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The response of foraging Argentine ants, *Linepithema humile*, to disturbance

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Abstract

Reducing the risk of predation is an important feature of the feeding behaviour of most animals. In social insects, foraging workers are particularly vulnerable, and the ability to trade-off mortality risk against food value may provide a considerable competitive advantage for the colony. We investigated the response of Argentine ants, *Linepithema humile*, to different kinds of disturbance while workers foraged on food of differing quality. The behaviour of disturbed individuals was influenced by group size, by the behaviour of nearby nestmates and by how much food had already been consumed. When in large groups, workers were less likely to leave the foraging arena and resumed feeding more rapidly. This response was even more marked among workers whose gasters were only partially replete. However, individuals took more time to resume feeding and became more likely to run away from a food source when greater numbers of ants were disturbed. These influences may allow foraging groups to maximise food intake while minimising the mortality of workers.

Introduction

Animals are regularly confronted with the conflicting requirements of foraging and avoiding predation, and would therefore benefit by making foraging decisions that reflect the value of a food source and its potential risk of predation (Sih 1980; Stephens and Krebs 1986; Dill 1987; Lima and Dill 1990). There is evidence among solitary animals to suggest that individuals can assess both of these factors and adjust their behaviour accordingly (reviewed in Lima and Dill 1990; Lima 1998). The foraging decisions of animals may also be influenced by their hunger level (Lima 1998) and the number of individuals in the foraging group (Pulliam and Caraco 1984; Lima and Dill 1990). For example, hungry animals may resume feeding more quickly following a disturbance than satiated animals, and animals in groups often engage in increasingly risky behaviour as group size increases (Lima and Dill 1990).

Unlike solitary animals, individual workers of eusocial insects collect food that is not only for their own consumption, but is also passed on to nestmates or the brood (Ydenberg and Schmid-Hempel 1994). Furthermore, the death of an individual worker does not result in the end of reproduction, and thus worker mortality is generally regarded as a cost that must be borne to varying degrees by the colony (Oster and Wilson 1978). Since individual workers may be willing to compromise their own interests if the costs to an individual are offset by benefits to the colony (Ydenberg and Schmid-Hempel 1994), variation in the response of foraging workers to a disturbance may reflect differences in their value to the whole colony. For example, physically worn or old individuals usually perform dangerous foraging activities and are relatively dispensable compared with younger individuals (Porter and Jorgensen 1981). Similarly, workers of the ant *Myrmica rubra* respond to threats by competing ants according to their age: the oldest workers attack the enemy while younger individuals retreat to the nest to recruit additional nestmates (Cammaerts-Tricot 1975).

Clearly, the ability of individual workers to respond simultaneously to more than one stimulus could result in a substantial competitive advantage (Nonacs and Dill 1990). Studies of social insects support this suggestion and reveal that individual foragers adjust their foraging behaviour according to the value of the food and the risk of mortality (Nonacs and Dill 1988, 1990; Nonacs 1990). However, we know little about whether this trade-off varies among individuals, the selective advantage of any behavioural flexibility, and how the decisions made by individuals are affected by other factors, such as group size.

We investigated the response of workers of the Argentine ant, *Linepithema humile*, to varying types of disturbance while feeding on food of differing quality. The ecologically dominant Argentine ant originated in South America, but has since been unintentionally distributed to many regions of the world, including Australia (Markin 1970; Hölldobler and Wilson 1990). Exploratory foraging and recruitment to food sources by workers of *L. humile* are facilitated by chemical trails (Aron *et al.* 1990; Deneubourg *et al.* 1990). When foraging workers of *L. humile* are disturbed, some individuals run away from the food while others resume feeding. Here, we examine how individual behaviour is influenced by food satiation, the kind of disturbance, the quality of food, and the number of disturbed conspecifics. We investigate group-level behaviours by subjecting groups of ants to a disturbance and observing how group size, food quality and the kind of disturbance influences their subsequent behaviour.

