

Emergence of group rationality from irrational individuals

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Evolutionary theory predicts that animal decision makers should be rational, meaning that they consistently choose fitness-maximizing options. Despite this, violations of rationality have been found repeatedly in humans and other animals. 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. Although past research on rationality has focused on individuals, many highly integrated groups, such as ant colonies, regularly make consensus choices among food sources, nest sites, or other options. These collective choices emerge from local interactions among many group members, none of whom take on the whole burden of decision making. We hypothesized that groups may evade the irrational consequences of individual limitations by distributing their decision making across many group members. We tested this in the well-studied case of collective nest-site selection by *Temnothorax* ants. We found that individual ants, but not colonies, strongly violated rationality when presented with a challenging nest-site choice. Specifically, isolated individuals irrationally switched their preference between 2 alternative nest sites based on their experience of an unattractive decoy. Given the same choice, intact colonies maintained consistent preferences regardless of the decoy's presence. Previous studies have stressed how distributed decision making can filter out random errors made by group members. Our results show that collectives can also suppress systematic errors that emerge from the decision heuristics of cognitively limited individuals. *Key words:* collective cognition, dynamic systems, decision-making, rationality. [*Behav Ecol*]

In its original economic setting, rational choice theory predicts behavior under the assumption that humans act to maximize utility, an implicit measure of net benefit (von Neumann and Morgenstern 1944). Applied to behavioral ecology, the theory makes an analogous assumption that natural selection has shaped animal decision making to maximize fitness (Stephens and Krebs 1986; Kacelnik 2006). This predicts the evolution of rational animals that rate options according to their fitness benefits and always choose the one with the highest value. The obvious test of this prediction—comparing the fitness outcomes of chosen and rejected options—is generally impractical. Instead, rationality is assessed by looking for adherence to certain consistency principles implied by maximization. For example, a preference for option A over option B should not be altered by addition of a third option, which is less preferred than either A or B. Immunity to such decoys is a hallmark of rationality known as independence from irrelevant alternatives (IIA) (Rieskamp et al. 2006).

Despite these predictions, violations of IIA and other rationality principles have been observed repeatedly in humans and other animals (Tversky 1969; Huber et al. 1982; Wedell 1991; Shafir et al. 2002; Bateson et al. 2003). Irrationality typically arises in challenging decisions involving options with multiple attributes such that no option is clearly superior in all attributes. In the decoy effect, for example, irrational shifts in preference are seen with addition of a decoy option that is clearly inferior to one target option but not to another (i.e., the decoy is asymmetrically dominated) (Huber et al. 1982). The decoy itself is rarely chosen, but its presence typically

increases preference for the dominating target. Such an increase violates the principle of regularity, which holds that an option's popularity should not be increased by the addition of new options to the choice set (Rieskamp et al. 2006).

Rationality violations seem to cast doubt on the optimizing power of natural selection, but an alternative explanation points to the influence of constraints unrecognized by classical rational choice theory. This classical theory assumes that decision makers have unlimited cognitive resources, but real animals operate under strong constraints both in the information they possess and the means to process it (Simon 1982). These constraints may select for simple heuristics or rules of thumb that economize on computation by either excluding information or processing it imperfectly (Gigerenzer and Todd 1999, 2000; Hutchinson and Gigerenzer 2005). In particular, it may be easier for an animal to compare the options in a choice set than it is to estimate the absolute fitness value of each one (Tversky and Simonson 1993; Shafir 1994; Bateson et al. 2003; Bateson and Healy 2005). In the decoy effect, only the dominant target is a clear winner in any pairwise comparison, thus enhancing its attractiveness to individuals using comparative heuristics. Selection may favor these heuristics if they work well in commonly encountered natural settings. However, these same rules may fail in certain predictable contexts, like the experimental paradigms that reliably yield irrational choice (Ariely 2008; Livnat and Pippenger 2008).

