

Original Article

Experience-dependent flexibility in collective decision making by house-hunting ants

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When making a decision, solitary animals often adjust to local conditions by using flexible evaluation and decision criteria, even though these may occasionally lead to irrationality. By contrast, collective decision making in large animal groups—such as, nest choice by emigrating ant colonies—is usually considered to rely on robust, fixed preference rules and to be immune to irrationality. Here, we show that familiarization with available nest sites prior to emigration can lead to flexible collective decisions in the house-hunting ant *Temnothorax albipennis*. Colonies allowed to inspect a mediocre nest site while their home nest is still intact usually develop an aversion toward that nest. We found that aversion strength was not determined by the quality of the familiar nest only but was also influenced by the quality of the home nest. As a result, nest choice in later emigrations depended strongly on the quality of the previously experienced home nest, allowing colonies to adjust to the local quality of available sites. Additionally, we found that in a worst-case scenario where the only alternatives are of even lower quality, developing an aversion toward a mediocre nest can occasionally lead to poor collective decisions. We discuss whether the observed flexibility in collective choices necessarily requires experience-dependent changes in individual decision criteria and develop a new analytical model of nest choice in house-hunting ants showing that a fixed-threshold decision strategy at the individual level can lead to experience-dependent, flexible decisions at the colony level. *Key words*: ants; collective decision making; irrationality; nest choice; previous experience. [*Behav Ecol* 22:535–542 (2011)]

INTRODUCTION

Animals are often faced with choices that may have an important impact on their fitness (Bateson 1983; Pyke 1984; Clobert et al. 2001). In temporally and spatially varying environments, search strategies and decision criteria need to be flexible to adjust to local conditions and ensure efficient decision making in various circumstances. Many solitary animals achieve such flexibility by taking into account the quality of previously encountered alternatives when assessing a given option (e.g., insects: *Gryllus lineaticeps*, Wagner et al. 2001; *Drosophila melanogaster*, Dukas 2005; *Ips pini*, Reid and Stamps 1997; fish: *Gasterosteus aculeatus*, Bakker and Milinski 1991; and birds: *Taeniopygia guttata*, Collins 1995). Although it usually confers crucial fitness benefits on individuals (Collins et al. 2006), taking into account previous alternatives when making a decision can also occasionally lead to irrationality. An animal is considered rational if its preference between 2 options with stable fitness-related values is consistent across contexts (Bateson and Healy 2005). Violations of rationality

brought about by variations in the background context (i.e., options encountered in the past) or in the local context (array of available options) have however been reported multiple times in humans and animals (Tversky and Simonson 1993; Doyle et al. 1999; Waite 2001; Schuck-Paim et al. 2004; Bateson and Healy 2005; Houston et al. 2007). Although well studied in solitary animals, flexibility in decision criteria and associated irrationality have received little attention in group-living animals (but see (Edwards and Pratt 2009; Sasaki and Pratt 2011)). The aim of this study was to investigate these issues further in the context of collective decision making by house-hunting ant colonies.

Temnothorax ants dwell in fragile nests, such as hollow acorns, twigs or rock crevices, and colonies often have to relocate into a new nest site (“nest emigration”; Möglich 1978). During emigrations, colonies are usually able to select the best among several sites (Franks et al. 2003, 2006). This collective decision making ability emerges from distributed mechanisms. When their nest has been damaged, a minority of workers (“scouts”) leaves the old nest to look for potential new nest sites. When they have found a suitable site, scouts start recruiting other workers to it by tandem running (Möglich 1978; Franks and Richardson 2006). Recruits then assess the site independently and may in turn initiate recruitment. Because ants recruit more readily to high than to low-quality nest sites (Mallon et al. 2001; Robinson et al. 2009), this generates a positive feedback cascade leading to faster population growth in better sites. This difference is further amplified by a quorum rule, whereby workers switch from slow recruitment by tandem running to a 3 times faster transport of brood and nestmates when the population in the new site reaches a certain value, or quorum threshold (Pratt et al.

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Table 1
Characteristics of different types of nests

	Brightness	Headroom (mm)	Entrance width (mm)
Good nest type 1	Dark	1.8	2
Good nest type 2	Dark	1.1	2
Mediocre nest	Bright	1.1	2
Poor nest	Bright	1.1	20

2002, 2005; Sumpter and Pratt 2009). Because the quorum is generally reached earlier in better nest sites, this ensures that all or most transport is directed toward the best option (Pratt et al. 2005; Sumpter and Pratt 2009).

Emigrating *Temnothorax* colonies have been shown collectively to behave rationally (i.e., have consistent preferences) when choosing between 2 unknown nest sites in the presence or absence of an irrelevant decoy (Edwards and Pratt 2009), in contrast with several instances of irrational decision making by solitary animals (Bateson and Healy 2005; Sasaki and Pratt 2011). This suggests that criteria for nest preference are stable at the colony level, in agreement with previous studies showing high consistency in nest preference among colonies and over time (Franks et al. 2003). However, recent studies showed that nest choice in *Temnothorax albipennis* can be altered by prior familiarization with some or all available nest sites (Franks et al. 2007; Stroeymeyt et al. 2010). In particular, colonies which familiarized themselves with a mediocre nest site prior to emigration developed an aversion toward that nest and avoided it in later emigrations when choosing between that nest and an otherwise identical, but unfamiliar site (Franks et al. 2007). Here, we investigated whether this familiarization process allows colonies to adjust their acceptance criteria to the local distribution of available nests, and whether this might lead to apparent collective irrationality in certain conditions.

