

## RESEARCH ARTICLE

# Experience, corpulence and decision making in ant foraging

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### SUMMARY

**Social groups are structured by the decisions of their members. Social insects typically divide labour: some decide to stay in the nest while others forage for the colony. Two sources of information individuals may use when deciding whether to forage are their own experience of recent task performance and their own physiology, e.g. fat reserves (corpulence). The former is primarily personal information; the latter may give an indication of the food reserves of the whole colony. These factors are hard to separate because typically leaner individuals are also more experienced foragers. We designed an experiment to determine whether foraging specialisation is physiological or experience based (or both). We invented a system of automatic doors controlled by radio-tag information to manipulate task access and decouple these two sources of information. Our results show that when information from corpulence and recent experience conflict, ants behave only in accordance with their corpulence. However, among ants physiologically inclined to forage (less corpulent ants), recent experience of success positively influenced their propensity to forage again. Hence, foraging is organised *via* long-term physiological differences among individuals resulting in a relatively stable response threshold distribution, with fine-tuning provided by short-term learning processes. Through these simple rules, colonies can organise their foraging effort both robustly and flexibly.**

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### INTRODUCTION

Division of labour is found at many levels in biological organisation; it occurs within cells, between cells within tissues, between organs within organisms, and within societies such as our own and those of social insects (de Sousa Lopes and Roelen, 2010; Hix et al., 2009; Maynard-Smith and Szathmáry, 1998; Oster and Wilson, 1978; Vickaryous and Hall, 2006). Where division of labour occurs, the tasks required for the function of the higher level of organisation (e.g. society) are unevenly distributed among the component parts (e.g. individuals). Key issues include the level of specialisation, the process of task allocation, and the mediation of flexible responses to changes in task demands. Social insect colonies are often organised from the bottom up – with workers deciding flexibly for themselves what to do next on the basis of both their own task response thresholds and socially derived information (Amdam and Omholt, 2003; Beshers and Fewell, 2001; Franks and Tofts, 1994; Gordon, 1996; Robinson, 1987). One important decision is whether to stay in the nest or to leave it to forage, a task essential for colony survival but risky for the individuals involved (Richardson et al., 2011; Richardson et al., 2010). In the present study, we analysed the foraging decisions that underpin this division of labour, and analysed, within a social context, the relationships between response thresholds, experience and individual nutritional physiology.

For solitary animals, the decision to forage is driven primarily by the animal's nutritional needs, modulated by environmental factors, e.g. predators or weather (Lima and Dill, 1990; Stephens

et al., 2008). For animals living in family groups, decisions are more complex. Animals may forage not just to meet their own needs, but also to provide for others, e.g. offspring or mates (Hinde and Kilner, 2007; McCarthy and Ball, 2008). Providing for others is taken to extremes in the eusocial insects, such as bees, wasps, ants and termites, in which a minority of individuals may supply the whole colony, while others stay in the nest. Environmental factors such as temperature (Ruano et al., 2000) and light intensity (Narendra et al., 2011) are important in regulating foraging in social insects. Beyond these factors, social insect foragers must cater for the needs of many individuals, and so the colony needs to be able to modulate its foraging effort when demands change. Colony-level flexibility can be facilitated by a distribution of response thresholds to the foraging stimuli (e.g. returning ants or brood hunger signalling). Usually, only low-threshold individuals will forage and the food they provide will keep the stimulus level low, but when demand increases, the stimulus level will reach the foraging thresholds of more individuals, so the foraging workforce will increase (Bonabeau and Théraulaz, 1999; Robinson, 1987). Task specialisation may be enhanced further if individuals have response thresholds that change according to experience such that the threshold for a particular task decreases after that task has been performed (Ravary et al., 2007; Théraulaz et al., 1998). Threshold adjustment could be mediated quickly by learning from experience or more slowly through physiological changes, such as laying down fat reserves or activating glands (Franks and Tofts, 1994; Robinson, 2009). However, memory

carries primarily individual-specific information (though acquired in a social context) whereas fat reserves may carry information about the state of both the individual and the colony, in terms of how much food has been available recently.

