Ant colonies outperform individuals when a sensory discrimination task is difficult but not when it is easy

Takao Sasaki[a,1], Boris Granovskiy[b], Richard P. Mann[b], David J. T. Sumpter[b], and Stephen C. Pratt[a]

[a]School of Life Sciences and Center for Social Dynamics and Complexity, Arizona State University, Tempe, AZ 85287; and [b]Department of Mathematics, Uppsala University, 751 06 Uppsala, Sweden

"Collective intelligence" and "wisdom of crowds" refer to situations in which groups achieve more accurate perception and better decisions than solitary agents. Whether groups outperform individuals should depend on the kind of task and its difficulty, but the nature of this relationship remains unknown. Here we show that colonies of *Temnothorax* ants outperform individuals for a difficult perception task but that individuals do better than groups when the task is easy. Subjects were required to choose the better of two nest sites as the quality difference was varied. For small differences, colonies were more likely than isolated ants to choose the better site, but this relationship was reversed for large differences. We explain these results using a mathematical model, which shows that positive feedback between group members effectively integrates information and sharpens the discrimination of fine differences. When the task is easier 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.

group cognition | psychophysics | social insects | biological complexity

In many taxa, from bacteria to humans, individuals cooperate to evaluate their environment and make collective decisions (1, 2, 3, 4). By combining multiple assessments, these groups attain more precise estimates and make more accurate decisions than solitary animals (5, 6, 7). For example, when many diverse individuals independently estimate a quantity (e.g., humans guessing the number of marbles in a jar), the group's average estimate is often close to the actual value (8–10). Similarly, groups of fish can better distinguish between stimuli than individuals (1), and pairs of homing pigeons take more efficient routes than solitary birds (11). Condorcet's Jury Theorem and the Central Limit Theorem show that the accuracy of a group of independent decision makers improves with group size (12–16).

Despite these expectations of group advantage, many examples of collective failure have been documented (6, 17, 18). People in groups sometimes arrive at absurd decisions they would not likely make on their own (19). Collectives fail even in estimation tasks, for which they should be especially good at filtering out random errors made by individual members (10). The problem is that groups often violate the assumption of independent decision making that is central to the wisdom of crowds (1, 19). 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 (20, 21, 22). These interactions may either improve intelligence by integrating multiple assessments or hurt it by amplifying mistakes (23). Understanding which outcome will happen requires a comparison between individual and group performance across a range of challenges.

House hunting by *Temnothorax* ants provides an excellent model system for this approach (24–30). Colonies are able to select the better of two nest sites, even when few if any individual ants have the opportunity to assess more than one option (24). A collective decision instead emerges from a competition between

recruitment efforts at different sites (31). To facilitate this decentralized decision making, these ants use positive feedback in the form of tandem running recruitment and a quorum rule, whereby transport to a nest site accelerates when a threshold number of visiting ants is exceeded (32, 33). At the same time, if ants are experimentally isolated, they can still distinguish two sites of different quality, allowing the decision making of individuals to be compared with that of colonies (34, 35). This approach has shown that colonies can effectively compare a larger option set than individuals (35) and that they are less vulnerable to irrational preference shifts induced by decoys (34). No study, however, has determined how group advantage varies as the difficulty of the task changes.

To address this issue, we adapted methods typically used to study sensory discrimination in individual humans or animals (36–40). *Temnothorax rugatulus* subjects (either an individual, a small colony, or a large colony) were given a series of choices between a constant nest, with a very dim interior light level, and a comparison nest (Fig. 1). The comparison nest was always brighter than the constant nest, but its exact brightness was varied across tests 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 (26, 27). 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.