In a first experiment, we show that developing an aversion toward a mediocre nest site can induce poor decisions if the only other alternative is of even lower quality, although most colonies are able to overcome their initial aversion and select the better option. In a second experiment, we show that the intensity of aversion toward a mediocre nest site does not only depend on the absolute quality of that site but also on the quality of the current nest. We then discuss 3 possible decision-making strategies that may account for our results: 1) direct comparisons by individuals; 2) adjustment of individual acceptance threshold through experience of the current nest; and 3) fixed individual acceptance thresholds leading to flexibility at the colony level. Because the latter possibility has never been theoretically investigated before, we develop a 2-stage analytical model exploring in which conditions this scenario could account for our results.

MATERIALS AND METHODS

Nest-site preference in *T. albipennis* depends on several nest characteristics, such as darkness, headroom, and entrance width (Franks et al. 2003). Accordingly, we designed 4 types of artificial nests ranging from high to very low quality ("good," "mediocre," and "poor," Table 1). All nests were made of a cardboard perimeter sandwiched between 2 glass slides (56 × 70 mm) and had an internal cavity of 35 × 50 mm. Darkness in good nests was obtained by covering the nest with opaque cardboard.

Experiments were performed under natural sunlight in large Petri dishes (22 × 22 × 2.2 cm) with Fluon-coated walls. Emigration was induced by removing the top glass slide of the old nest. Emigrating colonies could choose between

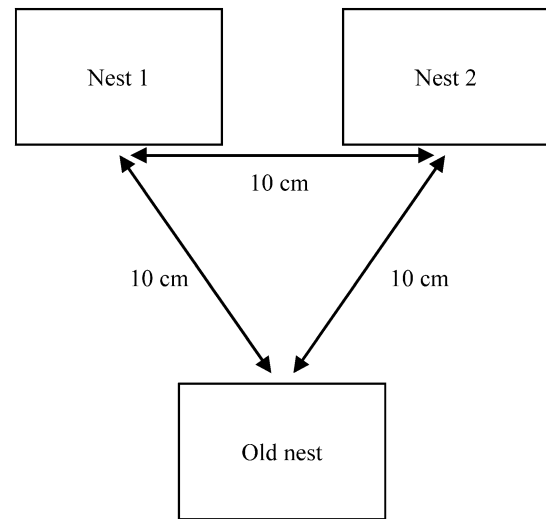


Figure 1

Diagram of experimental setup. Colonies were positioned along one side of the exploration arena. After an acclimatization/exploration period, emigration was induced and colonies were allowed to choose between 2 equidistant nests (Nests 1 and 2) placed along the opposite side of the arena. The quality (poor or mediocre) and status (familiar or unfamiliar) of nests 1 and 2 varied between experiments; in each experiment, the position of both nests (to the left or to the right) was pseudorandomized among colonies.

2 equidistant available nest sites (Nest 1 and Nest 2) that could be either familiar (i.e., previously explored by workers) or unfamiliar (i.e., never encountered before; see Figure 1). The position of the new nests relative to the old nest was pseudorandomized among colonies for each experiment (i.e., the position of both new nests was randomly allocated, subject to Nest 1 being on the left of the old nest for half the colonies and on the right for the other half). Nest choice was recorded after 24 h. A colony was deemed to have chosen a nest only if all brood items were in that nest; otherwise it was considered split.

Both experiments consisted of 2 replicates in which colonies emigrated simultaneously. Successive replicates were separated by more than 1 week to minimize memory of the previous situation, which is not expressed after 6 days (Langridge et al. 2004).

Experiment 1

Colonies housed in good old nests (type 2) were induced to emigrate and choose between a mediocre and a poor nest (Table 1) under 2 treatments. In the "Informed" treatment, colonies were allowed to examine the mediocre nest for 1 week prior to emigration, whereas the poor nest was introduced to the arena just before the onset of emigration. These colonies therefore had a choice between one mediocre familiar nest and one poor unfamiliar nest. In the "Naïve" treatment, colonies were allowed to acclimatize to the exploration arena for 24 h—time enough for *Temnothorax* ants to familiarize themselves with a novel environment (Aron et al. 1986). Both mediocre and poor nests were then simultaneously introduced to the arena just before the onset of emigration. These colonies therefore had a choice between 2 unfamiliar nests. Twenty colonies were tested each under both treatments (Naïve then Informed).

Experiment 2

Colonies housed in either a mediocre (treatment 1) or a good nest (type 1, treatment 2) were allowed to examine a mediocre

nest (“familiar nest”) for 6 days prior to emigration. Another mediocre nest (“unfamiliar nest”) was then introduced to the arena just before the onset of emigration. Colonies therefore had a choice between one familiar and one unfamiliar, otherwise identical mediocre nest. Twenty colonies were tested each under both treatments; 10 colonies were first exposed to treatment 1, whereas the others were first exposed to treatment 2. To relate nest choice to exploration intensity, we recorded for each colony the number of workers present in the familiar nest daily at a fixed time. Observations were carried out at 14 h on every day of exploration (except on the third day) and at the onset of emigration. Additionally, 18 colonies were observed continuously for 1 h each during exploration to record the number of workers entering and leaving the familiar nest during this period. Observation bouts were evenly spread throughout the exploration period, subject to day and time of observation being kept identical under both treatments for each colony.

