new nest is perceived more favourably, and the colony as a whole should therefore show a faster increase in the cumulative number of recruitment acts. From reviews of the video record of each emigration, we recorded the time of every 10th transport (that is, the time that the 10th, 20th, etc., nestmate was carried into the new nest). Time was measured relative to the destruction of the old nest. We omitted tandem runs from the recruitment counts, because these sometimes ended outside of camera range, and thus could not be counted reliably. Tandem runs are much rarer than transports, especially in short-distance emigrations like those observed here (Pratt et al. 2002). Moreover, their exclusion was not expected to affect the good and poor treatments differentially.

We fitted to these data a logistic growth equation:

$$N = \frac{K}{1 + \left(\frac{K}{N_0} - 1\right)e^{-rt}}$$

where N is the cumulative number of transports, t is the time since the start of emigration (opening of the old nest), K is the asymptotic limit of the number of transports, N_0 is the number of transports at time zero, and r is the rate of growth of transports. The value of N_0 was set to 0.01, because the function cannot be fit using the true value of zero. We used the fitted value of r as the measure of recruitment rate, and thus perceived site quality, for each emigration. We fitted a linear model to test for an effect of treatment on r . The model included a term for adult population, to statistically control for any confounding effect of the number of ants available to become recruiters. It also included a term for treatment session, to control for possible effects of season, ageing or emigration experience. The paired design allowed us to include colony identity as a random effect, to control for consistent differences between colonies. The full model is given by $r_{cst} = \mu + \zeta_c + \beta_s + \beta_t + \beta_p P_c + \varepsilon_{cst}$, where μ is the intercept, ζ_c is the random effect of colony c , β_s is the fixed effect of treatment session s , β_t is the fixed effect of treatment t , β_p is the regression coefficient for colony population, P_c is the population of colony c , and

Table 1. Nest type preferences shown by 12 colonies in binary choice tests

Comparison	Proportion of colony in latter nest ($\bar{X} \pm SD$)	Test statistic	P
Poor vs mediocre	0.84 ± 0.11	70	0.009
Mediocre vs good	0.77 ± 0.10	48	0.03
Poor vs good	0.92 ± 0.06	55	0.002

In each comparison, the proportion of each colony's members moving to the latter-named site was measured. A Wilcoxon signed rank test detected departures of this proportion from 0.5, the expected value in the absence of any preference between the sites.

ε_{cst} is a random error term. Normality of the error terms was confirmed with a Shapiro–Wilks test, and equality of variances with an F test. All model fitting and tests were performed with the statistical package R (Venables & Ripley 2002).

To confirm that r accurately mirrors the ants' assessment of nest site quality, we carried out the fitting procedure on data from a previously published experiment in which colonies moved successively to nests of good or mediocre design (Pratt 2005b; Pratt & Sumpter 2006). All ants were individually marked, allowing us to directly estimate a scout's rate of recruitment initiation. We found that slower rates of initiation to the mediocre nests were matched by lower estimates of r , as expected if r is a good aggregate measure of individual recruitment latencies.

Measurement of Population

We estimated colony populations for each emigration, both to test for an effect of adult numbers on emigration speed and to assay overall colony condition. Brood populations were measured from the videotaped emigrations by counting each brood item as it was carried into the new nest. The adult population was tracked by keeping a running tally of the total number of adults inside the new nest throughout the emigration. We used the maximum of this number as an estimate of the adult population of the colony. This gave a lower bound on adult population, as there were always some workers outside the nest.

RESULTS

Colonies moved consistently faster after recent experience of good nests than after recent experience of poor nests. Of 12 colonies, nine experienced faster growth in cumulative transport number (higher r) in the good treatment (Fig. 1). In a linear model that included effects of treatment, adult population and treatment session on r , the effect of treatment was statistically significant (good: $r = 0.32 \pm 0.11$; poor: $r = 0.23 \pm 0.09$; ANOVA: $F_{1,9} = 16.2$, $P < 0.01$). The effect of treatment session was also significant, such that colonies moved faster on their first test, independent of treatment type (first session: $r = 0.32 \pm 0.10$; second session: $r = 0.22 \pm 0.09$; ANOVA: $F_{1,9} = 18.9$, $P < 0.01$). Adult population had no significant effect (ANOVA: $F_{1,9} = 2.7$, $P = 0.14$).

