

Précis of *Psychology Of A Superorganism*

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Introduction

One of main goals in cognitive psychology is to understand the mechanisms by which organisms acquire, process, and store information from the environment [1]. Researchers have demonstrated the cognitive abilities of not only humans but also other species, from insects to primates [1-4]. In this dissertation, I investigated collective cognition, in which a colony of individual ants together process information and act as a single cognitive unit [5-7].

In this research, I applied concepts and methods developed in psychology to animal groups. Psychologists have focused on individual cognition and described it in detail. Because a cohesive animal group acts as a single cognitive unit, I can apply the very same psychology approaches to animal groups to investigate different aspects of collective cognition. This interdisciplinary method allowed me to analyze cognition at both the ultimate level (e.g. are certain collective cognitive abilities superior to those of individuals?) and the proximate level (e.g. how do individuals collectively achieve these abilities?).

I have used social insects to investigate collective cognition. Because of the high genetic relatedness among colony members, individuals gain fitness benefits from the their colony's success, rather than their own [8]. This has allowed selection to shape extremely unified collective behavior, and thus colonies of social insects can be considered as a superorganism, analogous to a single organism [8-10]. Superorganisms offer some of the most compelling and well-studied examples of collective cognition [11-18].

The research presented here focuses on collective cognition in the ant *Temnothorax rugatulus* (Formicidae: Mymicinae) (Figure 1). Colonies typically live in fragile rock crevices, and are adept at collectively choosing a new home if their old nest becomes inadequate [15,19,20]. House-hunting in this genus has grown into a leading model system for group cognition, driven by its many practical advantages. First, their colony size is relatively small, ranging from 50 to 250 ants, so it is relatively easy to identify each ant by marking



Figure 1. *Temnothorax rugatulus* colony showing small colony size and individual marking.

them with unique colors. Second, not only are colonies adept at consistently choosing a favored nest among a group of inferior ones [15], but individuals are adept as well (Chapter 2). Thus, I was able to assess and compare the cognitive abilities of colonies and individuals. Third, because they achieve such good decisions mainly by a series of observable recruitment behaviors (see below for details), I was able to record how information is transmitted among individuals and link these mechanisms to collective cognitive abilities.

These features have let the house-hunting behavior of *Temnothorax* colonies be well documented [17,21-27]. Laboratory observation, where individual ants can be easily tracked, has revealed how a colony can select the better of two nest sites, even when few if any individual ants have the opportunity to assess more than one option. Instead, comparison emerges from a competition between recruitment efforts at different sites. The key elements of this competition are two behavioral rules followed by the scout ants responsible for carrying out the emigration (Figure 2a,b). First, if a scout finds a potential new nest, her probability of recruiting nestmates to it depends on the site's quality, as determined by its entrance size, floor area, cavity thickness, light level, and many other features [19]. The ants she summons follow the same rule, creating positive feedback that drives up site population at a quality-dependent rate. Second, the scouts accelerate their recruitment once the site population surpasses a threshold. Because better sites are likely to reach the threshold earlier, this quorum rule amplifies the difference in population growth, and the colony is quickly directed towards the best nest (Figure 2c,d) [17,26].

