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Animal behaviour

Rational time investment during collective decision making in *Temnothorax* ants

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The study of rational choice in humans and other animals typically focuses on decision outcomes, but rationality also applies to decision latencies, especially when time is scarce and valuable. For example, the smaller the difference in quality between two options, the faster a rational actor should decide between them. This is because the consequences of choosing the inferior option are less severe if the options are similar. Experiments have shown, however, that humans irrationally spend more time choosing between similar options. In this study, we assessed the rationality of time investment during nest-site choice by the rock ant, *Temnothorax albipennis*. Previous studies have shown that collective decision-making allows ant colonies to avoid certain irrational errors. Here we show that the same is true for time investment. Individual ants, like humans, irrationally took more time to complete an emigration when choosing between two similar nests than when choosing between two less similar nests. Whole colonies, by contrast, rationally made faster decisions when the options were more similar. We discuss the underlying mechanisms of decision-making in individuals and colonies and how they lead to irrational and rational time investment, respectively.

1. Introduction

Evolutionary theory predicts that animals should make decisions that maximize their fitness [1]. Economic theory similarly predicts that humans make decisions that are rational, meaning that they maximize 'utility', an implicit measure of the satisfaction obtained from a choice [2]. This parallel suggests that both humans and animals should adhere to certain decision principles that characterize rational choice [3,4]. However, behavioural psychologists have found reliable violations of these principles when humans are presented with particular decision-making challenges [5,6]. Behavioural ecologists, in turn, have presented these challenges to animals and found similar violations of rationality [7–12]. The significance of these violations has been debated; they may reflect cognitive constraints favouring decision heuristics that work well in ecologically relevant contexts but fail in specific contexts [3,4,13]. The study of these failures offers potential insights into underlying decision-making processes.

Studies on animals have typically assessed rationality principles like transitivity or regularity, which specify which option should be selected from a choice set [5,6]. However, rationality also applies to the amount of time invested in decision-making, especially when time is scarce and valuable, as is often the case for both humans and other animals [14–16]. For example, imagine a timed task in which you are offered a series of choices between two images, each portraying a different number of dots. For each presentation, you choose one image, and you are rewarded according to the number of dots in your choice. Because there is a limited amount of time for the task, your ultimate reward depends both on how well you choose the image with more dots in each pair, and also on how many choices you complete. In some trials, the better option has 10 dots and the other has nine dots. In other trials, the
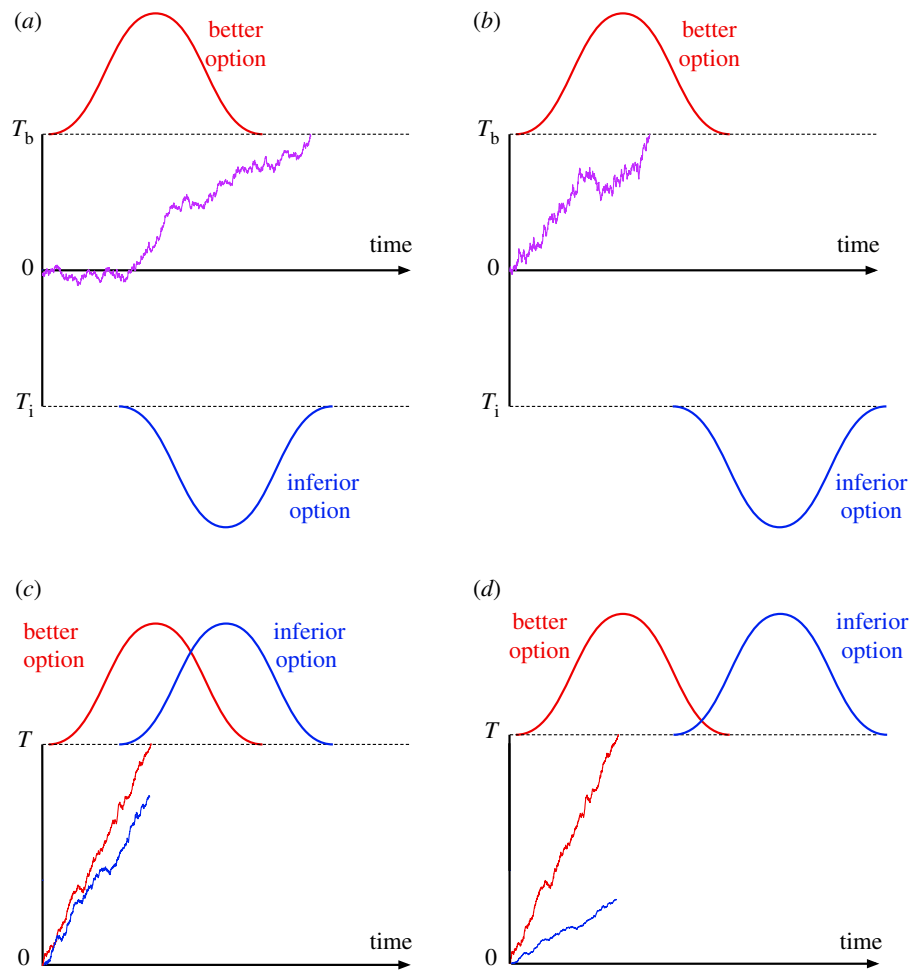
Figure 1. Illustrations of the accumulation of evidence over time for competing options in the tug-of-war model (top row) and the horse race model (bottom row). In both models, a decision is made when accumulation of evidence reaches a threshold. In the tug-of-war model, each option has its own threshold (T_b and T_i), and a decision is made when the difference between accumulated evidence for each option hits a threshold. When options are similar (a), the difference will be small and will take longer to reach a threshold than when options are less similar (b). In the horse race model, on the other hand, decision-making is faster when the options are more similar (c) than when they are different (d). In this model, evidence for each option accumulates independently; the inferior option occasionally censors the better option, and it does so more severely as the quality of the options becomes similar.