Materials and Methods

Sample populations

This study was conducted during the summer of 1998–99 in various parks throughout the coastal suburb of Seaholme, Melbourne, Victoria. The parks have been extensively modified for recreational purposes and comprise fields of grass, patches of tall vegetation and very large numbers of nests of *L. humile*, which were found at the base of eucalyptus trees and various flowering shrubs. *L. humile* is a unicolonial, polydomous, polygynous species (*sensu* Bourke and Franks 1995), characterised by few, if any, colony boundaries, extensive intermixing of queens and workers between colonies, and very low levels of within-colony relatedness (Kaufmann *et al.* 1992; but see Tsutsui 2000). A single nest of *L. humile* comprises a cluster of entrance holes, each of which is surrounded by a small pile of debris. It is not known how many colonies were observed in this study.

The behaviour of *L. humile* workers was observed at artificial foraging arenas. The foraging arenas were plastic Petri dishes, 90 mm in diameter, lined at the base with cotton wool and taped to 15-cm square pieces of white cardboard. The Petri dishes were filled with 20 mL of honey solution, which evenly soaked the cotton wool. Data was collected from a total of 317 nests; no nest was used in more than one trial in each experiment. Individual nests included in each experiment were at least 10 m apart to reduce the possibility of testing the same group of foraging workers twice. Previous work on *Iridomyrmex sanguineus* suggests that foraging workers are faithful to particular groups of nest entrances (McIver 1991). Typically, the experiments involved observing the behaviour of feeding ants following a disturbance. Thus, experiments were not conducted if the ants were already disturbed by environmental conditions, such as rain or strong wind.

Group response of foraging workers to pheromone disturbance

This experiment examined whether the quality of the food source and the nature of a disturbance influenced the behaviour of foraging ants. One of three different concentrations of honey solution (15%, 50% and 85%, diluted by water) were placed in the foraging arenas, and the ants foraging at this food source were subject to an airborne disturbance. The disturbance was caused by a burst of air, derived from a lens puffer (hurricane blower) that was forced through a short length (<5 cm) of plastic tubing, which was attached to a hole in a plastic vial. A second tube was attached to another hole at the opposite end of the vial, and thus the air passed through the vial into the second tube that was positioned 5 cm above the foraging arena.

There were two disturbance treatments in which either air (control) or air plus alarm pheromone (experimental) was blown down onto the foraging ants. In the experimental treatment, approximately 30 ants were placed in the plastic vial, whereas the vial contained no ants in the control treatment. Muslin was placed over both openings of the vial to prevent the ants escaping down the tubes. The vial was tapped

several times before each trial in order to agitate the captured ants, which we assumed would release alarm pheromone. A different puffer was used for the control and experimental treatments, and the plastic tubing and vials used in each treatment were kept separate to prevent contamination of control air disturbances with alarm pheromone. A new group of ants, collected from another nest at least 10 m away, were placed in the vial at the start of each experimental trial.

Four nests were chosen each day and each was randomly assigned a foraging arena with 15%, 50% or 85% honey solution. Foraging arenas were placed 30 cm from the most active nest entrance at midday. The number of ants feeding at each foraging arena was recorded at 1500, 1800, 1900 and 2000 hours. Each nest was randomly assigned an airborne disturbance treatment, which was applied after the 1900-hours recording, when there were usually large numbers of workers feeding. This time was chosen to ensure that the ants had established foraging trails, but had not obviously depleted the quantity of food in the foraging arena. The number of ants that immediately resumed feeding following the disturbance was recorded.

Response of disturbed ants with or without an engorged gaster

This experiment examined whether the decision of an individual worker to resume feeding following a disturbance was affected by whether its gaster was engorged with food. Workers of *L. humile* feed until their gaster is engorged to twice its normal size (Markin 1970). The disturbance in this experiment involved touching the gaster of the ant with a blade of grass.

At midday of each day in which the trials were conducted, we placed a foraging arena 5 cm from the most active nest entrance of 20 nests. Once an obvious foraging trail had been established (usually 5–10 h later), we recorded the number of ants inside the foraging arena of the first nest, and then immediately disturbed an ant that was feeding near the centre of the food source. We recorded the time that the disturbed ant spent running and the trial ended when the focal ant fed continuously for more than 10 s or climbed over the rim of the Petri dish. We then repeated the experimental procedure consecutively for five more ants. We alternated the condition (with or without an engorged gaster) of the disturbed ant between consecutive disturbances, and also alternated the condition of the first ant to be disturbed at each nest. Trials in which the blade of grass accidentally touched the head of the worker were excluded because these ants subsequently groomed themselves excessively.