If comparative heuristics lie behind irrational choice, then a different pattern may arise in the collective decisions of highly integrated groups, such as insect societies. In these "superorganisms," selection at the group level has yielded sophisticated colony-level adaptations, including the ability to reach consensus on the best of several options. A colony's choice arises in a highly decentralized way without the need for direct comparisons between options by individual ants

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Received 26 July 2010; revised 5 October 2010; accepted 13 October 2010.

(Couzin et al. 2005; Pratt and Sumpter 2006; Seeley et al. 2006; Hölldobler and Wilson 2008; Gordon 2010). The process is well illustrated by nest-site selection in *Temnothorax* ants, which typically live in preformed natural cavities, such as rock crevices or hollow nuts (Franks et al. 2002; Pratt et al. 2005; Pratt and Sumpter 2006; Robinson et al. 2009). In the laboratory, colonies thrive in artificial cavity nests made of glass and wood or cardboard. When presented with 2 such nests of different design, a homeless colony can assess each on the basis of multiple attributes and emigrate to the better one (Pratt and Pierce 2001; Franks, Mallon, et al. 2003). This decision arises from a complex algorithm based on competition between recruitment efforts by scout ants, few of which assess more than one candidate (Mallon et al. 2001; Pratt et al. 2005; Pratt and Sumpter 2006; Robinson et al. 2009). In a study of 9 emigrations by *T. albipennis*, for example, only 27% of scouts visited both sites in time to influence the colony's decision (Robinson et al. 2009). The majority with knowledge of only one site nonetheless drive the decision process because they start to bring nest mates to their site with a probability that depends on its quality (Mallon et al. 2001; Pratt 2005). As a result, population growth at the better site outstrips its competitor, ultimately making it the colony's choice.

We hypothesized that this highly distributed mechanism may save colonies from the irrational consequences of comparative heuristics. This is because a colony's choice emerges from the behavior of many ants that have each assessed only a single site and thus have no opportunity to make comparisons. Consistent with this idea, an earlier study found that colonies of *T. curvispinosus* choosing among nest sites were immune to the decoy effect (Edwards and Pratt 2009). Likewise, house-hunting colonies of *T. albipennis* were found to show transitive preferences, fulfilling another expectation of rationality (Franks, Mallon, et al. 2003). These studies, however, looked only at the decisions of whole colonies and not those of individual ants. Thus, the colony's immunity did not necessarily reflect the suppression of individual errors. It may instead have been a simple result of the particular set of options presented. For example, the trade-off between targets may have been too weak, allowing a strong preference for one target to mask or eliminate smaller decoy effects.

In this study, we carried out a direct test of the hypothesis that collective decision making can eliminate the irrational errors to which individuals are vulnerable. To do this, we challenged both colonies and isolated individuals of *T. rugatulus* with the decoy effect taking care that the target options were closely balanced in attractiveness to maximize the decision challenge. We predicted that a lone ant required to select a site by herself would be vulnerable to the same irrational outcomes seen in solitary animals. A colony, in contrast, should be rationally consistent because it does not rely on comparisons by individuals.

MATERIALS AND METHODS

Nest designs

To test for the decoy effect, we designed 2 target nests A and B that posed a trade-off between entrance size and interior illumination. These attributes are important to *Temnothorax*, with colonies showing a strong preference for smaller entrances and darker interiors (Pratt and Pierce 2001; Franks, Mallon, et al. 2003; Pratt 2005). Nest A had a smaller entrance than nest B (2 vs. 5.5 mm) but a brighter interior (525 vs. 2 lux). We settled on these particular designs through a series of preference tests with different candidates until we found a pair of targets for which ants showed roughly equal preference. We also designed 2 asymmetrically dominated decoy nests. Decoy

D_A was dominated by A but not by B: It shared A's entrance size, but it had a brighter less preferred interior (1400 lux), and it was not dominated by B because of the latter's larger less preferred entrance size. Decoy D_B , in contrast, was dominated by B but not by A: It equaled B in illumination but trailed it in entrance size (9.5 mm), and it was not dominated by A because of the latter's brighter less preferred interior. Figure 1 summarizes the dominance relationships between targets and decoys.

