

# Speed versus accuracy in collective decision making

Nigel R. Franks\*, Anna Dornhaus, Jon P. Fitzsimmons and Martin Stevens

Centre for Behavioural Biology, School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, UK

We demonstrate a speed versus accuracy trade-off in collective decision making. House-hunting ant colonies choose a new nest more quickly in harsh conditions than in benign ones and are less discriminating. The errors that occur in a harsh environment are errors of judgement not errors of omission because the colonies have discovered all of the alternative nests before they initiate an emigration. *Leptothorax albipennis* ants use quorum sensing in their house hunting. They only accept a nest, and begin rapidly recruiting members of their colony, when they find within it a sufficient number of their nest-mates. Here we show that these ants can lower their quorum thresholds between benign and harsh conditions to adjust their speed–accuracy trade-off. Indeed, in harsh conditions these ants rely much more on individual decision making than collective decision making. Our findings show that these ants actively choose to take their time over judgements and employ collective decision making in benign conditions when accuracy is more important than speed.

**Keywords:** speed–accuracy trade-off; collective decision making; ants; house hunting

## 1. INTRODUCTION

In decision making, speed and accuracy are often in opposition. Much time may be required to make an accurate decision between alternatives, because gathering, processing and evaluating information may be a lengthy process. If an animal has to make a swift decision it may therefore be less discriminating. This tension between speed and accuracy is so widespread that it has been termed the speed–accuracy trade-off paradigm (Busemeyer & Townsend 1993; Osman *et al.* 2000; Nikolic & Gronlund 2002). Nevertheless, empirical studies demonstrating the conflict between speed and accuracy in decision making are mostly investigations in the field of human performance and psychology (Osman *et al.* 2000; Vitevitch 2002; but see also Roitman & Shadlen (2002) for a study of monkeys and Chittka *et al.* (2003) for a study of bumble-bees). In many cases, people can actively choose their own compromise between accuracy and speed (consider for example, typing speed versus error rate). Here, we consider if social animals that employ collective decision making can also achieve a flexible, context sensitive, compromise between speed and accuracy.

Speed–accuracy trade-offs can occur for a large variety of reasons. For example, an animal may be so time limited that even though ideally it ought to be very discriminating (e.g. it should attempt to choose the best mate in a population) it does less sampling and misses good examples and accepts poor ones (Alatalo *et al.* 1988, 1990; Slagsvold & Dale 1994). Indeed, time-constrained animals or consumers might use a variety of techniques to decrease the breadth or the depth of their search (Gigerenzer & Goldstein 1996; Luttbeg 2002; Franks *et al.* 2003). Here, we are concerned with speed–accuracy trade-offs that occur when the organism has the information to make the appropriate choice but makes an error because it does not take the time to use the information

correctly. In other words, the subject makes an error of judgement rather than an error of omission.

There have been many studies showing, for example, that organisms can alter their behaviour in response to stress (e.g. hunger or a perceived risk of predation (Milinski & Heller 1978; Dukas & Ellner 1993; Lima 1998)). However, for the most part these are not examples of a speed–accuracy trade-off *per se* because such time-limited animals are not necessarily making errors, rather they are attempting to adjust their behaviour to maximize benefit to cost ratios. For example, a foraging mammal, under the threat of predation, might adjust its search path to stay closer to its burrow (Dall *et al.* 2001) or a consumer may change the breadth of its diet in response to time constraints (Lima 1998). To demonstrate explicitly a speed–accuracy trade-off the subject must be shown to exhibit more or less errors because it is acting more or less quickly. In terms of information processing, a speed–accuracy trade-off is most revealing if the subject has the necessary information to make an appropriate decision but the need for speed causes it to interpret such information erroneously.

Here we investigate a possible speed–accuracy trade-off in decision-making ants. The difficulty in achieving a suitable compromise between a swift decision and an accurate one is likely to be greatest when careful deliberation is required over multi-faceted options, the stakes are high (i.e. the fitness consequences are likely to be large) and many individuals are involved. All three of these issues are manifest in house hunting by complete colonies of social insects (Seeley & Buhrman 2001; Franks *et al.* 2002, 2003). Many attributes of several alternative potential homes may need to be considered while the whole colony is vulnerable because its old nest has been destroyed. Indeed, an insect society, under such circumstances, must simultaneously manage a crisis and rapidly achieve consensus over the best among many possible nest sites (Franks *et al.* 2002, 2003).