The poor treatment was associated with significantly lower brood populations and with a nonsignificant trend towards lower adult and total populations (Table 2, Fig. 2). To test whether these differences may have influenced emigration speed, we fitted a linear model predicting the difference in r for good (r_g) and poor (r_p) treatments for each colony as a function of the difference between total populations across treatments. We also included a term for the order in which treatments were presented, to account for the effect of this variable noted above. The results showed a significant effect of population difference on the difference in r between treatments (ANOVA: $F_{1,9} = 22.8$, $P < 0.01$).

Treatment session had no significant effect on any of the population measures (Table 2). Thus, there does not

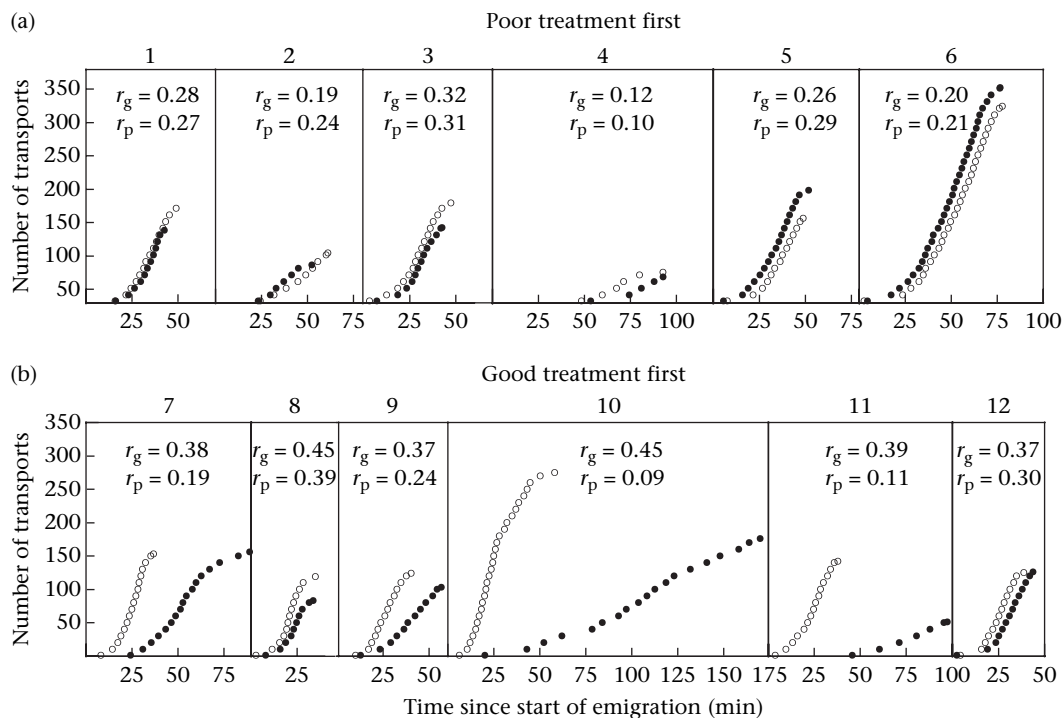


Figure 1. Cumulative number of transports as a function of time since the start of emigration (i.e. destruction of the old nest). Each panel shows two emigrations to a mediocre nest by a single colony, once after prolonged experience of good nests (○) and once after prolonged experience of poor nests (●). Colonies are grouped by which conditions they experienced first. For each colony, the parameters r_g and r_p give the estimated growth rate of a logistic equation fitted to the cumulative number of transports for good and poor conditions, respectively.

Table 2. Effects on colony population of nest experience and treatment session

	Nest experience				Treatment session			
	Good	Poor	$F_{1,10}$	P	First	Second	$F_{1,10}$	P
Adult	72±40	64±29	0.5	0.48	70±31	66±39	1.0	0.34
Brood	101±48	83±64	9.8	0.01	101±66	83±45	1.3	0.28
Total	173±86	147±88	4.0	0.07	171±94	150±81	1.7	0.22

Data are presented as mean number of individuals or brood items \pm SD. Populations measured in each emigration were modelled as linear functions of nest experience and treatment session, and tested by analysis of variance for effects of either factor. Colony identity was included as a random effect.

appear to have been a consistent pattern of growth or shrinkage over the interval from the first to the second emigration.