Results

As expected, both individuals and colonies made more accurate decisions as the choice became easier (Fig. 2*A*). However, the shapes of the discrimination curves were quite different. We 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 (41). 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 lx for
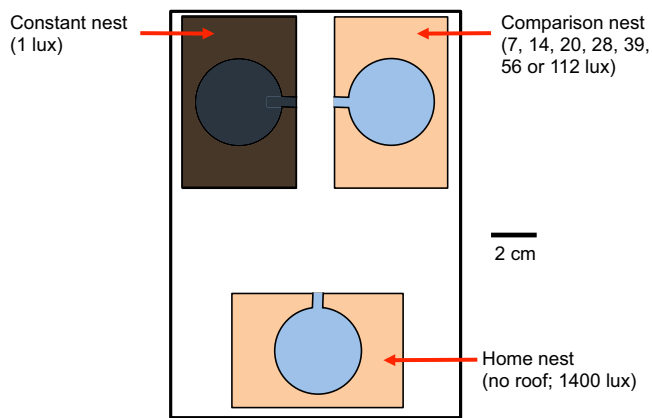
Fig. 1. Experimental arena for sensory discrimination tests. In each trial, subjects started in the home nest and were induced to choose between the constant and comparison sites. The constant nest was the same in all tests, with a very dim and highly favored interior light level. The comparison nest was always brighter than the constant nest, but its exact brightness varied across tests 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.

colonies and 32.3 lx for individuals (Monte Carlo test for $\alpha_{individual} > \alpha_{colony}$, $P = 0.0047$). When the choice was easy colonies no longer outperformed individuals, as shown by the higher asymptotic performance of individuals ($\lambda_{individual} = 0.93$) compared with colonies ($\lambda_{colony} = 0.80$; Monte Carlo test for $\lambda_{colony} < \lambda_{individual}$, $P = 0.050$). Large colonies marginally outperformed small ones across all differences (Fig. 2B), but this advantage was not statistically significant (*SI Appendix*, Fig. S2).

To explain these patterns we further investigated the mechanisms by which individual ants make a decision. We first considered the behavior of isolated ants, whose decision-making behavior is, in comparison with that at the colony level, relatively poorly understood. By observing lone ants as they chose between two sites of different quality, we established that they make multiple visits to each site, eventually accepting one of them as a new home with a probability that depends on site quality. Furthermore, their probability of choosing the better site grows with the number of times they compare sites (i.e., visit the two sites in succession; *SI Appendix*). On the basis of these observations we developed a simple Markov chain model of an ant choosing between a good nest A and a mediocre nest B. Every time the ant visits a site, she accepts it with a probability p that depends both on its quality and on the number of times i she has compared A and B:

$$p_A(i) = q_A$$
$$p_B(i) = q_B \left(\frac{2q_B}{q_B + q_A} \right)^i \qquad \text{[2]}$$

where $q_A > q_B$ are the intrinsic qualities of the nests. Under Eq. **2** the effect of each comparison is to reduce the probability of accepting the inferior nest, while leaving acceptance probability for the better nest unchanged. This model reproduces the positive effect of visit number on the likelihood of choosing correctly (*SI Appendix*, Fig. S5). It also assumes that this likelihood increases faster for larger quality differences between the nests (i.e., larger differences between q_A and q_B). This feature reflects the relative ease of distinguishing sites that are very different in quality.

We assumed that a similar process applies to individual ants within intact colonies, but in combination with social information. Consistent with earlier experimental work on the collective decision making of *Temnothorax* ants, we incorporated the use of quorums in our model (31). When the population of ants at a nest site surpasses a threshold, commitment to that site increases significantly (32, 33). With this addition, the site acceptance probabilities now depend on the number of ants at the site as follows:

$$p_A(i) = q_A + c \frac{N_A^2}{N_A^2 + T^2}$$
$$p_B(i) = q_B \left(\frac{2q_B}{q_B + q_A} \right)^i + c \frac{N_B^2}{N_B^2 + T^2} \qquad \text{[3]}$$

where N_A and N_B are the number of ants in the two nests, and T determines the population at which a quorum is reached and the probability of commitment increases sharply (42). The parameter c determines the relative weighting of individual assessment and social information ($c = 0$ for solitary ants).