Statistical analyses

All statistical analyses were performed using the software R version 2.8.1.

Nest choice patterns were compared between treatments using 2-tailed Fisher’s exact tests. Within treatments, nest preference was tested using exact binomial tests with a null hypothesis of random choice between both nests.

In experiment 2, the number of workers present in the familiar nest on daily scans was analyzed using a generalized linear mixed model (GLMM) with gamma error distribution, implemented using the function `glmmPQL` from R package MASS. We selected the model fitting our data best by using a stepwise backward procedure. The initial model included “colony” as a random factor, and fixed factors “treatment,” “colony size,” “day of observation,” “replicate,” and all first order interactions. The selection procedure allowed the removal of all interactions and of the main factor “replicate” from the model. The final selected model therefore included the significant effects treatment, colony size, and day of observation, and colony as random factor.

The number of entries and exits in/from the familiar nest during an observation bout was compared between treatments using paired *t*-tests on log-transformed data. Normality of data after transformation and equality of variances were checked using respectively Shapiro–Wilk’s tests ($n = 18$, $P > 0.100$ for all samples) and *F*-tests (Entries: $F = 0.58$, $P = 0.266$; Exits: $F = 0.71$, $P = 0.496$).

Modeling

We considered a scenario where each individual ant has an internal threshold for nest acceptance. There may be interindividual variation in thresholds within a colony, but thresholds are assumed not to vary over time. We developed a 2-stage model to investigate whether the flexibility of nest preference observed at the colony level in experiment 2 can be achieved under these assumptions. The first stage (“Pre-emigration phase”) describes exploration and commitment behavior prior to emigration; it is directly derived from the “acceptance threshold model” developed by Robinson et al. (2009; Robinson EJH, Franks NR, Ellis S, Okuda S, Marshall JAR, unpublished data). The second stage (“Emigration phase”) describes the commitment behavior of scouts during emigration. It is inspired by an existing model of opinion formation with recruitment (de la Lama et al. 2006, 2007; Revelli et al. 2009).

Pre-emigration phase (Stage 1)

We used a Markov chain model to describe the commitment behavior of ants to their old nest and to the familiar site

during the exploration period in the context presented in experiment 2 (see Appendix for details). We assumed that no recruitment occurs at that time. Ants can be either committed to a site or searching for a new site. Ants committed to either site can spontaneously abandon their commitment and start searching again. Ants discover nest sites independently, then assess their quality and compare it with an internal threshold, committing to them or rejecting them accordingly (Figure 7a; Robinson et al. 2009; Robinson EJH, Franks NR, Ellis S, Okuda S, Marshall JAR, unpublished data). As described in the Appendix, this Markov chain model rapidly converges to a limiting distribution of ants committed either to their old nest or to the familiar nest. It is therefore possible to calculate the average proportion of scouts committed to the familiar site at the end of exploration, that is, at the onset of emigration (“precommitted scouts”), as a function of the relative quality of the old nest and the familiar site.

Emigration phase (Stage 2)

We used a stochastic opinion formation approach to model expected nest choice in emigrations as a function of the relative quality of the alternatives and the proportion of scouts precommitted to the familiar site. Precommitted workers were assumed to remain permanently committed to the familiar nest during emigration (Figure 7b; see Appendix for details). Because colony-level aversion appears to be mediated by aversive pheromones affecting naïve workers in the same way as informed workers (Stroeymeyt N, Jordan C, Mayer G, Hovsepian S, Giurfa M, Franks NR, unpublished data), all other workers were assumed to be memory-less with regard to nests they had previously visited and rejected. We investigated specifically whether this new model can reproduce the results observed in experiment 2 (condition-dependent choice between one familiar and one unfamiliar, otherwise identical, mediocre nest sites). *T. albigennis* colonies have been shown to develop a collective aversion toward familiar, mediocre nest sites (Franks et al. 2007). However, such aversion could potentially be partly countered by the presence of scouts that are already committed to the familiar nest at the onset of emigration (i.e., precommitted scouts). Because the proportion of precommitted scouts depends on the quality of the old nest (see RESULTS from Stage 1), the resulting apparent colony-level aversion toward a familiar nest of fixed mediocre quality may also depend on the quality of the old nest. To test this hypothesis, we used the results of the pre-emigration phase (i.e., proportion of precommitted scouts, Stage 1) as input for the emigration phase (Stage 2; see Appendix for details).