DISCUSSION

These results show a clear effect of the nest quality experienced by ants on their subsequent emigration behaviour. However, the effect was the opposite of that predicted if ants adjust their selectivity to match the prevailing quality of sites in their vicinity. Under this hypothesis, ants should value a mediocre nest more highly if they have recently encountered only poor nests than if they have recently encountered only good nests. Because *T. curvispinosus* scouts encode their rating of a site's quality in the delay that they impose between finding the site and recruiting to it, the poor treatment was expected to induce a faster increase in the cumulative number of transports to the mediocre site. Instead, transport numbers increased significantly faster following the good treatment. Why should exposure to good nests lead to faster emigration to a mediocre nest? We consider three potential explanations: (1) condition dependence: ants in poor nests act more slowly because they are in poor condition, (2) size dependence: colonies were smaller after living in poor nests, and smaller colonies move more slowly and (3) urgency: ants in good nests perceive a greater sense of urgency after nest destruction than do ants in nests that are already poor.

The condition dependence hypothesis is based on the possibility that prolonged housing in poor-quality nests reduces the ants' health and slows down their activity during emigration. This idea receives some support from the significantly reduced brood populations after the poor treatment, compared to their numbers after the good treatment. This may indicate either higher brood mortality or lower brood production in the poor nests. Emigration speed, however, should depend more on the condition of the adult recruiters, and adult population was not significantly reduced by living in poor nests. Moreover, the effect of experience on emigration speed persisted when the analysis excluded the four colonies showing the largest population drop across treatments. Finally, even if the poor nests hurt colony condition, it is not clear that this should cause slower emigrations. In theory, animals in poor condition should make faster

decisions (Stamps et al. 2005; Stamps & Davis 2006). This is because limited energy reserves or physiological constraints on their search performance give them less time to invest in search and decision making (Davis 2007). Our study, in contrast, found that living in poor nests led to slower decisions.

The size dependence hypothesis is suggested by the trend towards smaller colony size after living in poor nests. Population declines may be due to greater mortality or delayed brood maturation in poor nests, and so are related to differences in the condition of individual ants. However, population could influence emigration speed independently of condition, through effects on the number or motivation of active ants. The population difference had a statistically significant effect on emigration speed, but the present data cannot distinguish whether this effect is causal or simply correlated with other changes in individual behaviour. In the related species *Temnothorax albipennis*, larger colonies can find nests more rapidly than smaller ones (Franks et al. 2006), but colony size has no effect on total emigration speed across an order of magnitude difference in worker number (Dornhaus & Franks 2006).

The urgency hypothesis is based on the fact that colonies experience a greater decline in nest quality when a good nest is destroyed than when a poor nest is destroyed. Ants may perceive this larger change as a more urgent need to emigrate quickly. Previous work has shown that ants significantly increase their search effort, reduce their recruitment latency and lower their quorum size under conditions of high urgency at the old nest (Franks et al. 2003a; Dornhaus et al. 2004; Pratt & Sumpter 2006). These changes lead to faster emigrations and form part of a strategy of context-dependent changes in relative emphasis on decision speed and accuracy. Our results may mean that a scout's estimate of emigration urgency is determined not only by the current state of the old nest, but by how much this state has deteriorated from recent conditions. Thus a colony in a poor nest may respond with less urgency to the opening of that nest than does a colony in a good nest, even though the nests are identical after opening. Our results cannot distinguish between a causal effect of urgency and a correlation with other changes. However, the urgency hypothesis is consistent with a general theoretical prediction that animals should become less selective as search becomes more costly or as the time available for search declines