When the model was used to simulate the nest discrimination experiment, the output matched our observation that both individuals and colonies become more accurate as the choice becomes easier (Fig. 3). It also reproduced the observed advantage of larger over smaller colonies across the entire range of difficulty (*SI Appendix*, Fig. S6). More 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 Fig. 2A and Fig. 3). To further test this prediction, we gathered more data for choices involving comparison stimuli on either side of the crossing point observed in the first experiment (*SI Appendix*, Fig. S3). Adding these data and refitting Eq. **1** gave revised discrimination thresholds $\alpha_{colony} = 6.6$ lx and $\alpha_{individual} = 30.9$ lx, and saturation levels $\lambda_{colony} = 0.78$ and $\lambda_{individual} = 0.89$. These data provided even stronger support for the better performance of groups on difficult tasks ($P = 0.0020$) and similar results for the better performance of individuals on easy tasks ($P = 0.052$).

Discussion

Groups are better than individuals in making difficult decisions, but the opposite effect is found when decisions are easy. The model suggests that the reason lies in the different assessment mechanisms operating at the level of individuals and colonies. For a difficult choice, solitary ants have a relatively high probability of accepting the worse nest, because they rely on quality-dependent acceptance probabilities that differ little for similar nests. Successive comparisons cause these probabilities to diverge, but the ant is likely to make her decision before this slow process has had much effect. Whole colonies, on the other hand, do much better at difficult choices, because they use social information to accentuate the quality difference between sites. Rather than rely on individual comparisons, the colony's choice emerges from a competition between recruitment efforts. Recruitment generates positive feedback on the number of ants at each site, with the better site slightly favored by its higher acceptance rate. The quorum rule amplifies this difference, allowing the colony to settle on the better site more frequently.

For very easy choices, the relative advantage is reversed between colonies and individuals. Acceptance probabilities now diverge quite rapidly with comparison, allowing solitary ants to make the right choice with high probability. For colonies, social information adds little benefit, and sometimes imposes a cost. This cost arises when random fluctuations yield a quorum for the inferior nest, locking the colony onto the wrong choice. In this situation, colonies get little advantage from individual comparison, even for easy choices, because the positive feedback process

Sasaki et al.

is quick, with most ants accepting one site without ever visiting the other one (24).