To our knowledge, speed–accuracy trade-offs have not been demonstrated before in collective decision making,

\* Author for correspondence (nigel.franks@bristol.ac.uk).

even though they have been predicted (Franks *et al.* 2002). The ant *Leptothorax albipennis* makes collective decisions through quorum sensing in its selection of the best available nest site. Only when the number of nest mates in a potential nest exceeds a quorum threshold do the ants effectively choose that nest by beginning to recruit with maximum speed. The quorum signifies that many ants have concluded independently that the potential nest is a suitable home (Pratt *et al.* 2002).

In this study, we demonstrate and explore a speed–accuracy trade-off by examining the rate of nest choice in both benign and potentially hazardous environments. Can an ant colony speed up its decision making in a hazardous environment and does this compromise accuracy even if it has discovered all of the options?

House hunting by colonies of the ant *L. albipennis* has been intensely studied and is remarkably sophisticated and thorough. For example, Franks *et al.* (2003) have shown that the ants take many attributes of alternative nest sites into account. In these ants, nest choice and colony emigration is a highly structured process that consists of several components: exploration, decision-making and migration. Recent studies have examined, in detail, the various elements of *L. albipennis* nest assessment and choice (Mallon *et al.* 2001; Franks *et al.* 2002, 2003; Pratt *et al.* 2002). For example, individual workers are able to assess the floor area of a potential new nest site (Mallon & Franks 2000; Mallon *et al.* 2001; Mugford *et al.* 2001) and colonies can choose the best nest among many, as determined by a diversity of cues, by using an additive decision-making strategy (Franks *et al.* 2003). Individual scouts hesitate for longer before recruiting their nest-mates if they have encountered a poor nest rather than an excellent one (Mallon *et al.* 2001). When they begin recruiting they do so by the very slow process of forward tandem running in which they typically lead only one nest-mate at a time from the old to the new nest site. Only later, after they have detected a quorum threshold—a sufficient number of nest-mates in a potential new nest—do they switch from recruitment by slow tandem running to recruitment by carrying, which is three times faster (Pratt *et al.* 2002). The choice of the best available nest may be made without individuals directly comparing the alternatives, though such direct comparison may also occur (Franks *et al.* 2002; Pratt *et al.* 2002). After the decision has been made and carrying has begun, the ants may also employ reverse tandem running, in which one ant will lead another from the new nest site back to the old one. The function of forward tandem running is to take nest-mates to the new nest site where they can assess it for themselves and also to teach them the route so that they can also become active recruiters (Möglich 1978; Pratt *et al.* 2002). When an ant is being lead in a tandem run, it can probably learn landmarks (Pratt *et al.* 2001; McLeman *et al.* 2002) but when an ant is being carried its head is in a poor orientation to learn the route. The function of reverse tandem runs may be to show additional ants the (reverse) route so that they can actively help in retrieving nest-mates from the old nest site.

The quorum-sensing procedure, for the switch from slow to fast recruitment, allows the decisions of many members of the colony to be collated (Franks *et al.* 2002; Pratt *et al.* 2002). The number of ants at the quorum

threshold is usually sufficiently high that a single scout would not have recruited them all. Hence, the quorum sensing is a method of gathering information on the ‘opinions’ of others. Nevertheless, individual scouts may sometimes directly compare nest sites and choose the best one (Franks *et al.* 2002; Pratt *et al.* 2002). Thus, in *L. albipennis*, decision making during house selection is a mixture of individual and collective decision making.

The quality of a potential nest site is effectively encoded in the delay before initial recruitment (Mallon *et al.* 2001) and by the time taken to achieve a quorum threshold (Pratt *et al.* 2002). If an ant has found only a low-quality nest site by initially hesitating to recruit at all and then by recruiting only through slow-tandem-running, a lag is built into the emigration process that may enable the colony to find a better alternative new nest site. In other words, the decision-making process in these ants appears actively to employ time-lags, which may favour accuracy (Franks *et al.* 2002). Here we will determine if these ants can speed up their decision making in a harsh environment and if this results in reduced accuracy.

In a series of experiments, we determined if colonies could decide upon a single new nest quicker in harsh rather than benign conditions. We then performed an experiment to examine if greater speed in decision making reduces accuracy.

## 2. METHODS

Sixteen *L. albipennis* ant colonies were collected in Dorset, England, in September 2002. The ant colonies were kept in small Petri dishes of 10 cm × 10 cm × 1.9 cm, with Fluon coated walls to prevent the ants escaping, and housed in nests made by sandwiching a cardboard perimeter (1 mm thick) between two glass microscope slides (50 mm × 75 mm). The nesting cavity was 35 mm × 28 mm, and had an entrance tunnel 3 mm wide and 4 mm long. All experiments were run under diffuse even illumination on a low-vibration bench. The ants were fed with dead *Drosophila* and honey solution and given water to drink *ad libitum*, except during emigrations. For each emigration, each ant colony was placed in a large 22 cm × 22 cm × 2.2 cm Petri dish but only at the start of the experiment, so that no scouts had a prior opportunity to discover the new nest or nests.