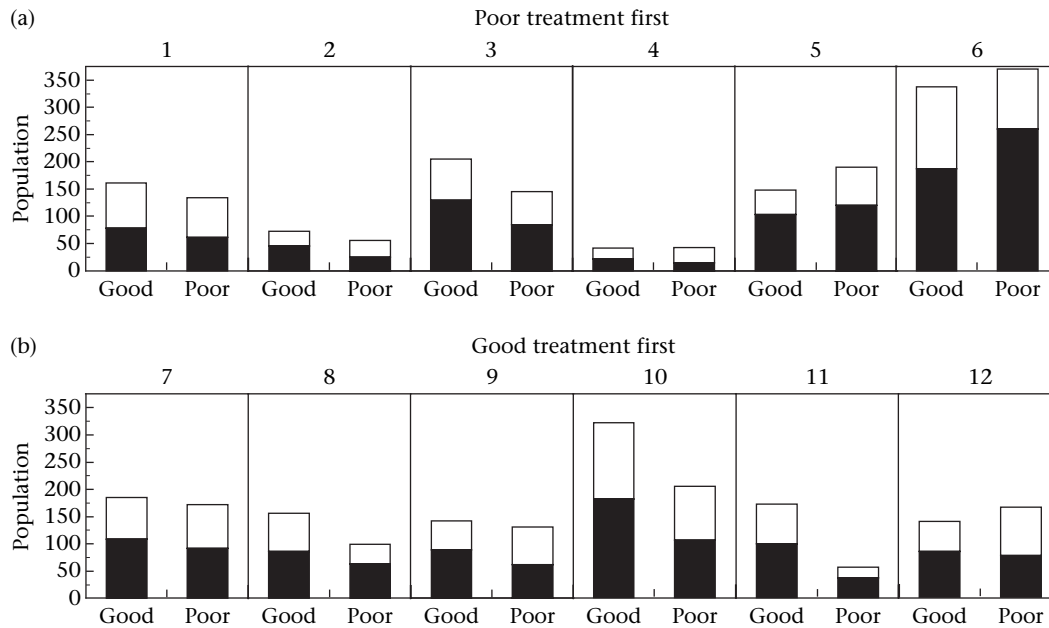


Figure 2. Population of each colony, measured after experience with good nests or poor nests. Colonies are grouped by which conditions they experienced first. ■: brood items; □: adults.

(Ward 1987; Real 1990; Baker & Rao 2004; Hutchinson & Halupka 2004; Stamps et al. 2005; Krishnan 2007). If a sharp decline in current nest quality is a reliable cue that the colony is dangerously exposed and needs a new shelter fast, then colonies are expected to be less selective following such a decline.

The effects of emigration urgency, colony condition and colony size on selectivity will require direct experimental testing, but what of the hypothesis examined in this study? We found no evidence that ants use their prior experience to adjust selectivity based on predicted encounter rate with good nests. This may mean that ants do not use their prior experience in this way, perhaps implying that the quality distribution of nest sites does not vary enough to make the strategy a useful one. However, it is also possible that any such effect was masked by differences in colony size or perceived urgency in the two treatments, or that our experimental design did not include salient cues about average nest site quality. One such cue might be intact, unoccupied nests available for inspection while the colony remained in its old nest. We presented new sites only during the crisis of nest destruction and emigration. A recent study has shown that *Temnothorax albipennis* colonies can learn about nearby empty sites and later retrieve this information (Franks et al. 2007b). When ants in a good-quality nest were presented with an empty mediocre site, scouts found and explored the site, but the colony did not move into it. A week later, when a second mediocre site was added and the old nest simultaneously destroyed, the colony soon moved, but it nearly always chose the newly added nest, despite its identical design to the first site. This suggests that the ants retained a memory of their earlier rejection of the first site and used it to guide their emigration behaviour. Although the context was quite different from the one explored in our study, the observation shows

that ants can learn about surrounding unoccupied nests, a potential source of information on average site quality worthy of further exploration.

Habitat choice is modified through learning processes in many animals faced with decisions about where to live (Davis & Stamps 2004; Forstmeier & Weiss 2004; Fontaine & Martin 2006; Davis 2007), but the present study also shows that experience can influence nest site choices by animal collectives such as ant colonies. A colony's choice can only be changed by altering the rules followed by the individual workers from whose disparate acts a collective decision emerges. Our results suggest that a key target for modification by experience is the time delay after which an ant accepts a particular site as a candidate worthy of nestmate recruitment. Future work will be needed to determine whether recruitment delays are affected by changes in an ant's condition, the internal scale against which she rates sites, her judgment of the need to emigrate, or some combination of these factors. These results suggest a rich vein for analysis of how experience-dependent alterations of individual behaviour adaptively influence colony-level phenotypes.

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