In the model, decision quality depends on the social information factor, c (*SI Appendix*, Fig. S7). Poor decisions can occur both when no pooling of information occurs ($c = 0$) and when ants rely too much on the presence of nestmates ($c > 1$). In the latter case, colonies get locked into their nest choices very quickly, leading to suboptimal decisions for easy problems, as occurred in our experiments. This locking on to suboptimal options through positive feedback is a recurring feature of group decision making (12), observed both in fish (1) and in trail-laying ants (23). There exists, however, an intermediate range of c values whereby colonies outperform individuals for both easy and difficult problems (*SI Appendix*, Fig. S7). We may conclude then that the colonies in our experiments did not achieve the
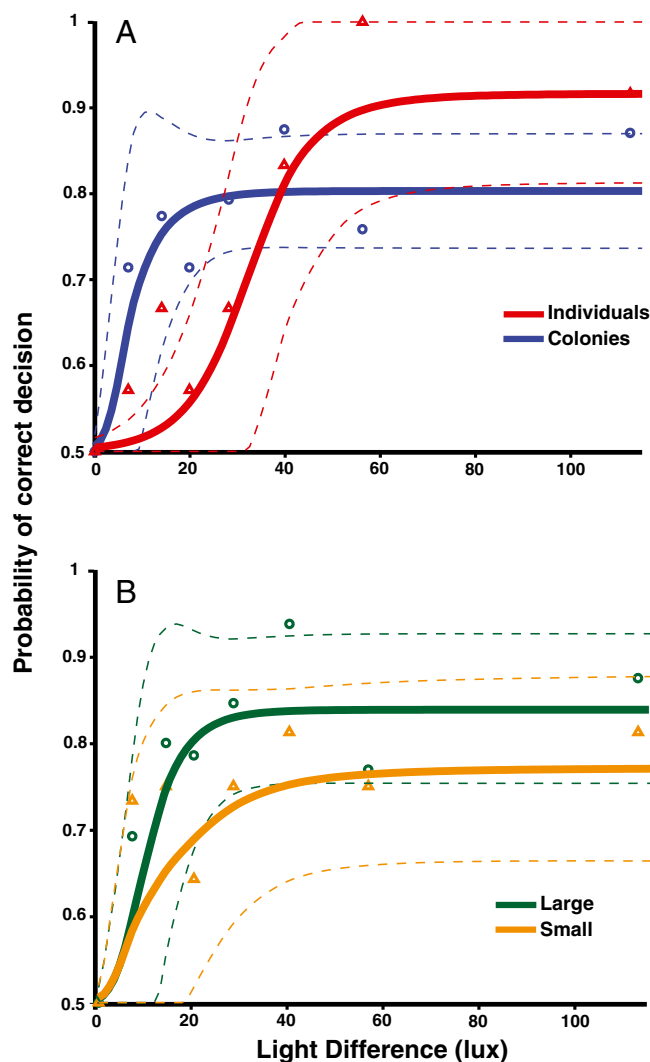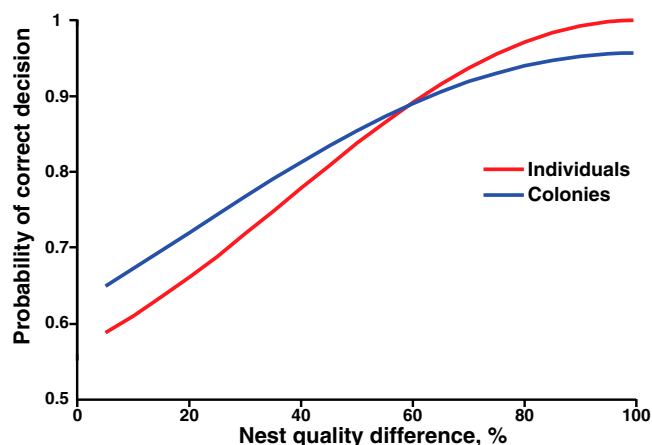

Fig. 3. Proportion of simulated individuals and colonies (population 100) selecting the better of two nests. Colonies perform better when the quality difference between the nests is small, but individuals choose more accurately when the difference is greater. In the corresponding experiments, a nest's quality is set by its brightness, with darker nests being more attractive. For these simulations, $q_A = 0.20$, and q_B varies between 0.19 and 0.001. The quorum parameter $c = 1.1$.

maximum possible accuracy. This result may be partially explained in terms of a speed–accuracy tradeoff. The colony's decentralized mechanism sacrifices some level of accuracy to make a more rapid decision (43–46). Our model predicts such a tradeoff for easier choices, with greater individual accuracy coming at the cost of much slower decision making (*SI Appendix*, Fig. S8). This is consistent with the observation that individuals take much longer to arrive at a decision than is typical for colonies (35). However, there is not always a speed–accuracy tradeoff (47). When the choice is difficult, by sharing the burden of nest assessment, colonies make decisions both faster and more accurately.

The patterns of collective and individual performance that we have observed in ants may also be relevant to many other taxa. Nonlinear responses to social information are known in many animal groups, including humans (48), fish (1) and cockroaches (49). Studies in honey bees have shown that social interactions do not always improve collective foraging, depending on the distribution of food (50, 51). Our study confirms this point and further demonstrates that these interactions sometimes even lower collective performance.

Although the wisdom of crowds has been acknowledged for decades, its failure or "madness of crowds" (52) has been recognized for even longer (17). Our work suggests that "madness" and "wisdom" are inescapably entwined. Enhanced group cognition is a clear benefit of living together (12–16), but in situations in which decision making should be straightforward there is a cost to relying on the judgment of others.