### (a) *Can colonies speed-up their decision-making in a harsh environment?*

#### (i) *Experiment 1*

This experiment examined the decision making and emigration behaviour of each of the colonies in both windy (harsh) and calm (benign) conditions. The new nest was placed directly in front of the old one with 6 cm between their entrances. The ants were induced to emigrate by removing the glass roof of their current nest. This event was taken as the start time for the experiment. All new nests were identical to the old nests except that each new nest had a red cellophane cover. For the ants this creates an effectively dark nest but allows the observer to count its occupants.

Benign conditions were created by keeping the lid on the large Petri dish. In addition, a small brush was used to paint some thin lines of water, along the edge of the dish in positions which would not interfere with the nest choice or emigration, to generate a relatively high humidity, estimated with a TFA hygrometer at 50% or 60%.

Harsh conditions were created by using a Petri dish without a lid so that air could be blown over the open old nest. The airflow, generated by a Rena 301 aquarium aerator, was directed over the nest cavity, with the end of the air tube 2 cm above the level of the base of the Petri dish and 6 cm away from the nest. The average airflow was *ca.* 35 ml s<sup>-1</sup>. A clamp was needed to hold the air tube in place. This might also act as a landmark for the emigrating ants (McLeman *et al.* 2002). Hence a similar clamp was placed in a similar position in the calm condition experiments.

Each colony was tested under both conditions, with at least one week between the emigrations. At any one time, two colonies were emigrated, one in the benign and one in the harsh conditions. Each round of testing involved swapping the side of the laboratory bench that each treatment was given on, and changing the experimenter who observed the emigration in each condition; these procedures were taken to remove as many confounding factors as possible. Running each colony in both conditions facilitated a paired data analysis and controlled for possible confounding factors such as different colony sizes and worker to brood ratios etc.

The air stream used to create harsh conditions was such that the ants were almost certain to notice it and it would be a powerful cue that their old nest had been destroyed. Complete nests are probably fairly draft free. There was evidence that the ants, in the open, were affected significantly by the wind, as many workers immediately huddled around items of brood in the exposed old nest, perhaps to protect the brood items, and were far less active than in the calm condition.

#### (ii) *Experiment 2*

This experiment also examined the decision making and emigration behaviour of all of the colonies in both harsh and benign conditions. However, it tested for the generality of the response to harsh versus benign conditions by using a different simulation of a stressful environment. The harsh environment was a simulation of the presence of potential predators. The potential predators of *L. albipennis* include formicine ants such as *Lasius niger* and *Lasius flavus*. Both may produce formic acid as a weapon and/or as an alarm signal (Hölldobler & Wilson 1990). Therefore, we aimed to simulate the presence of predators and hence a harsh environment through the presence of formic acid fumes.

The overall design of the experiment was similar to that in experiment 1, with each colony forced, by the destruction of their old nest, to emigrate to a new nest, 6 cm away from the old one. In this experiment however, all the large Petri dishes were lidded. To create harsh conditions a small plastic vial containing 5 ml of 5% formic acid solution was placed immediately behind the old nest. This vial was capped only with a piece of nylon mesh to prevent any ants entering while the formic acid fumes could diffuse freely from it. In the control, benign environment, an identical vial contained water rather than formic acid. The two vials were placed in the respective large Petri dishes 30 min before the start of the emigration.

Additionally, for safety, the lids of both Petri dishes were made airtight with a thin layer of Vaseline. The procedure and data recording for this experiment were the same as in experiment 1 except that observations were terminated after 1 h. All colonies were tested in both conditions in the same paired design as in experiment 1 above.

In other experiments, we determined that these ants are not killed or apparently harmed by long-term exposure to 5% formic acid fumes. (Earlier work also suggested that such formic acid

was fatal if the ants made contact with it in solution.) But could they detect the fumes and would such fumes form a density gradient within the experimental arenas? To determine this we set up a large Petri dish containing a container of acid, in a position where it would be present in the main experiment. In the Petri dish, we also placed three pieces of damp Whatman pH indicator paper (Type CF cat. no. 2613991). This was used to estimate the rate of diffusion of the acid throughout an experiment. One piece of pH indicator paper was placed where the old nest would be, and two other pieces were placed 10 cm and 18 cm away from the formic acid source. After 35 min, the pH paper placed where the old nest would be in the experiments indicated pH 4, whereas the other two pieces still showed pH 7. After 18 h, all pieces of indicator paper showed a pH of 4. This result shows that the diffusion of the acid fumes was well suited to the duration of the experiments. Leaving the acid in the Petri dish 30 min before the experiment allows the old nest to be within the diffusion gradient of the acid during the emigration, and critically, during the quorum threshold acceptance. Also, the diffusion of the acid is slow enough so that the new nest was unlikely to be significantly contaminated during the decision-making process. It was also observed throughout the emigrations that any ants that approached the formic acid vial antennated rapidly and then quickly ran away: no such comparable behaviour was seen in the presence of a water vial.