Response of ants disturbed singly or with others

This experiment examined whether the behaviour of a foraging ant was influenced by the behaviour of nestmates. The experiment comprised four treatments in which 1, 5, 10 or 20 ants were disturbed by touching their abdomens with a blade of grass. Prior to each trial, a blade of grass was held over the foraging arena for 15 s to minimise any effects caused by differences in the length of time for which a hand was above the ants. No obvious changes in activity were observed.

At midday of each day in which the trials were conducted, we placed a foraging arena 5 cm from the most active nest entrance of 20 nests. Once an obvious foraging trail had been established, we recorded the total number of ants inside the foraging arena, and then applied the disturbance. We recorded the time that the last ant that was disturbed spent running and whether it either resumed feeding or left the foraging arena. A trial ended when that focal ant fed continuously for more than 10 s or climbed over the rim of the foraging arena. Data from trials in which the grass accidentally touched the head or antennae of the last worker to be disturbed were excluded from the analysis.

All statistical analyses were performed using SYSTAT 7.01 for Windows. Data that were not normally distributed were log-transformed in order to improve distributions; such transformations are indicated in the text.

Results

Group response of foraging workers to pheromone disturbances

Prior to the experimental disturbances, the number of ants at the foraging arena was significantly influenced by an interaction between the time of observation and the concentration of honey in the foraging arena (repeated-measures ANOVA: $F_{6,240} = 6.23$, $P < 0.0001$). There was a marked increase in the number of ants feeding at the 50% and 85% concentrations of honey, but little change in the number of ants feeding at the 15% concentrations (Fig. 1).
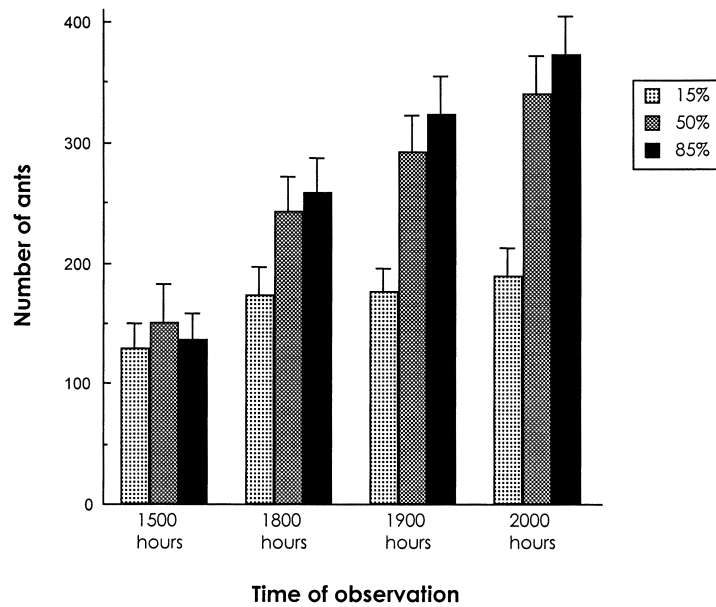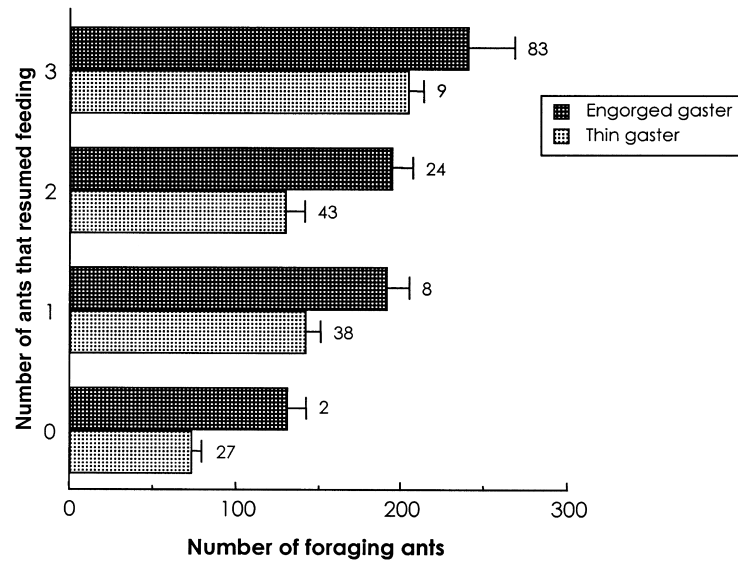
Fig. 1. The mean number of ants feeding in foraging arenas containing different concentrations of honey. Bars are standard errors.
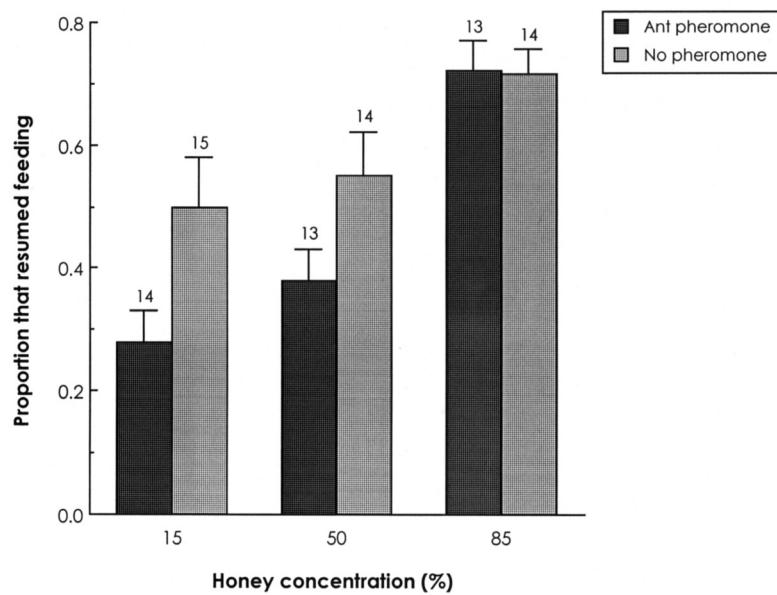
Fig. 2. The proportion of ants that immediately resumed feeding after an air disturbance, when foraging on different concentrations of honey. Bars are standard errors, with sample sizes above.