Materials and Methods

Nest Designs. To measure decision-making performance, we offered subjects binary choices between two kinds of nest: a constant nest and a comparison nest. The constant nest was the same in all choices, with an interior light level of 1 lx. The comparison nest was always brighter than the constant nest, but its specific light level was varied across trials (7, 14, 20, 28, 39, 56, or 112 lx). 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 2-mm entrance opening was cut out of the side of the nest (*SI Appendix*, Fig. S1). The floor of the cavity consisted of a single glass slide, whereas the roof was made from two stacked slides. Interior illumination was adjusted by placing transparent neutral-density filters (Rosco Cinegel) between the two roof slides. This design prevented ants from directly contacting the filters, which can sometimes build up an electrostatic charge that the ants find repellent. Nests were illuminated by two standard fluorescent light fixtures suspended

Fig. 2. The proportion of correct choices made as a function of site illumination difference. (A) Colonies (red triangles) outperform individuals (blue circles) when the illumination difference is small (<40 lx), but individuals perform better for larger illumination differences. (B) Large colonies (green circles) perform better than small colonies (yellow triangles) over the entire range of tested illumination differences, although this difference is not statistically significant. Thick lines represent fitting to the psychophysics function specified in Eq. **1**, with parameters sampled from the Bayesian posterior distribution calculated from the data. Dashed lines give 95% confidence intervals.

37 cm above the bench on which all experiments were carried out. This provided even illumination of 1,400 lx at the benchtop, as measured by a Lutron LX-101A light meter. Each fixture had a single 8,000K T-8 full-spectrum daylight bulb (All-Glass Aquarium).

Subjects. Thirty-two colonies of *T. rugatulus* were used for the colony-level tests. Half of them were small (20–80 workers), and half were large (150–250 workers). An additional eight medium-sized colonies (100–130 workers) provided 16 worker ants (2 ants per colony) for the individual tests. Only a minority of workers in *Temnothorax* colonies participate actively in nest-site scouting and transport of nestmates and brood items, whereas the rest of the colony waits at the home nest (24, 33). 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 emigrations (34).

Colonies were collected in the Pinal Mountains near Globe, AZ (N 33° 19.00′, N 110° 52.56′, W). All had at least one queen, with worker populations ranging from 20 to 250 and brood populations ranging from 20 to 280. We estimate that 25–100 ants (one-third of each colony's worker population) actively participated in scouting, site assessment, and recruitment (53). Each colony was housed in a nest like those described above, but without any light filters. Each nest was kept in a plastic box (11 cm × 11 cm), the walls of which were coated with Fluon to prevent the ants from escaping. Each box was provided with a water-filled plastic tube capped with cotton and an agar-based diet that was refreshed weekly (54).

Experimental Procedure. In each test, a subject (either an individual or a colony) was made to choose between a constant nest and a comparison nest. The comparison nest was always brighter than the constant nest, but its exact brightness varied across tests to provide an array of challenges of varying difficulty. Each subject was tested once for each of the seven comparison nests. The sequence of comparisons was varied across subjects to control for order effects. Four distinct orderings were used, with equal numbers of subjects assigned to each (*SI Appendix*, Fig. S1).

Tests of individuals began with placement of a home nest against one wall of a rectangular plastic arena (17.8 × 12.7 cm) with Fluon-coated walls. Two brood items were deposited just outside the nest entrance, and a single ant was placed in the arena. The ant was then given 12 h to find the nest and to move the brood inside. This procedure ensured that the subject was aware of both the home nest and the brood items. Constant and comparison nests were then placed against the arena wall opposite from the home. To induce a move to one of these nests, the roof of the home nest was removed. The ant's choice was assayed after 12 h by recording the nest to which she had carried the brood items. Each of 16 individuals was to be tested seven times (once for each comparison nest); however, two individuals died and one lost her mark (see below) during the experiment. Thus, a total of 106 trials were conducted. In all trials, subjects successfully moved the brood items to the home nest, but 12 trials had to be excluded from further analysis because

the subject failed to move to a target nest. Between trials, subjects were returned to their original colony. Each subject was marked with a unique paint drop on its gaster so that it could be identified and retrieved for subsequent trials. Before each experiment, all glass slides were washed in a commercial dishwasher, and the experimental arena was cleaned with ethanol. Balsa slats were made fresh for each experiment and never reused.

