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Animal behaviour

Ants learn to rely on more informative attributes during decision-making

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Evolutionary theory predicts that animals act to maximize their fitness when choosing among a set of options, such as what to eat or where to live. Making the best choice is challenging when options vary in multiple attributes, and animals have evolved a variety of heuristics to simplify the task. Many of these involve ranking or weighting attributes according to their importance. Because the importance of attributes can vary across time and place, animals might benefit by adjusting weights accordingly. Here, we show that colonies of the ant *Temnothorax rugatulus* use their experience during nest site selection to increase weights on more informative nest attributes. These ants choose their rock crevice nests on the basis of multiple features. After exposure to an environment where only one attribute differentiated options, colonies increased their reliance on this attribute relative to a second attribute. Although many species show experience-based changes in selectivity based on a single feature, this is the first evidence in animals for adaptive changes in the weighting of multiple attributes. These results show that animal collectives, like individuals, change decision-making strategies according to experience. We discuss how these colony-level changes might emerge from individual behaviour.

1. Introduction

Evolutionary theory predicts that animals act to maximize their fitness when choosing among a set of options, such as what to eat or where to live. Decision-making is relatively straightforward for simple options differing in only one attribute. For example, if two flower patches offer honeybees identical nectar but are found at different distances, the closer one, requiring less time and energy to exploit, should clearly be preferred. It becomes more difficult, however, if options vary in multiple ways, especially if no option is superior in all attributes [1]. Thus for honeybees, if flowers offer different qualities and quantities of nectars at different distances, it likely becomes harder to determine the best choice.

Decision-makers have a variety of strategies to handle these situations, many of which involve ranking attributes [1]. For example, the weighted additive strategy assigns a weight to each attribute according to its importance. An option's value is determined by summing each attribute score multiplied by its weight, and the option with the highest total score is preferred. This strategy has been observed in multiple contexts for many taxa, from insects to humans [2,3]. It is often assumed that weights are constant [2]. However, the validity of attributes can vary across time and place, and animals might increase their fitness if they adjust weights accordingly [1,2]. For example, if bees live in an environment where all flowers have similar nectar quality but very different shapes (and thus different ease of access to nectar), do they learn to weight shape more than nectar in judging each option?

We tested this hypothesis by studying nest site selection in the ant *Temnothorax rugatulus*. These ants typically live in fragile rock crevices and are adept at collectively choosing a new home if their old nest becomes inadequate [4]. In the laboratory, they can be induced to emigrate and choose between two or more artificial nests of different design [5,6]. Their choices reveal preferences based on

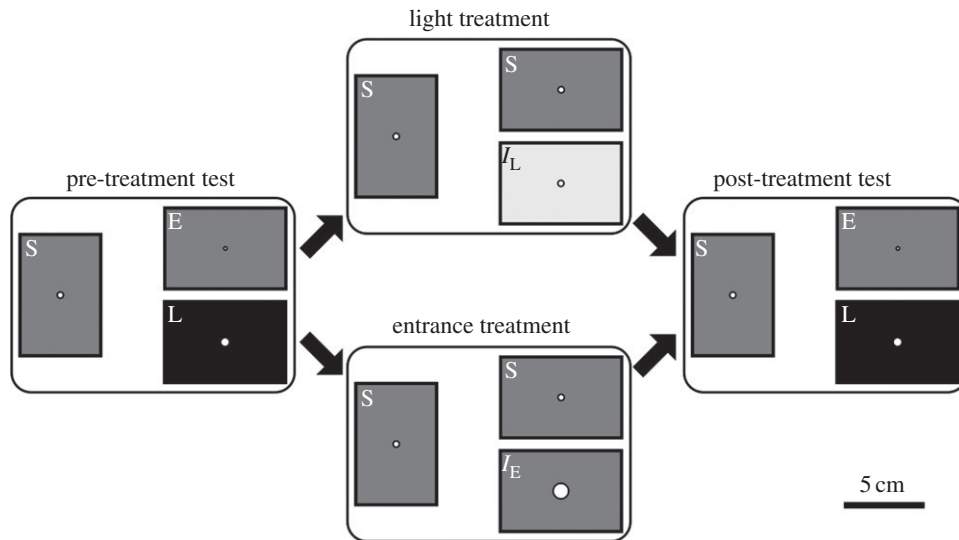


Figure 1. Experimental assessment of the effect of experience on attribute weights. An initial binary choice between sites E and L showed how colonies weighted entrance size and interior light level. Colonies then made a series of four choices in which only one attribute provided distinguishing information. In each choice, they chose between a standard nest (S) and another that was inferior to the standard nest in one attribute, but identical to it in the other. For half the colonies, the inferior attribute was light (I_L); for the other half it was entrance size (I_E). Finally, colonies repeated the original choice to determine whether experience had altered their preferences.

