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RESEARCH ARTICLE

Private information alone can trigger trapping of ant colonies in local feeding optima

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ABSTRACT

Ant colonies are famous for using trail pheromones to make collective decisions. Trail pheromone systems are characterised by positive feedback, which results in rapid collective decision making. However, in an iconic experiment, ants were shown to become 'trapped' in exploiting a poor food source, if it was discovered earlier. This has conventionally been explained by the established pheromone trail becoming too strong for new trails to compete. However, many social insects have a well-developed memory, and private information often overrules conflicting social information. Thus, route memory could also explain this collective 'trapping' effect. Here, we disentangled the effects of social and private information in two 'trapping' experiments: one in which ants were presented with a good and a poor food source, and one in which ants were presented with a long and a short path to the same food source. We found that private information is sufficient to trigger trapping in selecting the poorer of two food sources, and may be sufficient to cause it altogether. Memories did not trigger trapping in the shortest path experiment, probably because sufficiently detailed memories did not form. The fact that collective decisions can be triggered by private information alone may require other collective patterns previously attributed solely to social information use to be reconsidered.

KEY WORDS: Group decision making, Organisation, Memory, Ants, Social information, Pheromone trails

INTRODUCTION

Social insect colonies are a major model for understanding decentralised decision making. In a classic paper, Beckers et al. (1990) demonstrated that colonies of the ant *Lasius niger* can adaptively choose the better of two food sources. This is explained as follows: ants feeding at the higher quality food source deposit more pheromone. The attractiveness of pheromone trails increases non-linearly with their strength, so more ants follow the trail to the better food. These ants themselves feed and also deposit pheromone, resulting in a positive feedback cycle, amplifying the difference in recruitment to the two food sources. Such a pheromone-based positive feedback mechanism can lead to rapid collective decisions, but is vulnerable to outdating, as Beckers et al. (1990) demonstrated: if a poor quality feeder is initially provided to the colony, and a good feeder is added later, the ants fail to switch to the new feeder. This is again explained by recruitment initially only taking place to the poor feeder, resulting in a strong pheromone trail. When the higher quality feeder is provided, the colony is incapable

of refocusing its foraging effort, because the established pheromone trail outcompetes any incipient trails to alternative food sources. The ant colony is 'trapped'. This trapping effect has been demonstrated in other ants, and in mathematical models and simulations (Beckers et al., 1990, 1993; Camazine et al., 2003; Czaczkes, 2014; Grüter et al., 2012; Nicolis and Deneubourg, 1999). A very similar process is described in a classic paper by Goss et al. (1989), who showed that Argentine ants, *Linepithema humile*, are capable of choosing the shorter of two routes to a feeder, but are incapable of switching paths if the longer path is provided first. This result was also replicated with *L. niger* (Beckers et al., 1992). Ants may manage to avoid trapping via different recruitment mechanisms (Shaffer et al., 2013), differential pheromone response strengths (de Biseau et al., 1991), spontaneous errors in trail following (Dussutour et al., 2009), or by employing negative feedback mechanisms (Czaczkes, 2014; Grüter et al., 2012) or repellent pheromones (Robinson et al., 2005).

The collective decisions of ant colonies – both their initial decision and the trapping effect – are well explained by pheromone deposition, and many models using only pheromone deposition have duplicated these results (Beckers et al., 1993; Camazine et al., 2003; Czaczkes, 2014; Nicolis and Deneubourg, 1999). However, the ants are considered homogeneous, with no individual differences in information or behaviours, ignoring any potential private information they may have. But ignoring private information may be an oversimplification, and can lead to important group-level effects being missed (Czaczkes et al., 2015a).

Many social insects make extensive use of private information, such as route memory, to guide their behaviour (Collett et al., 2013; Kohler and Wehner, 2005; Mangan and Webb, 2012; Wystrach et al., 2011). Private information has several benefits over social information; memorised routes are often followed more rapidly than pheromone trails, and can be followed at a later date without reinforcement (Collett et al., 2003; Salo and Rosengren, 2001). Collectively, using private information in addition to public information allows ant colonies to make composite collective decisions based on both information sources, distributing their workforce efficiently amongst several food sources in a changing environment (Czaczkes et al., 2015a). Indeed, when private information (e.g. memories) and social information (e.g. pheromones) conflict, many species, including *L. niger*, follow private information preferentially (Aron et al., 1993; Grüter et al., 2011; Harrison et al., 1989), even if the memory is weak and the trail strong (Grüter et al., 2011). A single visit to a food source may suffice for a strong memory to be formed (Grüter et al., 2011; Kohler and Wehner, 2005; Mangan and Webb, 2012). Thus, route memories could just as effectively explain the trapping effect: if many ants have a memory of the original food source, they might ignore incipient trails to new food sources, and continue strengthening recruitment to the original food source. Private information may also restart pheromone-based positive feedback to

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the initial feeder, allowing it to outcompete the new feeder. Here, we repeated two classic trapping experiments: trapping to the poorer of two food sources as in Beckers et al. (1990) and trapping in the longer of two paths as in Goss et al. (1989) and Beckers et al. (1992). However, here we attempted to disentangle the effects of social and private information.