To investigate foraging decisions and the roles played by physiological state and recent experience, we used the ant *Temnothorax albipennis*, in which an individual's corpulence (fat reserves) correlates strongly and negatively with its likelihood of foraging (Blanchard et al., 2000). Similar correlations are seen in several other social insects (Ament et al., 2008; O'Donnell and Jeanne, 1995; Porter and Jorgensen, 1981; Toth and Robinson, 2005; Yang, 2006). In *T. albipennis*, previous work shows that this relationship cannot be explained as a side effect of differences in age, location within the nest or general activity level (Robinson et al., 2009a; Robinson et al., 2009c). In addition, this relationship between leanness (low corpulence) and foraging is not merely triggered by hunger in these ants, because lean ants that have collected food pass this food to nestmates by trophallaxis, remain lean and continue to forage (Robinson et al., 2009c). This suggests the hypothesis that ants could base their decision to forage on a flexible response threshold linked to their corpulence level, i.e. foraging when the stimulus to forage reaches this threshold. This is supported by the finding that when demand for foragers is increased, the ants which respond are the leanest of the remaining ants, irrespective of their age or previous spatial position in the nest (Robinson et al., 2009a). However, if lean ants are more likely to forage, they will naturally build up foraging experience. In natural situations these lean, experienced ants could base their decision to forage either on their corpulence or on their memory of foraging experience, or both.

To separate the effects of these usually correlated properties (corpulence and foraging experience), we designed an experiment in which an ant's corpulence and recent experience provide conflicting information. We used automatic doors combined with radio-frequency identification (RFID) technology to manipulate which ants were able to leave the nest to forage during a setup period, to create a negative correlation between the recency of foraging success and leanness (low fat reserves). During a test period we then assessed whether the ants that left the nest were the leanest or those with recent foraging success, given that we had experimentally decoupled these factors. This experiment allowed us to test whether individuals rely more on highly flexible short-term personal information or use socially influenced physiological cues that change more slowly when deciding whether to forage, and thus whether foraging is a physiological specialisation, an experience-based behavioural specialisation or whether both act in combination.

## MATERIALS AND METHODS

### Experimental colonies

Nine complete queenright *Temnothorax albipennis* (Curtis) colonies were collected from Dorset, UK, in April and July 2009. Colonies were maintained in the laboratory according to established protocols (Franks et al., 2006). Five colonies were used for the main experiment and four colonies were used for the calibration of corpulence measurements. Colonies included brood of all stages (eggs, larvae, pre-pupae and pupae).

For each experimental colony, we tagged every worker with an RFID microtransponder (500×500×120 µm, mass 89 µg; PharmaSeq, South Brunswick Township, NJ, USA) glued to the thorax using established protocol (Robinson et al., 2009b; Robinson et al., 2009c). We then photographed each ant [Canon EOS-1 Ds Mark II camera (Reigate, Surrey, UK) with a 100mm macro lens

and a ring flash] on a background with a printed scale, in order to measure its gaster width to assess pre-trial corpulence (see Corpulence calibration). An RFID reader was also used to record the RFID microtransponder for each ant, so its identification (ID) could be matched to its corpulence. RFID readers (PharmaSeq) comprised a Hitachi HL6738MG laser that provided 35 mW of energy to the passive tags and an antenna to detect the radio ID signal (Robinson and Mandecki, 2011).

### Exit control system

For each trial, the tagged colony was then allowed to move into a nest with an automatic RFID-controlled door (Fig. 1), placed in a 23×23 cm arena. The door was magnetically held in the open position while the ants transported the brood and queen into the nest. Once all of the brood was inside, the door was activated. From this time, ants attempting to leave the nest passed under an RFID reader, which read and recorded their RFID tag and then opened the door for 7 s, allowing the ant to pass through into the entrance corridor. A second reader at the far end of the corridor recorded the ant as it actually entered the foraging arena (Fig. 1A). For the RFID-controlled door, there was a 'permitted' list and a 'denied' list of ant IDs. Only ants on the 'permitted' list (initially all ants) could open the door and leave the nest. When any ant returned to the nest, its movement down the entrance corridor was detected by a webcam (Logitech Quickcam Communicate Deluxe, Slough, Berks, UK) and this opened the door again for 7 s, allowing the ant to re-enter the nest chamber. After an ant was recorded by the RFID reader and passed through the door, there was an insensitive period during which the motion sensing was inactive (6 s), to prevent the door re-opening behind the departing ant. Similarly, when the motion sensor had opened the door, there was an insensitive period (6 s) during which the RFID reader recorded the ant as it entered the nest chamber, but did not re-open the door behind the ant.

There were two ways that ants might avoid operating the RFID-controlled door but still exit the nest. One way was to 'tailgate' through after a departing ant that had opened the door; the other way is to go 'contraflow' when an entering ant had opened the door. We minimised these two problems by tuning the duration of the door-open time and the insensitive periods during preliminary experiments. We optimised these time periods to give one ant enough time to pass through the door, but not enough time for a second ant to 'tailgate' through after it or to push past in 'contraflow'. The corridor was the width of one ant to prevent ants passing one another. In addition, if an ant on the 'denied' list was detected trying to leave the nest, the door was closed immediately and automatically (if it was open) and remained closed for 7 s. These precautions eliminated all 'contraflow' exits and reduced the 'tailgating' rate to just 1.4%. Ants that tailgated during the experiment were excluded from the analysis.