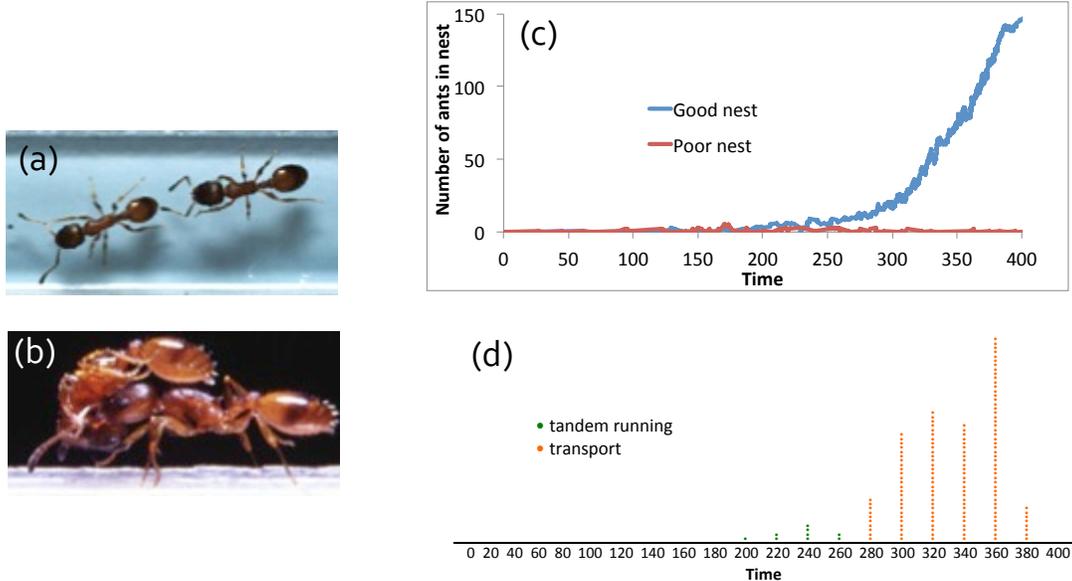


Figure 2. (a) Tandem running: a leader attracts a single nest-mate to follow her to the new nest. (b) Transport: recruiter physically carries nest-mates, one at a time. Transport is much faster and more stable than the tandem running. Recruitment behavior switches from tandem-running to transport when the population reaches a certain number, or quorum (c and d). This quorum rule amplifies the difference in population growth, and the colony is quickly directed towards the best nest. The recruitment acts in (d) are all towards the good nest.

Overview of Dissertation Studies

Individual ants make direct comparison

To carry out this program, I first had to confirm that isolated ants can independently compare options and make decisions. The collective decision-making mechanism described above does not require any single ant to compare multiple sites. However, this does not mean that individuals are incapable of doing so. In fact, during the course of an emigration, some ants do see more than one site and are disproportionately likely to recruit to the better one [19]. Another study, however, showed that ants do not use memory for choosing a site, and thus make no comparisons [28]. Regardless of the validity behind these studies, these migration data are inconclusive because the ants' behaviors might be influenced by their nestmates. In the first study of my dissertation, I tested this hypothesis by isolating each ant from their fellow workers. A single ant was placed in a small arena with two nests and given a small pile of brood. In short order, she moved the brood into one of the sites, thereby indicating her choice. I first gave two nests, one good and one poor, as a binary choice and measured how likely individual ants chose the good nest over the poor one. Then I estimated the proportion expected to choose the good nest in a "memoryless" Markov model based on the assumption that they do not make direct comparisons. The expected proportion choosing the good nest is significantly worse than the empirical result ($\chi^2 = 6.89$, $df = 1$, $N = 24$, $p < 0.01$) (Table 1). These results strongly suggest that, even in the absence of any social information, individual ants can effectively compare two sites of different quality and choose the better one.

	Choice	
	Good	Poor
Expected	15.05	8.95
Data	21	3

Table 1 Expected and actual frequencies of choices for good and bad nests. Solo ants were significantly more like to choose the good than expected.

Emergence of group rationality from irrational individuals (published in *Behavioral Ecology*)

In my first application of this finding, I tested for rationality in *Temnothorax* ants. Evolutionary theory predicts that animal decision makers should be rational, meaning that they consistently choose fitness-maximizing options. Despite this prediction, violations of rationality principles have been observed repeatedly in humans and other animals [29-33]. For example, a preference for option A over

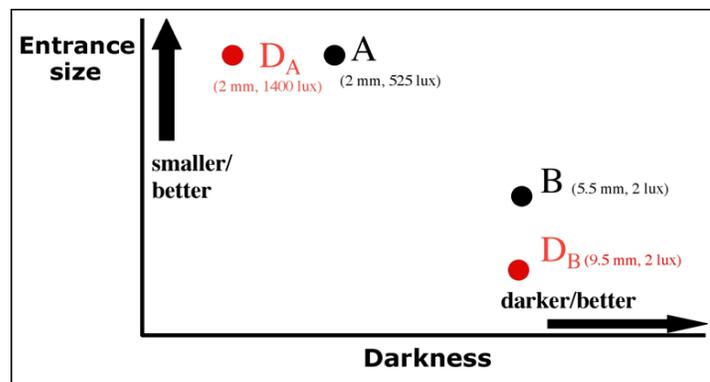


Figure 3. Attributes of nests used in preference tests. The choice between target nests A and B imposes a tradeoff in two attributes: A is better than B in regard to entrance size but B is better than A in regard to darkness. Decoy nests D_A and D_B are asymmetrically dominated by the targets: D_A is clearly worse than A but not B, while D_B is clearly worse than B but not A.