Each nest was made from a balsa wood slat (2.4-mm thick) sandwiched between glass microscope slides (50 × 75 mm). A circular cavity (38-mm diameter) was cut through the middle of the slat, and a round entrance hole was drilled through the center of the roof. The roof was composed of 2 identical slides stacked on top of one another. Interior illumination was adjusted by placing transparent neutral density filters (Rosco Cinegel) between the roof slides. This design prevented ants from directly contacting the filters, which can sometimes build up an electrostatic charge that the ants find repellent. All filters had a 9.5-mm diameter hole to accommodate the nest entrance. Consistent hole size ensured that illumination was independent of entrance size.

Nests were illuminated by 2 fluorescent light fixtures suspended 37 cm above the bench on which all experiments were carried out. This provided even illumination of 1400 lux at the benchtop as measured by a Lutron LX-101A light meter. Each fixture had a single 8000 °K T-8 full-spectrum daylight bulb (Aqueon Products All-Glass Aquarium, Franklin, WI).

Subjects

Fifty-three colonies of *T. rugatulus* were used for the colony-level tests. An additional 6 colonies provided 53 worker ants for the individual tests. Only a minority of workers in *Temnothorax* colonies participate actively in nest-site scouting and transport of nest mates and brood items, whereas the rest of the colony waits at the home nest (Mallon et al. 2001; Pratt 2005). In order to ensure that we tested only these active ants, we placed brood items outside of the colony's nest and selected workers that attempted to retrieve them. We reasoned that ants willing to leave the nest and retrieve brood were likely to carry out similar tasks during colony emigration.

Colonies were collected in the Pinal Mountains near Globe, Arizona. All had at least one queen, with worker populations ranging from 120 to 250 and brood populations ranging from 8 to 90. Each colony was housed in a nest like those described above but with a small entrance (2.0-mm diameter) and no light filter. Each nest was kept in a plastic box (11 × 11 cm), the walls of which were coated with Fluon to prevent the ants

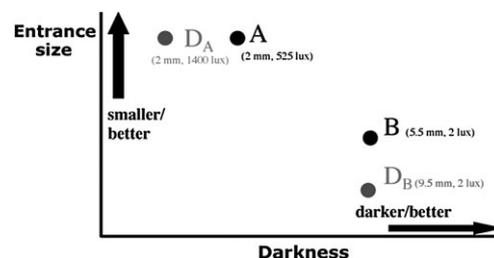


Figure 1

Attributes of nests used in preference tests. The choice between target nests A and B imposes a trade-off in 2 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, whereas D_B is clearly worse than B but not A.

from escaping. Each box was provided with a water-filled plastic tube capped with cotton and an agar-based diet that was refreshed weekly (Bhatkar and Whitcomb 1970).

Individual experiment

We first performed binary preference tests between targets A and B to confirm that the trade-off between entrance size and cavity illumination posed a significant decision-making challenge. If so, we predicted that each nest design would be chosen roughly half the time. The 2 nests were placed adjacent to one another against one wall of a small experimental arena with Fluon-coated walls (17.8×12.7 cm). We placed 3 brood items inside each nest and then introduced a single test subject into the arena. The subject was placed on the arena floor near the center of the wall opposite to the location of the nests. To determine her preference, we took advantage of the tendency of ants to gather scattered brood into a preferred location (Franks and Sendova-Franks 1992). The ant's choice was assayed after 12 h by recording the site to which she had carried all 6 brood items. In this and all other preference tests, the position of the target nests was randomized to control for directional bias.