better option again has 10 dots, but the inferior one has only four dots. Humans perceive the first trial, in which the difference in quality between options is smaller, as more difficult than the second trial and spend more time to make a decision [14]. However, a rational actor would show the opposite pattern, investing less time when the consequences of choosing the inferior option are less severe [14]. Since a mistake costs only one dot in the first trial but six dots in the second trial, it is irrational to spend more time in the first trial, thus paying unnecessary opportunity costs of missing out on rewards from additional trials. This relationship between task difficulty and relative reward—more difficult tasks often give smaller relative rewards—has been widely overlooked, but this seemingly paradoxical relationship exists in many ecologically important situations [14,17].

Models of information processing can account for why an animal might show irrational time investment. In a wide variety of animals, from flies to humans, two-choice decisions are well described by sequential-sampling models [18–21]. This is a large and varied class of models, but all of them share common elements. The subject is viewed as receiving streams of noisy information for two options. The brain integrates these streams over time, arriving at a decision when its accumulated activity level reaches a threshold. In the widely

applied drift-diffusion model, also known as the 'tug-of-war' [22], the brain tracks the difference between streams of information accumulated for each option, and the decision depends on whether the difference first hits an upper or lower threshold (figure 1a). This captures the idea that the decision-maker comparatively evaluates the two options. When two options are more similar (and thus more difficult to discriminate), the difference between streams is small, leading to a weak drift toward the superior option and a longer latency to reach a decision. This can lead to an irrational time investment (figure 1b).

Another kind of sequential-sampling model, the 'horse race' [22], instead predicts rational time investment. As in the tug-of-war model, a decision is made when accumulated activity reaches a threshold. Unlike the tug-of-war, the information streams for the two options do not interact but instead accumulate independently (figure 1c,d). That is, the decision-maker makes no direct comparison between options but processes each one separately. This model predicts that, as two options become harder to discriminate, time to reach a decision shortens due to cross-censoring between the underlying latency distributions for each option. Censoring means that longer latencies for either option become less probable, because of the likelihood that the other option will have

Table 1. Choices by each subject (individuals and colonies) for the good nest versus the mediocre nest (left) and for the good nest versus the poor nest (right).

	choice			choice	
	good nest	mediocre nest		good nest	poor nest
individuals	19	5	individuals	25	1
colonies	17	9	colonies	27	2

already reached its threshold. In particular, the right tail of the distribution for the better option gets censored more by the left tail of that for the inferior option as the quality of the inferior option increases (figure 1*c*). As a result, the expressed latencies for the better option become shorter. A similar effect leads to shorter latencies for the inferior option, in cases where it is chosen. Thus, latencies decrease, regardless of the choice made, as the quality of the inferior option increases.

