



Strategies for choosing between alternatives with different attributes: exemplified by house-hunting ants

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We tested the decision-making abilities of emigrating ant colonies. The colonies had to choose a new nest site when presented with two or more potential nest sites, each with different attributes or different combinations of attributes. For *Leptothorax albipennis* colonies in the laboratory, darkness of the nest cavity, internal height of the cavity and width of the entrance were all important attributes. The colonies ranked these attributes: darkness of the nest site was more important than internal cavity height, which in turn was more important than entrance width. These choices conform to the logic of transitivity. In addition, the colonies used a sophisticated decision-making strategy in which they took all alternatives and all attributes into consideration. Furthermore, the ants, in effect, weighed the different values of different attributes. They also chose the best nest when presented with only one excellent nest among four mediocre ones or one excellent nest in an array of one excellent, one good and one mediocre. Altogether, our results suggest that these ant colonies, in deciding upon a new home, used a weighted additive strategy, one of the most computationally expensive and thorough decision-making strategies.

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Animals choosing nest sites or mates may benefit if they can select the best among numerous alternatives. Their decision making will be more difficult, however, if each alternative has different values for its different attributes. In this study, we considered which decision-making strategy is used by certain house-hunting ant colonies when they must decide between different alternative nest sites each with different attributes. We examined choices of nest sites, which attributes of nest sites were valued and how different types of attribute were rated relative to one another. If ants rank nest site attributes, does their ranking of alternatives and attributes obey the logic of transitivity? That is, if they prefer A to B and B to C, do they also prefer A to C? Do they weigh and sum different attributes to derive a score for each potential nest site to facilitate well-informed decisions?

Many of the general issues that we raise concerning the strategy of decision making (when there are several

alternatives each with many different attributes) may also apply during mate choice (see Gibson & Langen 1996). A female may need to evaluate the quality of alternative males, each of which may have multiple courtship signals. For example, a peahen, *Pavo cristatus*, may need to evaluate not only the length of the peacock's train, but also the number of eye spots in it and the brilliance of the feathers (Petrie et al. 1991; Petrie 1994). Most experimental studies, however, compare only one trait at a time (Andersson 1994; Ryan 1997). Therefore, in many cases it is not clear whether females combine the many attributes of males into an overall measure of quality or simply use a single criterion such as territory size as a proxy. Furthermore, experiments to disentangle the role of many different attributes might be difficult to perform (Wittenberger 1983; but see Kodric-Brown & Nicoletto 2001; Künzler & Bakker 2001).

One obvious difference between mate choice and nest choice is that potential mates may exchange sexually selected signals whereas potential nest sites have to be searched for cues that might indicate their value. Nevertheless, in both mate choice and nest choice individuals may need to choose between numerous alternatives each with various attributes.

Because nest sites have easily manipulated physical properties, nest site choice by social insects can provide

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ideal experimental opportunities to explore the strategy of decision making when several alternatives and many attributes per alternative need to be evaluated. For example, honeybees, *Apis mellifera*, evaluate, among several other factors, (1) the volume of the potential nest site cavity; (2) the size (cross-sectional area) of the entrance; (3) the height of the entrance above the ground; (4) the height of the entrance above the internal floor of the cavity; and (5) the compass bearing of the entrance (see Seeley 1977, 1982; Seeley & Morse 1978; Witherell 1985). These variables are likely to be of adaptive significance because they will determine whether there is room for the colony to grow in the new cavity and to store sufficient honey for overwintering and how well the cavity can be defended and maintained at a certain temperature. However, studies have not yet determined how different attributes of a potential nest site are weighted. For example, it is not known how honeybees rank different types of nest site attribute or if such rankings show transitivity. For studies of the importance of housing variables in species other than social insects see, for example, Elwood & Neil (1992).

In general, how might decision making be achieved given a plethora of alternatives each with several attributes that differ quantitatively or qualitatively? Do animals simplify their decision making by using procedures to reduce the breadth (the number of alternatives considered) or depth (the number of attributes considered) of their evaluations? People making consumer choices may either simplify and speed-up or make more rigorous their decision making by using one of the following strategies (see Simon 1955; Payne et al. 1993).

(1) The satisficing strategy is a procedure that minimizes the breadth of the search. This algorithm proceeds by considering each alternative in turn and by choosing the first one that suffices for each and every necessary attribute. Here one might imagine the decision maker using a checklist with tick boxes (Fig. 1). One negative result for any attribute would terminate the evaluation and another alternative would be considered. This method would be quick because no attempt is made to find the best of all the alternatives, merely one that suffices. In this algorithm, there is no ranking or weighting of attributes and no direct comparisons of alternatives. It is, therefore, computationally simple. It invokes, at each point, the binary decision: does the attribute currently under consideration suffice? The search ends when an alternative is found that is satisfactory for all attributes that matter.