The motion-sensing software was Webcam Zone trigger 2.380, Pro Edition (Omega Unfold, Greenfield Park, QC, Canada). LabVIEW 8.5 software (National Instruments, Newbury, Berks, UK) was used for taking inputs from Zone Trigger and from the RFID readers and providing the appropriate output to control current to a solenoid which, when active, magnetically opened the door (Fig. 1B).

### Experimental protocol

Each trial began with 2 days of exploration ('pre-set-up exploration period') for the colony to settle in to their new nest and explore the arena (Fig. 1C). All ants were initially on the 'permitted' list, so could exit and enter the nest freely. Water was available, but no

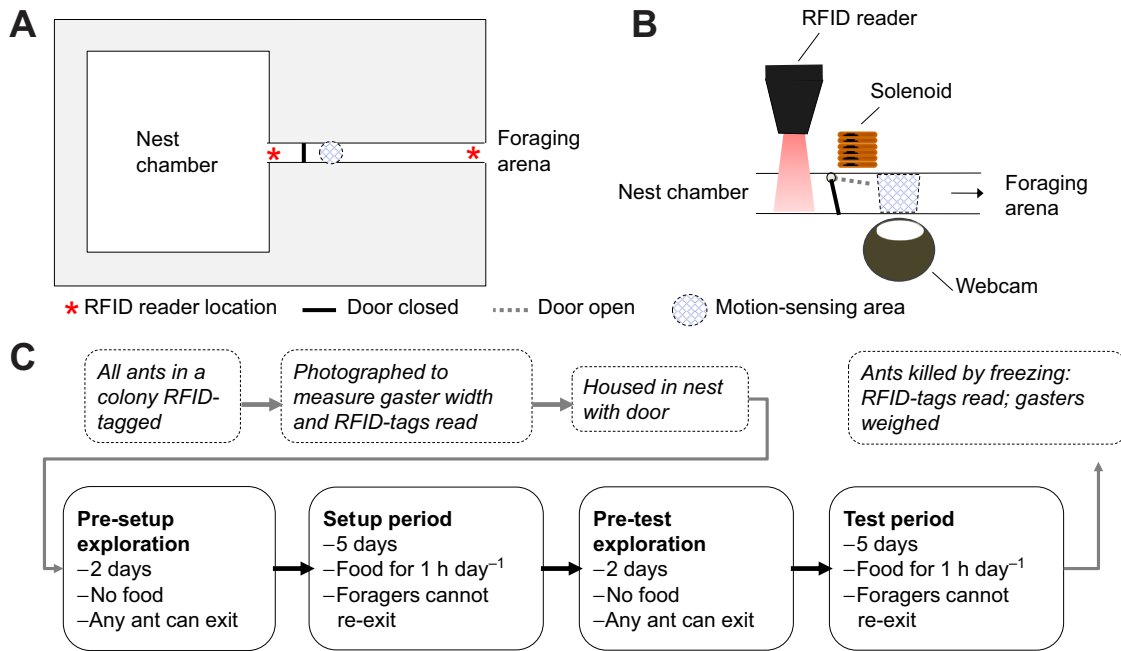


Fig. 1. Experimental methods. (A) Top view of nest with automatically controlled door, showing locations of radio-frequency identification (RFID) readers (\*) and motion-sensing area (hatched). (B) Side view of entrance corridor showing the door closed (solid line) and open (broken line) positions. (C) Timeline of a trial (solid lines) with pre-trial and post-trial processes (broken lines).

food was provided. After this period, the ‘set-up period’ (5 days) began. During this period, food (0.1 ml of 1:9 honey:water solution) was provided for one ‘feeding hour’ each day (13:00–14:00 h). Water was removed 30 min prior to food placement and returned to the arena after food removal. During the feeding hour, any ant that approached the food was photographed before she fed (for corpulence estimation from gaster width). If the ant then fed from the honey solution, the ant’s RFID tag was read using a hand-held reader. This automatically transferred the ant’s ID from the ‘permitted’ to the ‘denied’ list. Reading the RFID tag did not disturb feeding. After feeding, the ant could re-enter the nest by motion triggering the door, but it could not leave again. The volumes imbibed by the ants were sufficiently small that the food never became appreciably depleted during a feeding hour. This procedure was repeated daily, each day adding more ants to the ‘denied’ list. The attempts of these ‘denied’ ants to leave the nest were recorded by the RFID reader controlling the door.