We then used a similar procedure to determine whether the presence of a decoy site changes preference between A and B. The procedure was modified to ensure that each subject experienced the decoy nest before making her choice. We first placed the decoy nest alone in the arena against one wall. We then deposited 3 brood items just outside the entrance of the decoy and introduced a single test subject to the arena. The arena was checked periodically to see whether the ant had moved the brood inside. All ants did so within 12 h, confirming that they had experienced the decoy. After this, the procedure was identical to the binary choice experiment. Target sites A and B, each containing 3 brood items, were placed near the center of the arena wall opposite from the decoy. Preferences were assayed after 12 h by recording the site that contained all 9 brood items (the 6 in the target nests as well as the 3 from the decoy nest). We used this 2-stage method rather than simultaneous presentation of all 3 options because the latter approach leaves open the possibility that the ant makes a decision without first visiting the decoy, thus undermining the essential condition for testing the decoy effect.

Twenty ants were given the binary choice between A and B; 16 were tested with decoy D_A , and 17 with decoy D_B . Each ant was tested only once. No ant ever chose the decoy. Nine ants did not choose a nest (2 in the binary test, 2 in the presence of decoy D_A , and 5 in the presence of decoy D_B) and so were excluded from the analysis.

Colony experiment

To confirm that colonies showed similar preferences to those of individuals, we performed binary preference tests between targets A and B. The procedure was identical to that for individuals except that all members of the colony, rather than a single ant, were removed from their home nest and deposited in a test arena containing the target sites.

Then, to test the effect of decoys on whole colonies, we used a similar procedure to that for individual ants. First, a colony was introduced to the experimental arena in its home nest, and an empty decoy nest (either D_A or D_B) was placed nearby. The colony was then induced to migrate to the decoy by removing the roof of its home nest. All colonies successfully migrated within 12 h. Target nests A and B were then placed against the arena wall opposite from the decoy. In contrast to the individual experiment, the roof of the decoy was removed to induce

migration. We assayed nest-site preference by recording the site occupied by the colony 12 h later. Colonies usually showed an unambiguous preference, but they sometimes split between sites. If one site contained more than 90% of colony members, including all queens and brood items, we designated that as the colony's choice. If no site achieved this criterion, we did not record a preference. This occurred only 8 times out of 60 migrations. Thirty colonies were tested, each one receiving both the D_A and the D_B treatments in counter-balanced order.

Preparation

Before each experiment, all glass slides were washed with dish soap and rinsed with distilled water. Light filters were gently wiped with ethanol, and the experimental arena was cleaned with ethanol. Balsa slats were made fresh for each experiment and never reused.

Analysis

Preferences in the binary choice were assayed with a binomial test. The presence of a decoy effect was tested with a χ^2 test of independence. That is, we tested the null hypothesis that the preference between targets A and B was independent of the type of decoy present. The alternative hypothesis was that the 2 decoy types drive target preference in opposite directions with D_A making A more popular and D_B making B more popular. The statistical package R (v. 2.9.0) was used for all analyses, and Yate's continuity correction was applied in all χ^2 tests.

RESULTS

Individual ants show irrational preference shifts

In the binary choice between A and B, individual ants showed no strong preference for either site, with 9 choosing A and 9 choosing B (2-tailed binomial test: $P = 1.0$). This result confirmed that the trade-off between entrance size and dimness posed the desired decision-making challenge to individuals. In the presence of an asymmetrically dominated decoy, however, the preference between A and B was significantly altered. Target A was preferred to B in the presence of D_A , but B was preferred to A in the presence of D_B ($\chi^2 = 7.79$, degrees of freedom [df] = 1, $N = 26$, $P < 0.05$) (Figure 2). Thus, the addition of a decoy option to the choice set caused individuals to violate regularity by increasing their preference for the dominant target.

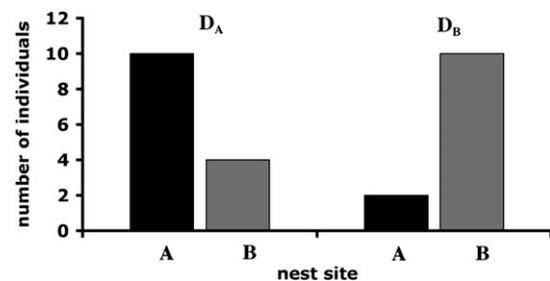


Figure 2

Nest-site preference by individual ants depended on which decoy nest was present. In the presence of D_A , more ants chose A, whereas in the presence of D_B , more ants chose B ($\chi^2 = 7.79$, $N = 26$, $P < 0.05$).

