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RESEARCH ARTICLE

Does the history of option quality affect nest site choice in the Acorn ant?

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Abstract
During decision – making, animals consider not only the current but also the past quality of options. For example, when humans evaluate performance (e.g. sales) of employees, they do not only consider the average performance but also the trend of performance; ascending performance is often viewed as more favorable than descending performance. In our study, we test if non-human animals have a similar bias when they are evaluating options using house-hunting by the acorn ant, *Temnothorax curvispinosus*, as our model system. Our data show that when nest-site quality is static over time, ant colonies tend to prefer the nest site which was better (i.e. darker) between two nest options. However, when the nest quality changes over time—one improves and the other worsens—more colonies choose the low-quality, but improving, nest than the high-quality, but worsening, nest. These results suggest that a continuous change of option quality may influence evaluation. We discuss alternative explanations for our results, possible mechanisms, and potential ecological benefits for keeping track of the nest-site quality.

Keywords Decision making · Cognitive bias · Collective cognition · *Temnothorax*

Introduction

Decision making, such as when to forage and where to live, has been extensively studied in animal behavior because its outcomes often have an impact on the decision-maker's fitness (Bateson 1983; Stephen and Krebs 1986). Thus, it is critical for animals to integrate not only the current but also the past information during decision making (Bitterman 1976; Couvillon and Bitterman 1984; Wendt et al. 2019b). For example, when bees have higher expectations for a feeder (e.g. a higher concentration of sucrose solution), they consume the food significantly less (Bitterman 1976). This contrast effect can also be observed using continuous change instead of one-off change. For example, when humans evaluate performance (e.g. sales) of employees, ascending performance is often viewed as more favorable than descending performance (DeNisi and Stevens 1981). Rhesus monkeys have shown a similar bias; when monkeys receive different sequences of options, they prefer the ascending sequence to the descending one (Blanchard et al. 2014). Because the contrast effect using continuous change requires a long-term memory, this effect has been mainly tested in primates, especially humans. Thus, there has still been little empirical investigation into whether gradual changes in choice quality influence decision making in "simpler" organisms, such as social insects.

In this study, we tested this continuous contrast effect using nest site choice by the acorn ant, *Temnothorax curvispinosus*, as our model system. The colonies of this diurnal species typically have fewer than one hundred workers and live in plant cavities, such as acorns and hollow twigs (Bengston and Dornhaus 2012). The fragility of their nest sites likely necessities frequent emigrations (Möglich 1978), and the emigration process of this genus has been well documented based on laboratory research (Mallon et al. 2001; Franks et al. 2002; Pratt and Sumpter 2006; Sasaki and Pratt 2018). When the home nest site is damaged, about a quarter of the colony workers serve as scouts, searching for new sites (Pratt 2005). When scouts discover potential nest sites, they assess several features (Franks et al. 2003; Sasaki et al. 2013), including interior light levels (darker

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nests are preferred) and entrance sizes (smaller sizes are preferred). Scouts that discover a better site are more likely to initiate recruitment and, in turn, recruited workers do the same, creating a positive feedback loop that enables colonies to choose the best nest site among several in their environment (see Sasaki and Pratt 2018 for the details of this collective nest-choice process). Even when the home site is intact, some scouts explore their environment (Dornhaus et al. 2004). If they encounter any potential sites, they assess them and use this information later when their home nest becomes uninhabitable (Stroeymeyt et al. 2010, 2011a). These results suggest that colonies can remember not only locations but also the quality of potential nests. This ability is particularly important for colonies because the quality of their potential nest sites can change over time in nature. For example, acorns in wet areas can decay faster than ones in dry areas. Thus, some good-quality acorns could become worse than others over time. Therefore, we hypothesized that nest choice in ant colonies is influenced by the trend (i.e., ascent or descent) of nest quality (DeNisi and Stevens 1981; Blanchard et al. 2014). In our study, we adjusted light levels in two potential nest-options over time with one option becoming darker (improving) and the other becoming brighter (worsening). Although the nest quality was identical during the nest choice, we anticipated that colonies would prefer the improving nest over the worsening nest.