In this study, we consider the implication of these information processing models for time investment by the rock ant, *Temnothorax albipennis*. These ants typically live in fragile rock crevices and emigrate if their old nest becomes inadequate [23]. Rapid emigration is likely to be critical, because ants on the move or inhabiting a damaged nest are more vulnerable to predators, desiccation and other threats. Colonies can select the better of two nest sites using a quality-dependent recruitment system that generates positive feedback, amplified by a quorum rule [24,25]. Their decision emerges from interactions among many ants, rather than being guided by the informed decision-making of a single ant. However, if a single ant is experimentally isolated from her colony, she can independently compare two sites of different quality and choose one of them [12,26,27]. This allows for comparison of individual and collective cognitive abilities when faced with the same decision challenge. A recent study took advantage of this to show that the decision-making process of *T. albipennis* colonies matches the horse race model while that of individual ants fits the tug-of-war model [28]. This led us to predict that individual ants would make irrational time investments, but colonies would behave rationally. We tested this by offering subjects (either whole colonies or single ants) two-choice tasks between nests that were either similar or different in quality.

2. Material and methods

To test for the irrational time investment, we made three types of the target nest cavity, designated as 'good', 'mediocre' and 'poor'. Nest designs were identical except for their interior illumination, which was dim for the good nest, brighter for the intermediate nest and brighter still for the poor nest. These differences were based on the strong preference for dimmer nests shown by *Temnothorax* ants [26,29].

A total of 47 colonies of *T. albipennis* were used in the experiment: 30 colonies were used for the colony-level tests and an additional 17 colonies provided 68 worker ants (four ants per colony) for the individual tests. We presented subjects (whole colonies or single ants) with two binary choices, one between a good nest and a poor nest (GvsP) and the other one between a good nest and a mediocre nest (GvsM). The first choice had a greater difference in quality than the second one. Note that the better option, and thus the more likely to be selected, was

identical in both choices; the only difference between these choices was the worse option. Half of the subjects faced the GvsM choice first and the other half faced the GvsP choice first.

In each test, migration was induced by removing the roof of the home nest. We then recorded the whole arena for 13 h using a high-resolution video camera (Sony FDR-AX100E). We later watched these videos to determine which nest the subject migrated to and how long it took to do so. In both individual and colony tests, the decision-making latency was defined as the time between the removal of the home nest roof and transport of the last brood item to the new site [28]. We used the last transport because the colony's choice emerges from the lengthy process of recruitment that moves the colony, rather than being determined by the earliest recruitment acts (see [28] for a more detailed justification of this decision latency criterion).

We were mainly interested in how latency to choose the good nest would be affected by its similarity to the inferior alternative; hence we first analysed only the cases where the good option was chosen, as in a previous human study [14]. This included most trials (44 out of 50 individual trials and 44 out of 55 colony trials in which a decision was made within 13 h; table 1). We fit a generalized linear mixed model to test for an effect of choice set on decision latency. For the individual data, each colony provided two ants, creating a potential problem with pseudoreplication. To account for this, we included the colony as a random effect in the model. For the colony data, we included numbers of workers and brood items as covariates.

To test the robustness of the outcome, we also considered all the data points, including cases where the poor nest was chosen or no nest was chosen within 13 h. For this analysis, we compared the latencies between conditions using Cox proportional-hazards regression, treating all cases in which neither nest was chosen as censored data.

See the electronic supplementary material for further details on experimental procedures and analysis.