At the end of the set-up period, the denied list was deleted, starting the ‘pre-test exploration period’ (2 days). All ants could leave the nest, but no food was present (Fig. 1C). Ants leaving to explore were recorded, but successful foraging was not possible. After this, the ‘test period’ began, following the same procedure as the set-up period, building up a new list of ‘denied’ ants, over the course of 5 days. Finally, the colony was killed by freezing, and for all ants the RFID tags were read and the gaster dry mass recorded.

#### Corpulence calibration

Corpulence can be approximated from gaster dry mass (Blanchard et al., 2000). This method was used to take corpulence measurements for each ant at the end of the trial, according to an established protocol (Robinson et al., 2009c). Dry mass has the advantage of being a quick and accurate way of assessing ant corpulence, but has the disadvantage that it cannot be measured *in vivo*. To establish a corpulence measurement that could be applied to live ants, we photographed 80

*T. albipennis* workers (20 from each of the four colonies, comprising a mixture of foragers and nest workers), and measured gaster width, gaster length and head width from these photographs using ImageJ (ImageJ 1.41o, public domain 2009, National Institutes of Health, Bethesda, MD, USA). Immediately after we photographed the ants, they were killed by freezing, and we subsequently dissected and dried the ants and measured their dry gaster mass compared with using gaster width alone. There was a strong positive correlation between gaster dry mass (log-transformed for normality) and gaster width ( $R=0.77$ ,  $N=80$ ,  $P<0.0001$ ) (supplementary material Fig. S1). Using instead a gaster area approximation calculated from gaster length and gaster width does not improve the correlation with gaster dry mass compared with using gaster width alone. Both gaster width and gaster dry mass also correlated with head width, a suitable proxy for exoskeletal size in this monomorphic species (Hölldobler and Wilson, 1990). The correlation between gaster width and gaster dry mass remained both strong and significant ( $R=0.74$ ,  $N=80$ ,  $P<0.0001$ ) even after partial correlation had been used to remove the effect of head width (see Table S1 in supplementary material). Gaster width (mm) can therefore be used to predict gaster dry mass (mg), using the relationship:  $\ln(\text{gaster mass})=6.3 \times \text{gaster width}-6.8$ ;  $R^2=59\%$  (supplementary material Table S1). As would be expected, there is some unexplained variation in this relationship, probably due, in part, to the water content of live ants. However, this relationship was sufficiently strong that gaster width could be used as a proxy for corpulence in the parts of our experiments when gaster dry mass data were unavailable.

#### Data analysis

We used generalised linear mixed models (GLMMs) to analyse our data, using colony as a random factor in all models. GLMM 1 tested whether corpulence of foraging ants increased over the course of the set-up period, using corpulence (gaster width at time of foraging) as the dependent variable, day of foraging as a fixed factor and a

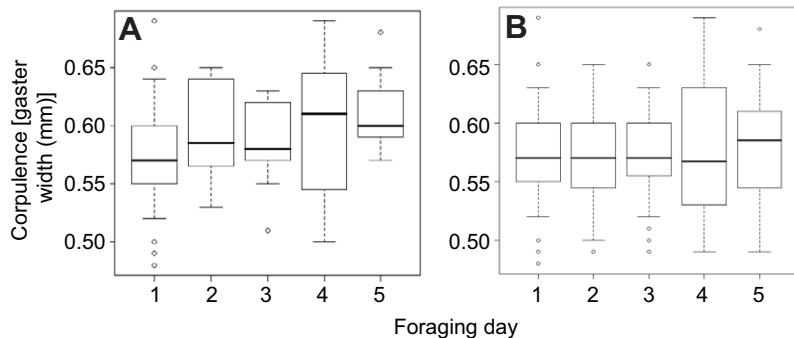


Fig. 2. Set-up period. (A) Corpulence of ants engaging in foraging increases significantly during the setup period. GLMM 1:  $t=2.70$ , d.f.=79,  $P<0.01$ . Day 1:  $N=42$ ; Day 2:  $N=8$ ; Day 3:  $N=9$ ; Day 4:  $N=12$ ; Day 5:  $N=14$ . (B) Corpulence of ants attempting to leave the nest does not change significantly during the setup period, indicating that the doors are successfully manipulating colony behaviour. GLMM 2:  $t=0.81$ , d.f.=151,  $P=0.42$ . Day 1:  $N=42$ ; Day 2:  $N=27$ ; Day 3:  $N=31$ ; Day 4:  $N=26$ ; Day 5:  $N=32$ . For both plots, black bars indicate median values and whiskers enclose the interquartile range.