Methods

Experimental procedure

Prior to the experiment, we induced a colony emigration to an empty home nest placed in the middle of the experimental arena (19 × 27 cm) (see Sasaki and Pratt 2018 for the detail of the emigration procedure). After 24 h, we introduced two kinds of potential target nests, namely an “improving” nest and a “worsening” nest, one on each side (Fig. 1a). These target nests were identical to the home nest except for the interior light level, which was controlled by putting light filters on the roof (see Supplementary Information for the detail of the nest design; Figure S1). The home nest (approx. 1 lx) was always darker than target nests to prevent early migration. The improving nest initially had a very bright interior light level (approx. 1600 lx) but became darker, and more preferable (Franks et al. 2003; Sasaki et al. 2019), over time (Fig. 1b). The interior light level of the worsening nest, on the other hand, was initially very dark (approx. 3 lx) but became brighter, and less preferable, over time (Fig. 1b). Note that the interior light level of the worsening nest was always darker, thus more preferable, than that of the improving nest until day 4. *Temnothorax* ants have low sensitivity to light within a bright range, and thus light levels were chosen based on this previous finding (Sasaki et al. 2013). Every morning until day 5, we adjusted the interior light level by replacing the light filters of the secondary roof. To minimize changing the environmental cues, we used the same glass slides for the secondary roof throughout the experiment. To test whether decisions were influenced by the trend in quality, both potential nests had the same interior light level (approx. 400 lx) on day 5. On the following day (day 6), the roof of the home nest was removed to induce an emigration. We chose five days as the duration of the experiment based on the previous studies, which showed that *Temnothorax* ants retain nest information for at least six days (Langridge et al. 2004; Santos et al. 2022). We assayed nest-site preference by recording the site occupied by the colony 12 h later. If one site contained more than 90% of colony members including all queens and brood items, we designated that as the choice. If no site achieved this criterion, we did not

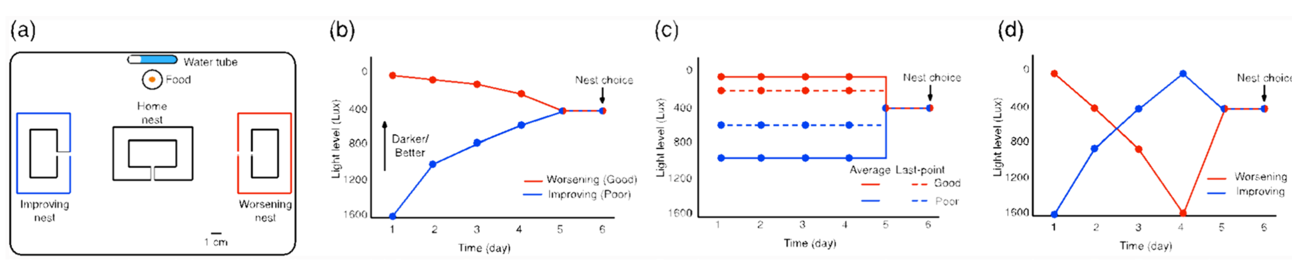

Fig. 1 (a) Experimental arena. The home nest containing a colony was placed in the middle of the arena box. Two target nests, the improving nest and the worsening nest, were placed at opposite sides of the arena. The sides of the target nests were counterbalanced across colonies. The food and the water tube were in the arena. (b) Experimental design for the trend condition. The interior light level of the improving nest became darker, and more preferable, over days (blue line), while that of the worsening nest became brighter and less preferable (red line). On the 5th day, the light levels of these nests became the same. On the following day, nest choice was induced by removing the roof of the home nest. (c) Experimental design for two control conditions. In both conditions, the light level of the target nest was constant over time until day 5. In the average condition, the light level of the target nest was the average of the light levels for each nest type (solid lines). In the last-point condition, the light level was the last level for each nest type (dashed lines). (d) Experimental design for the follow-up trend condition. While one nest became darker, and better, over time, the other became brighter, and worse, over time. The means of the interior light levels of these nests were same (approx. 700 lx)

record a preference. This occurred only once out of a total of 30 tests.

Until the roof of the home nest was removed on day 5, the interior light level of the home nest was always darker than that of the target nests, so the colony stayed at the home nest although some scouts might visit and assess these potential nests throughout the experiment. To confirm these visits and measure the number of scouts, we recorded the number of ants in the target nests at around 9 A.M. each day before the secondary roof was replaced for each of the 10 colonies. The food (an agar-based diet (Bhatkar and Whitcomb 1970) and Spam meat) and water tube were placed next to the home nest (Fig. 1a) throughout the experiment. The arenas had three photography LED lights above them and received 1540–1690 lx light intensity. Note that the interior light levels reported above are estimations based on the light transmittance (i.e. f-stop) of the light filters.