MATERIALS AND METHODS
Study species, housing and maintenance
Eight colony fragments (hereafter 'colonies') of the black garden ant, *Lasius niger* (Linnaeus), were collected from eight different wild colonies on the University of Regensburg campus and housed in plastic boxes (40×30×20 cm) with a layer of plaster of Paris on the bottom. Each box contained a circular plaster nest (14 cm diameter, 2 cm high). Colonies were queenless with 1000–2000 workers and small amounts of brood. Colonies were fed three times per week with Bhatkar diet, a mixture of egg, agar, honey and vitamins (Bhatkar and Whitcomb, 1970). Colonies were deprived of food for 4 days prior to each trial to give high and consistent motivation for foraging and recruitment. Water was provided *ad libitum*. For treatment 3 ('memory removed', see below) an additional colony fragment, also containing 1000–2000 workers, was taken from each of the eight original wild colonies.

Experiment 1 – collective food source choice experiment
The aim of this series of experiments was to reproduce the classical collective food-choice experiment of Beckers et al. (1990), in which *L. niger* colonies were shown to become trapped in exploiting a poor quality food source. In this series of experiments, however, the effects of route memory and trail pheromones on collective decision making were disentangled. The three treatments are largely identical, except that in the first treatment (1 – 'pheromone removed'), pheromone information was removed part-way through the experiment; in the second treatment (2 – 'memory+pheromone'), it was maintained; and in the third treatment (3 – 'memory removed') a separate, naive, colony was given access to the pheromone information of the first colony, resulting in only pheromone information being available initially. Experiments were carried out in one of two rooms with many salient visual landmarks available to the ants. Each colony was tested once a week, and tests were performed in different rooms on alternating weeks, so that each subsequent test on a colony was performed in a different room from the previous test. This was done to minimise memory 'spillover' between experiments. Both rooms were maintained at 21°C.

The initial stages of all three treatments were identical. A colony was given access via a card bridge to a large (28×43 cm) raised plastic-coated platform, covered in clean white paper. The two far corners of the platform were connected via card bridges (2×21 cm) to two circular feeder platforms (5.5 cm in diameter), also covered in paper. Each feeder platform had a 3×3 cm acetate platform, which would later serve as a feeder (see Fig. 1). The ants were allowed to explore the apparatus for 5 min, by which time ants were present on both feeder platforms. After 5 min, drops of 0.5 mol l^{-1} sucrose were placed on one of the acetate feeder sheets, and data collection began 1 min later. A photograph of each feeder platform was taken every 2 min for 15 min. Sucrose was reapplied as necessary, to ensure that all ants could feed when arriving at the platform. Three to five of the first few ants to reach the feeder were individually marked with a dot of acrylic paint on the abdomen. This allowed us to record the number of return visits the marked ants made to the feeder platforms in the first 15 min of the trial.
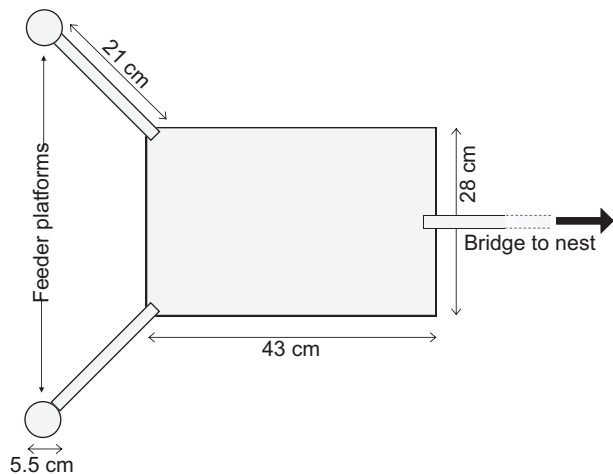

Fig. 1. Experimental setup for experiment 1. For the first 15 min, 0.5 mol l^{-1} sucrose solution was provided on one feeding platform. Afterwards, in treatment 1 (pheromone removed), ants were removed from the platform, the paper covering the setup was replaced, and the setup was cleaned with ethanol. The 0.5 mol l^{-1} sucrose solution was replaced and 1 mol l^{-1} solution was placed on the other feeder. The colony was once again given access to the platform and observed for a further 30 min. Treatment 2 followed the same protocol but the paper was retained and the setup was not cleaned. For treatment 3, a 'follower' colony was given access to the setup after it had been cleaned to remove any trail pheromone present.