Gaussian error structure. GLMM 2 applied the same model to ants attempting to leave the nest during the set-up period but prevented by the automatic doors. GLMM 3 tested whether corpulence or recent experience is the better predictor of foraging in the test period, using day of foraging as the dependent variable, corpulence (gaster mass) and experience as fixed factors, and a Poisson error structure. In addition, head width was included as a covariate. Two versions of GLMM 3 were run, using different measurements of experience. For GLMM 3a, experience was defined as minimum number of days since the last successful foraging trip (exact number known if the ant foraged in the set-up period; set as 8 days if the ant did not forage during the trial). We focused on successful foraging trips to avoid potentially confounding factors from ants engaged in different extra-nest tasks (e.g. scouting for new nests) possibly using different cues to leave. To check the relevance of the success of foraging trips, GLMM 3b was a repeat of GLMM 3a, but calculated experience on the basis of the number of trips each ant made outside the nest during the pre-test exploration period (no food available). GLMM 4 tested for predictors of whether an ant foraged at all during the test period, using corpulence (gaster mass) and experience (whether ant foraged at all during the setup period) as fixed factors, and a binomial error structure. The approximation for corpulence (gaster mass *versus* gaster width) used in each model is the one measured closest in time to when the behaviour under test was observed. The two measurements correlated strongly (see Results). A small number of ants (13%) lost their tags during the course of the two-week trials. These ants were subsequently confined to the nest, because they could not trigger the automatic door to open. Only ants that retained their tags to the end of the trial were included in the analyses. To compare correlation coefficients we used Fisher's  $r$ -to- $z$  transformation before applying a two-tailed  $z$ -test. Statistical tests were performed in R version 2.7.2 (R Foundation for Statistical Computing, Vienna, Austria).

## RESULTS

### Setup: manipulating foraging task access

The setup period aimed to create a negative correlation between recent foraging success and corpulence. During the setup period, over the course of the five foraging sessions the ants leaving the nest were increasingly more likely to be more corpulent (Fig. 2A), meaning that at the end of the period, the ants with the most recent experience of foraging success were more corpulent than those with less recent success. To demonstrate that this significant trend is not part of an intrinsic cycle within the colony, the corpulence of ants attempting to leave the nest (including those on the 'denied' list unable to leave) is shown in Fig. 2B. The corpulence of the ants attempting to leave does not change over the course of the foraging period, indicating that it is the manipulation of the exit-controlling doors that causes the change in Fig. 2A. The rate of attempts to leave

by individuals on the 'denied' list during the setup period was significantly higher than the rate of exits made by the same ant prior to their being placed on the 'denied' list (Wilcoxon paired test:  $V=3073$ ,  $N=84$ ,  $P<0.0001$ ). This provides further evidence that the doors were actively preventing attempted exits, because ants that were on the denied list clearly continued to make repeated attempts to leave the nest. This difference was not due to a general increase in activity over this time period, as the rate of trips outside the nest per ant prior to being added to the 'denied' list did not increase over the pre-setup exploration and set-up periods [Page trend test:  $L=487$ ,  $m=5$  colonies,  $n=7$  days, not significant (NS)], nor did the rate of attempts to leave per ant made by ants on the 'denied' list increase over the foraging period (Page trend test:  $L=207$ ,  $m=5$  colonies,  $n=5$  days, NS).

The corpulence of individual ants did not vary significantly over the course of the 2-week trials. Initial corpulence (measured from gaster width) and final corpulence (measured from gaster dry mass) were strongly correlated (Spearman's  $\rho=0.77$ ,  $N=438$ ,  $P<0.0001$ ). This remained significant when the first-order partial correlation was used to remove the effects of correlation with head width ( $r=0.73$ ,  $N=438$ ,  $P<0.0001$ ). This is a similar strength of correlation to that found in the corpulence calibration test, which photographed a sample of ants and then immediately killed and weighed them ( $r=0.74$ ,  $N=80$ ,  $P<0.0001$ ). These two correlation coefficients do not differ significantly ( $z=0.12$ ,  $P=0.90$ ), nor do the actual regression slope coefficients ( $t=0.71$ , d.f.=511,  $P=0.48$ ), indicating that a gap of two weeks between measurements does not decrease the accuracy of corpulence estimates, nor does it change the relationship between the two measurements. In case the foragers vary in corpulence more than other ants, the photographs taken during foraging were compared for ants that were active in both foraging periods. Once more, the corpulence measurements were highly consistent ( $r=0.88$ ,  $N=27$ ,  $P<0.0001$ ). This shows that the relative corpulence of ants within a colony remains consistent over a two-week timescale, and that final corpulence of the ants can be taken to be a good approximation of their corpulence throughout the trial.