Following an air disturbance, the ants either resumed feeding or ran away from the food. Those ants that resumed feeding often started running again after contact with disturbed ants. The proportion of ants that resumed feeding (i.e. the number of ants feeding after disturbance/number of ants feeding before disturbance) was influenced by the kind of air

Fig. 3. The relationship between the number of ants that resumed feeding after a grass disturbance and the mean number of ants in the foraging arena shortly before the disturbance. Bars are standard errors, with sample sizes to the right.

disturbance (two-way ANOVA: $F_{1,77}$ = 7.39, $P < 0.009$) and the concentration of honey ($F_{2,77}$ = 16.86, $P < 0.0001$; interaction, $F_{2,77}$ = 2.03, $P > 0.13$). This proportion was higher for ants feeding on 85% honey concentrations, and was reduced after an experimental disturbance, when the ants were exposed to additional alarm pheromone (Fig. 2).

The number of ants feeding at each foraging arena at 2000 hours was not affected by the scent of the air disturbance experienced by the foragers 1 h earlier (two-way ANOVA: $F_{1,77}$ = 0.34, $P > 0.5$), but was strongly influenced by the concentration of honey in the foraging arena ($F_{2,77}$ = 12.20, $P < 0.0001$; interaction: $F_{2,77}$ = 1.06, $P > 0.35$).

Response of disturbed ants with or without engorged gasters

Foraging workers that were stroked with a blade of grass immediately ceased feeding, ran in unpredictable directions, and either resumed feeding or ran over the edge of the foraging arena. Since only three ants of each state (either with or without an engorged gaster) were disturbed at each nest, the number of ants of each state that resumed feeding after the disturbance varied between zero and three.