After 15 min, the sucrose was removed, as was the bridge allowing the colony access to the platform. All the ants on the apparatus were replaced in their plastic box. One of the three different treatments was then applied.

Treatment 1 – pheromone removed
The paper covering the platform and feeder platforms, and the bridges connecting the platform to the feeders were discarded, so as to remove any pheromone that had been deposited. This method has been used in previous experiments, and produces reliable behavioural changes (Czaczkes et al., 2013). In case any pheromone had seeped through the paper, the platform, feeding platforms and acetate feeder sheets were cleaned with ethanol. Lastly, fresh paper was placed over the platform and feeder platforms, providing an identical substrate to that in the first half of the experiment, and covering any traces of pheromone that may have remained. Fresh card bridges were used to reconnect the feeder platforms to the main platform; 0.5 mol l^{-1} sucrose solution was reapplied to the same feeder, and similar drops of 1 mol l^{-1} sucrose were placed on the other feeder platform. The original card bridge was used to reconnect the ant colony with the platform, and a photograph of each feeder platform was again taken every 2 min for 30 min. Marked ants, when found, were removed from the colony, to avoid confusion with other marked ants in future experiments. After 30 min the experiment was ended, all the ants were replaced in the box, and the apparatus was again cleaned with ethanol.

Treatment 2 – memory+pheromone
This treatment was identical to treatment 1, except that the old, marked, paper overlays were reused, and the platforms were not cleaned with ethanol. The ants were, as above, removed from the apparatus, and only allowed access again once food was present on both feeder platforms. Data collection proceeded as described for treatment 1.

Treatment 3 – memory removed
As it is not possible to remove the memories of the ants, we used a two-colony fragment design, with one colony fragment acting as

a 'pheromone trail donor', and a second colony fragment acting as a 'follower', as in previous experiments (Czaczkes et al., 2011; Evison et al., 2012). Paired colony fragments were collected from the same wild colony, and so constituted two fragments of one colony. Workers moved from one fragment to another elicit no aggression, while workers from other source colonies are immediately attacked. This demonstrates that the two fragments can effectively be considered the same colony.

The first part of the experiment (as detailed above) was carried out by the 'pheromone trail donor' colony. After 15 min, the ants were removed, and the paper overlays and card bridges retained. The apparatus was not cleaned with ethanol. Instead of reconnecting the donor colony to the platform, we connected the follower colony. Data collection proceeded as described for treatment 1. A few minutes before the first 15 min phase came to an end, 5–10 ants from the follower colony were allowed to feed at a separate 0.5 mol l^{-1} feeder and return to the nest, so as to perform physical recruitment displays and alert the follower colony ants to the presence of food, and ensure they were in the correct motivational state, as motivational state can affect pheromone following behaviour (Czaczkes et al., 2013; Witte, 2001).

Each colony was tested twice in each treatment: once with the 0.5 mol l^{-1} feeder on the right and once with it on the left, resulting in 16 trials per treatment, and 48 trials in total.

Experiment 2 – collective path choice experiment

The aim of this series of experiments was to reproduce the collective path choice experiment of Goss et al. (1989) and Beckers et al. (1992), in which *L. humile* and *L. niger* colonies were shown to become trapped in using an established longer path to a food source, when a new, shorter path is presented. In this series of experiments, however, we attempted to disentangle the effects of route memory and trail pheromones on collective decision making.

The methods used in this experiment were effectively identical to those used in experiment 1, except that instead of two feeders of different qualities, a diamond maze with two paths of different lengths leading to one feeder was used (see Fig. 2). The maze was based on those used by Beckers et al. (1992), Goss et al. (1989) and, more recently, Dussutour et al. (2004, 2006). The long (poorer) path

was provided for the first 15 min, and both paths were provided for the remaining 30 min. The three treatments described in experiment 1 were applied: pheromone removed, memory+pheromone and memory removed.

Statistical analysis

The statistical analysis of experiments 1 and 2 was identical. For convenience, we describe the analysis for experiment 1 only.

The number of ants on each feeder platform was counted every 2 min from the photographs. Only data from the second phase of the experiments (after the 1 mol l^{-1} sucrose was provided) were analysed, although data from both stages are presented in the figures. Statistical analysis was carried out in R 3.1.0 (R Core Team, 2012). First, to test whether colonies became trapped, the proportion of ants on the poor (0.5 mol l^{-1}) feeder was averaged. For each treatment, we tested whether the average proportion was different from 0.5 using a two-tailed sign test (H_0=0.5).