### Test period: foraging decisions

At the start of foraging period 2, the cues from an ant's recent experience conflicted with cues from its corpulence. Specifically, ants with the most recent successful foraging experience had higher corpulence than those with less recent experience (Fig. 2A). In addition, the leanest ants have not only been prevented from acquiring recent experience of foraging success, but have acquired experience of failing to leave the nest. If ants use their own recent foraging success as a cue to decide to forage, the ants that foraged first in the test period should be those with the least amount of time since their last successful foraging trip (i.e. those foraging near the end of the setup period). Conversely, if ants use their corpulence



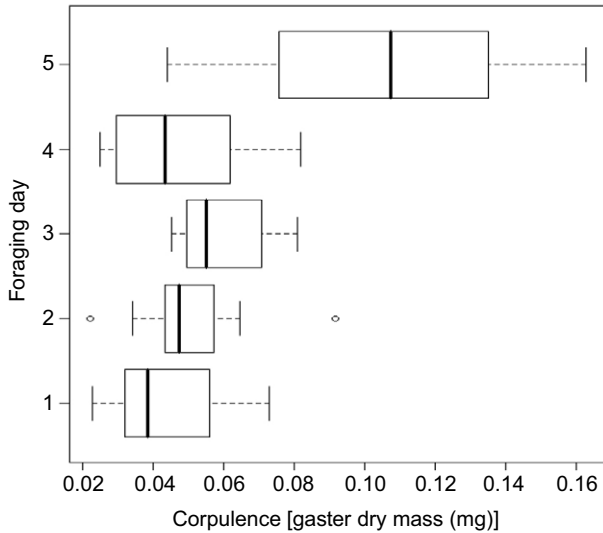


Fig. 3. In the test period, leaner ants forage earlier. GLMM 3a:  $t=2.34$  d.f.=40  $P<0.05$ . Day 1:  $N=15$ ; Day 2:  $N=15$ ; Day 3:  $N=12$ ; Day 4:  $N=9$ ; Day 5:  $N=4$ . Black bars indicate median values, and whiskers enclose interquartile range.

to decide to forage, leaner ants should forage first, irrespective of the time since they have foraged. GLMM 3a, with time since the ant last foraged and corpulence as predictors, found that only corpulence has a significant effect on the order in which the ants leave the nest, with leaner ants foraging earlier, irrespective of time since previous foraging success (Fig. 3). If, instead of representing experience as time since successful foraging, experience is represented as the number of trips out of the nest during the pre-test exploration period (none of which will have been successful foraging trips) again, corpulence is the only significant predictor (GLMM 3b). Head width had no significant effect on ant behaviour in any of the models. These results support the use of corpulence information over recent foraging experience when the two are in conflict.

At a coarser level, we can compare those ants that left the nest to forage at any point during the test period with those that stayed inside. Here again, corpulence is a significant predictor, with leaner ants leaving the nest (GLMM 4:  $t=4.62$ , d.f.=442,  $P<0.0001$ ). However, there is also a significant interaction between corpulence and successful foraging experience, in terms of whether an ant foraged successfully at any point during the set-up period (GLMM 4:  $t=4.04$ , d.f.=442,  $P=0.0001$ ). Lean ants that have had a recent (<1 week) successful foraging trip are more likely to forage than ones that have not been successful recently (Fig. 4). At this level, the cues from corpulence and experience do not conflict because, overall, ants that foraged in the set-up period were leaner than those that did not.

### DISCUSSION

Our results clearly show that corpulence, or some close physiological correlate of corpulence, influences an ant's decision about whether to forage. This physiological information has more influence than recency of foraging success, when the two are in conflict. Combined with previous results showing that corpulence is a better predictor of propensity to forage than age, general activity level or previous location within the nest (Robinson et al., 2009a), these results support

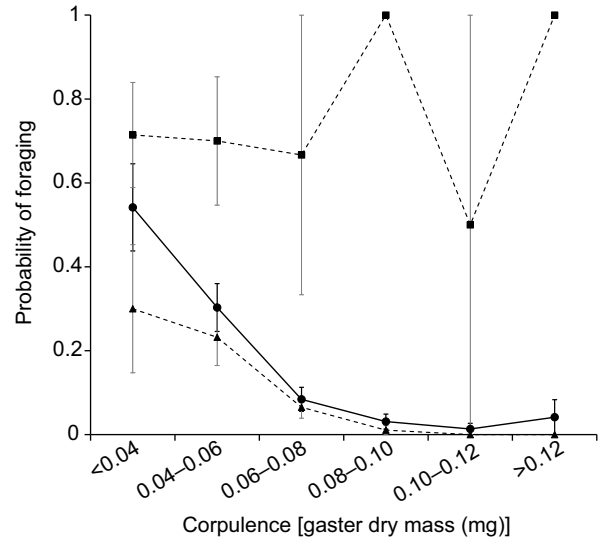


Fig. 4. The relationship between probability of foraging and corpulence for all ants (solid line and circles), ants that have had a recent successful foraging trip during the past week (squares), and ants that have not recently foraged successfully (triangles). The sample sizes for highly corpulent ants with successful foraging experience are (necessarily) very low, hence the large standard error bars and fluctuations in the signal in that part of the graph. However, the general pattern for all ants (solid line) is, the leaner the ant, the more likely it is to forage. In addition, for very lean ants, those with recent foraging experience (squares) are more likely to forage again than ants that do not (triangles).