A repeated-measures ANCOVA, with the total number of ants in the foraging arena as the covariate, was used to compare whether the state of the ants (with or without a replete gaster) affects their decision to resume feeding. This analysis revealed that the number of ants that resumed feeding within each trial increased with the total number of ants that were present in the foraging arena ($F_{1,115}$ = 32.65, $P < 0.001$; Fig. 3), and that replete ants were less likely to resume feeding than ants with thin gasters ($F_{1,115}$ = 34.39, $P < 0.001$; Fig. 4). There was no significant interaction between these two variables ($F_{1,115}$ = 0.17, $P > 0.67$).

Among those ants that left the food following a disturbance, there was no significant difference in the time taken to leave the foraging arena between those ants with an engorged gaster (mean = 19.35 s, n = 195) and those with a thin gaster (mean = 19.03 s, n = 43;
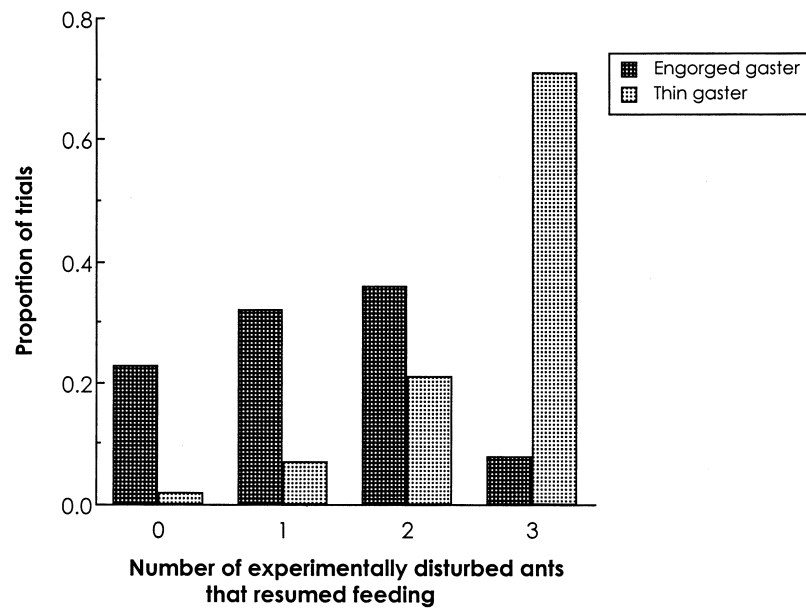
Fig. 4. The proportion of trials that resulted in either zero, one, two or three ants that resumed feeding after being disturbed by a piece of grass.

$t = 0.140$, $P > 0.2$). However, there was a significant difference in the time taken to begin feeding again between those ants with an engorged gaster (mean = 14.56 s, $n = 149$) and those ants with a thin gaster (mean = 8.92 s, $n = 305$; $t = 5.821$, $P < 0.001$).

Response of ants disturbed singly or with others

The last worker to be disturbed at each nest either started feeding again or ran over the edge of the foraging arena. The proportion of these workers that resumed feeding was smaller when greater numbers of ants were initially disturbed ($\chi^2 = 40.52$, d.f. = 3, $P < 0.001$) (Fig. 5). The time taken for an individual to resume feeding after the disturbance was not normally distributed and a log-transformation was applied. The log-transformed time was influenced by an interaction between the number of ants initially disturbed and the total number of ants feeding at the time of the disturbance (two-way ANOVA: $F_{3,192} = 3.43$, $P < 0.02$). The time taken for a worker to resume feeding increased when more ants were experimentally disturbed, but decreased if there were more ants feeding at the time of the disturbance (Fig. 6). The log-transformed time taken for a worker to reach the edge of the foraging arena was not affected by the number of ants initially disturbed ($F_{3,110} = 0.94$, $P > 0.4$; interaction: $F_{3,110} = 2.037$, $P > 0.1$), but increased with the total number of ants present ($F_{1,110} = 13.99$, $P < 0.004$). This increase was also observed in the previous experiment.