(2) Elimination by aspects. In this procedure, there is both a ranking of attributes and the use of a binary satisficing rule. Not all attributes are necessarily considered. The procedure evaluates all alternatives for the most important attribute and rejects those that do not suffice for that attribute (Fig. 1). It then considers remaining alternatives for the second most important attribute and rejects those that do not suffice for that attribute and so on until only one alternative remains. (In practice, this strategy may involve a final random choice if more than one alternative remains at the end of the process.) Elimination by aspects is a process of satisficing that does

not necessarily consider all of the attributes. It is therefore only partially rational. As such it is arguably less sophisticated than the satisficing strategy, but it may also facilitate fast decision making, in this case, by decreasing the depth of the search.

(3) The lexicographic heuristic proceeds by ranking all of the alternatives for this attribute and then choosing the alternative with the highest rank for this attribute. If there are ties it considers the next most important attribute and continues as necessary (Fig. 1). All alternatives are considered and compared but the depth of the search may be reduced, that is not all attributes may be evaluated.

The more important the decision the more thorough should be the evaluation: unless, of course, speed is paramount. Both of the following strategies evaluate each and every attribute of each and every alternative. That is, they make no attempt to decrease either the depth or breadth of the evaluation.

(4) The equal weight heuristic. In this procedure, there is no ranking of attributes. Each attribute of every alternative is scored and multiplied by the same coefficient (i.e. equal weight; Fig. 1). This is followed by a pooling of such subscores for each alternative to give a grand total for each alternative. This facilitates complete comparison of every alternative across all attributes but simplifies by giving each attribute equal weight.

(5) The weighted additive strategy. In this procedure, attributes are ranked. Each attribute of every alternative is scored and multiplied by a coefficient that weights appropriately the different intrinsic values of the different types of attribute (Fig. 1). This is followed by a pooling of such subscores for each alternative to give a grand total for each alternative. This permits a complete weighted comparison of every alternative across all attributes.

The weighted additive strategy is the most thorough of all of the above decision-making strategies. It considers each and every attribute of each and every alternative, giving each attribute a score according to its importance. If honeybees, for example, were using this strategy the relative importance of each attribute of a potential nest site would be evaluated in terms of its potential influence on the inclusive fitness of the members of the colony.

Seeley & Buhrman (2001) have shown that honeybee colonies can select the single most desirable nest out of an array of five, in which the other four nest sites were acceptable but mediocre. They further suggested that honeybees may be using an advanced weighted evaluation strategy. However, as yet, experiments to confirm this are lacking. The relative weightings of different nest site attributes have not been shown for house-hunting honeybees.

Leptothorax ant colonies are good subjects for studies of nest choice (Mallon & Franks 2000; Pratt & Pierce 2001). *Leptothorax albipennis* colonies naturally occur in nests within thin fissures in rocks (Franks et al. 1992). Although they can build a wall of debris within such a nest (Franks et al. 1992; Franks & Deneubourg 1997) they can do little to repair its roof or floor after damage by disturbance or weathering. Indeed, it seems that entire colonies are well adapted to frequent emigrations to

Satisficing

E.g.		Alternatives			
		A	B	C	D
	Attributes (not ranked)	1	✓	✓	✓
		2	X	✓	✓
		3		X	✓
		4			✓

C suffices and is chosen

Elimination by aspects

E.g.		Alternatives			
		A	B	C	D
	Most important	1	✓	✓	X
	Attributes (ranked)	2	X	✓	X
		3			
	Least important	4			

First C, then A and D are eliminated. B is chosen

Lexicographic heuristic

E.g.		Alternatives			
		Ranking across alternatives for given attributes in order of decreasing importance			
		A	B	C	D
	Most important	1	4th	3rd	= 1st
	Attributes (ranked)	2		1st	= 2nd
		3			
	Least important	4			

C is chosen

Equal weight heuristic

E.g.		Alternatives			
		A	B	C	D
		(Subscore × weight)			
	Attributes (not ranked)	1	4×5	3×5	2×5
		2	3×5	4×5	2×5
		3	1×5	2×5	2×5
		4	1×5	2×5	2×5
	Scores		45	55	40
					50

B is chosen

Weighted additive strategy

E.g.		Alternatives			
		A	B	C	D
		(Subscore × weight)			
	Attributes (ranked: differentially weighted)	1	4×6	3×6	2×6
		2	3×5	4×5	2×5
		3	1×4	2×4	2×4
		4	1×2	2×2	2×2
	Scores		45	50	34
					43