the idea of a corpulence-related response threshold distribution. The corpulence threshold model predicts that ants will leave the nest to search for food when the stimulus to forage reaches their individual threshold, linked to their level of fat reserves. Our results suggest that this system is robust to short-term fluctuations in foraging success, because lean individuals persist as foraging specialists even when prevented from finding food. This system also has the potentially beneficial property that during normal foraging, the only ants to be outside the nest will be those that are lean and may, therefore, be less valuable to the colony if lost during this dangerous task (Tripet and Nonacs, 2004). If demand increases due to loss of these foragers or due to colony growth, the ants that respond will be the next least valuable in terms of fat reserves. In addition, this system should be very responsive to colony hunger levels. Our results show that corpulence does not change rapidly in response to experience; therefore, lean ants are not simply responding to urgent individual hunger. However, it is to be expected that over longer periods of time, corpulence could change. If the colony begins to starve, ants will gradually use up their fat reserves, and the combination of increased stimulus to forage (hunger signals) and decreased thresholds (as corpulence diminishes) would promote a rapid and persistent response to the need for a greater food influx. Individual corpulence thus could include social information about the state of the colony, as well as effectively acting as a proxy for long-term individual experience. Further work will be required to determine how flexible and reversible the corpulence levels are.

Our results suggest that experience of simply leaving the nest and searching the environment does not affect an ant's propensity to forage; however, recent foraging success does appear to have some influence on future decisions. Lean ants that have made a successful foraging trip in the last week are more likely to leave

the nest to forage than equally lean ants with no recent foraging success. Our finding that only successful foragers are more likely to forage again precludes the idea of a second underlying physiological factor making some lean ants more likely to leave the nest than others. If such a second factor were to exist we would expect the number of trips made in the absence of food to correlate with later decisions to leave; our findings contradict this. Normally, leanness (low fat reserves) will tend to correlate with experience, so in nature both influences on an ant's decision will be in accord.

Frequent foraging may decrease corpulence even further, because foraging ants will use up energy in locomotion and transport, and tend to pass on the food they collect to nestmates (Sendova-Franks et al., 2010). Thus, initial minor differences in leanness or foraging success could be exacerbated by positive feedback to establish foraging specialists. In the ant *Cerapachys biroi*, early experience of foraging success correlates with long-term propensity to perform a task (Ravary et al., 2007). In *T. albipennis* such a correlation could be established through the combination of memory in the short term and longer-term physiological differentiation.

Our study can also be seen as a task-group removal experiment, because the normal foragers are excluded from performing that task. However, unlike most removal experiments, we achieve this whilst keeping colony size constant. The threshold reinforcement model of Théraulaz et al. predicts that if a task group A is removed from a colony and a group of individuals B take over performing that task, then when group A is returned, group B should continue in that task, because their thresholds for that task will have decreased (Théraulaz et al., 1998). This is not what was found in our experiment: ants that foraged recently did not continue to forage when the excluded ants were allowed to return to their task. Our results suggest that task thresholds did not change over this timescale, perhaps because thresholds are related to slow-changing physiological attributes. More work is required to test longer-term effects. Our results suggest that even if thresholds do not change over this timescale, short-term memory effects may still contribute to longer-term changes. This may occur if experience is used to fine-tune the physiological threshold system. For example, our data suggest that an ant that repeatedly fails to forage successfully will become slightly less likely to forage again, although it is still lean. As such an ant is now foraging less often, it may be more likely to receive food from returning foragers, and will use up less energy, and become more corpulent, making it even less likely to forage in future. In this way, experience effects may allow ants to change their physiological specialisation.

In general, a positive feedback loop between behaviour and physiology would be expected to lead to high levels of specialisation. It has been hypothesised that leaner ants may make more effective foraging specialists, because they may be more mobile, and have a greater capacity for feeding in the field (Blanchard et al., 2000; Porter and Jorgensen, 1981). Our results suggest that successful foragers are more likely to forage again, which could be expected to lead to intrinsically more competent foragers becoming specialists. Through repeated foraging trips, these ants also have the opportunity to learn routes to good foraging sites and perhaps to hone navigational skills (Beverly et al., 2009; Graham et al., 2010). However, previous experimental investigation has found no evidence for a correlation between propensity to forage and task performance in *T. albipennis* (Dornhaus, 2008). The task performance experiment by Dornhaus measured the rate of foraging trips in a simple laboratory environment (Dornhaus, 2008). It may be that differences in performance would only be evident in a more natural and more challenging foraging environment (Chittka and Muller, 2009). Another possibility is that

the division of the workforce into lean outside workers and corpulent inside workers is driven by evolutionary pressures to regulate colony nutritional provisioning and to protect food stores, rather than to promote individual foraging efficiency.