To compare the behaviour of colonies between treatments, we used generalised linear mixed-effect models, in the LME4 package (Bates et al., 2014), with a Gaussian distribution family. Proportion data were logit-transformed, following Warton and Hui (2001) and Shi et al. (2013). All the data points collected from the last 30 min of each experiment were used. We added time as an additional explanatory effect, and trial nested inside colony as random effects. As the proportion of ants on the two feeders adds up to 1 for any one point in time, we only analysed the proportion of ants on the originally presented poor feeder. The model formula was thus:

$$\text{Proportion of ants on poor feeder}$$
$$= \text{treatment} \times \text{time} + (\text{random effect: colony/trial}).$$

In experiment 2, we adjusted the number of ants by the length of the paths, as the longer path has more area, and thus both can contain more ants and retains ants that travel along it for longer. As the longer path was 1.4 times longer than the short path, the number of ants on the long path was adjusted by dividing by 1.4. The number of ants on the short path was not adjusted. Adjusted proportions were thus calculated from the adjusted number of ants.

As we had no *a priori* expectations about effect sizes, effective sample sizes (i.e. the number of colonies used) were chosen based
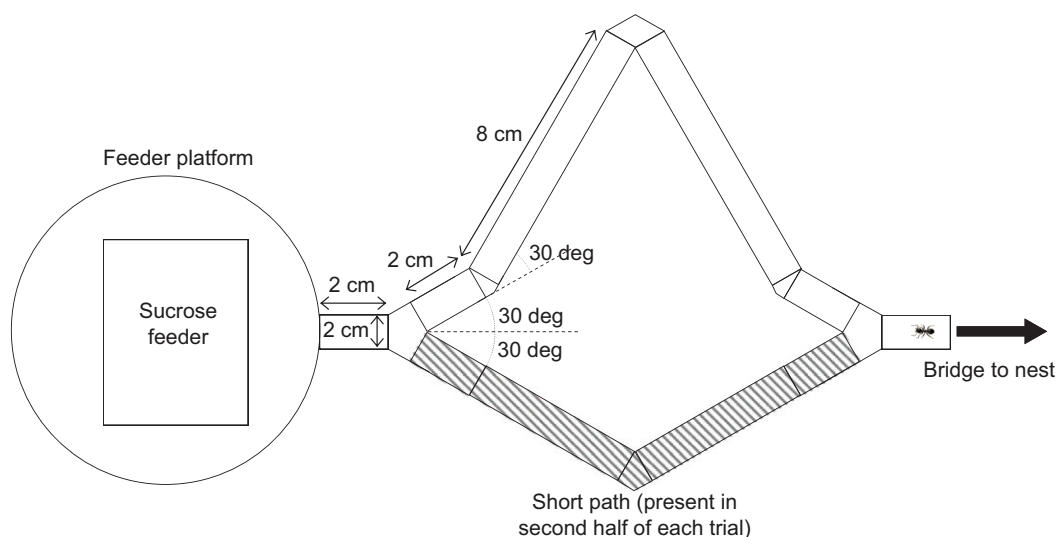

Fig. 2. Experimental setup for experiment 2. For the first 15 min of the experiment, the maze consisted of only the long path (unshaded area). After minute 15, the first maze was replaced by a complete maze, including the short path (shaded). The figure, including the image of the ant, is to scale.

on practicability and availability of colonies, rather than power-related considerations. No data were excluded from the study. The order in which each colony experienced each treatment was pseudo-randomised, providing an even distribution of treatment order between colonies.