#### (b) *Is accuracy impaired by speed?*

##### (i) *Experiment 3*

This experiment was similar in design to experiment 1, using the same windy (harsh) treatment and calm (benign) control, but presented the ants with a choice between two new nest sites. One such nest was of higher quality than the other as shown by Franks *et al.* (2003). Both new nests were dark, with a nest entrance 1 mm wide by 4 mm long and a cavity of 33 mm × 25 mm. The better nest had a cavity with an internal height of 1.6 mm and the worse nest had a cavity only 0.8 mm in height. The ants will colonize both of these nest types if nothing better is available (Franks *et al.* 2003). The new nests were set with their entrances both exactly 6 cm away from the old nest entrance and placed symmetrically in the large Petri dish. The positions of the good and mediocre nests alternated in each subsequent experiment as a further control.

In all three experiments we recorded the following.

- (i) The number of ants in each new nest each minute, and then every 5 min once the number of ants in the new nest rose to more than 20 and our censuses became estimates rather than exact counts.
- (ii) The maximum number of ants observed in the nest within each minute before the onset of carrying. These observations were used to estimate the quorum thresholds.
- (iii) The number of forward and reverse tandem runs to and from each new nest.
- (iv) The time that elapsed between the opening of the old nest and the discovery of a new nest.
- (v) The time that elapsed between the discovery of a new nest and the first carrying of brood or adult nest mates to it.

All recordings were taken over the course of 1 h (unless the emigration was completed in less than 1 h).

In experiment 3, we also recorded: (i) which of the two new nests, good or mediocre, the ants initially accepted (i.e. the one to which they first carried a brood or adult nest-mate); (ii) which

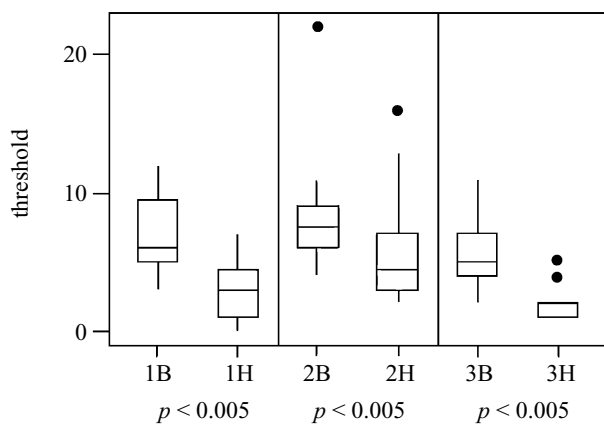


Figure 1. Quorum threshold box plots. Experiment 1, benign and harsh conditions (1B and 1H); experiment 2, benign and harsh conditions (2B and 2H) and experiment 3, benign and harsh conditions (3B and 3H). The horizontal line within the box represents the median. The box encompasses the inter-quartile range, i.e. the middle half of the data (i.e. Q1 to Q3). The whiskers are the lines that extend from the top and bottom of the box to the lowest and highest observations that are still inside the region defined by the following limits: lower limit,  $Q1 - 1.5(Q3 - Q1)$ ; upper limit,  $Q3 + 1.5(Q3 - Q1)$ . Outliers are points beyond these lower and upper limits and are plotted with a filled circle. In each case, in which there is no horizontal line within the box, the median value corresponds to the bottom of the box. The results of Wilcoxon signed rank tests are presented under each experiment. n.s., not significant. See text for details.

nest they chose by the end of the experiment; and (iii) how many adult or brood nest-mates were carried to the mediocre nest in the benign and harsh environments.