Colonies show rationally consistent preferences

Like individuals, colonies showed no strong preference in the binary choice, with 11 choosing A and 12 choosing B (2-tailed binomial test: $P = 1.0$). In contrast to individuals, however, colony preferences were unaffected by asymmetrically dominated decoys ($\chi^2 = 0.734$, $df = 1$, $N = 52$, $P = 0.392$) (Figure 3). Preferences were not identical between the 2 treatments, but the difference was nonsignificant and opposite to the direction predicted by the decoy effect and observed in the individual experiment. This result cannot be attributed to low sample size as power analysis showed that this sample size is adequate to detect an effect as strong or stronger than that seen in the individual experiment (power = 0.98 for $\alpha = 0.05$).

To exclude the possibility that removal of the decoy roof was responsible for the difference between individuals and colonies, we repeated the D_B treatment but allowed colonies to spontaneously abandon the undamaged decoy (colonies were unwilling to abandon undamaged D_A nests). If the decoy influences preferences in the same way seen for individuals, we expected to see a preference for B over A in these tests. Instead, we again saw only a nonsignificant trend in the opposite direction (9 chose A and 6 chose B; 2-tailed binomial test, $P = 0.607$).

DISCUSSION

The consistency of colony preferences in these experiments confirms an earlier result from *T. curvispinosus* (Edwards and Pratt 2009). That study examined only colony-level behavior, but the new results show clearly that lone ants are strongly influenced by decoys that have no effect on colonies. Similar sensitivity has been shown for individuals of many other species, but the decoy effect observed here was especially strong. For example, some earlier studies found no violation of regularity but only of the weaker constant ratio rule, which holds that the relative popularity of 2 options should not be changed by adding a third option (Bateson et al. 2002). Other studies found regularity violations but in response to only 1 of the 2 decoys offered (Bateson et al. 2003). The stronger effect in our study may be due to our careful selection of equally preferred targets posing a challenging trade-off between attributes. More importantly, it shows that the rational consistency of colony behavior was not simply a function of our choice set—instead, colonies showed clearly rational behavior in a context that induced strong departures from rationality in lone ants.

This contrast between group and individual reverses a traditional view that collectives are prone to amplification of individual irrationality. Our results instead suggest that an appropriately structured collective can prevent irrationality by avoiding the

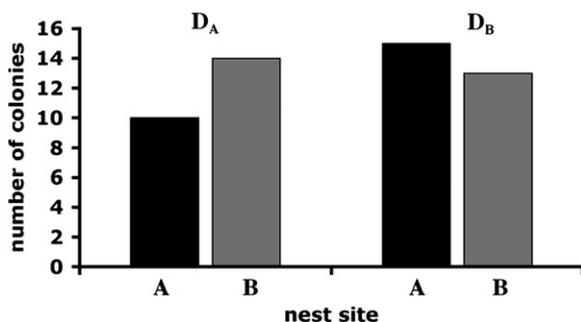


Figure 3 Nest-site preference by colonies was not affected by decoy type ($\chi^2 = 0.734$, $N = 52$, $P = 0.392$).

overburdening of individual cognitive abilities. A plausible scenario is that lone ants cannot adequately process information for all 3 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 (Hastie and Dawes 2001; Bateson and Healy 2005). In a collective setting, such comparisons are unnecessary because each ant need assess only one site or at most compare it to her current home. 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 (Pratt et al. 2005; Pratt and Sumpter 2006). The result is emergence of a rational group decision from ants prone to individual irrationality.