Ethical statement

All work reported here complies with the rules and guidelines of the country in which the experiment was carried out. No explicit ethical committee approval was needed.
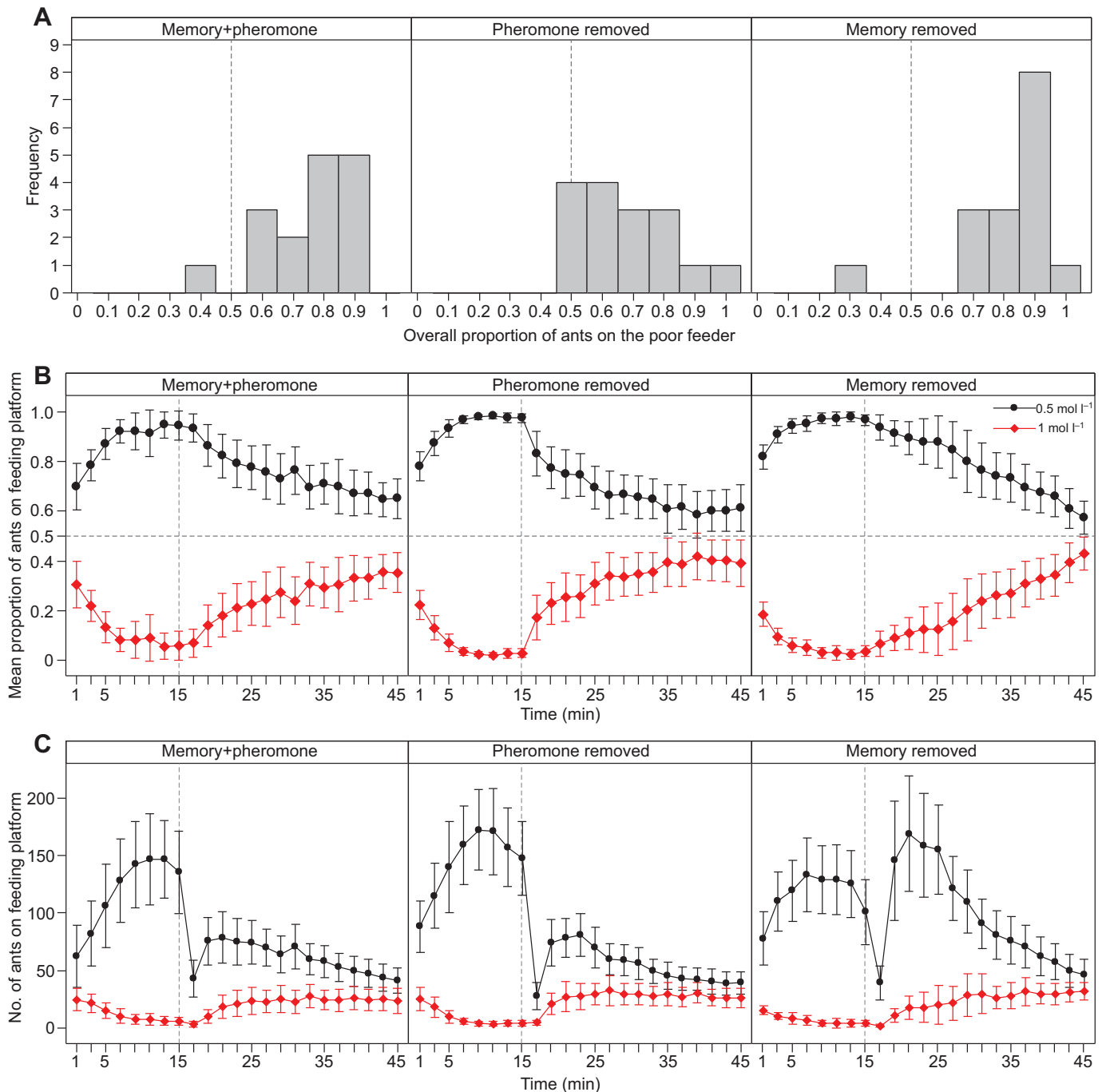

Fig. 3. Experiment 1: collective food source choice. (A) The overall proportion of ants on the poor (0.5 mol l^{-1}) feeder platform for each trial. The proportion of ants on the poor feeder platform every 2 min, for 30 min after the good (1 mol l^{-1}) feeder was added, was averaged to form a measure of whether the colony became 'trapped' in that trial. In only two of 48 trials was there a higher average proportion of ants on the good feeder. (B) Mean proportion of ants on each feeding platform. Here, 1 mol l^{-1} food was only provided after minute 15 (vertical dashed lines); prior to this time (left of the dashed line) there was no food on this platform. Symbols represent means±95% confidence interval (CI). (C) Mean number of ants on each feeding platform. As an unfed colony was used after minute 15 in the 'memory removed' treatment, their satiation is lower, resulting in more ants on the feeder. The decline in ant numbers between minutes 15 and 17 is due to all ants being removed from the setup at minute 15. Eight colonies were tested, and each colony was tested twice in each treatment: once with the poorer feeder on the left, and once with it on the right.

RESULTS
Experiment 1 – collective food source choice

In almost all trials, over all three treatments (pheromone removed, memory removed and memory+pheromone), the colonies remained trapped, with a higher proportion of ants exploiting the 0.5 mol l^{-1} feeder after a 1 mol l^{-1} sucrose source was made available (two-tailed sign tests, H_0=0.5, $P \leq 0.0005$ in all three treatments; see Fig. 3A).