### 3. RESULTS

The quorum thresholds associated with the initiation of carrying were significantly lower in the windy conditions than in the calm conditions. In experiment 1, the median quorum threshold for windy and calm conditions was 3 and 6 respectively (Wilcoxon signed rank test,  $N$  for test = 16; Wilcoxon statistic = 129.5;  $p < 0.005$ ; median difference = 4.25; figure 1). It was also significantly lower in acidic conditions than in humid ones. In experiment 2, the median quorum threshold for acidic and humid conditions was 4.5 and 7.5 respectively (Wilcoxon signed rank test,  $N$  for test = 14; Wilcoxon statistic = 89.0;  $p < 0.005$ ; median difference = 2.50; figure 1). In experiment 3 (as in experiment 1), the quorum threshold for the initiation of carrying was significantly lower in the windy conditions (median 2) than in the calm conditions (median 5) (Wilcoxon signed rank test,  $N$  for test = 16; Wilcoxon statistic = 136.0,  $p < 0.005$ ; median difference = 3.5; figure 1). The quorum thresholds for experiment 3 were taken from the first nest accepted; in all but one case this was from the superior nest. In seven out of 16 cases, the quorum threshold was 1 in the harsh conditions whereas it was greater than 1 in all 16 cases in the calm conditions (Fisher's exact test, two-tailed,  $p = 0.00679$ ). Effectively a quorum threshold of 1 might mean that only the deciding ant had visited the nest. Thus in harsh conditions individual

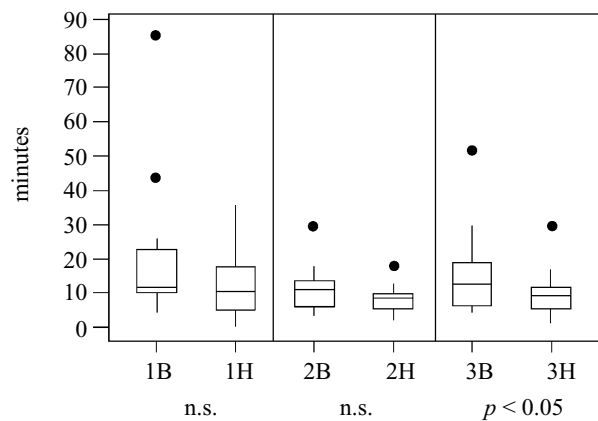


Figure 2. Decision times. The decision time is the period between first discovery and first carrying to a nest. Key to box plots and symbols as in figure 1.

ants may be relying entirely on their own assessments. These results suggest that the ants may be employing a lower quorum threshold in harsh conditions so as to make more rapid decisions.

The median decision times, defined as the period between first discovery and first carrying of an adult or brood nest-mate to a nest, in the nest choice experiment (experiment 3), were significantly shorter in the windy conditions (median 9 min) than in the calm conditions (median 12.5 min) (Wilcoxon signed rank test,  $N$  for test = 14; Wilcoxon statistic = 84.5;  $p < 0.05$ ; median difference = 3.50 min; figure 2). Furthermore, a similar, but not significant, trend to faster decisions in harsher conditions is also seen in both experiments 1 and 2 (see figure 2). The median decision times in experiment 1 were 10.5 min and 11.5 min in the windy and calm conditions, respectively. In experiment 2, the median decision times were 8.5 min and 11.0 min in the acidic and humid conditions, respectively. These results show that the ants, when given a choice, as in experiment 3, do make quicker decisions in harsher conditions. The differences in decision times that we have observed in our laboratory experiments are quite small. In the field the distances between nests is likely to be much larger and this may lead to bigger differences in decision times in harsh versus benign conditions.

In experiment 1, there was significantly more forward tandem running in calm conditions than in windy conditions (Wilcoxon signed rank test,  $N$  for test = 10; Wilcoxon statistic = 51.5;  $p < 0.05$ ; median difference = 1.00; figure 3). This is also seen in experiment 3 (Wilcoxon signed rank test,  $N$  for test = 13; Wilcoxon statistic = 91.0;  $p < 0.005$ ; median difference = 2.50). This is probably associated with the higher quorum thresholds and the longer times over which decisions are made in benign conditions. There is no significant difference in the amount of forward tandem running in humid conditions than in acidic ones (experiment 2). Thus the ants may perceive the windy conditions as harsher than the acidic conditions. This seems to be reflected in the higher quorum thresholds and greater numbers of forward tandem runs in the acidic conditions than in the windy conditions (figures 1 and 2). There was no significant difference in reverse tandem running either between calm and windy conditions

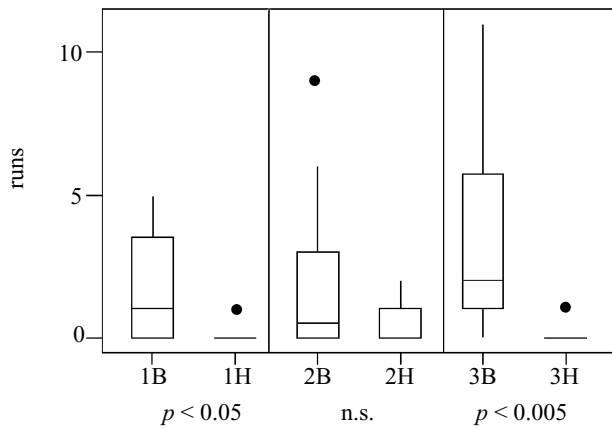


Figure 3. Forward tandem runs. Key to box plots and symbols as in figure 1.

