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DEATH IN THE DISTANCE: MORTALITY RISK AS INFORMATION FOR FORAGING ANTS

by

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(With 2 Figures)
(Acc. 17-V-1989)

The great success of ants as a group must be due in some degree to their ability to coordinate individual behaviours into mass action through effective communication. Where this coordination is both advantageous and evident is in foraging: ants have been shown to recruit nestmates into foraging behaviour by communicating quality, quantity and location of distant food sources (TAYLOR, 1977; DAVIDSON, 1978; COSENS & TOUSSAINT, 1985; HOLDER BAILEY & POLIS, 1987). Therefore, through information brought back by successful foragers, colonies are able to accurately track and react to changes in food availability.

Foraging efficiency can be further improved if workers inform each other of more than just food distribution and quality. For example, mortality rates of foragers are often high (WILSON, 1971) and this risk is unlikely to be homogeneously distributed in space: some areas or food patches should be safer than others. If so, mortality rates of workers would be reduced if colonies effectively channelled foragers away from areas containing dangerous predators or competitors. Ants do use alarm pheromones to mobilize groups of workers but these responses have been studied primarily in relation to nest disturbance or imminent threats to

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colony existence (reviewed by HÖLLDOBLER, 1978). The risks involved in foraging, while not immediately threatening colony existence, must substantially endanger the workforce. However, communication of risk in this context of everyday foraging has not been demonstrated.

Overall foraging behaviour of ants is clearly affected by mortality risk. Numerous studies of ants have shown that removal of above ground workers reduces activity levels (GENTRY, 1974; WHITFORD & BRYANT, 1979; MAC KAY, 1982; MUNGER, 1984; GORDON, 1986). Territory usage patterns in *Lasius neoniger* appear to reflect avoidance of aggressive competitors (TRANIELLO, 1983, 1989). NONACS & DILL (1988) found that *L. pallitarsis* (Provancher) foragers distinguish between nutritionally equivalent food patches based on associated mortality risk and choose the safer alternative. Further, when given choices between safe patches with poor food and dangerous patches with better food, the foragers' willingness to take risks is significantly correlated with the costs, in terms of lowered colony growth, of foraging in the safe patch. Colonies value safe and risky patches equally at the point where the gain in growth from the risky patch approximately equals the loss of forager biomass (NONACS, 1988).

Given that *L. pallitarsis* colonies respond adaptively to mortality risk, the next question to ask is how the individual workers become aware of such risk. Obviously, individual foragers should react upon encountering immediate danger. More interestingly, however, ants could later communicate that risk to nestmates, who could then respond to mortality risk without encountering it themselves.

Methods

To determine where workers become aware of or evaluate risk, it is necessary to differentiate between individual experience and communication between foragers at the colony. I tested for communication of distant danger by two sets of experiments: the first measured colony response to the initial return of successful foragers who had or had not encountered danger, and the second measured the response to addition of risk after colonies had begun to recruit to a food source.

In this first experiment, one laboratory *L. pallitarsis* colony was given access, via a single 90 cm Tygon tube, to a food patch after 24 h of food deprivation. In the food patch was a standard liquid and diet of either full strength (the good diet) or a 16-fold dilution (poor). When kept solely on one of these two diets colonies gained or lost biomass, respectively (see Nonacs [1988] for details of the diet and the origin and general maintenance of the colonies).

Movement along the trail was controlled by a series of hose clamps. When 3-4 ants were observed at or near the food patch, food of either full or 1/16 strength was added. The workers quickly found the solution and began to feed. At the same time, the trail was clamped shut near the colony exit (after making sure there were no other ants in the tube between the colony and food) to prevent more foragers from joining in.

Also at this time, in half of the trials I added a *Formica subnuda* to an "arena" located on the trail between the food and the colony. This arena was an enclosed section of the trail which had a tube-within-a-tube design. *L. pallitarsis* workers had to pass through the arena by way of the smaller, interior tube. This tube also had holes through which the foragers could enter into the larger, exterior tube in which the *F. subnuda* resided. The holes in the interior tube were of such a size, however, that although *L. pallitarsis* workers could pass freely, the much larger *F. subnuda* could not escape the arena. With this arena design, *F. subnuda* kill 1-2 *L. pallitarsis* per 100 successful foraging trips (NONACS & DILL, 1990). In the other trials (the controls), the arena was left empty.