B is chosen

Figure 1. Different decision-making strategies: satisficing, elimination by aspects, the lexicographic heuristic, the equal weight heuristic and the weighted additive strategy.

new nests (Franks & Sendova-Franks 1992, 2000; Backen et al. 2000; Pratt et al. 2001; McLeman et al. 2002). At certain times of year, colonies may occupy more than one nest site (Partridge et al. 1997), but for the rest of the year an emigrating colony might do best to stay together (Franks et al. 2002). Individual scouts leave damaged old nest sites and seek good new ones. They can measure accurately the floor area of such new nest sites (Mallon & Franks 2000; Mugford et al. 2001) and must select new sites that can house their entire colony of up to a few hundred workers, a single queen and numerous brood. Individual scouts hesitate for longer, before recruiting their nestmates, if they find a poor new nest site rather than a good one (Mallon et al. 2001). When they do begin recruiting they do so initially by the slow process of tandem running in which scouts literally lead single workers to the new nest. Pratt et al. (2002) have shown that such scouts assess the number of their nestmates in the new nest site to ensure quorate decision making. Scouts begin the much faster process of recruiting nestmates by carrying them only if they find a substantial number (ca. 9–17) of their nestmates in the new nest site. This quorum sensing enables the ants to take an opinion poll. Only when sufficient nestmates indicate their acceptance of a new nest site by their presence within it does the emigration proceed at maximum pace. Recruitment by carrying is three times faster than recruitment by tandem running and once such transport begins, a nest will be rapidly occupied (Pratt et al. 2002). In this paper, we are concerned with the assessments by scouts of certain nest site attributes (other than floor area which we held constant). Such assessments may cause colonies to show a preference for particular types of nest.

We conducted experiments on nest choice by colonies of the ant *L. albipennis*. The experiments involved 12 different nest types and over 340 colony emigrations. We used only those physical parameters of nest sites that are simplest to manipulate and least likely to interact. For example, we did not investigate nest temperature and humidity, not only because these might be difficult to control but also because individual ants might use only a single physiological measure to determine the influence of both of these variables through their interactive effect on their physiological state.

METHODS**Collection and Culturing of Colonies**

We collected colonies of *L. albipennis* each spring or summer (1998–2001) at a disused quarry in Dorset, U.K. They were cultured in the laboratory by housing each colony in a ‘holding’ nest made by sandwiching a piece of cardboard between two glass microscope slides, 75 × 50 mm (Sendova-Franks & Franks 1993). Over the course of these experiments we used two different ‘standard nests’, which were used for culturing the ants or as holding nests between choice experiments. One form of these standard nests had a floor area of 38 × 24 mm, the other a floor area of 33 × 25 mm. This difference was made to facilitate filming in other experiments. This

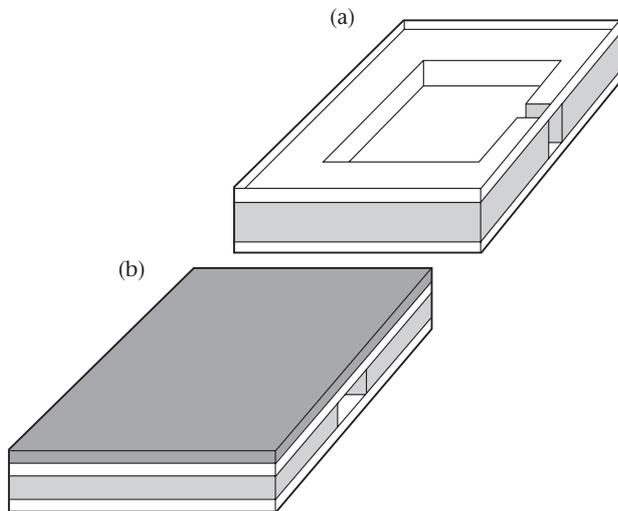


Figure 2. (a) A Bright, Thick, Narrow nest: the cavity was bright, and had 1.6 mm of headroom and an entrance that was only 1 mm wide. (b) A Dark, Thin, Wide nest: the cavity was dark (because the top microscope slide was covered with cardboard), and had 0.8 mm of headroom and an entrance 4 mm wide. Both nests were constructed from glass microscope slides, 75×50 mm, sandwiching cardboard.

difference in nest site floor area is too small to be recognized by the ants (Mallon & Franks 2000). Within each set of experiments, the floor area of all the nests was the same. For the holding nests, the thickness of the cardboard, and hence the internal height of the cavity, was 1 mm. Each nest had a single entrance in the middle of its longer side. The entrance of the holding nests was 2 mm wide (and 4 mm long). Holding nests were never covered with a top sheet of cardboard, that is they were always so-called Bright nests (see below). Each holding nest was placed in a petri dish, 100 × 100 × 17 mm, the walls of which were covered with Fluon to prevent the ants escaping. Except during experiments, the colonies were fed ad libitum with *Drosophila* larvae and honey solution and provided with a separate water supply.