Significant differences were found between all three treatments, in terms of the proportion of ants exploiting the poor (0.5 mol l^{-1})

feeder: a higher proportion of ants exploited the poor feeder in the memory removed treatment, followed by the memory+pheromone treatment and finally the pheromone removed treatment (Z>2.17, P<0.030; see Fig. 3B). Because a new colony was used after the first 15 min of the memory removed treatment, satiation was lower and thus the absolute number of ants was higher in the second half of this treatment (Fig. 3C). Comparisons between the memory removed and the other treatments should be made with caution. For example, the apparently stronger recruitment immediately after minute 15 in the memory removed treatment (see Fig. 3C) is due to lower
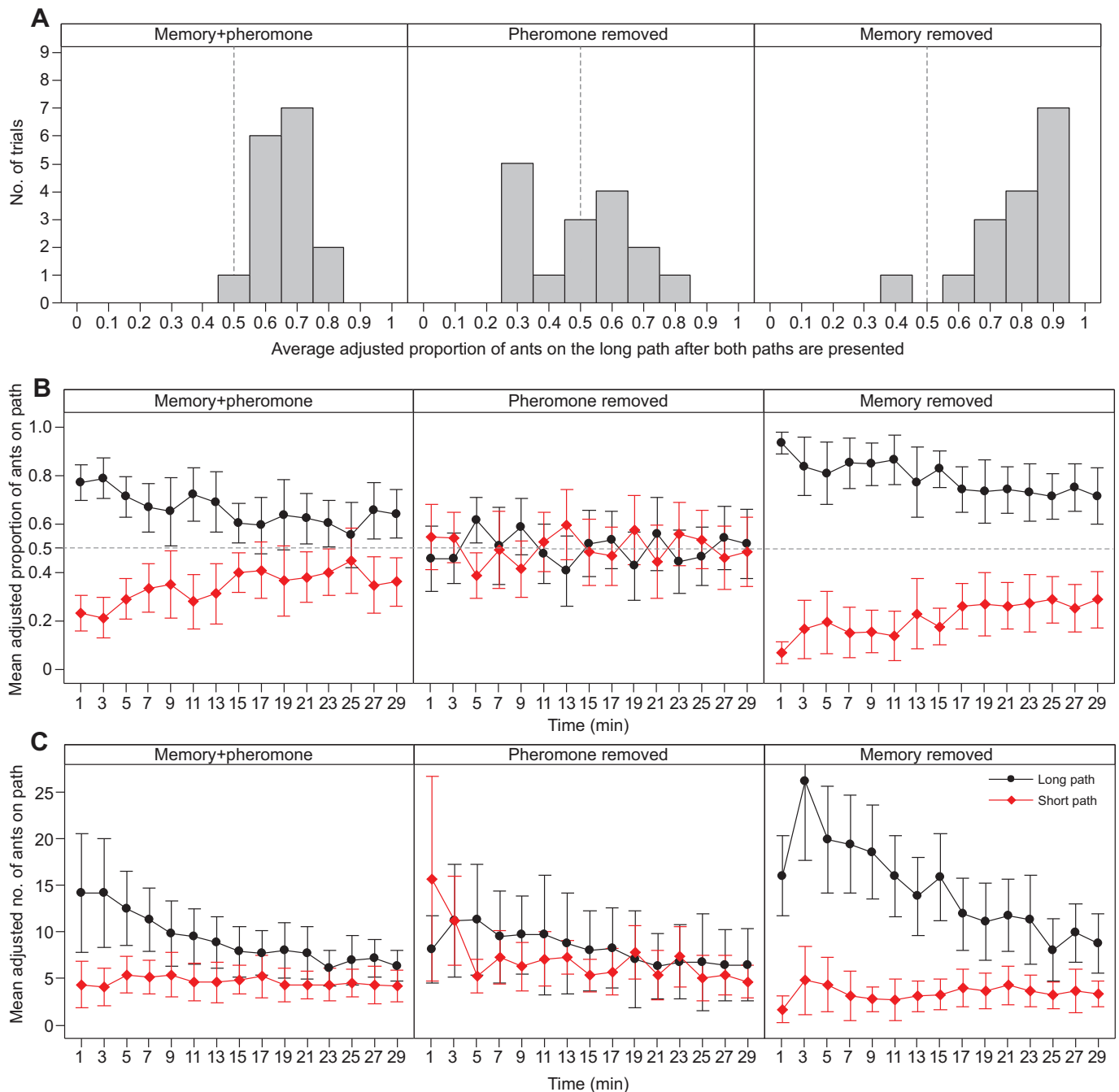

Fig. 4. Experiment 2: collective path choice. (A) The overall proportion of ants on the long path for each trial. The proportion of ants on the long path every 2 min, for 30 min after the short path was added, was averaged to form a measure of whether the colony became trapped in that trial. (B) Adjusted proportion of ants on each path every 2 min, according to treatment. Note that only data for the last 30 min, when both paths were present, are shown. Symbols are means±95% CI. (C) Adjusted number of ants on each path every 2 min, according to treatment. Eight colonies were tested, and each colony was tested in each treatment.

satiation in that treatment at that time. While not ideal, this is unpreventable, as providing the ants with food prior to the experiment, to equilibrate hunger levels across the treatments, would cause memories of that food location to be formed. The marked ants made on average 1.38 (s.d. 0.67) return visits to the original feeder before the second feeder was provided.