RESULTS

Experiment 1

After 24 h, all naïve colonies ($n = 20$) confronted with a choice between a mediocre and a poor nest chose the mediocre nest (Figure 2). This shows a very strong natural preference for the better alternative (binomial test: $P < 0.0001$). By contrast, informed colonies ($n = 20$), which were familiar with the mediocre but not with the poor site prior to emigration, chose either the mediocre nest ($n = 15$) or the poor nest ($n = 5$; Figure 2). Informed colonies therefore selected the poor nest significantly more often than naïve colonies (Fisher’s test: $P = 0.047$), indicating that they had developed an aversion to the familiar, mediocre nest, which was strong enough to induce assessment errors in some colonies. Nevertheless, informed colonies still displayed a preference for the mediocre over the poor nest (binomial test: $P = 0.041$). Most colonies had therefore been able to overcome their aversion to the familiar nest and selected it as the better option;

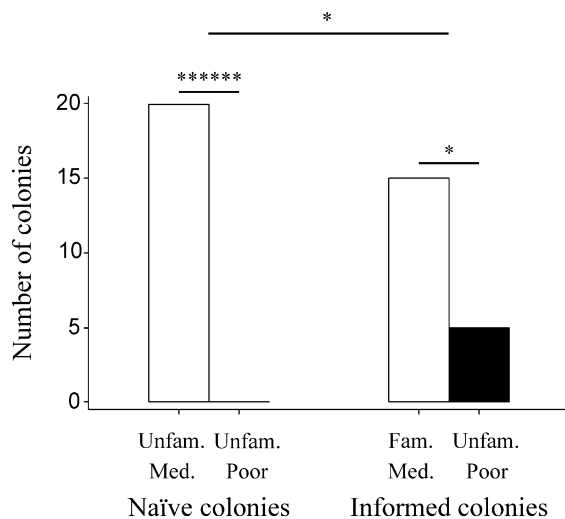


Figure 2

Nest choice by naïve and informed colonies (experiment 1). Number of naïve (left) or informed (right) colonies choosing the mediocre (Med., white bars) or the poor nest (Poor, black bars) 24 h after the onset of emigration, depending on the familiarity of each nest (Familiar: Fam., Unfamiliar: Unfam.). Binomial and Fisher's tests, * $P < 0.05$; ***** $P < 0.0001$. No colonies split.

however, the change in relative preference between the mediocre and the poor nest between both treatments reveals a form of collective irrationality.

Experiment 2

Exploration intensity was higher for colonies housed in mediocre than in good nests: during exploration, colonies housed in mediocre nests had more workers inside the familiar nest (Figure 3; GLMM: $p < 0.0001$) and higher traffic in and out of the familiar nest (Figure 4; paired t -test, Entries: $t = -2.55$, $P = 0.021$; Exits: $t = -3.08$, $P < 0.01$). This result indicates that evaluation of the current nest promotes or inhibits search for better alternatives.

Nest choice patterns differed marginally for colonies housed in a good or in a mediocre nest (Figure 5; Fisher's test: $P = 0.075$). The marginal P value obtained may be explained by the relatively low sample size ($n = 18$ colonies in each treatment), and the fact that choice was random in 1 of the 2 treatments (see below), which attenuates the difference between treatments. Colonies housed in a good nest had developed an aversion toward the familiar mediocre nest and preferred the unfamiliar option (Figure 5; binomial test: $P < 0.01$), in agreement with the results of Franks et al. (2007). By contrast, colonies housed in a mediocre nest did not show any preference for either nest but apparently chose randomly between them (Figure 5; binomial test: $P = 1$). Aversion intensity at the colony level therefore appeared not to be determined by the absolute quality of the familiar nest only but also by the quality of the home nest.

Modeling

The first stage of the model assumes that the proportion of scouts abandoning their commitment to their home nest and searching for alternative sites should increase when the quality of the home nest decreases; the number of scouts inspecting available nest sites should therefore increase as home nest quality decreases. Additionally, Stage 1 predicted that the proportion of scouts that commit to a familiar site

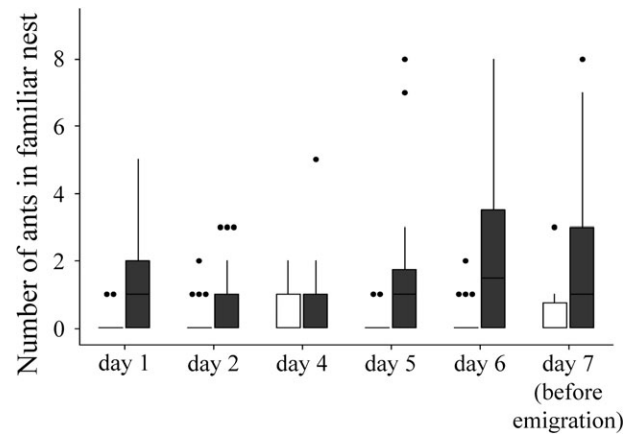


Figure 3

Number of workers in the familiar nest at different times during exploration (experiment 2). Interquartile range (rectangle), median (horizontal line), $1.5 \times$ interquartile range (vertical whiskers), and outliers (solid circles) are presented for colonies with a good (light gray, $n = 20$) or mediocre (dark gray, $n = 20$) old nest. All colonies were scanned daily at 14 h. The GLMM identified 3 factors significantly influencing the number of workers in the familiar nest: quality of the old nest ($P < 0.0001$); colony size ($P = 0.019$); and day of observation ($P < 0.005$).