Alternative Potential Nest Sites

The nest variables that we examined were Dark versus Bright, cavities that were either Thick or Thin and entrances that were Narrow, Medium or Wide. Dark nests had a piece of cardboard on top of the nest to prevent most light from entering the nest cavity; Bright nests had no such cover. Thick nests were constructed from 1.6-mm-thick cardboard, thin ones from 0.8-mm cardboard. Entrance widths were Narrow (1 mm), Medium (2 mm) or Wide (4 mm) (Fig. 2).

Thus a total of 12 different nest types could be presented to the ants. In addition, to determine whether the cross-sectional area of the nest entrance had any influence, we allowed certain colonies to choose between nests that were both constructed to be thick, that is to have 1.6 mm of headroom, but one of which had an extra piece of cardboard so that its entrance was low and wide

(0.8 × 4 mm) whereas the other had a high but medium-width entrance (1.6 × 2 mm). Hence, both potential new nest sites had entrances with cross-sectional areas of 3.2 mm².

Binary Choice Experiments

Each experimental arena was a large (220 × 220 mm) square petri dish, the sides of which were covered with Fluon. A pair of new potential nest sites was placed so that each was 100 mm away from the old nest site (entrance to entrance). This distance was large enough to allow the ants to make a clear decision between nest sites and small enough for us to view the whole emigration. The distances and directions between the old nest and each new nest site and between the two new nest sites were such that they formed an isosceles triangle. The distance between the entrances of the two new potential nest sites was 90 mm. We initiated the emigration by placing the colony in the arena and removing the uppermost glass slide from the original holding nest (Sendova-Franks & Franks 1993). The relative positions of the different alternative nest sites were randomized so as to eliminate the effects of any directional biases. After initiating the experiment, we then left the colonies for 48 h. No colonies in that time switched nests after moving into one nest. A colony was deemed to have chosen a nest site when all ants, bar a few foragers, were inside this nest site. Some colonies used both new nests and these were recorded as having split. After each experiment, each colony was required to emigrate back into a standard holding nest with the dimensions described above.

To determine whether the results differed significantly from a random choice, we conducted a two-tailed binomial test on each binary choice data set for colonies that had shown a preference (i.e. had not split; Fig. 3).

We ran as many as 15 replicates of each experiment simultaneously. Some colonies were involved in many different choice experiments (up to 17). These repetitive trials seemed to have no effect on the health of these colonies or on their decision making. We checked this, in part by running the following 'best-among-several' experiments towards the end of the entire experimental series, using the same colonies. These colonies made exactly the choices that could have been predicted from the binary choice experiments.

Best-among-several Experiments

These experiments were conducted in a circular arena, 1 m in diameter and 40 cm high, designed to present a minimum of visual landmarks. The arena walls were constructed of translucent white Plexiglas, and the base of transparent Plexiglas. The 40-cm Plexiglas walls, which were painted internally with Fluon, were further extended to a total height of 80 cm with plain light blue cardboard, also to minimize visual landmarks. The entire arena was placed under a lighting hood that presented