As the first of the fed ants returned to the colony, the clamp at the colony exit was opened for her and for all ants leaving for the food patch. For the next 20 min, the number of foragers leaving for the food patch was counted in 5 min periods. However, to standardize the initial information received across trials, the trail was closed to all other successful foragers trying to return to the colony for 5 min after the arrival of the first one. Thereafter for returning workers, the clamp was opened only if they had food. In other words, after a trial began any forager could freely leave the colony, but then she was "committed" to reaching the food patch, regardless of the danger along the trail. Upon reaching the food source, workers always fed irrespective of whether they encountered risk previously. Therefore, all returning ants had food and none returned having encountered only mortality risk. The colony was presented, in random order, with each combination of diet strength and risk four times. The colony was housed in clear Tygon tubing, which allowed the observation of worker behaviour both along the trail and within the colony.

The rationale for this protocol is that successful foragers bringing back food to the colony should stimulate other ants to forage. However, if the first and all subsequent foragers have experienced mortality risk and communicate this to the colony, then recruitment may be inhibited. Furthermore, the quality of the food (good or poor) may also affect how the patch is perceived and the response to the danger along the trail.

The above experiment has two drawbacks. First, determining the effects of risk requires comparing treatments of risk *versus* no-risk. The underlying assumption in this is that the colony would always recruit to the food source if risk were not present. Therefore, any difference between risk and no-risk treatments would be due to communication about the presence of the *F. subnuda* along the trail. There is, however, no internal control for the rate of recruitment prior to risk addition (*i.e.*, if the workers do not recruit in trials with risk, is that due to the risk or might they not have recruited under conditions of no-risk, as well?). Second, the foragers leaving the colony were manipulated such that they had to go past the *F. subnuda* and reach the food and could not retreat to the colony. Realistically, however, some foragers could be expected to abandon foraging prior to reaching the food. Therefore, both successful and unsuccessful (with respect to food) foragers would be returning to the colony.

In the second experiment, all the initial foragers of the above colony plus two more colonies (all consisting of a queen, larvae, eggs and >250 workers) were allowed to return from the food patch without encountering risk. If workers started to recruit to the food source, the trial was continued; if they did not, the trial was abandoned. Therefore, unlike the first experiment, there is no question whether the colonies perceived the food source as attractive prior to the appearance of the *F. subnuda*. Where recruitment occurred, the colonies were allowed 30 min of undisturbed use of the food patch (the pretreatment phase), which contained a diet either of good or poor quality as described above, or one of a four-fold dilution. This additional diet level is of moderate quality because colonies fed *ad libitum* on this diet would roughly maintain themselves, but would not grow (NONACS, 1988).

Another difference from the first experiment was that after the initial foragers returned the trails were divided, such that foragers had to follow one route to the food and a dif-

ferent one back to the colony (80 cm on one-way trails per 180 cm round trip). Trail directionality was maintained by using an ant "teeter-totter", which acted as a one-way valve. The teeter-totter was enclosed in a plastic sphere with access holes at top and bottom. Foragers approached the teeter-totter from above, through a Tygon trail. An unladen teeter-totter was balanced so that its pan rested directly under the top hole. When an ant stepped on the pan, her weight dropped the pan, preventing her from going back. The ant could step off the pan and exit the sphere only through the bottom hole. The empty pan would then spring back to its original position. The sides of the sphere were lightly greased with petroleum jelly to prevent foragers from climbing back up. Although foragers' travel times increased because they often hesitated in stepping on and off the pan, they readily used the teeter-totter. The divided trail likewise proved not to be an impediment to foraging. Apparently *L. pallitarsis* foragers mark trails both going to and coming from food sources. In the congener *L. neoniger*, foragers leave a persistent trail pheromone that serves as a long-term orientation guide (TRANIELLO, 1989).

After the pretreatment phase, one *F. subnuda* was introduced into arenas either on the route to the food (risk to food: RTF), on the route back to the colony (risk from food: RFF), or along both routes (risk both ways RBW). In control trials, *F. subnuda* were not added (no risk: NR). This design allows inferences about communication of mortality risk from the observed recruitment responses with the different locations of danger. For example, if no information about risk is transmitted with the incoming food, then workers in the colony should recruit to the food patch unless they encounter the danger themselves prior to reaching it. Because risk only on the trail back is never encountered before the food, this treatment (RFF) should not immediately inhibit recruitment rate. However, if both food and risk information is communicated within the colony, risk on the trail back could rapidly affect recruitment.