Tests of colonies followed a similar procedure. The colony in its old nest was placed next to a standard home nest in the center of the arena. The roof of the old nest was then removed to induce the colony to move into the home nest. In all cases, colonies finished migrating within 12 h. Then, target nests were introduced, and the roof of the home nest was removed to force a choice between the targets. The colony's choice was assayed by recording the nest to which a strong majority of colony members (>90%) migrated. Each of 16 colonies was tested seven times with different comparison nests, for a total of 112 trials. In nine trials colonies split, and in one trial the colony did not move to either target nest. These 10 trials were not included in the analysis. Order effects were controlled as for the individual tests (*SI Appendix*, Table S1).

Markov Chain Model. A Markov chain model was used to describe the *Temnothorax* house hunting process. In the model, each ant begins in the Exploring state, from which she can either find the better nest, entering state *A*, or the worse nest, entering state *B*. If the ant fails to find either nest, she continues exploring. Once at a site, she may also leave and find the other site, with some probability. With each subsequent nest visit, the ant enters state CA_i or CB_i, where i represents the number of comparisons she has made between nests. This number is incremented each time the ant goes from *A* to *B*, or from *B* to *A*. At each state the ant has a probability of accepting the nest she is currently assessing, modeled as the final states *a* and *b*. *SI Appendix*, Table S2 provides a summary of model states; *SI Appendix*, Table S3 the model's transition probabilities; and *SI Appendix*, Table S4 a description of the model parameters. The flowchart in *SI Appendix*, Fig. S4 summarizes all possible state transitions.

The probability of an ant committing to a particular nest is a function of the nest's intrinsic quality *q*, the number of times *i* she has compared it with the other nest, and social information mediated by a quorum rule, as given by Eq. **3**. Under the quorum rule, the probability of committing to a site increases in a step-like way with site population. For the purpose of calculating these populations (N_A and N_B), we added the number of fully committed ants (state *a* or state *b*) to 20% of the assessing ants (states *A* and CA_i or states *B* and CB_i). This reflects the approximate percentage of time actually spent by those ants inside the nest, where they can contribute to another ant's assessment of quorum attainment. A colony was considered to have chosen a nest when more than half of the ants were in the corresponding final state (*a* or *b*).