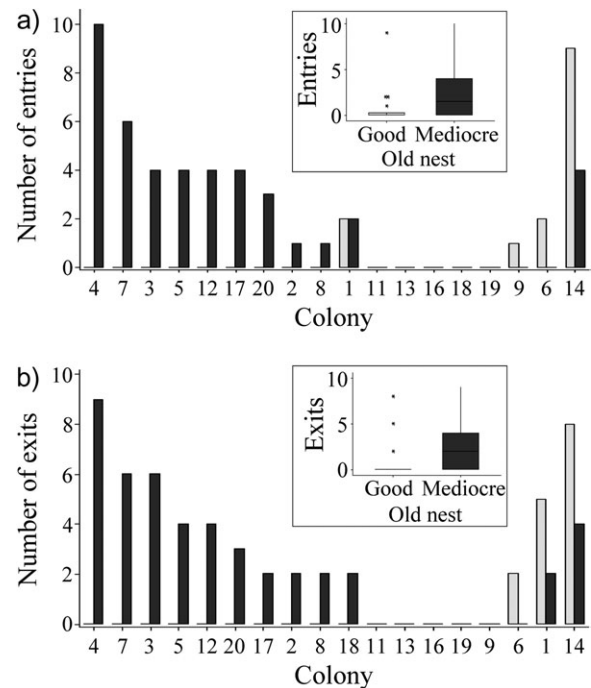


Figure 4

Traffic in and out of the familiar nest during exploration (experiment 2). Number of workers entering (a) or leaving (b) the familiar nest during a single 1-h observation bout for colonies with a good (light gray) or mediocre (dark gray) old nest. Inserts show the same data pooled for all colonies: interquartile range (rectangle), median (horizontal line), $1.5 \times$ interquartile range (vertical whiskers), and outliers (solid circles) are presented for colonies with a good (light gray, $n = 18$) or mediocre (dark gray, $n = 18$) old nest (paired t -test: Entrances, $P < 0.05$; Exits, $P < 0.01$). The number of entries and exits was highly correlated for each colony under both treatments (Pearson correlation coefficient $r = 0.935$; $P < 0.001$).

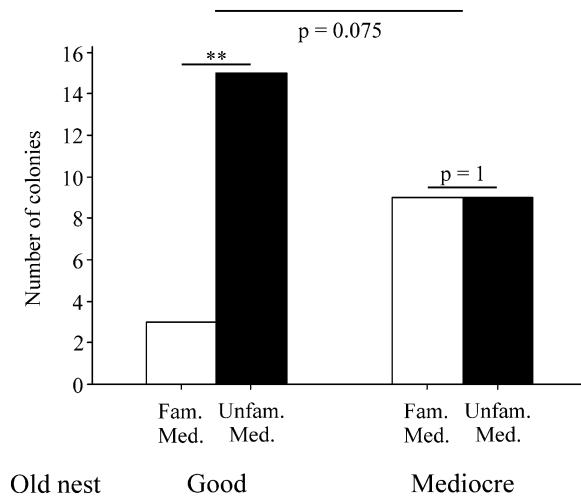


Figure 5
Nest choice by colonies housed in good or mediocre nests (experiment 2). Number of colonies choosing the familiar (white bars) or unfamiliar (black bars) mediocore nest 24 h after the onset of emigration, depending on the quality of their old nest. Binomial and Fisher's tests, $**P < 0.01$. Comparison of nest choice pattern between treatments used a 2-tailed Fisher's exact test. Under each treatment, there were 2 split colonies (not shown).

should increase when the relative quality of the home nest decreases (see Appendix). These predictions are in agreement with our data (experiment 2) showing both increased traffic (Figure 4) and residence (Figure 3) in the familiar site when the home nest was of lower quality.

The combined predictions from the 2-stage model on nest choice are shown in Figure 6: when the quality of the old nest was high during exploration, the unfamiliar site is more likely to be chosen during emigration (shaded region). Reducing the quality of the old nest relative to the familiar site (as indicated by the arrow) results in a decrease in the probability of choosing the unfamiliar nest, such that nest choice progressively becomes random (border line) then biased toward the familiar site (unshaded region), as the proportion of pre-committed scouts increases. This scenario is in agreement with the results observed in experiment 2: for a fixed (mediocre) quality of the familiar site, colonies with a good old nest indeed preferred the unfamiliar site, whereas colonies with a mediocre old nest chose randomly between familiar and unfamiliar sites (Figure 5).

Results from Stage 2 also indicate that the proportion of pre-committed scouts required for random colony choice is usually quite small, with a maximum possible value of approximately 30% (see Appendix and Supplementary Material).

DISCUSSION

Colonies of *T. albipennis* continually gather information about available nest sites and can use this information in later emigrations (Franks et al. 2007; Stroeymeyt et al. 2010). Here, we present 2 cases where this process induces changes in nest preference depending on previous conditions. Colonies that had familiarized themselves with a mediocre nest site before emigration indeed chose differently from naïve colonies (experiment 1) or chose differently depending on the quality of their home nest (experiment 2). Previous experience was already known to affect emigration dynamics in *Temnothorax* (Langridge et al. 2004; Healey and Pratt 2008); our results indicate that it can also influence collective nest choice.