Burrowing patterns in the cotton wool lining of foraging arenas

In the initial stages of recruitment to the foraging arena, the ants stood side by side on the rim of the foraging arena with their heads facing down into the honey solution. As the number of feeding ants increased, the perimeter of the food source became crowded, and workers began to occupy the central regions of the foraging arena. In 15% honey treatments, the perimeter of each foraging arena was usually unoccupied by 1900 hours and ants instead fed near the center. In contrast, the entire surface of the food was usually
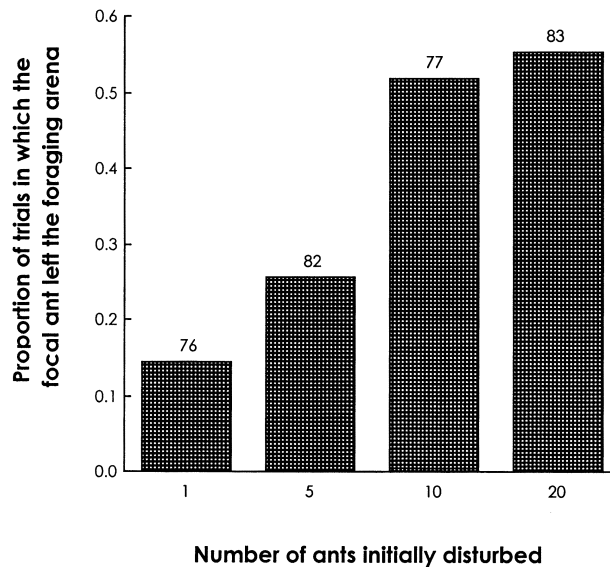
Fig. 5.   The proportion of trials in which the focal ant left the feeding arena as a function of the number of ants that were initially disturbed. Number of trials are indicated above each bar.

crowded by this time in the 50% and 85% honey treatments, and a series of shallow indentations in the cotton wool were visible by 2000 hours if several hundred ants had been feeding all afternoon. Small burrows, each of which was occupied by several workers, covered the cotton lining of the foraging arena by the next morning. A two-way ANOVA revealed that the number of burrows in the cotton wool increased with the maximum number of ants observed in the foraging arena ($F_{1,77} = 40.25$, $P < 0.0001$) irrespective of the concentration of honey available ($F_{2,77} = 0.89$, $P > 0.4$; interaction: $F_{2,77} = 0.3$, $P > 0.7$).

Discussion

When feeding workers of *L. humile* were disturbed, their decision to resume feeding or to leave the food was influenced by the amount of food they had consumed and the number and behaviour of nearby nestmates. Generally, as the size of group increased, disturbed individuals took longer to leave a foraging arena, and were quicker (and more likely) to resume feeding, particularly if their gasters were not replete. However, when more ants were disturbed, workers were more likely to run away from the foraging arena or took longer to resume feeding. Furthermore, when groups of ants were disturbed, the proportion of ants that immediately resumed feeding was greater if they were feeding on a more concentrated honey solution. These results are consistent with previous studies on ants, which suggest that as the value of a potential food source increases, individuals become more likely to take risks (Nonacs and Dill 1990, 1991).