1. Ward AJW, Sumpter DJT, Couzin ID, Hart PJB, Krause J (2008) Quorum decision-making facilitates information transfer in fish shoals. *Proc Natl Acad Sci USA* 105(19): 6948–6953.
2. Woolley AW, Chabris CF, Pentland A, Hashmi N, Malone TW (2010) Evidence for a collective intelligence factor in the performance of human groups. *Science* 330 (6004):686–688.
3. Couzin ID (2009) Collective cognition in animal groups. *Trends Cogn Sci* 13(1):36–43.
4. Nakagaki T, Yamada H, Tóth Á (2000) Maze-solving by an amoeboid organism. *Nature* 407(6803):470.
5. Surowiecki J (2005) *The Wisdom of Crowds* (Random House, New York).
6. Krause J, Ruxton GD, Krause S (2010) Swarm intelligence in animals and humans. *Trends Ecol Evol* 25(1):28–34.
7. Seeley TD (2010) *Honeybee Democracy* (Princeton Univ Press, Princeton).
8. Galton F (1907) Vox populi. *Nature* 75:450–451.
9. King AJ, Cowlishaw G (2007) When to use social information: The advantage of large group size in individual decision making. *Biol Lett* 3(2):137–139.
10. Lorenz J, Rauhut H, Schweitzer F, Helbing D (2011) How social influence can undermine the wisdom of crowd effect. *Proc Natl Acad Sci USA* 108(22):9020–9025.
11. Biro D, Sumpter DJT, Meade J, Guilford T (2006) From compromise to leadership in pigeon homing. *Curr Biol* 16(21):2123–2128.
12. Sumpter DJT (2010) *Collective Animal Behavior* (Princeton Univ Press, Princeton).
13. Condorcet M (1785) *Essay sur l"application de l"analyse de la probabilité des decisions: Redues et pluralité des voix* (Imprimerie Royale, Paris).
14. Simons AM (2004) Many wrongs: The advantage of group navigation. *Trends Ecol Evol* 19(9):453–455.
15. Hamilton WJ (1967) Social aspects of bird orientation mechanisms. *Animal Orientation and Navigation*, ed Strom RM (Oregon State Univ Press, Corvallis, OR), pp 57–71.
16. Wallraff H (1978) Social interrelations involved in migratory orientation of birds: Possible contribution of field studies. *Oikos* 30(2):401–404.
17. Kerr NL, Tindale RS (2004) Group performance and decision making. *Annu Rev Psychol* 55:623–655.
18. Bahrami B, et al. (2012) What failure in collective decision-making tells us about metacognition. *Philos Trans R Soc Lond B Biol Sci* 367(1594):1350–1365.
19. Janis IL (1972) *Victims of Groupthink: A Psychological Study of Foreign-Policy Decisions and Fiascoes* (Houghton Mifflin, Oxford).
20. Conradt L, Roper TJ (2005) Consensus decision making in animals. *Trends Ecol Evol* 20(8):449–456.
21. Detrain C, Deneubourg JL (2006) Self-organized structures in a superorganism: Do ants "behave" like molecules? *Phys Life Rev* 3(3):162–187.
22. Dussutour A, Fourcassié V, Jeanson R (2012) Key factors for the emergence of collective decision in invertebrates. *Front Neurosci* 6:121.
23. Goss S, Aron S, Deneubourg JL, Pasteels JM (1989) Self-organized shortcuts in the Argentine ant. *Naturwissenschaften* 76(12):579–581.
24. Mallon E, Pratt SC, Franks NR (2001) Individual and collective decision-making during nest site selection by the ant *Leptothorax albipennis*. *Behav Ecol Sociobiol* 50(4): 352–359.
25. Franks NR, Dornhaus A, Fitzsimmons JP, Stevens M (2003) Speed versus accuracy in collective decision making. *Proc Biol Sci* 270(1532):2457–2463.
26. Franks NR, Mallon E, Bray H, Hamilton M (2003) Strategies for choosing between alternatives with different attributes: Exemplified by house-hunting ants. *Anim Behav* 65(1):215–223.
27. Pratt SC (2005) Behavioral mechanisms of collective nest-site choice by the ant *Temnothorax curvispinosus*. *Insectes Soc* 52(4):383–392.

28. Pratt SC, Sumpter DJT, Mallon E (2005) An agent-based model of collective nest choice by the ant *Temnothorax albipennis*. *Anim Behav* 70(5):1023–1036.

29. Dornhaus A, Franks NR (2006) Colony size affects collective decision-making in the ant *Temnothorax albipennis*. *Insectes Soc* 53(4):420–427.

30. Pratt SC (2008) Efficiency and regulation of recruitment during colony emigration by the ant *Temnothorax curvispinosus*. *Behav Ecol Sociobiol* 62(8):1369–1376.

31. Franks NR, Pratt SC, Mallon EB, Britton NF, Sumpter DJT (2002) Information flow, opinion polling and collective intelligence in house-hunting social insects. *Philos Trans R Soc Lond B Biol Sci* 357(1427):1567–1583.

32. Pratt SC, Mallon E, Sumpter DJT, Franks NR (2002) Quorum sensing, recruitment, and collective decision-making during colony emigration by the ant *Leptothorax albipennis*. *Behav Ecol Sociobiol* 52(2):117–127.