The risk arenas were positioned in front of the teeter-totter so that foragers could retreat back to the colony and, therefore, unlike the first experiment, in RTF and RBW treatments foragers with risk experience could return to the colony both with and without food. The RFF treatment is similar to the first experiment in that mortality risk information is only brought back by fed workers. A trial consisted of recording the number of individuals crossing the two teeter-totter in 5 min periods for the 30 min pretreatment phase and for the 60 min treatment phase after the risk manipulation. Afterwards, any *F. subnuda* were removed and the colonies were allowed to satiate on full strength diet. Every colony had one trial with each combination of diet level and risk location. Between trials, colonies were kept without food for one day.

In both experiments it is assumed that after the first successful forager returns to the colony, behaviour of other ants in the colony is no longer spontaneous. Ants of the genus *Lasius* use chemical trails and have mass recruitment (ATTYGALLE & MORGAN, 1985). I observed in *L. pallitarsis* foragers abdomen dragging and trail following behaviour that typifies a chemical recruitment and signaling system. (See also recruitment responses to food in NONACS & DILL, 1988.) Because there is only one restricted trail from the colony to the food, any ant leaving the colony must encounter the pheromone trail and cannot be naive with respect to the presence of food. Therefore, increases in the number of ants recruiting to the patch are not likely to be due merely to quiescent ants spontaneously beginning to forage.

Besides inducing others to forage, ants can return for additional food loads, themselves. Therefore, to make inferences about recruitment response it is necessary to measure the rate at which individual ants collect loads. To do so, I marked the abdomens of several workers with a Pentel white marking pen and timed at least two round-trips to the food for each of these individually identifiable ants. For eight workers, the average round-trip time was 17.2 min (S.E. $\pm$ 1.3). (For all 33 recorded round-trips of the 8 workers, the mean was 16.3 min, with a range of 7.8 of 37.0 min). The average times for the first, second, third and last round-trip of the ants were 18.3, 15.4, 17.3 and 19.7

min, respectively. This indicates that foragers may work faster in the middle of trials, but they do not seem able to consistently bring back loads in under 15 min in this experimental apparatus.

Results

In the first experiment with the single trail, when the diet in the patch was full strength, recruitment in trials with the *F. subnuda* was not significantly different from trials without the larger ant ($t = 0.187$, NS, for the comparison of total number of foragers leaving the colony in 20 min). Furthermore, in both treatments the response “built” in that many more ants left for the food source in the later time periods than at the beginning of the trial (Fig. 1). In trials without risk, 305% more ants left for the food in the last 10 min than in the first 10 min. Likewise in trials with risk, 175% more ants left in the last 10 min. Given the round-trip estimated times of well over 10 min, it seems unlikely that the increase in the last 10 min can be attributed solely to foragers working faster. Therefore, returning ants must have continually recruited others

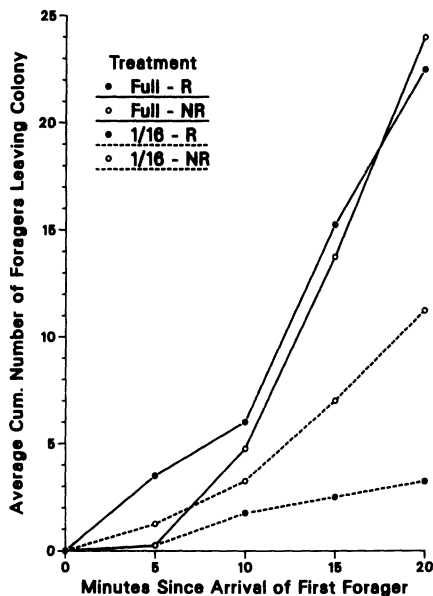


Fig. 1. Average ($n = 4$ trials) cumulative numbers of foraging leaving for the food patch over the 20 minutes after the arrival of the first successful forager. Full and 1/16 refer to the diets in the patch. R and NR mean that returning foragers either do or do not encounter risk on the trail respectively.

into foraging throughout the length of the trials, even where there was risk in the system.