Experiment 2 – collective path choice

The mean adjusted proportion of ants on the long path differed significantly from 0.5 in the memory+pheromone (median=0.666, P=0.0005) and memory removed (median=0.810, P=0.0005) treatments (see Fig. 4A). However, the mean adjusted proportion of ants on the long path was not different from 0.5 in the pheromone removed treatment (median=0.523, P=1.0). The mean adjusted proportion of ants on the long path was highest in the memory removed treatment, followed by the memory+pheromone treatment, and lowest in the pheromone removed treatment (see Fig. 4B,C). All pairwise comparisons were significant (Z>2.87, P<0.0026). The marked ants made on average 1.13 (median 1, s.d. 0.82) visits to the food source via the long path before the short path was introduced.

DISCUSSION

Our results demonstrate that an iconic phenomenon in collective decision making – trapping in local optima – can occur even after existing social information (trail pheromones) is removed. Even without pheromones present, when the new feeder was introduced, colonies not only failed to choose the higher quality food source but also preferentially exploited the poorer food source. Although the ability of ants to collectively choose a 1 mol l^{-1} over a 0.5 mol l^{-1} feeder is not perfect (Beckers et al., 1990), we would still expect different results in the memory only experiment if private information played no role in colony choice. The ants appear to be in the process of 'switching' to the new food source (Fig. 3B), but this is driven mostly by a reduction in the number of ants exploiting the 0.5 mol l^{-1} feeder, not by an increase in ants exploiting the 1 mol l^{-1} feeder (Fig. 3C). Thus, satiation, not switching, probably explains this apparent switching process. Because of satiation, lack of recruitment and low ant numbers at minute 45, it is highly unlikely that switching would have occurred if the experiment had run longer. It is also conceivable that this difference was to some extent a side-effect of cleaning the platform with ethanol in the pheromone-removed treatment, although the platforms were allowed to dry after ethanol washing.

We did not carry out a treatment in which both memory and pheromones were removed, and thus in principle some unexplained mechanism apart from memory or pheromones may also explain the collective patterns found in all three treatments. However, we can conceive of no other mechanism that would result in the predictable and strong collective decisions we describe. We thus remain confident that memories or trail pheromones were responsible for triggering the trapping observed in our experiments.

We showed that the trapping effect can occur even if the existing pheromone trail is removed, leaving only the memory of the food location as the trigger. *Lasius niger* have robust memories that can last at least 24 h (Czaczkes et al., 2014). In another ant that relies on aphid farming, *Formica rufa*, memories of specific feeding sites may be reactivated after months of winter dormancy (Rosengren and Fortelius, 1986). In our experiment, memories may have seeded a difference in recruitment after the second feeder was presented, allowing pheromone-based positive feedback to amplify this difference. However, because in this species memories are followed over pheromones when the two conflict (Grüter et al., 2011),

the trapping effect may have remained had no pheromones ever been laid.

Assuming that memorisation is stronger or quicker with stronger rewards (Al Toufailia et al., 2013), private information could also explain the initial collective choice. Indeed, ants that do not recruit at all still forage preferentially on the best of multiple food sources (Dussutour and Nicolis, 2013).

In contrast to the results of experiment 1, we found no evidence that memory triggered trapping in collective path use (experiment 2). This is perhaps not surprising as Beckers et al. (1992) report that the likelihood of ants taking one path to a food source is not affected by whether they took that path on a previous visit. Why are the results of two seemingly similar situations so different? We believe that the methods used in experiment 2 were flawed, in that we had in fact failed to achieve memory formation at the bifurcation point of the maze. Route memories in ants are formed in stages. During the first few visits to a food source, path integration is used to calculate the general heading and distance required to return to the nest (Collett et al., 2013). The currently accepted model of how ants learn and navigate a route involves holistically learning views along the entire route. When retracing a route, the current view seen by the ant is judged for familiarity against the holistic memory, and the ant turns towards the most familiar view (Baddeley et al., 2011, 2012; Knaden and Graham, 2016; Kodzhabashev and Mangan, 2015; Wystrach et al., 2013). Ants can also home towards specific landmarks in an otherwise unfamiliar location (Wystrach et al., 2011; Zeil et al., 2014). This model of ant navigation is, however, based on the behaviour of solitary foraging desert ants, which rely solely on private information for navigation. *Lasius niger* may be slower to learn complex routes than desert ants, and have been shown to struggle to learn doubly bifurcating routes (Czaczkes et al., 2013), making many mistakes on the first bifurcation, even after six return visits to a food source via the same path. This may well be due to an aliasing problem, with the view from the first and second bifurcations being very similar, but requiring opposite directions to be taken.