33. Pratt SC (2005) Quorum sensing by encounter rates in the ant *Temnothorax albipennis*. *Behav Ecol* 16(2):488–496.

34. Sasaki T, Pratt SC (2011) Emergence of group rationality from irrational individuals. *Behav Ecol* 22(2):276–281.

35. Sasaki T, Pratt SC (2012) Groups have a larger cognitive capacity than individuals. *Curr Biol* 22(19):R827–R829.

36. Fechner G (1966) *Elements of Psychophysics* (Holt, Rinehart, & Winston, New York), Vol I.

37. Gescheider G (1997) *Psychophysics: The Fundamentals* (Lawrence Erlbaum Associated, Mahwah, New Jersey).

38. Chittka L, Spaethe J, Schmidt A, Hickerlsberger A (2001) *Cognitive Ecology of Pollination: Animal Behaviour and Floral Evolution*, eds Chittka L, Thomson JD (Cambridge Univ Press, Cambridge, UK), pp 106–126.

39. Dyer AG, Chittka L (2004) Biological significance of distinguishing between similar colours in spectrally variable illumination: Bumblebees (*Bombus terrestris*) as a case study. *J Comp Physiol A Neuroethol Sens Neural Behav Physiol* 190(2):105–114.

40. Dyer AG, Spaethe J, Prack S (2008) Comparative psychophysics of bumblebee and honeybee colour discrimination and object detection. *J Comp Physiol A Neuroethol Sens Neural Behav Physiol* 194(7):617–627.

41. Wichmann FA, Hill NJ (2001) The psychometric function: I. Fitting, sampling, and goodness of fit. *Percept Psychophys* 63(8):1293–1313.

42. Sumpter DJT, Pratt SC (2009) Quorum responses and consensus decision making. *Philos Trans R Soc Lond B Biol Sci* 364(1518):743–753.

43. Chittka L, Skorupski P, Raine NE (2009) Speed-accuracy tradeoffs in animal decision making. *Trends Ecol Evol* 24(7):400–407.

44. Marshall JAR, Dornhaus A, Franks NR, Kovacs T (2006) Noise, cost and speed-accuracy trade-offs: Decision-making in a decentralized system. *J R Soc Interface* 3(7):243–254.

45. Passino K, Seeley TD (2006) Modeling and analysis of nest-site selection by honeybee swarms: The speed and accuracy trade-off. *Behav Ecol Sociobiol* 59(3):427–442.

46. Marshall JAR, et al. (2009) On optimal decision-making in brains and social insect colonies. *J R Soc Interface* 6(40):1065–1074.

47. Sumpter DJT, Zabzina N, Nicolis S (2012) Six predictions about the decision making of animal and human groups. *Managerial and Decision Economics* 33(5-6):295–309.

48. Milgram S, Bickman L, Berkowitz L (1969) Note on the drawing power of crowds of different size. *J Pers Soc Psychol* 13(2):79–82.

49. Amé JM, Halloy J, Rivault C, Detrain C, Deneubourg JL (2006) Collegial decision making based on social amplification leads to optimal group formation. *Proc Natl Acad Sci USA* 103(15):5835–5840.

50. Sherman G, Visscher PK (2002) Honeybee colonies achieve fitness through dancing. *Nature* 419(6910):920–922.

51. Dornhaus A, Chittka L (2004) Information flow and regulation of foraging activity in bumble bees (*Bombus* spp.). *Apidologie (Celle)* 35(2):183–192.

52. Mackay C (1841) *Memoirs of Extraordinary Popular Delusions and the Madness of Crowds* (Wordsworth Editions Limited, Ware, UK).

53. Pinter-Wollman N, Hubler J, Holley J, Franks NR, Dornhaus A (2012) How is activity distributed among and within tasks in *Temnothorax* ants? *Behav Ecol Sociobiol* 66(10):1407–1420.

54. Bhatkar A, Whitcomb WH (1970) Artificial diet for rearing various species of ants. *Fla Entomol* 53(4):229–232.

PSYCHOLOGICAL AND COGNITIVE SCIENCES

ECOLOGY