When the food source was 1/16 strength, the number of ants recruited into foraging was less than in the full strength treatment, independent of the presence of risk. However, unlike the case in the full strength treatment, significantly fewer foragers left for the food in the risk than in the no-risk treatment ($t = 3.720$, $df = 3$, $p < 0.01$). Recruitment in the no-risk treatment increased over time as it did with full strength food (albeit at a slower rate: a 146% increase in the last 10 min over the first 10), but with risk, there was no increase in the number of foragers leaving in the later time periods. In fact, 14% fewer ants left for the food in the last 10 min than did in the first 10 min. Returning foragers were observed exchanging food in all treatments, but only the combination of risk and poor food failed to elicit recruitment.

In the second experiment with the divided trail and three possible diets in the food patch, the numbers of foragers both going to the food and returning to the colony were counted. Given the necessarily close relationship between the numbers of outbound and incoming ants, however, I will restrict the data analysis mostly to incoming foragers because the number of food loads returned to the colony is the better descriptor of colony foraging rate.

The average numbers of foragers who returned in the first 30 and last 60 min in each treatment condition are shown in Fig. 2. ANOVA (repeated measures design) of the data for the first 30 min with factors of diet level, future risk location and time showed that foraging rate increased significantly only with time ($F = 14.09$; $df = 5, 10$; $p = 0.0003$). The building of the response was like that observed in the first experiment and indicated that the colonies found the food, by itself, attractive at all diet levels. All other main effects and interaction terms were not significant, indicating that the treatment groups behaved similarly prior to manipulation (left panels in Fig. 2).

ANOVA of the last 60 min showed a significant positive effect of diet quality ($F = 17.81$; $df = 2, 4$; $p = 0.010$), a significant interaction between risk location and time ($F = 1.90$; $df = 33, 66$; $p = 0.013$) and a marginally significant interaction between diet and risk location ($F = 2.96$; $df = 6, 12$; $p = 0.052$). The risk $\times$ time interaction indicates that the response to the addition of *F. subnuda* took some time to stabilize. An initially higher load return rate could be expected because foraging ants at the patch or on the trail opposite the *F. subnuda* would have been unaware of changes in risk. Therefore, I removed the first 10 minutes after risk addition from