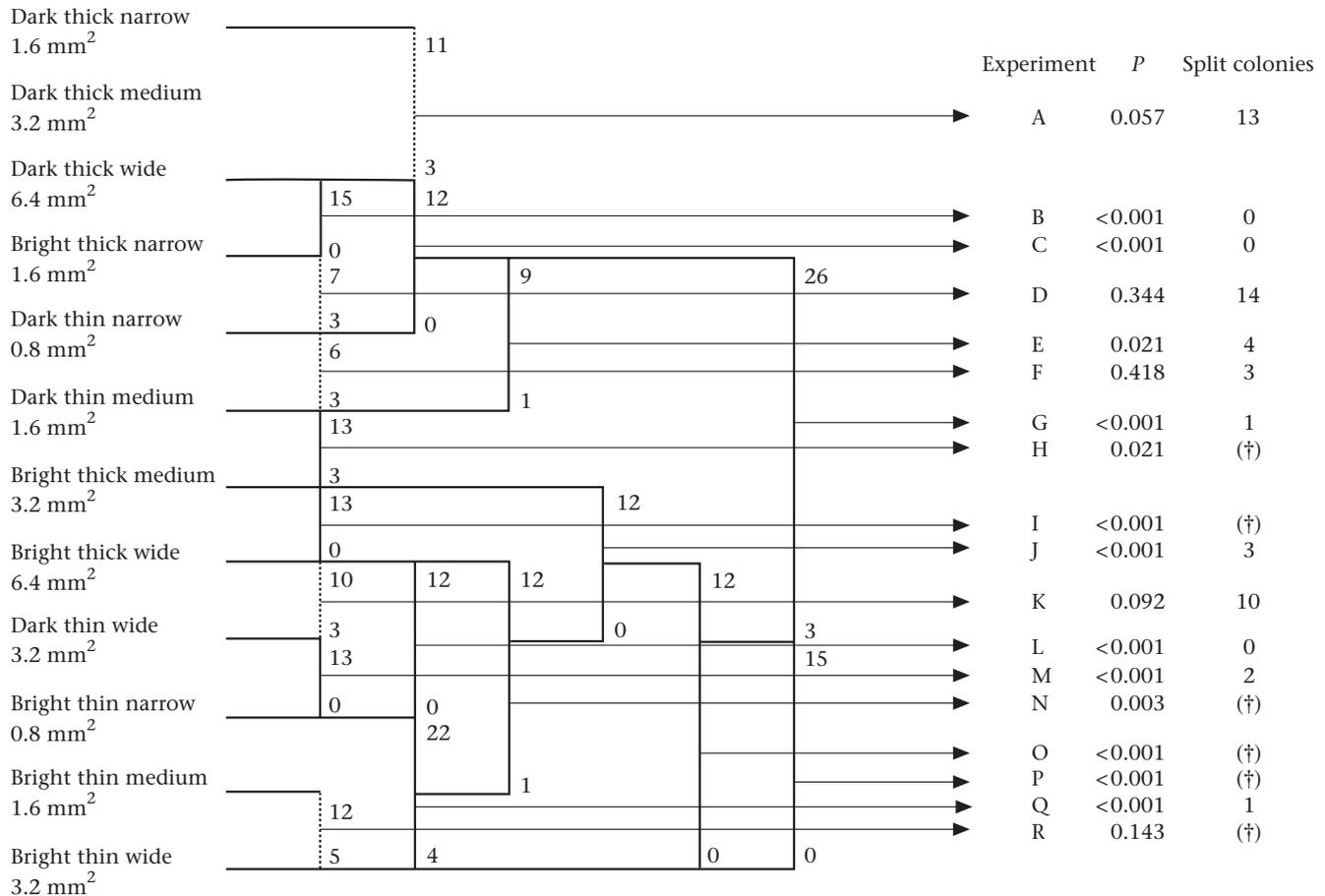


Figure 3. Experimental comparisons are bracketed and identified with a unique letter (A to R). Dark solid lines bracket significant results. Dashed lines bracket nonsignificant results. The numbers near the top and bottom of each such bracket indicate the number of colonies that chose that nest in each experiment. The *P* value for a two-tailed binomial test is given after each experiment's designation letter, followed by the number of colonies that split. The key to the experimental codes is also given in Table 1. In certain early trials (†) the number of colonies that split was not recorded, because in these trials very few colonies split. High proportions of splitting colonies are associated with indecision over evenly matched new nest sites (e.g. Experiments A, D and K).

extremely even overhead illumination, again to minimize directional biases.

First, we placed either three or five alternative nests equidistantly from the centre of the arena with a constant angular separation between neighbouring ones (120° for three nests or 72° for five nests). The distance between each nest entrance of a potential nest site and the centre of the arena was 7.5 cm. Then the old nest was placed so that the centre of its bottom microscope slide was exactly at the centre of the arena. We removed both the top microscope slide and the old cardboard walls of the old nest site to minimize any directional biases. We recorded which new nest the ants chose (or whether the colony split) 24 h after the old nest was placed in the arena. The position of the 'best' new nest site in the array was randomized for each trial.

RESULTS

In the experiment on the role of cross-sectional area of the nest entrance, 10 colonies chose the Bright, Thick

nests with Low \times Wide Entrances ($0.8 \times 4 = 3.2 \text{ mm}^2$) and seven chose nests that were Bright and Thick, with High \times Medium Entrances ($1.6 \times 2 = 3.2 \text{ mm}^2$). This difference is not significant (two-tailed cumulative probability binomial test that assumed that the probability of accepting a particular type of nest was 0.5: $P = 0.629$). This result can be compared with experiment I (13 colonies chose Bright, Thick, Medium, entrance $1.6 \times 2 = 3.2 \text{ mm}^2$; none chose Bright, Thick, Wide, entrance $1.6 \times 4 = 6.4 \text{ mm}^2$; two-tailed, cumulative probability binomial test: $P = 0.0002$). This comparison suggests that colonies are more concerned with the cross-sectional area of the nest entrance than its width per se. In general, however, nest entrance width (or cross-sectional area) seemed to be the least important variable for these ants (see, for example, experiment O in Table 1).