3. Results

Our results were consistent with our prediction that individuals would be irrational but colonies would be rational. Individuals took significantly longer to choose the good nest when the quality of choices was similar (GvsM) than when it was different (GvsP) ($t = 2.71$, d.f. $= 32.55$, $p = 0.01$) (figure 2), as humans do [14]. Colonies, by contrast, took significantly shorter in the GvsM choice than in the GvsP choice ($t = 3.20$, d.f. $= 12.25$, $p < 0.01$) (figure 2). There was no significant effect of the colony for the individual analysis ($p = 0.11$), indicating that an ant's decision latency was not influenced by its colony of origin. For the colony analysis, we found no effects of the numbers of workers and brood items ($p = 0.10$ and $p = 0.60$, respectively). When we included the cases where the subject chose the poor nest or neither nest, the patterns remained same, although the individual difference was no longer significant (electronic supplementary material).

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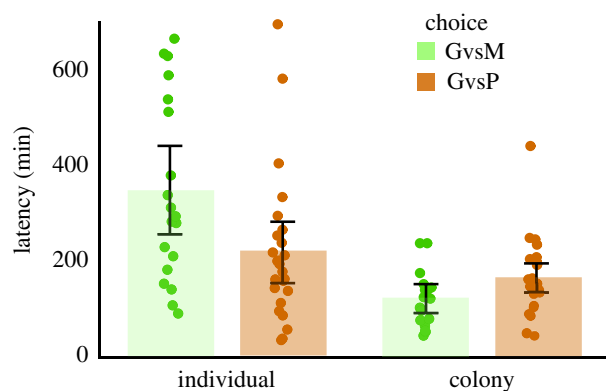
Figure 2. Decision-making latencies of individuals and colonies when choosing the good nest. Individuals make slower decisions when the options are more similar (i.e. good versus mediocre takes longer than good versus poor). On the other hand, colonies make faster decisions when the options are more similar. Dots represent data points and are horizontally jittered to improve clarity. Bar heights show average latencies and error bars show 95% confidence intervals.

4. Discussion

Our results match the predictions of the decision-making models previously attributed to individuals and colonies. Individual decisions follow the tug-of-war model [28], in which options are directly compared and greater similarity of options leads to longer decision latencies. Colony decisions instead follow the horse race model [28], in which options are evaluated independently and greater similarity leads to shorter latencies. The respective models are also consistent with observed behaviour. In a colony, few ants visit both sites; most of the work of decision-making is done by ants that have visited only one site [27]. Each ant assesses its site and initiates recruitment to it with a probability proportional to site quality. The colony's choice is the winner of competing processes of recruitment at each candidate site. These processes are largely independent; hence, the horse race model of independently accumulating streams is appropriate. Lone ants, by contrast, typically visit both options and directly compare them [12,27]. This opens the possibility that the neural processes underlying their choice involve interactions between information about each option. The presence of direct comparative evaluation of this kind makes the tug-of-war model more relevant.

The observed difference between colonies and individuals is consistent with previous evidence about irrational choice in

Temnothorax ants [12,30]. Isolated workers of *T. rugatulus* were found to irrationally switch their preference between two candidate nest sites based on their experience of an unattractive decoy. Given the same choice, whole colonies maintained consistent preferences regardless of the decoy's presence. Decoy effects like this are widespread in the decision-making of humans and other animals [6,11,31–33]. They are generally attributed to the use of comparative heuristics to simplify complex choices among multi-attribute options that pose difficult trade-offs [5]. As in the current study, colony-level rationality is attributable to the avoidance of such comparisons; the colony instead distributes assessment over many ants and evaluates options in parallel [27].

The colony behaviour seen here springs from the specific collective decision mechanisms used by *Temnothorax* ants, which lead to highly independent option evaluation that is well described by the horse race model. Other social animals might show different patterns, insofar as their decision tactics create interdependence between options. For example, honey-bee nest site selection resembles that of *Temnothorax* but with the key difference that scouts for one site actively inhibit recruitment by scouts from competing sites [34]. Analogous inhibition is expected in ants that recruit via pheromone trails, such as *Myrmecina nipponica* [35], because more developed trails (i.e. higher concentrations of trail pheromones) can suppress less developed ones [36]. Decision-making in these species may be better described by the tug-of-war model than the horse race model, implying different expectations about the rationality of their collective choices. This points to the value of a broader exploration of rationality in collective choice, to better understand how the diversity of decision mechanisms effects variation in collective performance.