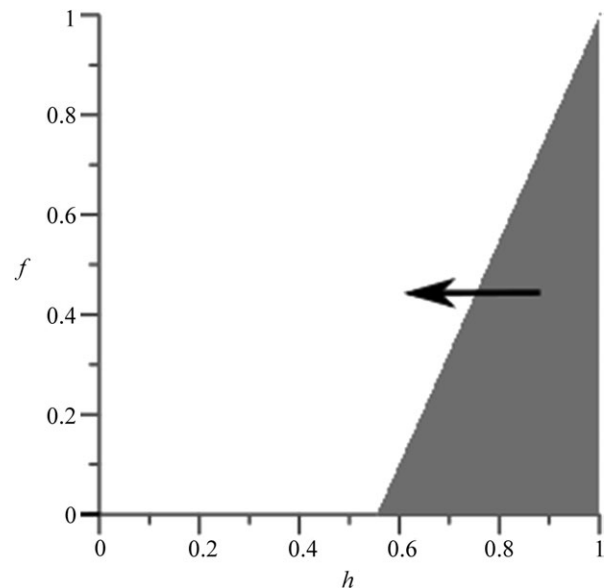


Figure 6
Predictions from combined pre-emigration and emigration phases for colony-level nest choice. The shaded region indicates the values of h and f in the pre-emigration phase (per visit acceptance probabilities of the old—or “home”—nest and familiar site, respectively, determined by their perceived qualities) in which the unfamiliar site is more likely to be chosen. In the unshaded region, the familiar site is more likely to be chosen. Along the line dividing the regions, the colony choice will be random. See Appendix for details.

Colonies changed their relative preference between 2 nest sites depending on previous conditions, although the absolute fitness-related values of these sites did not change. This can be seen as a form of irrationality (Waite 2001; Schuck-Paim et al. 2004; Bateson and Healy 2005; Houston et al. 2007). Our results therefore appear to contrast with a previous study (Edwards and Pratt 2009), where collective irrationality was not observed in colonies of a related *Temnothorax* species. However, in that study, the authors investigated a specific form of rationality—independence from irrelevant alternatives—by varying the local context: specifically, they tested whether the presence of a decoy nest affected the level of preference between 2 other nests, both nests being unknown at the time of emigration. By contrast, in our study, the apparent irrationality observed was induced by variations in the background context, that is, differences in experience with 1 of the 2 alternatives (experiment 1) or differences in the previously experienced home nest quality (experiment 2).

Apparent deviations from rationality are thought sometimes to occur as a side effect of decision heuristics that usually perform well or to reflect adaptive adjustments to the local context (Houston et al. 2007). The seemingly irrational decisions observed in this study may similarly reflect a process allowing colonies to adjust their preference criteria to experienced conditions. Previous experience can allow solitary animals to make flexible choices according to the local quality of potential mates (Bakker and Milinski 1991; Collins 1995; Reid and Stamps 1997; Wagner et al. 2001; Dukas 2005; Collins et al. 2006), habitats (Davis and Stamps 2004; Stamps and Davis 2006; Davis 2007), or food sources (Hodges 1981; Greggers and Menzel 1993). Previous experience could similarly confer ant colonies with greater flexibility in emigrations. We found that the strength of aversion toward a familiar nest site depended strongly on the quality of the home nest, that is, colonies developed an aversion toward a mediocre site only

if their home nest was of higher quality (experiment 2). This is particularly relevant because colonies are able to move to better sites while their own nest is still intact (Dornhaus et al. 2004), so a well-established colony is likely to occupy one of the best available nest sites in its surroundings. Developing an aversion toward sites of quality similar to that of the current nest would therefore be detrimental because it is unlikely that a much better site would suddenly become available, and aversion would merely delay emigration. By contrast, developing an aversion toward poorer sites can be beneficial, as it should allow colonies to focus their search for better alternatives (Franks et al. 2007). The quality of the home nest may therefore serve as an indicator to build reasonable expectations of the quality of future nests, and the optimal behavior may differ depending on these expectations. In that case, the ants' change in acceptance criteria according to old nest quality cannot be considered as irrational, but as an adaptive adjustment to local conditions.

Natural selection is thought to shape decision heuristics, which usually perform well in the context they evolved in, but may induce occasional mistakes or perform badly in novel contexts (Gigerenzer and Todd 1999; Houston et al. 2007). The apparent mistakes observed in experiment 1 (informed colonies choosing the poorer site) could similarly be a by-product of decision mechanisms allowing the combination of previous (aversion toward a familiar site) and current information (difference in quality between alternatives), which is usually beneficial (Franks et al. 2007; Stroeymeyt et al. 2010). However, contrary to previous work by Franks et al. 2007, where current information was irrelevant because colonies had to choose between 2 identical nest sites, experiment 1 staged a "worst-case scenario" in which previous and current information exerted opposite influences on nest choice. This conflict is likely to delay decision making, and it is uncertain which nest will be chosen. In our experimental conditions, site quality appeared to have a stronger effect than previous experience because most colonies overcame their initial aversion and selected the better option. The decision mechanisms therefore appear to be self-correcting and to reduce the risk of errors when previous experience is misleading. It is therefore likely that the apparent mistakes observed in experiment 1 are relatively infrequent in natural conditions.