Figure 2 and Table 1 give all the other results from the binary choice experiments. In general, the 12 different nest types can be ranked consistently on the basis of all of the experimental results.

Table 1. The preferences of colonies given a choice between two types of nest

Experiment		
Preferences		
P	Dark, Thin, Wide	> Bright, Thin, Wide AEBE
O	Bright, Thick, Wide (6.4 mm ²)	> Bright, Thin, Wide (3.2 mm ²)
Q	Bright, Thin, Narrow	> Bright, Thin, Wide AEBE
I	Bright, Thick, Medium (3.2 mm ²)	> Bright, Thick, Wide (6.4 mm ²)
Rankings and transitivity		
H	Dark, Thin, Medium (1.6 mm ²)	> Bright, Thick, Medium (3.2 mm ²)
L	Bright, Thick, Wide (6.4 mm ²)	> Bright, Thin, Narrow (0.8 mm ²)
M	Dark, Thin, Wide (3.2 mm ²)	> Bright, Thin, Narrow (0.8 mm ²)
B	Dark, Thick, Wide (6.4 mm ²)	> Bright, Thick, Narrow (1.6 mm ²)
N	Bright, Thick, Wide (6.4 mm ²)	> Bright, Thin, Medium (1.6 mm ²)
C	Dark, Thick, Wide (6.4 mm ²)	> Dark, Thin, Narrow (0.8 mm ²)
Weightings		
E	Bright, Thick, Narrow (1.6 mm ²)	> Dark, Thin, Medium (1.6 mm ²)
J	Bright, Thick, Medium (3.2 mm ²)	> Dark, Thin, Wide (3.2 mm ²)
G	Bright, Thick, Narrow (1.6 mm ²)	> Dark, Thin, Wide (3.2 mm ²)
Equalities		
A	Dark, Thick, Narrow	>(NS) Dark, Thick, Wide AEBE
D	Bright, Thick, Narrow (1.6 mm ²)	= Dark, Thin, Narrow (0.8 mm ²)
F	Dark, Thin, Narrow (0.8 mm ²)	= Dark, Thin, Medium (1.6 mm ²)
K	Bright, Thick, Wide (6.4 mm ²)	= Dark, Thin, Wide (3.2 mm ²)
R	Bright, Thin, Medium (1.6 mm ²)	= Bright, Thin, Wide (3.2 mm ²)

Preference is indicated by >. No significant choice: NS or =. Key attributes compared in Bold. AEBE=all else being equal.

Preferences

Experiments P, O, Q and I showed preferences when all else was equal (excepting nest entrance cross-sectional area in certain cases). The ants preferred nests that were Dark, Thick and had Narrow entrances (Table 1, Fig. 2).

Ranking of Attributes and Transitivity

Eight of the experiments tested the ranking of attributes (Table 1, Fig. 2): D, H and K tested whether light level is ranked higher than cavity height; C, L and N tested whether cavity height is ranked higher than entrance size; and B and M tested whether light level is ranked higher than entrance size. In general, light level was a more important attribute than cavity height, which was a more important attribute than entrance size. Nevertheless, the results of experiments D and K do not show the expected preferences but suggest that attribute importance may sometimes be context dependent (see Discussion). The results of experiments F and R show that colonies can be indecisive when nests differ only in the least important attribute, nest entrance width. Nevertheless, the results in Fig. 3 imply strongly that Bright, Thick, Narrow nests were much preferred to Bright, Thick, Medium nests even though these differed only in the least important attribute, entrance width, which sometimes had little influence (as in F and R).

The results of experiments B, N and C show transitivity particularly clearly. Thus in B, as expected, nests that were Dark and Thick (with a wide entrance) were preferred to nests that were Thick and Narrow (and Bright; Fig. 3, Table 1).

Weighting of Attributes

Experiments E, J and G show that attributes are weighted. Thus in experiment G, Bright, Thick, Narrow nests were preferred to Dark, Thin, Wide ones. This is likely to occur only if two preferred but lesser attributes in combination can outweigh one higher-ranking single attribute. A Thick cavity with a Narrow entrance can outweigh a Dark nest handicapped by poor lower-ranking attributes. The results of experiments E, J and G, which established that attributes are weighted, are some of the most important results in this series of experiments (Table 1, Fig. 3).