option B is altered with addition of a third option that is clearly inferior to one target option, but not another. Immunity to such decoys is a hallmark of rationality known as independence from irrelevant alternatives [34]. The significance of these violations remains controversial, but many explanations point to cognitive limitations that prevent animals from adequately processing the information needed for fully rational choice. Instead they rely on heuristics that usually work well but yield systematic errors in specific contexts. While past research on rationality has focused on individuals, many highly integrated groups regularly make consensus choices. These collective choices emerge from local interactions among many group members, none of whom take on the whole burden of decision-making. Thus, I hypothesized that *Temnothorax* colonies may evade the irrational consequences of individual limitations by distributing their decision-making across many minds.

To test for the decoy effect, I designed two target nests A and B that posed a tradeoff between entrance size and interior illumination (Figure 3). These attributes are important to *Temnothorax*, with colonies showing a strong preference for smaller entrances and darker interiors [17,23,35]. I also designed two asymmetrically dominated decoy nests, D_A and D_B (Figure 3). I first performed binary preference tests between targets A and B and confirm that the tradeoff between entrance size and cavity illumination posed a significant decision-making challenge for individuals and colonies (individuals: A:B = 9:9; colonies: A:B = 11:12). I then tested whether the presence of a decoy site changes preference between A and B. For individuals, the preference between A and B was significantly altered by the decoy: Target A was preferred to B in the presence of D_A , but B was preferred to A in the presence of D_B ($\chi^2=7.97$, $N = 26$, $p < .05$)(Figure 4a). Thus, the addition of a decoy option to the choice set caused individuals to increase their preference for the dominant target, in violation of regularity. In contrast, the decoys did not affect colony preferences between A and B ($\chi^2=8.59$, $N = 47$, $p = 0.353$)(Figure 4b).

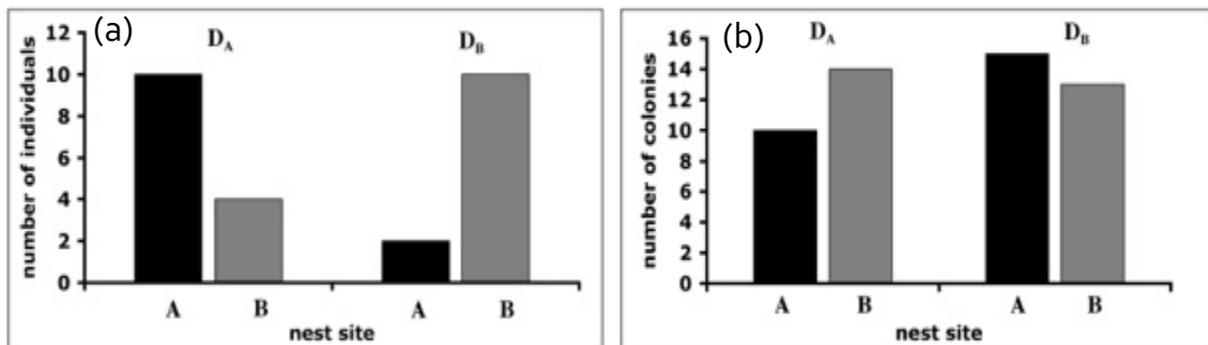


Figure 4. (a) Nest site preference by individual ants depended on which decoy nest was present. In the presence of D_A , more ants chose A, while in the presence of D_B more ants chose B. (b) Nest site preference by colonies was not affected by decoy type.

A plausible scenario of my findings is that lone ants cannot adequately process information for all three nests when inconsistencies among their attributes complicate assessment. Instead, ants may rely on simplifying heuristics based on pairwise comparisons, which are also implicated in the decoy effects seen in humans and other

animals [1,36]. In a collective setting, such comparisons are unnecessary, because each ant need assess only one site. This limited perspective imposes the best strategy for consistent choice: evaluate a given option the same way, regardless of the available alternatives. The separate evaluations of many ants are then integrated through a communication network and complex behavioral algorithm [1-4,25,26]. The result is emergence of a rational group decision from ants prone to individual irrationality.