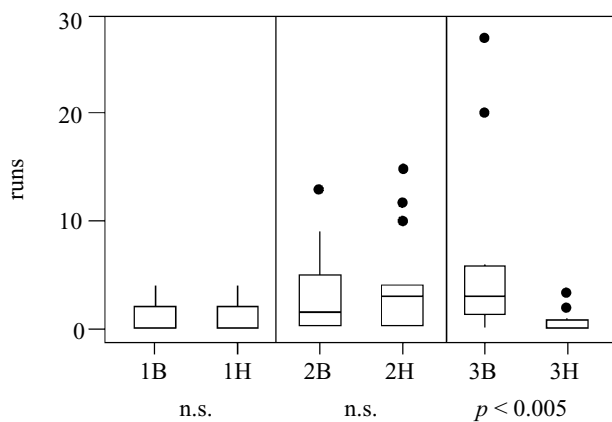


Figure 4. Reverse tandem runs. Key to box plots and symbols as in figure 1.

or between acidic and humid ones (experiments 1 and 2; figure 4). However, there was significantly more reverse tandem running in experiment 3 in the benign rather than the harsh conditions. All reverse tandem runs observed in experiment 3 were from the superior nest. In experiment 3, the median number of reverse tandem runs was three in the benign conditions and zero in the harsh conditions (Wilcoxon signed rank test,  $N$  for test = 13; Wilcoxon statistic = 87.5;  $p < 0.005$ ; median difference = 3.00). Reverse tandem running typically only occurs after carrying has started and therefore has no bearing on this aspect of decision making in nest choice.

In the nest choice experiment (experiment 3) in 30 of the 32 trials, both nests had been discovered before carrying occurred to either. Furthermore, there was no association between the conditions and which nest was discovered first (Fisher's exact test two-tailed  $p = 0.472$ ). In the benign conditions, the better nest was discovered first eight times and the worse nest eight times. In the harsh conditions, the better nest was discovered first five times and the worse nest 11 times. The better nest was accepted first in 31 out of 32 experiments and in all 32 trials the colonies resided in the better nest within 1 h. Thus even in harsh conditions the ants are eventually accurate in their nest choices. However, in this experiment, there was significantly more carrying of brood or adult ants to the worst of the two nests in the windy

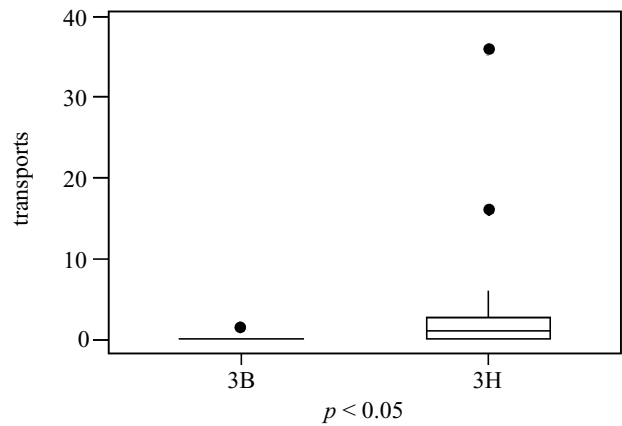


Figure 5. Numbers of adult or brood ants carried to the mediocre nest in experiment 3. Key to box plots and symbols as in figure 1.

conditions than in the calm conditions (Wilcoxon signed rank test,  $N$  for test = 11; Wilcoxon statistic = 59.0;  $p < 0.05$ ; median difference = 1.0; figure 5). In all 11 cases, in experiment 3, in which carrying occurred to the mediocre nest the better nest had already been discovered. Taken together these results show that the ants make faster decisions in harsh conditions and consequentially they are more error prone even though they had discovered all of the alternatives.