Under this scenario, the group paradoxically benefits by limiting the information available to each of its members. In laboratory emigrations by *Temnothorax* colonies, such limited information is the rule: Most ants do not visit more than one of the available candidate sites or do so only after decision making is well underway (Mallon et al. 2001; Robinson et al. 2009). This is not necessarily an adaptive response by the colony but a constraint imposed by the great difference in scale between ants and the area they must search. It is unlikely for each ant to find more than one site in time to influence the colony. Some ants, however, do get to visit more than one site. What impact might they have on the colony's choice? Robinson et al. (2009) suggest that even these knowledgeable ants refrain from making comparisons partly to avoid the resulting risks of irrational inconsistency. Our results, however, contradict this idea. If informed individuals do not compare options, then we should not have seen any influence of the decoy on the preferences of isolated ants. Instead, decoys strongly changed individual preferences between A and B. In a colony setting, however, this effect may have relatively little influence on the collective decision. Even if some ants show irrational behavior, their influence is likely swamped by the much larger number of ants that do not have the opportunity to compare sites.

Although a long line of research has noted the error-reducing potential of collective choice, the focus has been on random errors that can be cancelled out by a straightforward process of summation (Grunbaum 1998; Conradt and Roper 2003; Franks, Dornhaus, et al. 2003; Simons 2004; Surowiecki 2004; Ward et al. 2008). For example, a group of migrants may average their noisy estimates of the proper travel direction to achieve a more precise heading. In contrast, the decoy effect and other cases of irrational choice involve systematic preference changes that cannot be cancelled out by summing the choices of many independent decision makers (Livnat and Pippenger 2008). Collective choice can only limit these errors if it allows individuals to show qualitatively different behavior in the social context than they do when alone. For the ants, the key difference is that lone ants must make comparisons, but ants in the social context need not. Comparison of options is instead an emergent property of the colony as a whole.

This reasoning suggests that differences in the structure of individual and group cognition explain the contrast we observed. However, we must also consider whether the explanation lies in other differences between the 2 cases. An obvious methodological difference is that lone ants spontaneously abandoned the intact decoy nest to choose one of the targets, whereas colonies left the decoy only after its roof was removed. Destruction of their nest might spare colonies from the decoy effect if ants rapidly forget the attributes of their ruined home. This possibility is discounted by the behavior of colonies that

were allowed to abandon an intact nest just like the lone ants. Colonies did this only when living in decoy D_B , but their preferences were indistinguishable from those of colonies forced from D_B by removal of its roof. That is, they showed no preference for the dominant target just as expected under rational choice. This is consistent with earlier work that found an effect of home nest quality on emigration behavior even after the home was destroyed (Healey and Pratt 2008).

Another possible confounding factor is the unnatural isolation of ants in the individual experiments. This may have caused very different motivational states or preference functions than the same ants would show in a colony context. For example, isolated ants might hastily seek any haven for their brood rather than deliberating over the best nest. This possibility is countered by the slow decision speeds of these ants; rather than rush into any shelter, they spent at least as long as whole colonies before moving the brood to their final choice. The first check of experimental arenas was typically made 3 to 5 h after introducing the target nests; although most colonies had made a decision by this point, few individuals had. More importantly, lone ants and colonies showed very similar preferences in the binary choice when only the target sites A and B were present, suggesting that the lack of social context did not strongly alter preferences. Even if isolation did influence choice behavior, this would not change the essential irrationality of the lone ants' behavior compared with that of colonies. Whatever a decision-maker's preferences, they should remain consistent in the presence of an unattractive decoy. Lone ants strongly violated this expectation, whereas colonies did not.

These findings emphasize the importance of context in evaluating decision-making behavior. Like other ants, *Temnothorax* are obligately social, typically making nest-site choices collectively rather than relying on fully informed individuals. In this sense, the ants are ecologically rational (Stephens et al. 2004)—their behavior maximizes fitness in natural settings, if not in the experimental context of isolated ants. The finding that rationality is attained by the group, despite the potential for irrationality by individual members, suggests a novel advantage to group living and one that may also prove relevant to other social animals.

FUNDING

“JumpStart” grant from the Graduate & Professional Student Association at Arizona State University and Office of Naval Research grant N00014-08-1-0696.

We would like to thank Douglas Kenrick and Becca Neel for useful comments.

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