References

1. Stephen DW, Krebs JR. 1986 *Foraging theory.* Princeton, NJ: Princeton University Press.

2. Von Neumann J, Morgenstern O. 1944 *Theory of games and economic behavior.* Princeton, NJ: Princeton University Press.

3. Kacelnik A. 2006 Meanings of rationality. In *Rational animals?* (eds MD Breed, J Moore), pp. 87–106. Oxford, UK: Oxford University Press.

4. Bateson M. 2010 Rational choice behavior: definitions and evidence. *Encycl. Anim. Behav.* **3**, 13–19.

5. Tversky A, Kahneman D. 1974 Judgment under uncertainty: heuristics and biases. *Science* **185**, 1124–1131. (doi:10.1126/science.185. 4157.1124)

6. Tversky A, Kahneman D. 1981 The framing of decisions and the psychology of choice. *Science* **211**, 453–458. (doi:10.1126/science.7455683)

7. Tversky A. 1969 Intransitivity of preferences. *Psychol. Rev.* **76**, 31–48. (doi:10.1037/h0026750)

8. Bateson M, Healy SD, Hurly TA. 2003 Context-dependent foraging decisions in rufous

hummingbirds. *Proc. R. Soc. Lond. B* **270**, 1271–1276. (doi:10.1098/rspb.2003. 2365)

9. Huber J, Payne JW. 1982 Adding asymmetrically dominated alternatives: violations of regularity and the similarity hypothesis. *J. Consum. Res.* **9**, 90–98. (doi:10.1086/208899)

10. Wedell DH. 1991 Distinguishing among models of contextually induced preference reversals. *J. Exp. Psychol. Learn. Mem. Cogn.* **17**, 767–778. (doi:10. 1037/0278-7393.17.4.767)

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royalsocietypublishing.org/journal/rsbl   Biol. Lett. **15**: 20190542

11. Shafir S, Waite TA, Smith BH. 2002 Context-dependent violations of rational choice in honeybees (*Apis mellifera*) and gray jays (*Perisoreus canadensis*). *Behav. Ecol. Sociobiol.* **51**, 180–187. (doi:10.1007/s00265-001-0420-8)

12. Sasaki T, Pratt SC. 2011 Emergence of group rationality from irrational individuals. *Behav. Ecol.* **22**, 276–281. (doi:10.1093/beheco/arq198)

13. Gigerenzer G, Goldstein DG. 1996 Reasoning the fast and frugal way: models of bounded rationality. *Psychol. Rev.* **103**, 650–669. (doi:10.1037/0033-295X.103.4.650)

14. Oud B, Krajbich I, Miller K, Cheong JH, Botvinick M, Fehr E. 2016 Irrational time allocation in decision-making. *Proc. R. Soc. B* **283**, 20151439. (doi:10.1098/rspb.2015.1439)

15. Chittka L, Skorupski P, Raine NE. 2009 Speed–accuracy tradeoffs in animal decision making. *Trends Ecol. Evol.* **24**, 400–407. (doi:10.1016/j.tree.2009.02.010)

16. Stephens DW, Krebs JR, John R. 1986 *Foraging theory*. Princeton, NJ: Princeton University Press.

17. Pirrone A, Stafford T, Marshall JAR. 2014 When natural selection should optimize speed-accuracy trade-offs. *Front. Neurosci.* **8**, 73. (doi:10.3389/fnins.2014.00073)

18. DasGupta S, Ferreira CH, Miesenbock G. 2014 FoxP influences the speed and accuracy of a perceptual decision in *Drosophila*. *Science* **344**, 901–904. (doi:10.1126/science.1252114)

19. Kaneko H, Tamura H, KawashimaA T, Suzuki S. 2006 A choice reaction-time task in the rat: a new model using air-puff stimuli and lever-release responses. *Behav. Brain Res.* **174**, 151–159. (doi:10.1016/j.bbr.2006.07.020)

20. Bogacz R. 2007 Optimal decision-making theories: linking neurobiology with behaviour. *Trends Cogn. Sci.* **11**, 118–125. (doi:10.1016/j.tics.2006.12.006)

21. Brunton BW, Botvinick MM, Brody CD. 2013 Rats and humans can optimally accumulate evidence for decision-making. *Science* **340**, 95–98. (doi:10.1126/science.1233912)