multiple nest attributes, including interior light level and entrance size [5]. Our experimental strategy was to test whether their relative weighting of these two attributes changes if they are exposed to an environment in which only one attribute is useful in distinguishing candidate sites.

2. Material and methods

The experimental design is shown in figure 1. We first established a baseline by offering colonies a choice between two target nests E and L. Nest E had a smaller entrance than nest L, but a brighter interior (see the electronic supplementary material for details of nest design). Because these ants have a strong preference for smaller entrances and darker interiors [5], this choice imposed a trade-off between the two attributes. We designed the nests to achieve roughly equal preference in the baseline tests.

In the treatment phase, colonies underwent a series of four trials. In each trial, they were induced to move from a standard home nest and choose between two sites: another standard nest and one that was inferior to the standard nest in one attribute, but identical to it in the other. For half the colonies, the inferior attribute was light level (the light treatment); for the other half, the inferior attribute was entrance size (the entrance treatment; figure 1). Each emigration usually ended with the colony moving to the standard home nest, because this was superior to the alternative in all choices. Thus, colonies spent the entire treatment phase living in and moving to standard nests. The only difference between treatments was the nature of the rejected nest, and the criterion (light level or entrance size) that was used to reject it.

Once the treatment phase was complete, colonies were again presented with the original binary choice between sites E and L. This test assessed whether the treatments had changed the ants' attribute weightings. Specifically, increases in the relative weighting of light level could be detected as an increase in preference for L, whereas increases in the weighting of entrance size could be detected as an increase in preference for E.

To avoid any bias owing to differences among colonies in how they weight the two attributes, we took account of their initial preferences when assigning them to treatments. Half of the colonies that chose E in the baseline test were placed in the entrance

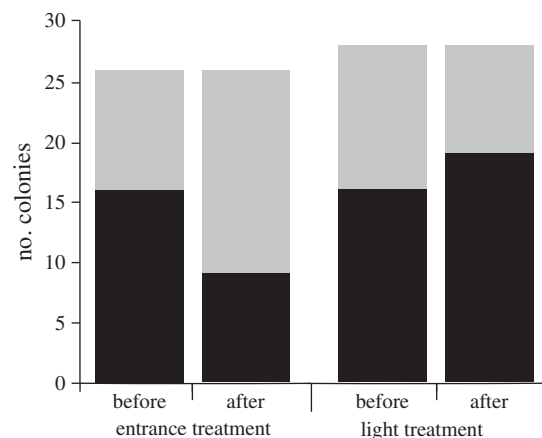


Figure 2. Nest site preferences of colonies before and after treatments in which either entrance or light level were informative for decision-making. In each treatment, colonies shifted their preference toward the option favoured by the informative attribute. E (light shaded) and L (dark shaded) stand for the small entrance nest and the darker nest, respectively.

treatment and the other half in the light treatment. Those that chose L were divided in a similar fashion. See the electronic supplemental material for further details on experimental procedures.

3. Results

In both treatments, colonies shifted their preference toward the site favoured by the informative attribute (figure 2). Of the 26 colonies assigned to the entrance treatment, only 10 chose nest E before the treatment, but this rose to 17 after the treatment. Conversely, for the 28 colonies in the light treatment, the number preferring L increased from 16 to 19. Closer examination of each colony's choices before and after treatment confirms this pattern (table 1).