Groups have a larger cognitive capacity than individuals (published in *Current Biology*)

In the next study, I directly tested if colonies can handle more information than individuals. Increasing the number of options can paradoxically lead to worse decisions, a phenomenon known as cognitive overload [5-7,37]. This happens when an individual decision-maker attempts to digest information exceeding its processing capacity. Highly integrated groups, such as social insect colonies, make consensus decisions that combine the efforts of many members, suggesting that these groups can overcome individual limitations [5,6,8,38]. Therefore, I hypothesized that *Temnothorax* colonies are less vulnerable to cognitive overload than individual ants.

I induced either whole colonies or isolated ants to select a new nest in one of two conditions. In the simpler condition they chose between only two nests, one good and one poor. In the more challenging condition, they chose among eight options, four good and four poor (Figure 5A). Good nests differed only in having a smaller entrance, a strongly favored feature [8-10,15]. I found that individuals performed significantly worse when the number of options was eight rather than two, indicating that they experienced cognitive overload ($\chi^2 = 4.18$, $N = 43$, $df = 1$, $p < .05$) (Figure 5B top). In the two-nest condition, over 80% of ants chose a good nest, but in the eight-nest condition, only 50% did, indistinguishable from random performance. Colonies, on the other hand, performed equally well with either two or eight options, with at least 90% choosing a good nest in each condition ($\chi^2 = 0.36$, $N = 40$, $df = 1$, $p = 0.55$) (Figure 5B

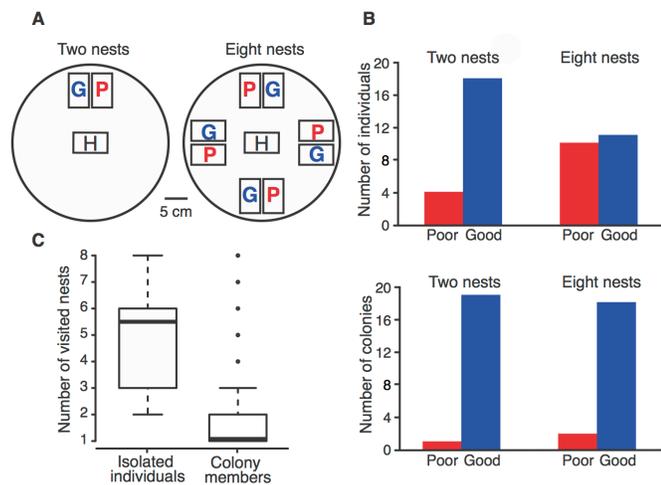


Figure 5. (A) Experimental arenas. Subjects (whole colonies or isolated ants) were made to abandon their home nest (H) and choose a new one from an array of either two or eight good (G) and poor (P) nests. (B) Numbers of subjects choosing good or poor nests in each treatment. Isolated ants made worse decisions with eight options than with two (top chart), but colonies nearly always chose a good nest regardless of the number of options (bottom chart). (C) In the eight-nest condition, isolated ants visited more nests than did individual colony members. Boxes delimit the 1st and 3rd quartiles, the horizontal line indicates the median, and whiskers show the range. Open circles are outliers.

bottom). Thus colonies achieved a significantly higher decision performance in the face of increased processing load than did individuals (partial χ^2 test: $\chi^2 = 8.75$, $N = 3$, $df = 3$, $p = 0.03$).

I hypothesized that colonies better handle higher option numbers because their members do not have to assess as many sites as isolated individuals. If so, I predicted that each colony member visits a smaller number of nests than an isolated ant. To test this, I repeated the eight-nest treatment, but counted the number of sites visited by each ant. The results of this second experiment confirmed my prediction: isolated ants assessed significantly more sites than did colony members (Wilcoxon rank test: $W = 1819$, $N_{\text{isolated}} = 10$, $N_{\text{colony}} = 209$, $p < 0.01$) (Figure 5C). Importantly, although each colony member visited very few sites, the colony collectively assessed all eight sites. These results confirm that the colony avoids cognitive overload by sharing the burden of assessment among members.

A crowd is wise for hard tasks but not for easy ones (published in *Proceedings of the National Academy of Sciences*)

In the fourth study, I tested collective intelligence by comparing decision-making performance of *Temnothorax* colonies and individuals. “Collective intelligence” refers to situations where groups achieve more accurate perception and better decisions than solitary agents [11-18,39-43]. Although collective intelligence has been supported empirically and theoretically, many examples of collective failure have been documented [15,19,20,42,44,45].