In addition to the "trend" condition described above, we also conducted two additional conditions as control conditions. In both the control conditions, the procedure was identical to the one used for the trend condition except that the interior light levels of the target nests were constant over time until day 4. In the "average" control condition and the "last-point" control condition, the interior light levels of the target nests were the average of the light levels for each nest type (1024 lx for the improving nest and 88 lx for the worsening nest) and the last level for each nest type (565 lx for the improving nest and 200 lx for the worsening nest), respectively (Fig. 1c). On day 5, the light level for the target nests became identical (400 lx), and the roof of the home nest was removed to induce emigration. Out of the 30 tests conducted for each of the two control conditions, six tests in the average condition and two tests in the last-point condition did not achieve the consensus criterion.

We used 30 colonies (see Supplementary Material for the detail of the subjects), all of which were tested for each condition, and the order of the conditions was randomized for each colony. The interval between the tests was at least two weeks. Before each test, all glass slides were washed using a commercial dishwasher, and the experimental arena was cleaned with ethanol. Cardboard plates were made fresh for each test and never reused.

Colonies in the trend condition chose the improving nest over the worsening nest more frequently than the ones in the average condition did, suggesting that the nest-quality change influenced the nest preference (i.e. the nest with improving quality became more preferable than the one with worsening quality). However, because there was not a significant preference for the poor nest site (improving nest) in the trend condition (see Results for details), one possible alternative hypothesis was that the nest-quality change impaired the ability to assess nest quality (Burns et al. 2016), leading to no nest-site preference. To test this hypothesis, we collected additional 29 colonies (see Supplementary Material for the detail of the subjects) and ran another experiment similar to the trend condition. In this "follow-up trend" condition, we also changed the qualities of two nests—one improved and the other worsened over time—but, unlike the trend condition, the quality of the improving nest was better than that of the worsening nest in later days (days 3 and 4; Fig. 1d). Note that the means of these over-time qualities were the same (approx. 700 lx). All colonies were tested only once, and four colonies did not achieve the consensus criterion. In the follow-up trend condition, we did not record the number of ants in the target nests each day as we did for the trend and control conditions.

Analysis

Preferences in the binary choice were assayed with a χ^2 goodness of fit test. The effect of the nest-quality change was tested with a χ^2 test of independence. We removed the choices that did not achieve the criterion for consensus. We ran a generalized linear mixed-effects model (GLMER) using colony size (the numbers of workers and brood) and order of the test as fixed effects and colony ID as a random effect. The statistical software R (v. 4.1.2) was used for all analyses. The data and code can be accessed online (Tyler et al. 2023).

Results

In both the control conditions, the good nest was preferred more than the poor nest, though it was statistically significant only for the average condition ($\chi^2 = 6.0$, df = 1, $p = 0.014$; Fig. 2) but not for the last-point condition ($\chi^2 = 2.29$, df = 1, $p = 0.13$; Fig. 2). In the trend condition, on the other hand, colonies chose the poor improving nest more frequently, though not significantly ($\chi^2 = 0.33$, df = 1, $p = 0.56$; Fig. 2), than the good worsening nest. This preference in the trend condition was significantly different from that of the average condition ($\chi^2 = 4.90$, df = 1, $p = 0.02$) but not from that of the last-point condition ($\chi^2 = 2.18$, df = 1, $p = 0.14$; Fig. 2). The preferences in the average and last-point conditions were not significantly different ($\chi^2 = 0.70$, df = 1, $p = 0.40$; Fig. 2). In the follow-up trend condition, the improving nest was chosen significantly more often than the worsening nest ($\chi^2 = 4.84$, df = 1, $p = 0.02$; Fig. 2). The generalized linear model showed that the numbers of workers ($p = 0.10$) and brood ($p = 0.10$) and order of the test ($p = 0.13$) do not have significant effects on the nest-site choice.

The daily observation data showed that one scout was found in the target nests on average (Fig. 3 and Figure S2), suggesting that scouts actively assessed the nests until the nest choice. These data further showed that ants in the control conditions