Our results show that *T. albipennis* colonies are influenced by the quality of their home nest when assessing a new nest site. How is this achieved? The literature on mate choice by solitary animals suggests several possible mechanisms allowing individuals to take into account the quality of previously encountered options when assessing a new candidate. Individuals can compare potential mates or use an internal acceptance threshold which they adjust through step-by-step updating after each encounter or according to average mate quality (Bakker and Milinski 1991; Collins 1995; Luttbegg 1996; Reid and Stamps 1997; Bateson and Healy 2005; Collins et al. 2006). Such flexibility in individuals could explain the colony-level flexibility in assessment criteria observed in our experiments. For example, ants could compare encountered available sites with their current nest and develop an aversion only toward sites of lower quality ("comparison hypothesis"). Comparisons of nest sites by individuals have indeed been suggested in many empirical and theoretical studies (Mallon et al. 2001; Dornhaus et al. 2004; Pratt et al. 2005; Marshall et al. 2006; Pratt and Sumpter 2006). However, recent studies have questioned the existence of individual comparisons and suggested that apparent comparisons at the collective level could emerge from individual decision rules based on absolute evaluation of nest sites and fixed acceptance thresholds (Robinson et al. 2009; Robinson EJH, Franks NR, Ellis S, Okuda S, Marshall JAR, unpublished data). It is possi-

ble that these thresholds are adjusted through prolonged experience with the current nest's quality ("adjusted-threshold hypothesis"), so that ants housed in lower quality nests would have lower standards than ants housed in higher quality nests, which would also explain the results from experiment 2.

Here, we investigated a third novel scenario, related to the following question: can flexible, experience-dependent collective decisions emerge from fixed-threshold decision rules in individuals ("fixed-threshold hypothesis")? We combined a fixed acceptance threshold model of pre-emigration commitment (Stage 1) with a stochastic decision-making emigration model (Stage 2) and show that fixed thresholds at the individual level can produce flexible choices at the colony level. This is because the quality of the home nest determines the proportion of ants that are dissatisfied with it and search for alternative sites, which in turn influences future collective decisions. Additionally, fixed thresholds in individuals can also result in variable aversion strength if there is intracolony variation in acceptance thresholds. Indeed, in that case, different subsets of workers are involved in searching and assessing new sites depending on the context. For example, for colonies housed in a good nest, only workers with a high acceptance threshold would leave the nest and look for alternatives. Most of these workers should therefore reject the familiar mediocre site when they visit it because its quality falls well below their acceptance threshold. This results in strong aversion toward that site at the colony level. By contrast, for colonies housed in a mediocre nest, exploring workers have a greater range of thresholds, and those with lower thresholds can be expected to commit to the familiar mediocre site, whereas those with higher thresholds should reject it. In this case, our analytical results show that the influence of these categories of workers can cancel out for biologically plausible parameters (see Appendix and Supplementary Material), resulting in the observed absence of aversion to the familiar nest at the colony level. One prediction of this scenario is that exploration intensity will depend on the absolute quality of the home nest: if workers use a fixed-threshold rule to decide whether to leave their nest and look for better alternatives, then exploration intensity should be higher for colonies housed in lower quality nests. Our observations are in agreement with this prediction (Figures 3 and 4). By contrast, a recent study in a related *Temnothorax* species seems to indicate a certain degree of experience-induced flexibility in individual decision criteria (Sasaki and Pratt 2011). It is therefore not possible at present to select or rule out definitively any of the 3 scenarios (comparison, adjusted thresholds, or fixed thresholds) presented above.

Irrationality is usually considered as evidence for comparative evaluation mechanisms at the individual level (Waite 2001; Schuck-Paim et al. 2004; Bateson and Healy 2005). Here, we have observed seemingly irrational decisions at the colony level induced by variations in the background context (i.e., previous experience). This may be indicative of a comparative strategy at the colony level. However, our analytical results demonstrate that this does not necessarily require comparative evaluation in individuals but could emerge from individuals using absolute evaluation coupled with threshold-based decision rules. Interestingly, the same individual decision strategy was previously suggested to protect colonies from irrationality induced by variations in the local context (i.e., composition of the choice set; Edwards and Pratt 2009; Robinson EJH, Franks NR, Ellis S, Okuda S, Marshall JAR, unpublished data). This simple individual rule has therefore the potential to allow colonies both to make robust decisions based on current information and to adjust their acceptance criteria according to

previous information. This is a new illustration of the principle that complex collective properties can emerge from the interaction of simpler units (Camazine et al. 2001; Couzin 2007, 2009). We hope our results will stimulate new studies to investigate how individual decision-making strategies relate to apparent collective strategies, and how previous experience can influence decision making in animal groups without necessarily requiring experience-dependent changes in individuals.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>.

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APPENDIX

Pre-emigration phase (Stage 1)

We modeled ants as independently discovering nest sites, assessing their quality (with noise) and comparing it with an internal threshold, then accepting or rejecting them accordingly. We made 2 modifications as follows: Robinson E.J.H., Franks N.R., Ellis S., Okuda S., and Marshall J.A.R. (unpublished data) modeled site acceptance during emigration and considered that once scouts accept a site, they remain committed to it until the end of emigration and may start recruiting. In the pre-emigration period, however, we considered that committed scouts do not recruit but may subsequently abandon their commitment and assess other sites.