The problem is that groups often violate the assumption of independent decision-making that is central to collective intelligence [15,40,46]. Theories assume that individual assessments are made in isolation, and then integrated by a centralized process such as vote counting or averaging. Real groups instead rely on decentralized mechanisms in which interactions and positive feedback bring the group to consensus [17,21-27,47-49]. These interactions may either improve intelligence by integrating multiple assessments, or hurt it by amplifying mistakes [19,50]. Understanding which outcome will happen requires a comparison between individual and group performance across a range of

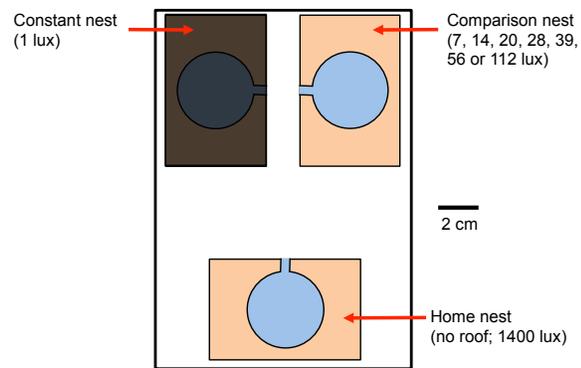


Figure 6. Experimental arena for sensory discrimination tests. In each trial, subjects started in the home nest and were induced to choose between the constant and comparison sites. The constant nest was the same in all tests, with a very dim and highly favored interior light level. The comparison nest was always brighter than the constant nest, but its exact brightness varied across tests in order to provide an array of challenges of varying difficulty. Nests consisted of a cavity cut into a wood partition, with a glass ceiling and floor. Cavity light level was modified by adding transparent neutral density filters to the ceiling. Numbers in parentheses indicate interior light levels.

challenges.

To address this issue, I adapted methods typically used to study sensory discrimination in individual humans or animals [17,26,51-55]. *Temnothorax* subjects (either an individual or a colony) were given a series of choices between a constant nest, with a very dim interior light level, and a comparison nest (Figure 6). The comparison nest was always brighter than the constant nest, but its exact brightness was varied across tests in order to provide an array of challenges of varying difficulty. All subjects were expected to prefer the constant nest in every test, because these ants have a strong and unambiguous bias toward darker sites [17,19,23]. Thus, any choice of the comparison nest could be taken as a failure to discriminate the options. Discrimination ability was measured in terms of the functional relationship between the brightness of the comparison nest and the probability of choosing the constant nest.

As expected, both individuals and colonies made more accurate decisions as the choice became easier (Figure 7). However, the shapes of the discrimination curves were quite different. I fitted separate sigmoidal response functions to the colony and individual data:

$$P(\text{correct choice}) = 0.5 + 0.5 \frac{\lambda}{1 + e^{-\frac{(x-\alpha)}{\beta}}} \quad (1)$$

where x is the difference in brightness between the constant and comparison nests, α is the discrimination threshold (i.e., the smallest detectable difference in illumination), β is a scale parameter, and λ is the asymptotic level of discrimination [28,56]. When the differences were small (i.e. difficult choices), colonies more precisely discriminated options than individuals did. Specifically, the median discrimination threshold α was 7.4 lux for colonies and 32.3 lux for individuals (Monte Carlo test for $\alpha_{\text{individual}} > \alpha_{\text{colony}}$, $p = 0.0047$). When the choice was easy colonies no longer outperformed individuals, as shown by the higher asymptotic performance of individuals ($\lambda_{\text{individual}} = 0.93$) compared to colonies ($\lambda_{\text{colony}} = 0.80$) (Monte Carlo test for $\lambda_{\text{colony}} < \lambda_{\text{individual}}$, $p = 0.050$).

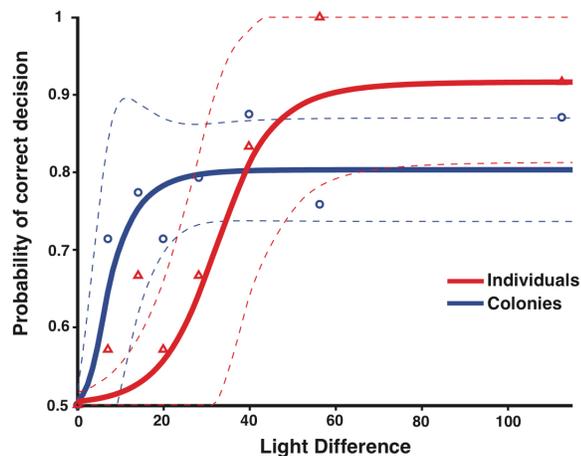


Figure 7. The proportion of correct choices made as a function of site illumination difference. Colonies (red triangles) outperform individuals (blue circles) when the illumination difference is small, but individuals perform better for larger illumination differences. Thick lines represent fitting to the psychophysics function specified in equation 1, with parameters sampled from the Bayesian posterior distribution calculated from the data. Dashed lines give 95% confidence intervals.