In experiment 2, the marked ants had made on average 1.13 visits to the food source in the first 15 min. One visit to a food source is sufficient for ca. 75% of *L. niger* ants to make a correct decision at a single T-bifurcation (Grüter et al., 2011), but is not enough for ants to correctly learn an intermediate turn in a doubly bifurcating maze (Czaczkes et al., 2013). We strongly suspect that in experiment 2 the ants had not formed a strong enough memory to be able to reliably use it for navigation. Specifically, as the turn made at the bifurcation is reversed half-way along the maze, this would produce very similar panoramic views to a turn in the opposite direction at the bifurcation entrance, because of the small size of the maze setup relative to the size of the room. This in turn would cause strong uncertainty about which view from the bifurcation is most familiar. This is in contrast to experiment 1, where the view when approaching the two food sources is very different, and becomes more different as the ants travel further away from the nest, allowing ants many opportunities to correct their path. Thus, while we attempted to test the role of memory in collective path selection and path trapping, we failed to elicit the formation of an appropriate memory directing the ants along the long path. Another, not mutually exclusive possibility is that the ants were also using path integration-based navigation, which is often used in the first few visits of ants to a food source (Collett and Collett, 2000). This would result in ants at the bifurcation being drawn straight ahead, leading to a random choice between the two routes. Hence, we would urge readers not to conclude that trapping in the use of a non-ideal route could not be driven by route memories. Ideally, the ants in

experiment 2 would have been allowed to make at least five return visits via the long path before the presentation of the short path, allowing well developed memories to form (Czaczkes et al., 2013). However, this was not possible, as the colony satiates within ca. 45 min of *ad libitum* feeding (see Figs 3C and 4C), and foragers would not manage to make five return visits in that time. It is also unlikely that adding more, or more salient, landmarks would increase learning speed (Grüter et al., 2015).

Instead of attempting to demonstrate collective trapping in the use of a long path, one could demonstrate trapping in the exploitation of a more distant feeder. Experiments and simulation have shown that ants can preferentially exploit closer food sources (Detrain et al., 1999; Dussutour et al., 2009). A similar setup to that described in experiment 1 could be used, but with the two feeders offering a sucrose solution of the same molarity, and the initially presented feeder being more distant than the second feeder.

When studying collective decision making, there is a strong tendency to simplify individual agents. However, without taking into account individual complexity or differences in knowledge or abilities, collective behaviour patterns may be misinterpreted, or missed altogether (Czaczkes et al., 2015a; Jandt et al., 2015; Schürch and Grüter, 2014). Private information, and individual differences, can have a profound effect on collective decision making and group behaviour (Aplin et al., 2014; Couzin et al., 2005; Herbert-Read et al., 2013; Jandt et al., 2015; Michelena et al., 2010). A reliance on private over social information will be especially advantageous when expert individuals are present, and when there is a danger of information cascades (Conradt, 2011; Rieucau and Giraldeau, 2011). Relying on private information, alone or coupled with social information, also allows different group members to make different decisions (Czaczkes et al., 2015a; Schürch and Grüter, 2014). Individual decisions can be to some degree independent of the decisions of other group members. The group decision comprises both the individual and collective decision-making mechanisms, and groups are not confined to making consensus decisions; rather, each individual can make their own personal decision. This may allow a group to utilise resources more efficiently in situations where a consensus is not required (Czaczkes et al., 2015a; Schürch and Grüter, 2014; Sueur et al., 2011). The utilisation of social information together with other information sources seems to be the rule, not the exception, for both individuals and groups (Beauchamp et al., 1997; Czaczkes et al., 2015b; Rieucau and Giraldeau, 2011; Templeton and Giraldeau, 1996). Private information should thus always be considered explicitly when explaining collective decision making in groups.

Author contributions
T.J.C. conceived the project, analysed the data and wrote the manuscript. A.K.S. collected the data for experiment 1. F.A.M.K. collected the data for experiment 2. J.H. revised the manuscript and assisted with experimental planning. All authors approved the manuscript.

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