We modeled this as a discrete-time Markov-process whose state transitions are represented in Figure 7a (see Supplementary Material for details). We assumed that probability h of accepting the old (or "home") nest is greater than probability f of accepting the familiar site. This can occur for several reasons: the old nest can be of physically higher quality or merely perceived as better due to the presence of nest mates, brood, and the queen. Additionally, even if old and familiar sites are of the same perceived quality, if we assume a distribution of acceptance thresholds in the colony, then those scouts dissatisfied with the old nest and discovering the familiar site will have a higher average threshold than those scouts staying in the old nest, leading to a correspondingly lower probability of accepting the familiar site.

The model outlined above predicts the pattern seen in the experimental data of higher entrance and exit rates at the familiar site when the home site is of lower quality (Figure 4; see Supplementary Material for details). Additionally, it converges to a limiting distribution over its states, which predicts the increased residence observed in the familiar site when the quality of the old nest is lower (Figure 3; see Supplementary Material for details).

The limiting distribution of the model can be used to calculate the average proportion of scouts committed to the familiar site when emigration is induced, for given relative site qualities. This proportion increases when the quality of the old nest relative to the familiar nest decreases and can be used as an input parameter for the stochastic decision-making model described below (see Supplementary Material for details).

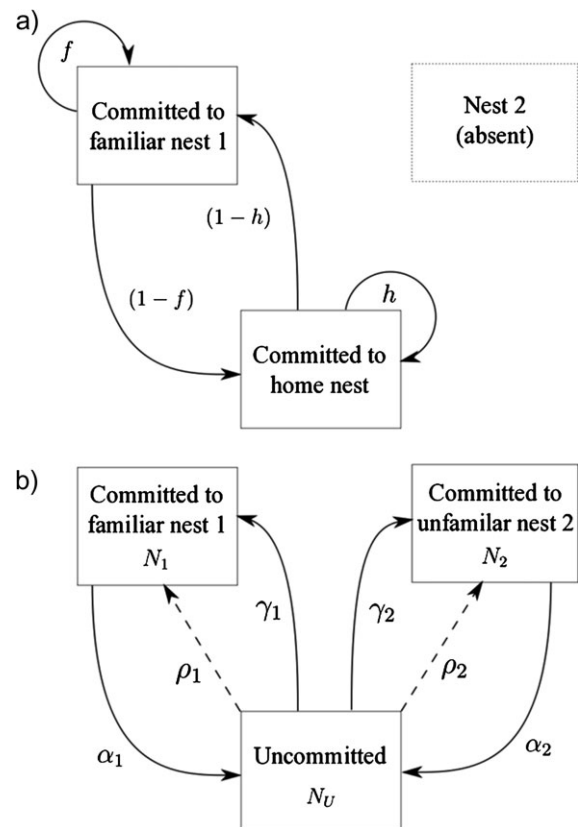


Figure 7
State transition diagrams (a) for the pre-emigration phase (Stage 1) and (b) for the emigration phase (Stage 2). Solid lines indicate spontaneous transitions and dashed lines indicate recruitment.

Emigration phase (Stage 2)

To model nest choice by emigrating colonies, we applied an existing stochastic model of opinion formation with recruitment by de la Lama et al. (2006, 2007). The states and transitions in this continuous-time model are depicted in Figure 7b: Ants may either be committed to the familiar nest (N_1), committed to the unfamiliar nest (N_2) or uncommitted to either nest (N_U). Uncommitted ants may spontaneously discover and commit to either nest or be actively recruited by committed ants and commit to either nest. Committed ants may also spontaneously abandon their commitment and become uncommitted. These 6 rates may in general be independent.

We further assume that the precommitted scouts from the pre-emigration commitment model (φ) remain permanently committed to the familiar nest during the decision-making process (Revelli et al. 2009). These ants may not spontaneously abandon their commitment to the familiar nest but crucially may recruit uncommitted ants to become committed to nest 1. These precommitted ants may partly counter the aversion to the familiar nest, depending on their proportion among total scouts, which itself depends on the relative qualities of the old and familiar nests.

This model begins with a microscopic, continuous-time master equation description of the transitions. From this, the macroscopic equations for the proportion of the colony in each state, as well as the fluctuations about these, may be derived. These results are then used to calculate the conditions for which we may expect equal probabilities that the majority of scouts are committed to either nest as a function of the parameters of the model, in particular the proportion of precommitted scouts φ . As φ is a function of the nest-quality parameters h and f in the pre-emigration model, we can find, under certain generalized assumptions, the values of h and f required for random nest choice, as depicted in Figure 6 (see Supplementary Material for details).

Figure 6 may help explain the results observed in experiment 2 (Figure 5): Reducing the quality of the home site for a fixed quality

of familiar nest results in an increased proportion of precommitted scouts, which counter the effect of aversion to the familiar nest. If the old home nest is good and the familiar site is mediocre (experiment 2, treatment 2), the system will be in the shaded area of Figure 6, that is, greater chance of choosing the unfamiliar than the familiar site. This indicates that precommitted scouts are not enough to compensate the effect of aversion to the familiar site. Keeping the quality of the familiar site constant, reducing the perceived quality of the old nest will move the system parallel to the horizontal axis as indicated by the arrow. This will reduce the chances of the unfamiliar site being chosen, passing through random nest choice (line), as the proportion of precommitted scouts increases (experiment 2, treatment 1). Finally, low enough old nest quality should result in a greater chance of choosing the familiar than the unfamiliar nest, as precommitted scouts are sufficiently numerous and influential to overcome the effects of aversion.

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