A further dimension, not addressed by our study, is the regulation of protein intake. Compared to carbohydrates, we would expect colony protein levels to be less strongly linked to worker corpulence, because protein is used primarily by the larvae for growth and represents only a minor proportion of worker reserves (Blanchard et al., 2000). However, the protein requirements of larvae could still be part of the stimulus to which the less corpulent ants respond by foraging. Further work is required to investigate nutrient-specific regulatory mechanisms.

Our experiments investigate which ants in the colony decide to forage, but when to forage is also important. The timing of ant exits from the nest, particularly in the case where no ants are returning, can be modelled using a record dynamics approach, which accurately describes the rapidly decreasing exit rates observed (Richardson et al., 2010). Heterogeneity in exit probabilities is implicated in the production of this pattern of exits (Richardson et al., 2011). Our results suggest that this heterogeneity could come from the corpulence-related threshold distribution within the colony. This is supported by the observation of Richardson et al. that colonies composed entirely of callow (newly eclosed) individuals do not follow record dynamics, but rather their exits fit a null model (a homogeneous Poisson process) (Richardson et al., 2011). Colonies composed of only callows vary less in both corpulence and experience than colonies with normal demography (Robinson et al., 2009a), so we would expect their heterogeneity in exit probabilities to be reduced, explaining the loss of record dynamics. A rapid reduction in exit rate (such as that described by record dynamics) when no ants are returning is thought to be adaptive, because it protects colonies from wasting resources when conditions are adverse (Greene and Gordon, 2007). Hence, the corpulence-related foraging threshold distributions may play a role in regulating foraging effort in response to external pressures, as well as in response to a colony's internal needs.

The contribution of corpulence to the regulation of division of labour may be much more widespread among the social insects than is realised. One clear example of the role of fat reserves is in honeybees (*Apis mellifera*), where manipulation studies demonstrate a causal relationship between lipid depletion and the age-correlated behavioural switch to extra-nest tasks (Toth et al., 2005). Furthermore, in single-cohort honeybee colonies, body mass at eclosion correlates with which task is performed later (Vance et al., 2009). This phenomenon may have been overlooked in other species, because there is frequently a correlation between corpulence and age (MacKay, 1983; Porter and Jorgensen, 1981; Toth and Robinson, 2005; Tschinkel, 1998). Age is usually taken into account in studies of division of labour, because age-task correlations are known to be widespread (Oster and Wilson, 1978; Robinson, 1992; Seeley, 1982). In *T. albipennis* for a given corpulence, age does not predict division of labour, but if corpulence were to be excluded from the analysis, a weak age-corpulence correlation means that age would appear to predict task (Robinson et al., 2009a). Similarly, we found no relationship between morphology (head width) and foraging behaviour in this species; however, there is a weak relationship between head width and corpulence, which could lead to an apparent relationship between morphology and behaviour. Including age or morphology and excluding corpulence when conducting analyses of task allocation could mask the importance of physiological differences.

Our work suggests that foraging task allocation in ants can be organised using a system combining long-term physiological differences between individuals which result in a relatively stable response threshold distribution, with short-term learning processes adding fine-tuning. Through these simple rules, workers can organise the provisioning of the colony and manage allocation of foraging effort in a manner robust to minor environmental changes and yet offering flexibility when required.

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Table S1. Both gaster width and gaster mass are correlated with head width (a proxy for exoskeletal size), so first-order partial correlations between these three intercorrelated variables were calculated to determine the correlation between gaster width and gaster mass when the effect of head width is removed

First-order partial correlations	<i>r</i>	<i>r</i> <sup>2</sup>	<i>t</i>	<i>P</i>
Gaster width × gaster dry mass (excluding head width)	0.74	0.54	9.5	<0.0001
Head width × gaster width (excluding gaster dry mass)	0.43	0.19	4.2	0.0001
Head width × gaster dry mass (excluding gaster width)	0.10	0.01	0.9	0.37

Correlation between head width and gaster width ( $r=0.53$ ,  $N=80$ ,  $P<0.0001$ ).

Correlation between head width and log-transformed gaster dry mass ( $r=0.35$ ,  $N=80$ ,  $P<0.01$ ).

The correlation between gaster width and gaster dry mass remains strong and significant even when adjusted to control for the effects of correlation with head width:  $r=0.74$ ,  $N=80$ ,  $P<0.000$ .