   As expected, more workers were recruited to foraging arenas that contained higher concentrations of honey than to arenas with low concentrations (see also Nonacs and Soriano 1998). Mass-recruiting ants, such as *L. humile*, use pheromones to communicate the location and quality of food sources (Hölldobler and Wilson 1990). The quantity of pheromone a worker adds to a pheromone trail varies with the nutritional state of the colony and increases with the quality of available food. A slight increase in the quantity of
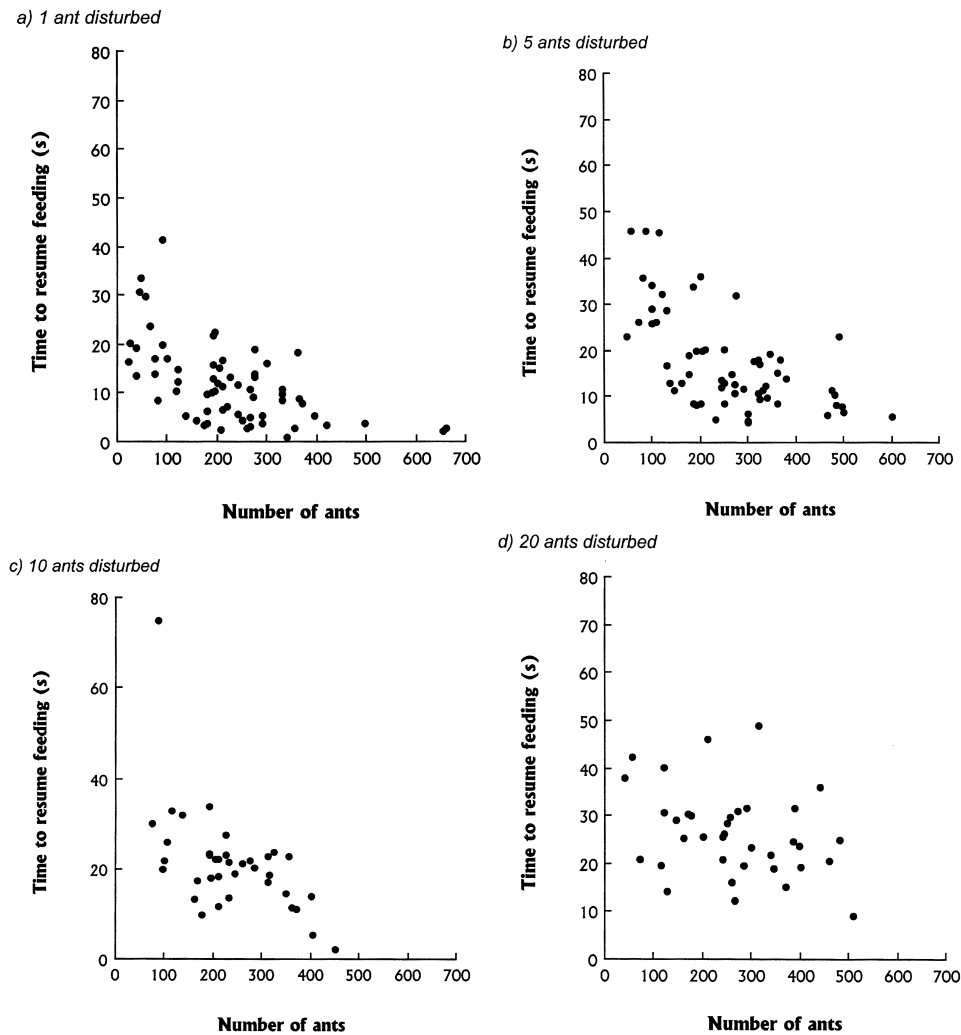
Fig. 6. The relationship between the time taken to resume feeding and the number of ants in the foraging arena when (*a*) one, (*b*) five, (*c*) ten, and (*d*) twenty ants were disturbed. These values were log-transformed for the analysis.

pheromone voided per worker can lead to a large increase in the number of ants recruited to a food source (Wilson 1962, 1971; Deneubourg *et al.* 1986; Breed *et al.* 1987; Hölldobler and Wilson 1990). As the food source becomes crowded or the colony approaches satiety, the probability that an individual will add to the pheromone trail declines, causing a reduction in the recruitment of workers.

The different responses of workers with replete or empty gasters may reflect a trade-off between efficient food-gathering behaviour and the need to avoid excessive mortality (Hölldobler and Wilson 1990; Nonacs and Dill 1991). Foragers exposed to an elevated mortality risk may either return to the nest or remain foraging. The former might result in an inadequate supply of food to the colony, especially if workers respond in this way when the risk of mortality is negligible. In contrast, ignoring all potential threats could subject the

colony to unacceptably high levels of worker mortality (Nonacs and Dill 1988, 1991). Since all foraging workers are unlikely to be similarly valuable to the colony, variation in worker behaviour may allow foraging groups to fine tune their response to disturbance. Workers with relatively replete gasters may be more valuable to the colony than workers with relatively empty gasters (Nonacs 1990; Nonacs and Dill 1990), and these valuable workers could avoid hazards by returning to the nest. In contrast, workers that have just started feeding are relatively expendable and hence may risk remaining at the food source to feed. Alternatively, workers with replete gasters may have less manoeuvrability, and thus flee more readily because they are more vulnerable.