22. Kacelnik A, Vasconcelos M, Monteiro T, Aw J. 2011 Darwin's 'tug-of-war' vs. starlings' 'horse-racing': how adaptations for sequential encounters drive simultaneous choice. *Behav. Ecol. Sociobiol.* **65**, 547–558. (doi:10.1007/s00265-010-1101-2)

23. Dornhaus A, Franks NR, Hawkins RM, Shere HNS. 2004 Ants move to improve: colonies of *Leptothorax albipennis* emigrate whenever they find a superior nest site. *Anim. Behav.* **67**, 959–963. (doi:10.1016/j.anbehav.2003.09.004)

24. Pratt SC, Mallon E, Sumpter D, Franks N. 2002 Quorum sensing, recruitment, and collective decision-making during colony emigration by the ant *Leptothorax albipennis*. *Behav. Ecol. Sociobiol.* **52**, 117–127. (doi:10.1007/s00265-002-0487-x)

25. Pratt SC. 2005 Behavioral mechanisms of collective nest-site choice by the ant *Temnothorax curvispinosus*. *Insectes Soc.* **52**, 383–392. (doi:10.1007/s00040-005-0823-z)

26. Sasaki T, Granovskiy B, Mann RP, Sumpter DJT, Pratt SC. 2013 Ant colonies outperform individuals when a sensory discrimination task is difficult but not when it is easy. *Proc. Natl Acad. Sci.* **110**, 13 769–13 773. (doi:10.1073/pnas.1304917110)

27. Sasaki T, Pratt SC. 2012 Groups have a larger cognitive capacity than individuals. *Curr. Biol.* **22**, R827–R829. (doi:10.1016/j.cub.2012.07.058)

28. Sasaki T, Pratt SC, Kacelnik A. 2018 Parallel vs. comparative evaluation of alternative options by colonies and individuals of the ant *Temnothorax rugatulus*. *Sci. Rep.* **8**, 12730. (doi:10.1038/s41598-018-30656-7)

29. Franks NR, Mallon EB, Bray EH, Hamilton MJ, Mischler TC. 2003 Strategies for choosing between alternatives with different attributes: exemplified by house-hunting ants. *Anim. Behav.* **65**, 213–223. (doi:10.1006/anbe.2002.2032)

30. Edwards SC, Pratt SC. 2009 Rationality in collective decision-making by ant colonies. *Proc. R. Soc. B* **276**, 3655–3661. (doi:10.1098/rspb.2009.0981)

31. Latty T, Beekman M. 2010 Irrational decision-making in an amoeboid organism: transitivity and context-dependent preferences. *Proc. R. Soc. B* **278**, 20101045. (doi:10.1098/rspb.2010.1045)

32. Waite TA. 2001 Intransitive preferences in hoarding gray jays (*Perisoreus canadensis*). *Behav. Ecol. Sociobiol.* **50**, 116–121. (doi:10.1007/s002650100346)

33. Bateson M, Healy SD, Hurly TA. 2002 Irrational choices in hummingbird foraging behaviour. *Anim. Behav.* **63**, 587–596. (doi:10.1006/anbe.2001.1925)

34. Seeley TD, Visscher PK, Schlegel T, Hogan PM, Franks NR, Marshall JAR. 2012 Stop signals provide cross inhibition in collective decision-making by honeybee swarms. *Science* **335**, 108–111. (doi:10.1126/science.1210361)

35. Cronin AL. 2013 Synergy between pheromone trails and quorum thresholds underlies consensus decisions in the ant *Myrmecina nipponica*. *Behav. Ecol. Sociobiol.* **67**, 1643–1651. (doi:10.1007/s00265-013-1575-9)

36. Czaczkes TJ, Grüter C, Ratnieks FLW. 2015 Trail pheromones: an integrative view of their role in social insect colony organization. *Annu. Rev. Entomol.* **60**, 581–599. (doi:10.1146/annurev-ento-010814-020627)

37. Sasaki T, Stott B, Pratt SC. 2019 Data from: Rational time investment during collective decision making in *Temnothorax* ants. Dryad Digital Repository. (http://dx.doi.org/10.5061/dryad.m0d4b17)