#### 4. DISCUSSION

Our experiments demonstrate a classic trade-off between speed and accuracy in decision making. In harsh conditions, the ants employ lower quorum thresholds, and thus decide to accept a nest more individually and quicker. Crucially, we have observed, in the choice experiment (experiment 3), that numerous ants discovered both nests before either was accepted (figure 1). Thus the colonies had information about both nests. Hence their frequent carrying to the mediocre nest in harsh conditions is, at the colony-level, effectively an error of judgement not an error of omission. Moreover, it is a genuine error because both new nests were equidistant from the old one and hence neither nest would involve a less costly emigration. In addition, those items first carried to the mediocre nest later had to be transported to the good one.

The consistent use of lower quorum thresholds in harsh conditions appears to be associated in all our experiments with a trend to quicker decisions. A high quorum threshold favours accuracy in the nest selection process but does so at the cost of speed, as more scouts have to accumulate in a nest site before it is chosen. In harsh conditions, individual ants put less emphasis on collating the 'opinions' of a fairly large sample of their nest-mates. They use lower quorum thresholds and in effect rely more on their own direct assessment of a nest site. In addition, individual ants might decide more quickly and with less information if they are less likely to make direct comparisons of alternative nests in harsh conditions. In benign conditions, individual ants can make direct comparisons between alternative nests (Franks *et al.* 2002; Pratt *et al.* 2002). Thus at the individual level, in harsh conditions,

there may be errors of omission rather than errors of judgement. In benign conditions, the use of a high quorum threshold not only favours collective decision making but it also promotes more sampling by individuals because it creates a time-lag in which they may directly discover better nests. Thus the use of variable quorum thresholds may have dramatic effects on the speed–accuracy trade-off and may influence both colony-level and individual decision making.

In adjusting its speed–accuracy trade-off a colony can vary the importance of choosing the best available nest against the immediate safety of its members. Our laboratory experiments show colonies making speed-dependent errors (e.g. carrying to the inferior nest even when they have discovered the better one first). However, in the field this speed–accuracy trade-off probably represents a good compromise. Essentially, the colonies can balance their long-term and short-term prosperity. In harsh conditions, workers individually choose refuge nests quickly so that nest mates can be swiftly taken out of danger. In benign conditions, workers can collectively choose the best available nest, which may allow colony members to maximize their long-term inclusive fitness.

Slow initial recruitment by forward tandem running is part of the decision-making process. Hence, there was more forward tandem running, when the ants take longer to decide, in benign conditions. In harsh conditions there is less time for tandem running and less is observed perhaps because the quorum thresholds are set lower and/or because the ants also rely more on quick individualist decision making. Our results for reverse tandem running confirm the prediction that reverse tandem running has no role in the decision-making process (Pratt *et al.* 2002).

In the nest choice experiment (experiment 3), all the colonies eventually established themselves in the better of the two available nests even in harsh conditions. This is strong evidence for the overall robustness of the organization of nest choice and emigrations by these ants. Despite the significantly greater amount of carrying to the poorer of the two nests, in the harsh conditions in experiment 3, the ants can quickly re-unite in the better of the two nests. Thus, even though there is a speed–accuracy trade-off in the collective decision making of these ants, they also have an additional mechanism for rectifying their decisions. Even though they might be thought of as using the rule of thumb ‘any port in a storm’, if they find they can cope with the conditions they will latterly all choose the best available nest site. Their decision-making systems are clearly robust, flexible and forgiving (i.e. error tolerant).

The fascinating corollary of our findings is that these ant colonies choose to take their time when they are making decisions over potential nest sites in benign conditions. They could decide quicker but only at the cost of reduced accuracy. The behavioural rules they employ under benign conditions favour accuracy over extreme speed. This is consistent with the very sophisticated additive decision-making strategy employed by these ants when they are house hunting (Franks *et al.* 2003).

We thank Elizabeth Langridge, Jay Denny, Ana Sendova-Franks, Innes Cuthill, Alasdair Houston and Mark Steer for discussions of the issues raised in this paper. A.D. thanks the German Academic Exchange Service (DAAD) for their support. Tragically, Jon Fitzsimmons was killed in a canoeing acci-

dent in July 2003. His co-authors dedicate this paper to his memory. He was a hugely valued friend and, at 22 years of age, his scientific career had only just begun.