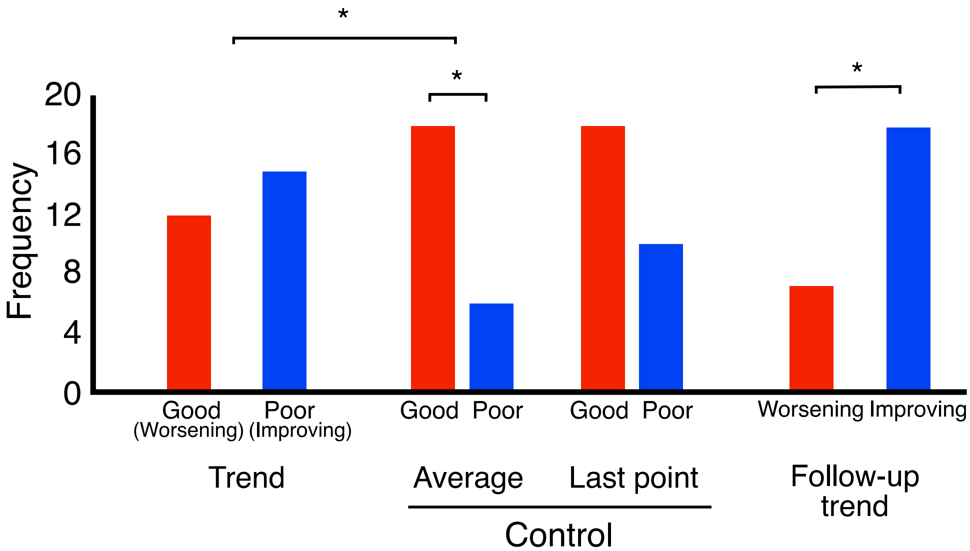

Fig. 2 Nest-site preference in the trend condition ("Trend"), the control conditions ("Average" and "Last point") and the follow-up trend condition. To make the nest names consistent across the conditions, we used the same names for the target nests, good and poor nests, in all the conditions, except for the follow-up trend condition. In the trend condition, the worsening nest and improving nest were the good nest and the poor nest, respectively, because the former always had better quality than the latter. In both control conditions, the good nest was preferred more to the poor nest, although it was statistically significant only for the average condition. The pattern of the trend condition was significantly different from that of the average condition. In the follow-up trend condition, the improving nest was significantly more preferred than the worsening nest. The asterisk indicates $P<0.05$

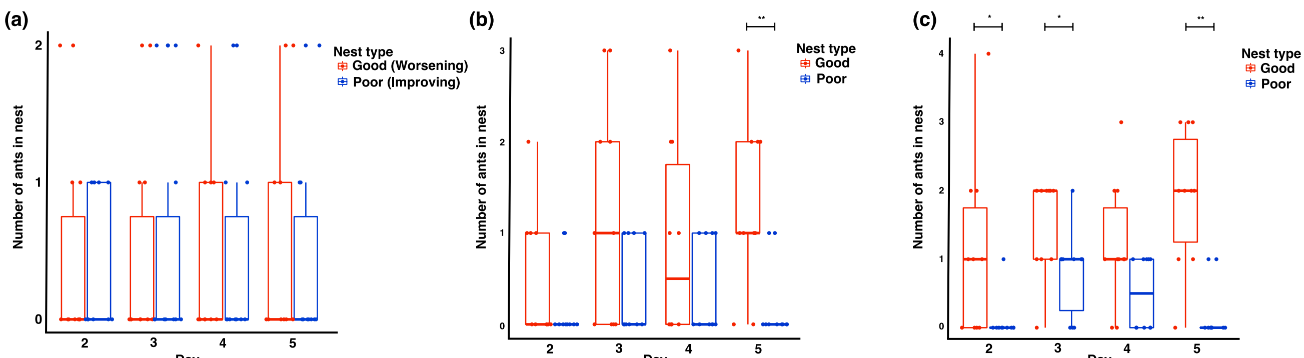

Fig. 3 Number of ants in each target nest over four days (day 2nd to 5th). (a) Trend condition, (b) last-point condition and (c) average condition. While there was not a significant difference for the number of ants between the good (worsening) nest and the poor (improving) nest in the trend condition, there were significant differences on certain days in the control conditions (Day 5 in the last point condition and Days 1, 2 and 5 in the average condition). All data points overlay boxplots. Each box extends between the lower and upper quartiles, a horizontal line within the box indicates the median, and whiskers show the range of the data, except for outliers. * and ** indicate $p<0.05$ and $p<0.01$ based on the Wilcoxon test, respectively

visited the better nest significantly more often than the worse nest (Fig. 3). In the trend condition, however, ants did not visit the improving nest more often than the worsening nest (Fig. 3).

Discussion

Our study shows that a continuous change of option quality influences evaluation in ants. That is, when the nest-site quality was static with a large difference between the good and poor nests (the average condition), colonies preferred the nest site which had been better (i.e. darker) between the two possible nests, as a previous study showed (Stroeymeyt et al. 2010). However, when the nest quality changed over time—one improved and the other worsened—colonies were significantly more likely to choose the low-quality, but improving, nest than the high-quality, but worsening, nest compared to the colonies in the static average condition. Note that although the nest-site quality changed once before the nest choice (i.e. the good nest became worse, while the poor nest became better), colonies still preferred the good nest. These data confirmed that the gradual change was important for the nest-site evaluation.