To compare preference shifts between conditions, we fitted a logistic regression model, using the statistical package R

Table 1. Contingency tables classifying colonies by their choices before and after treatment. Colonies that initially chose the nest favoured by the informative attribute tended to select the same option after treatment; colonies that initially chose the disfavoured nest tended to switch their preference. Thus, in the entrance treatment, colonies that initially chose nest L were more likely to change than those that initially chose E. The opposite pattern was seen in the light treatment.

entrance treatment				light treatment					
		before treatment					before treatment		
		E	L	sum			E	L	sum
after treatment	E	6	11	17	after treatment	E	3	6	9
	L	4	5	9		L	9	10	19
	sum	10	16			sum	12	16	

(v. 2.15.2). The response variable was post-treatment choice (E or L) and the predictor was treatment (light or entrance; electronic supplementary material, table S1). The model showed a significant effect of treatment (Wald test: $\chi^2 = 5.73$, d.f. = 1, $p = 0.02$) as well as a significant overall goodness of fit (likelihood ratio test: $\chi^2 = 6.08$, d.f. = 1, $p = 0.01$). The odds ratio was 3.99, meaning that the odds of choosing nest E after the entrance treatment (or nest L after the light treatment) were approximately four times greater than the odds of choosing E after the light treatment (or L after the entrance treatment). To determine whether each colony's pre-treatment preference affected this pattern, we re-fitted the model by adding pre-treatment choice and its interaction with treatment as predictor variables. We found no effect of these new variables (likelihood ratio test: $\chi^2 = 0.71$, d.f. = 2, $p = 0.70$), suggesting that colonies do not show consistent differences in their preferences. To assess the predictive accuracy of the simpler model, we calculated Somer's D, a measure of association between the observed choices of each colony and the choice probabilities predicted by the model. The resulting value of 0.33 means that experimental treatment is only moderately predictive of each colony's choice. The data thus indicate that treatment has a significant effect on preference, but other factors must also have a substantial influence on each colony's choice.

4. Discussion

Our study shows that animals can change weights on option attributes according to experience. Past studies on animal decision-making have mainly focused on how experience affects a single attribute [7,8]. Those studies tested whether decision-makers change their selectivity according to the average quality of options available in their environment [9]. We instead created an environment where only one attribute distinguishes options and showed that colonies learn to emphasize that attribute.

Experience has long been known to influence decision-making by solitary animals [10,11]. Our work extends this finding to groups, reinforcing recent results in *Temnothorax* ants [5,12,13]. Collective nest choice is a distributed process, with most scouts assessing only one candidate site. Rather than compare sites with one another, they instead compare a single site to an internal scale and then decide whether to recruit nest-mates there [14,15]. Thus, the effects we observed can best

be interpreted as changes to the weightings of this internal scale. One possible mechanism is suggested by the scarcity effect in psychology [16], where emphasis is placed on attributes for which high quality cases are rare. Thus, if an ant repeatedly encounters sites with a low value for a given attribute (implying that high values are rare), she might increase the weighting for this attribute. Over repeated emigrations, this strategy would reinforce weights for more variable attributes.

Alternatively, some scouts may have the opportunity to compare both sites during the emigration and could use this information to change their internal scale. Experiments in *T. albipennis* show that scouts retain memories of site quality obtained before emigrations begin [13]. Similar memories might allow ants to compare multiple sites and determine which attributes best differentiate them. Understanding the degree to which such comparisons matter, and the precise behavioural mechanisms responsible, must await future studies.

In evaluating preference tests, it is important to distinguish changes in attribute weightings from changes in motivational state [17]. A recent study on *T. curvispinosus* found the counter-intuitive result that colonies with experience of good nests more readily accepted a mediocre site than did colonies with experience of poor nests [12]. A simple interpretation of this result is that colonies responded with a greater sense of urgency when forced to abandon a good site compared with a poor site, because of the larger drop in site quality. To avoid such state-dependent effects, we took pains to ensure that colonies lived in identical nests in both the light and entrance size conditions. That is, the better option was always the standard home nest, and the only difference between conditions was the design of the inferior nest, which was rarely chosen. This design allows us to conclude that the treatment effects reflect changes to the ants' internal standards rather than their motivational state.

What could be the benefit of flexible weights? Because the environment can change across time and place, reliability of attributes is not constant. In a dense, uniformly dark forest, light level is less useful in distinguishing good from bad nests than it would be in an open forest where some areas are much darker than others. Reducing the number of attributes that need to be considered may also improve the quality of decision-making, by lessening the burden on each ant's limited cognitive abilities. Even in humans, it has been suggested that faster and more accurate decisions can be made by focusing on only one reliable attribute and

ignoring others [18]. Ants may also use simple heuristics like this to maximize their fitness [19].

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Data accessibility. All data can be found in the electronic supplementary material.

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