Best-among-several Experiments

The first best-among-several experiment involved a choice between five nests: the 'best' or 'most desirable', was Dark, Thick, Narrow and the other four were Bright, Thin, Narrow. We thus had one excellent nest versus four we knew the ants would choose if there was nothing better (see Experiment Q in Fig. 3). We decided a priori to have five replicates and to score only those in which the colony did not split. Four colonies chose the best nest and one split. We considered this result as four out of four, because all four colonies that chose one nest chose the best. This is significant at $P=0.002$ with a one-tailed binomial test based on a probability of success per trial of 0.2. We used a one-tailed test because one nest had been determined a priori to be excellent. We also obtained a highly significant result ($P=0.006$) when we counted the one ant colony that split as a failure.

The second best-among-several experiment determined whether colonies could choose well when given three nests each of different quality: Dark, Thick, Narrow versus Bright, Thick, Narrow versus Bright, Thin Narrow. We decided a priori to do 15 replicates, so that we could use a chi-square test with expected frequencies of 5 ($=15/3$). We also decided a priori, for statistical reasons, to record choice as a majority decision. In other words, if a colony split we recorded its preference according to where most of it came to be housed. On this basis, 14 colonies chose Dark, Thick, Narrow and one chose Bright, Thick, Narrow ($\chi^2_2=24.4$, $P<0.0001$). Even in this experiment splitting was rare: nine of the 14 colonies that chose the Dark nest had every ant and brood item in that nest. The majority of the remainder had only a couple of workers and one or two brood items in another nest.

Clearly, these ants can choose the best nest both when presented with many nests (i.e. five) and also when three different types of nest made the choice potentially difficult.

DISCUSSION

The results of the binary choice experiments are such that we can rank all of the nest types in a consistent hierarchy (Fig. 3). The ants generally preferred dark nests to bright ones, thick ones to thin ones and those with narrow rather than medium or wide entrances, when other factors were held constant. Furthermore, they typically preferred dark nests to thick ones and thick ones to those even with the narrowest entrances. In addition, their preferences obeyed the logic of transitivity. Thus, for example, they preferred dark, thick nests to thick ones with narrow entrances (Table 1, Fig. 3).

There are, however, two types of situation in which colonies were sometimes indecisive. First, they were indecisive when given the choice between narrow and medium entrances or medium and wide (experiments F and R) with all else being equal. Nevertheless, the results in Fig. 3 strongly imply that Bright, Thick, Narrow nests were much preferred to Bright, Thick, Medium nests even though these differed only in the least important attribute, entrance width (cf. experiment F). Second, colonies were also indecisive when combinations of good lower-ranking attributes apparently balanced a single higher-ranking attribute, or even a high- and low-ranking attribute in combination (see experiments D and K). Thus some of our results suggest that attribute importance may be context dependent. For example, we expected Dark, Thin, Narrow nests to be preferred to Bright, Thick, Narrow ones, because in general Darkness ranked above Thickness. Yet here the ants were indecisive (experiment D: see also experiment K). Perhaps they get confused in these circumstances because Darkness is only marginally more desirable than Thickness and the third variable, nest entrance width, in these experiments, could not be used as a tiebreaker.

The results of experiments E, J and G are a key to understanding which decision-making strategy these ants use. These experiments show that a most desirable

attribute such as a dark nest can be outweighed by a combination of other desirable but lower-ranking attributes (Table 1, Fig. 3). For example, colonies consistently chose Bright, Thick, Medium-entrance nests to Dark, Thin, Wide-entrance ones (J). Such experiments show that colonies are weighting the different attributes, even down to the least important ones, in addition to ranking them.

Thus our experimental results show that these ants have (1) consistent preferences; (2) rank different attributes; (3) exhibit transitivity in their preferences; and (4) weight the different attributes.

The results of both of the 'best-among-several' experiments show that the ants can choose the single most desirable nest (as predicted from the binary choice experiments) when it is one among four equally mediocre ones, or when it is the most desirable one among three that range from excellent, through good, to mediocre.

Altogether, these experiments clearly confirm that these ants are using a more thorough search and decision-making protocol than the satisficing or elimination by aspects strategies. They are ranking all of the attributes of nests. They do not merely take the first that satisfices, but reliably seek out the best as shown by both of the best-among-several experiments. This eliminates both the satisficing and the elimination by aspects procedures. Furthermore, given that the least important attribute (nest entrance width) can be influential and, when summed with the middle-ranked attribute (nest thickness), can outweigh the highest-ranked attribute (darkness of the cavity), it is clear that the ants are also not using the lexicographic heuristic. In short, the ants are not reducing either the breadth or depth of their search. Our experiments show that these ants are using a highly sophisticated and extremely thorough additive strategy such as the equal weight heuristic or the weighted additive strategy.