To explain these patterns I further investigated the mechanisms by building a mathematical model. The output of the model matched my observation that both individuals and colonies become more accurate as the choice becomes easier (Figure 8). Interestingly, the model showed the distinctive crossing of discrimination curves seen in the data, with colonies doing better at difficult choices and individuals doing better for easier ones (compare Figure 7 and Figure 8). That is, positive feedback between group members effectively integrates information and sharpens the discrimination of fine differences. When the task is easier, however, the same positive feedback can lock the colony into a suboptimal choice. These results suggest the conditions under which crowds do or do not become wise.

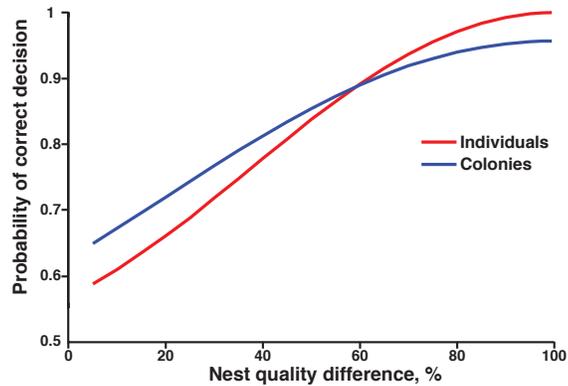


Figure 8. Proportion of simulated individuals and colonies (population 100) selecting the better of two nests. Colonies perform better when the quality difference between the nests is small, but individuals choose more accurately when the difference is greater. In the corresponding experiments, a nest's quality is set by its brightness, with darker nests being more attractive.

Chapter 4: Ants adjust attribute weights according to prior experience (published in *Biology Letters*)

In the last study, I investigated if *Temnothorax* colonies collectively learn to rely on more informative attributes. Choosing the best among a set of options is challenging when options vary in multiple attributes. Decision makers have a variety of ways to handle these situations, but many strategies involve ranking attributes [29-33,57]. 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 many taxa, from insects to humans [23,34,58]. It is often assumed that weights do not change across different contexts [17,23,35,58]. However, because the validity of attributes can vary across time and place, animals might increase their fitness if they adjust weights accordingly [57,58]. 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 weigh shape more than nectar in judging each option?

I tested this hypothesis by studying nest site selection in *Temnothorax* colonies. In the experiment, I first measured how colonies weighed two important nest attributes (entrance size and interior brightness), then exposed them to treatments in which one or the other attribute was more informative, and finally re-measured to determine whether they had modified their attribute weightings accordingly (Figure 9). In the treatment phase, colonies made a series of four choices. Prior to the first choice, each colony was induced to move into a standard home nest. In each choice, they chose between one site identical to the standard home nest 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 level; for the other half, the inferior attribute was entrance size. Each emigration usually ended with the colony moving to the standard home nest, because this was superior to the alternative in all choices.

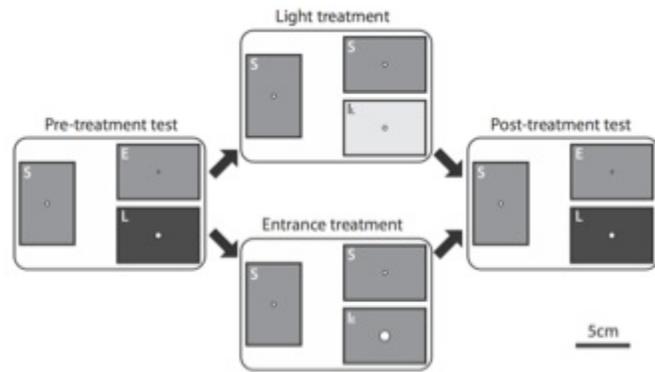


Figure 9. Experimental assessment of the effect of experience on attribute weights. An initial binary choice between sites E and L showed how colonies weighted entrance size and interior light level. Colonies then made a series of four choices in which only one attribute provided distinguishing information. 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.