One may wonder if changing the nest quality "confused" ants in the trend condition so that they were not able to accurately assess the nest quality. Indeed, colonies in the trend condition did not have a significant preference for either nest site (Fig. 2). To test this, we ran one additional experiment, where one nest improved and the other worsened over time, like the trend condition, but the quality of the worsening nest was not always better than that of the improving nest. Our results showed that, although the means of these nest qualities were the same, more colonies chose the improving nest over the worsening nest, rejecting the hypothesis that the nest-quality change reduces the ability for evaluating nest quality. This is consistent with past research: when *Temnothorax* colonies are presented with two nest sites that fluctuate in quality over time, they are still capable of choosing the nest with higher average quality (Franks et al. 2015).

While our results suggest that nest choice was influenced by the trend of nest quality, they can be also explained by "short-term" memory—the colonies could choose the nest solely based on its quality on the 4th day. That is, the choice was random in the trend and last-point conditions because the nest-quality difference on the 4th day was small. Furthermore, in the average and follow-up conditions, where the difference was large on the 4th day, the colonies chose the darker nest on that day. In this "short-term" memory scenario, what our data showed was not that the colonies considered the nest quality change but instead that they simply relied on the nest quality on the final day before the quality of the target nests became identical. This is a plausible hypothesis, which our data cannot reject. Additional experiments, such as the trend condition with larger changes, are needed to directly test this hypothesis.

If ants keep track of nest-site quality, how do they do it? One parsimonious mechanism, which does not require use of memory in individual ants, is that ants use chemical marks, such as chemical footprints (Wüst and Menzel 2017), which they secrete from adhesive structures on their tarsi as they walk (Geiselhardt et al. 2010). These chemical footprints can be used as a cue during nest assessment—a nest with more footprints is evaluated more favorably. Ants in the control conditions indeed visited the better nest significantly more often than the worse nest (Supplementary Information). However, in the trend condition, our data showed neither that (1) ants visited the improving nest more often than the worsening nest, nor that (2) ants increased or decreased the frequency of the visit towards the improving nest or the worsening nest, respectively, over time (Supplementary Information). Therefore, our data still do not fully support that ants use chemical cues during nest evaluation, especially in the trend condition. However, because the data for these visits are limited (one observation per day), future research should test this hypothesis rigorously by recording more observations each day.

Another possible mechanism for keeping track of the nest-site quality is that scouts remember the quality of each nest site. *Temnothorax* ants are known to remember the quality of available nest sites prior to emigration (Stroeymeyt et al. 2010, 2011b) and through repeated emigrations at least for six days (Sasaki and Pratt 2013). Furthermore, an associative learning experiment has recently shown that *Temnothorax* ants remember environmental cues for at least three days (Santos et al. 2022). These studies suggest that scouts have the cognitive ability to detect the change in the nest-site quality over time.

What could be the benefit of keeping track of nest-site quality? Because *T. curvispinosus* colonies live in acorns and hollow twigs, which are very fragile, quality of their nest sites is not constant. It may be critical for scouts to detect a change in nest quality because this change indicates that the potential nest site starts collapsing, decaying, or being exposed to the sun more due to seasonal changes. In the wild, while it is common for nest site quality to deteriorate, its improvement is probably rare. Therefore, scouts may be more sensitive to the worsening nest site (i.e., avoiding it) than the improving nest (i.e. being attracted to it). This bias—a loss is perceived as psychologically more severe than a gain—has been found in humans (Kahneman and Tversky 2018) and other animals (Kacelnik and Bateson 1996; Wendt et al. 2019b), known as loss aversion. Furthermore, because natural decay typically occurs slowly over the course of days, the timescales of nest-site quality change may be important. If we used a shorter timescale (e.g. all the changes occur in a day instead of over five days), we might not see the contrast effect. This could be because, for example, scouts would not make enough nest visits in this time to able to detect changes of nest-site quality. By investigating cognitive biases like this in non-human animals, we understand deeper not only how they process information but also how these cognitive biases affect their fitness (Sasaki and Pratt 2013, 2018).

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00040-024-00969-0.

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Data availability The data and R code are available online (doi:https://datadryad.org/stash/share/gokTGmFJjlBptNW-CC8SKtINOhbFDoBdgRqFLKYsSeE).

Declarations

Competing interests The authors declare no competing interests.

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