Furthermore, the satisficing, elimination by aspects and lexicographic strategies are not likely to be used by these ants given the way in which their decision making is organized (Mallon et al. 2001; Franks et al. 2002; Pratt et al. 2002). The satisficing strategy is inherently a sequential one, in which candidates are considered one at a time and either rejected or accepted. The ants' strategy is inherently nonsequential, because different individuals consider different candidate nests simultaneously (Pratt et al. 2002). The other two strategies (elimination by aspects and lexicographic) are also difficult to reconcile with the behaviour of individual ants, which condense their overall evaluation of a site into a single score and associated behavioural choice: how long to wait before initiating recruitment (Mallon et al. 2001). They simply hesitate for longer before recruiting their nestmates when they encounter a less desirable nest site. When they encounter a good one they hardly hesitate at all. Furthermore, the opinions of numerous ants are effectively pooled by the quorum sensing (Pratt et al. 2002) that occurs before the crucial switch from slow recruiting by tandem running to fast recruitment by carrying behaviour. Given all of these findings, it seems unlikely that the ants could add new attributes successively to their

measure of overall nest quality, on the basis of comparison with other potential nest sites. In short, the highly parallel nature of a colony's mechanisms for gathering information and coming to a decision are consistent with an additive strategy.

The experimental results per se do not allow us to determine whether the ants are using the equal weight heuristic or the weighted additive strategy. This is because, in practice, it is possible for equally weighted attributes to appear as if they are consistently ranked (i.e. to appear to have different weighting coefficients). This might occur simply because the value of each attribute presented might, by chance, be such that it always scores highly or poorly and therefore appears as if it is ranked consistently even though the maximum possible subscore for each different attribute is the same.

Nevertheless, given that these ants are weighting the attributes and apparently (doing something equivalent to) summing subscores, we speculate that they are more likely to be using a weighted additive strategy than an equal weight heuristic. We suggest that the weighted additive strategy is a more parsimonious explanation for naturally selected decision makers. The equal weight heuristic is less sophisticated and thorough than the weighted additive strategy but it is just as difficult and time consuming. For example, the summing of subscores is unlikely to be intrinsically easier if they are given equal weights. Furthermore, it is unlikely that the different nest attributes we examined would have the same maximum potential influence on the fitness of the ants. Therefore, they should not be given equal weight.

The reason that the ants prefer dark nests might be that this is a good way for them to judge quickly the integrity of the existing walls of a cavity in the field. That is, does the nest have gaps that would allow rainwater to flood it? A small entrance may aid them in defending their nest and a cavity that has reasonable internal height (headroom) may make it easier for the ants to tend their brood (personal observations). *Leptothorax* ants are opportunistic users of available nest sites, which may often be limited or subject to take over (Herbers 1986; Foitzik & Heinze 1998). *Leptothorax albipennis* ants are skilled at building dry stone walls within nest cavities (Franks et al. 1992; Franks & Deneubourg 1997) and they could easily block a wide entrance to a nest. Nevertheless, they prefer small fixed entrances, possibly because potential invaders could easily remove loose debris. One next step will be to determine how the nest site variables we have examined influence the (inclusive) fitness of the ants.

In conclusion, social insect colonies are model systems for studying the mechanisms, tactics and strategies of decision-making systems in biology. It would be interesting to know which decision-making strategies animals use during mate choice when they are presented with numerous alternatives each with different attributes (e.g. Collins et al. 1994; Dale & Slagsvold 1996; Slagsvold & Drevon 1999). New methods of using computer animations in mate choice experiments have opened up the possibility of teasing apart the influence of many separate traits. Indeed, using this method Künzler & Bakker (2001) have shown that female sticklebacks, *Gasterosteus aculea-*

tus, respond to multiple secondary sexual signals presented by artificial animated males. A valuable next step in such mate choice experiments would be to determine which decision-making strategies females use when they are presented with numerous alternatives each with different attributes.

Our findings strongly suggest that these ant colonies are using one of the most thorough, computationally expensive, and time-consuming, decision-making strategies. However, time costs will be reduced because these superorganisms are distributed decision makers. When an old nest is destroyed workers go off in all directions and work concurrently on their separate evaluations. The colony, as a collective decision maker, can both process large amounts of disparate information and be almost everywhere at once.

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