The response of workers of *L. humile* to a disturbance varied according to the quality of food and the kind of disturbance. Since the number of workers at the food source was correlated with the concentration of honey, it is difficult to separate the influence of honey concentration with group size *per se*. When groups of feeding workers were disturbed, the proportion of ants that immediately resumed feeding was smaller if the food source was of low quality or the level of disturbance was greater. This pattern suggests that the colony trades-off foraging efficiency against the risk of injury (e.g. Nonacs and Dill 1990). Workers appeared to be less tolerant to risk of injury when feeding on low-quality food as they were relatively unwilling to resume feeding after disturbance; even fewer workers resumed feeding after a greater disturbance. The lack of difference in the response of workers foraging on 85% honey solution to the two kinds of air-borne disturbances may arise because the value of the food source was sufficiently high that most ants were unwilling to respond to any relatively minor disturbance.

As group size increased, disturbed individuals generally spent less time running around and resumed feeding more quickly. Ants of many species, including *L. humile*, begin running in haphazard directions if alarmed, probably to increase the rate of social interaction with other ants (Adler and Gordon 1992; Gordon *et al.* 1993; see also Frehland *et al.* 1985). A heightened rate of social interaction increases the speed with which information can spread through a group and may allow individuals to assess environmental danger more rapidly (Adler and Gordon 1992; Gordon *et al.* 1993). Rapid rates of social encounter are facilitated by large or dense groups (Pacala *et al.* 1996). Hence, the decrease in time taken to resume feeding with increasing group size may reflect a heightened rate of information collection and therefore a more rapid decision by disturbed individuals. In small groups, disturbed individuals may need to search for a longer time to collect the same amount of information from nestmates.

The time taken for a disturbed individual to resume feeding was longer if more ants were initially disturbed. If a disturbed worker encounters other workers that are not similarly alarmed, the level of danger in the environment is probably minimal, making it energetically wasteful to continue running and alarming other individuals. In contrast, widespread danger and a high risk of mortality may be indicated by many workers being similarly disturbed over a short time. Under these conditions, individuals may attempt to maximise communication with nestmates in order to collect or provide updated information.

Ants that quickly resumed feeding after a disturbance often began running again after interacting with several alarmed nestmates. In addition, the behaviour of most workers in a group was not visibly affected when only single ants were disturbed: anecdotal observations suggest that feeding ants start running only after contact with several disturbed workers. Thus, it is possible that alarm signals used by disturbed *L. humile* workers have a modulatory effect on feeding conspecifics. That is, instead of initiating an alarm response in every feeding nestmate with which it interacts, it may only slightly increase the

probability of becoming alarmed. Although information conveyed during modulatory communication may have a general nature, it can nevertheless elicit specific responses in individuals if the context in which the signal is received supplies a specific meaning (Nieh 1998). Alarm signals in *L. humile* may convey the message 'run around', but the liklihood that an individual will respond in this way may depend on other influences, such as the number and behaviour of surrounding conspecifics. An advantage of a modulatory alarm signal might be that it reduces the tendency of large groups of feeding workers to become alarmed by a single, perhaps misguided, worker.

If running is a means of collecting information, then the path shape can determine the probability that an individual will discover new information. Gordon (1995) recently showed that when *L. humile* workers searched for food in undisturbed but novel foraging arenas, their path shapes became increasingly linear as group size decreased. Theoretical results suggest that this could serve to increase the discovery rate of the group (Adler and Gordon 1992). Some of the behaviours that we observed may result from the path shape of individuals. For example, ants that were disturbed in small groups may have been more likely to leave sources of food not because the food was of low quality, but rather because their path shapes after the disturbance were relatively linear. Similarly, disturbed ants may have taken longer to leave a foraging arena as group size increased not because the food was of higher quality, but rather because their path shapes became relatively convoluted.

Although colonies of *L. humile* are extensive, local nest sites can be short-lived and are often found close to a source of food (Hölldobler and Wilson 1990). The appearance of burrows in the cotton wool lining of some foraging arenas may represent an attempt to establish a new nest, although few workers remained in the burrows after most of the food had been consumed. Alternatively, the workers may create the burrows in order to increase the surface area of the food. This would allow larger numbers of workers to access the food simultaneously and thus increase the rate of food returned to the colony. Field observations support this idea: very similar burrowing patterns were found on mouse carcasses, which often attract very large numbers of foraging workers. In both situations, the burrows formed only when large numbers of workers were recruited to the food source and the surface area of the food became limited.

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