In both treatments, colonies shifted their preference toward the site favored by the more informative attribute (Figure 10). Of the 26 colonies assigned to the entrance treatment, only 10 chose nest E before the treatment, but this rose to 17 after treatment. Conversely, for the 28 colonies in the light treatment, the number preferring L increased from 16 to 19. A generalized linear model showed a significant effect of treatment on post-treatment preference (odds ratio = 3.98, $p = 0.018$), but no effect of pre-treatment choice (odds ratio = 0.62, $p = 0.41$). This means that the odds of choosing nest E after the entrance treatment (or nest L after the light

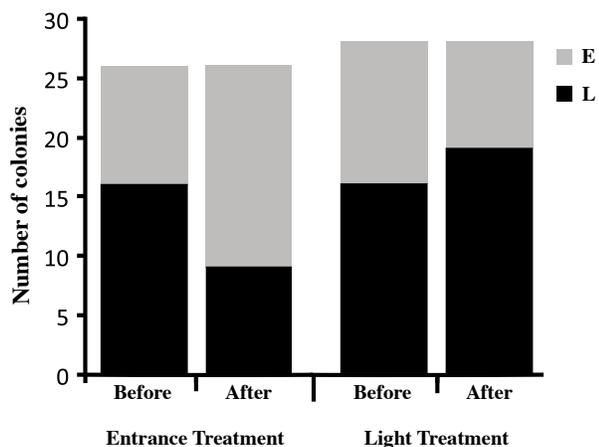


Figure 10. Nest site preferences of colonies before and after treatments in which either entrance or light level were informative for decision-making. In each treatment, colonies shifted their preference toward the option favored by the informative attribute. E (light shaded) and L (dark shaded) stand for the small entrance nest and the darker nest, respectively.

treatment) were approximately four times greater than the odds of choosing E after the light treatment (or L after the entrance treatment).

Experience has long been known to influence decision-making by solitary animals [1,59]. My work extends this finding to groups, reinforcing recent results in *Temnothorax* ants [60-62]. 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 nestmates there [19,63]. Thus, the effects I 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 [64], 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 [61]. 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 behavioral mechanisms responsible, must await future studies.

Conclusion

These results demonstrate novel advantages of group living. It has been shown that individuals can gain benefits in many ways by forming a group [65]. My research shows a very different kind of benefit to group living: improved cognition. Although all my studies were conducted in the laboratory, the superior cognitive abilities of groups should also be beneficial in nature, where nest site selection is likely a frequent and important task for colony survival and reproduction [20,66,67]. Future work is required to investigate exactly when and how the collective advantages are used in their natural habitat.

My studies investigated several cognitive tasks in which collective cognition succeeds or fails. Although collective cognition should theoretically be superior [68,69], many examples of collective failure have been documented [45]. There are at least two problems with the underlying theoretical assumptions. The first problem is that they typically ignore or simplify individual cognitive abilities and conclude that groups always have superior cognition [70]. However, it has been shown that these abilities are often more complex than assumed [71-73]. The second problem is that theories assume that individual assessments are made in isolation, and then integrated by a centralized process such as vote counting or averaging. Real groups instead rely on decentralized mechanisms in which interactions and positive feedback bring the group to consensus [74]. The violation of these assumptions suggests that groups may not make better decisions than individuals under certain circumstances. In this dissertation research, I

overcame the challenges described above using the house-hunting *Temnothorax* ant, which provides a detailed understanding of individual cognitive abilities and of information transfer among group members.

Recent studies have noted the similarities between information processing of a social insect colony and that of the brain [5,7,75,76]. It has further been suggested that both systems achieve statistically optimal decision-making [13]. Emergent processes of individual cognition have been a major topic in many fields, including psychology and biology, but they remain largely unknown. This is partially because neurons are connected in a very complex way and it is hard to untangle or manipulate them. The workers of a social insect colony are, on the other hand, much less tightly integrated. This difference makes it straightforward to isolate individual insects (Chapter 2) and to manipulate colony organization by adding and removing certain individuals [77]. By taking advantage of these parallels between a colony and a brain, future studies can use social insect colonies for deeper understanding of emergent processes of cognition.

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