## REFERENCES

- Alatalo, R. V., Varlson, A. & Lundberg, A. 1988 The search cost in mate choice of the pied flycatcher. *Anim. Behav.* **36**, 289–291.
- Alatalo, R. V., Lundberg, A. & Rätti, O. 1990 Male polyterritoriality and imperfect female choice in the pied flycatcher, *Ficedula hypoleuca*. *Behav. Ecol.* **1**, 171–177.
- Busemeyer, J. R. & Townsend, J. T. 1993 Decision field-theory: a dynamic cognitive approach to decision-making in an uncertain environment. *Psychol. Rev.* **100**, 432–459.
- Chittka, L., Dyer, A. G., Bock, F. & Dornhaus, A. 2003 Bees trade-off foraging speed for accuracy. *Nature* **424**, 388.
- Dall, S. R. X., Kotler, B. P. & Bouskila, A. 2001 Attention, ‘apprehension’ and gerbils searching in patches. *Ann. Zool. Fennici* **38**, 15–23.
- Dukas, R. & Ellner, S. 1993 Information-processing and prey detection. *Ecology* **54**, 1337–1346.
- Franks, N. R., Pratt, S. C., Mallon, E. B., Britton, N. F. & Sumpter, D. J. T. 2002 Information flow, opinion polling and collective intelligence in house-hunting social insects. *Phil. Trans. R. Soc. Lond. B* **357**, 1567–1583. (DOI 10.1098/rstb.2002.1066.)
- Franks, N. R., Mallon, E. B., Bray, H. E., Hamilton, M. J. & Mischler, T. C. 2003 Strategies for choosing between alternatives with different attributes exemplified by house-hunting ants. *Anim. Behav.* **65**, 215–223.
- Gigerenzer, G. & Goldstein, D. G. 1996 Reasoning the fast and frugal way: models of bounded rationality. *Psychol. Rev.* **103**, 650–669.
- Hölldobler, B. & Wilson, E. O. 1990 *The ants*. Berlin: Springer.
- Lima, S. L. 1998 Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Adv. Study Behav.* **27**, 215–290.
- Luttbeg, B. 2002 Assessing the robustness and optimality of alternative decision rules with varying assumptions. *Anim. Behav.* **63**, 805–814.
- McLeman, M. A., Pratt, S. C. & Franks, N. R. 2002 Navigation using visual landmarks by the ant *Leptothorax albipennis*. *Insect. Soc.* **49**, 203–208.
- Mallon, E. B. & Franks, N. R. 2000 Ants estimate area using Buffon’s needle. *Proc. R. Soc. Lond. B* **267**, 765–770. (DOI 10.1098/rspb.2000.1069.)
- Mallon, E. B., Pratt, S. C. & Franks, N. R. 2001 Individual and collective decision-making during nest site selection by the ant *Leptothorax albipennis*. *Behav. Ecol. Sociobiol.* **50**, 352–359.
- Milinski, M. & Heller, R. 1978 Influence of a predator of the optimal foraging behaviour of sticklebacks (*Gasterosteus aculeatus*). *Nature* **275**, 642–644.
- Möglich, M. 1978 Social organization of nest emigration in *Leptothorax* (Hym., Form.). *Insect. Soc.* **25**, 205–225.
- Mugford, S. T., Mallon, E. B. & Franks, N. R. 2001 The accuracy of Buffon’s needle: a rule of thumb used by ants to estimate area. *Behav. Ecol.* **12**, 655–658.
- Nikolic, D. & Gronlund, S. D. 2002 A tandem random walk model of the SAT paradigm: response times and accumulation of evidence. *Br. J. Math. Stat. Psychol.* **55**, 263–288.
- Osman, A., Lou, L. G., Muller-Gethmann, H., Rinkenauer, G., Mattes, S. & Ulrich, R. 2000 Mechanisms of speed–accuracy trade-off: evidence from covert motor processes. *Biol. Psychol.* **51**, 173–199.

- Pratt, S. C., Brooks, S. E. & Franks, N. R. 2001 The use of edges in visual navigation by the ant *Leptothorax albipennis*. *Ethology* **107**, 1125–1136.
- Pratt, S. C., Mallon, E. B., Sumpter, D. J. T. & Franks, N. R. 2002 Quorum sensing, recruitment, and collective decision-making during colony emigration by the ant *Leptothorax albipennis*. *Behav. Ecol. Sociobiol.* **52**, 117–127.
- Roitman, J. D. & Shadlen, M. N. 2002 Response of neurons in the lateral intraparietal area during a combined visual discrimination reaction time task. *J. Neurosci.* **22**, 9475–9489.
- Seeley, T. D. & Buhrman, S. C. 2001 Nest-site selection in honeybees: how well do swarms implement the ‘best-of-N’ decision rule? *Behav. Ecol. Sociobiol.* **49**, 416–427.
- Slagsvold, T. & Dale, S. 1994 Why do female pied flycatchers mate with already mated males: deception or restricted mate sampling. *Behav. Ecol. Sociobiol.* **34**, 239–250.
- Vitevitch, M. S. 2002 Influence of onset density on spoken-word recognition. *J. Exp. Psychol. Hum. Percept. Perform.* **28**, 270–278.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.