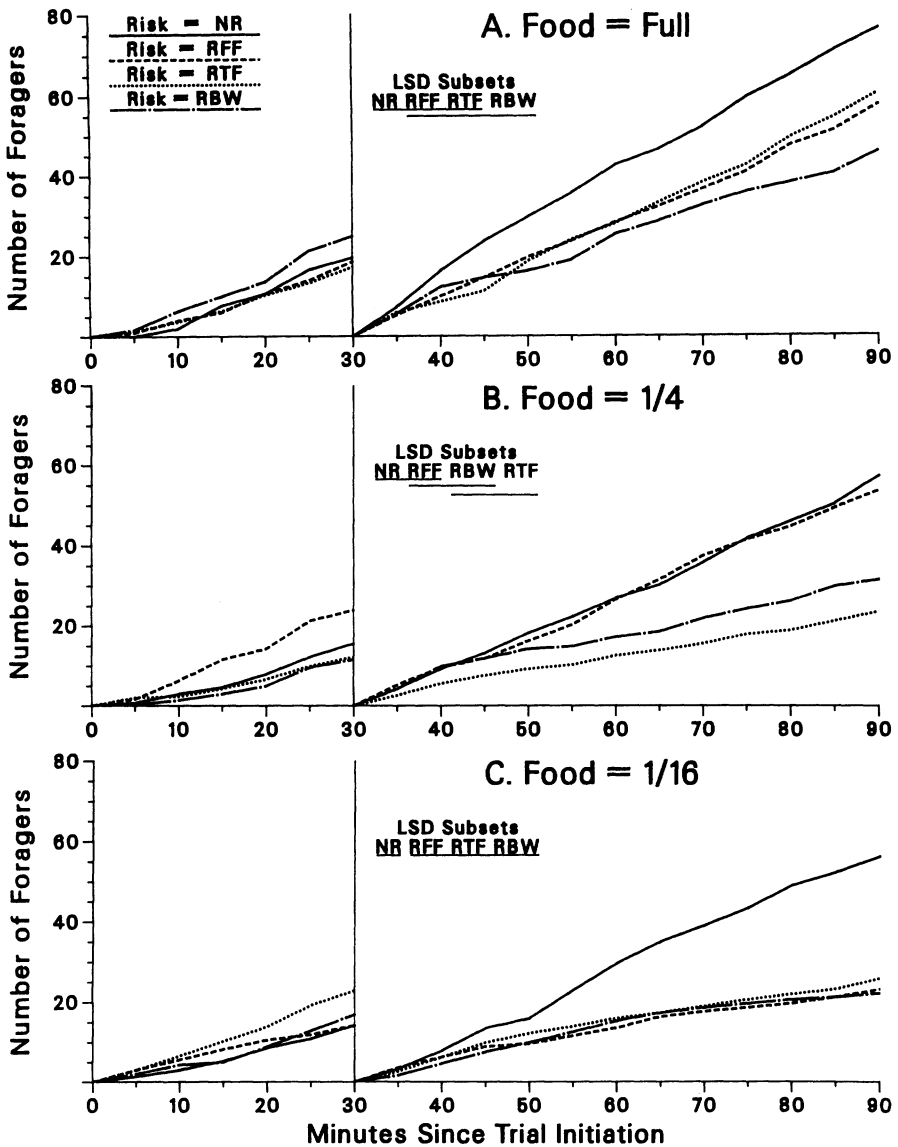


Fig. 2. Returning foragers over time. The lines connect the cumulative number of returning foragers from the food patch at consecutive five minute periods, for each of the four risk treatments, averaged over the three colonies. At 30 minutes, *F. subnuda* were released into the risk arenas either only on the way back from the food (RFF), only on the way to the food (RTF), or on both routes (RBW). In the no risk treatment (NR), *F. subnuda* were not present. The diet levels in the food patch were full, 1/4 or 1/16 strength for A, B, and C, respectively. The LSD subsets are treatments which were not significantly different by Least Significant Difference analysis at $\alpha = 0.05$.

the data set to examine behaviour when there were likely to be few naive foragers on the trials. ANOVA on the data for the last 50 min no longer shows a significant interaction between risk location and time ($p = 0.147$), suggesting that after the initial information lag, responses to risk were stable. The interaction between diet level and risk location was now highly significant, however ($F = 5.88$; $df = 6, 12$; $p = 0.005$), indicating that the eventual colony response to risk was dependent upon food quality.

I used analysis by Least Significant Difference (SOKAL & ROHLF, 1981; $\alpha = 0.05$) to elucidate the effects on the total number of returning ants of risk location at each diet level. When diet level was full strength, load return rates remained high for all treatments (Fig. 2A), although significantly fewer foragers returned with RBW than under the NR condition. When diet level was 1/4 strength, recruitment declined similarly in both treatments in which risk was encountered along the trail to food (Fig. 2B). Significantly fewer loads were collected with RTF than under either NR or RFF conditions. When diet level was 1/16 strength, risk anywhere caused significant and similar declines in loads collected compared to NR treatment condition (Fig. 2C).

An alternative hypothesis to explain the results of the second experiment without evoking communication of risk is that individual ants decided to stop foraging after encountering risk, *i.e.*, they chose not to make additional trips. With a round-trip time of approximately 16-17 min, a forager can collect 4 loads of food in the 60 min treatment phase. Twenty foragers, therefore, can collect 80 loads in an hour, which is close to the maximum number observed in the full strength food, no risk condition (Fig. 2A). If 20 workers did all the foraging and did not return for additional loads after encountering risk, this could explain the reduced cumulative number of loads returned to colonies at the end of trials with moderate or poor food sources (Figs 2B & C). This explanation, however, is at odds with the results of the first experiment in which individual experience alone cannot explain the inhibition of foraging with risk and a poor food patch (*i.e.*, less than four ants, on average, left the colony and personally experienced risk [Fig. 1]). Furthermore, three lines of evidence within this experiment suggest that this hypothesis is insufficient here, as well. First, if individual experience were the sole determinant of colony foraging responses, then the RFF condition should have been equal to the RTF condition in inhibiting recruitment. If anything, RFF should have had the greater effect because of risk being the last experience on a foraging trip. It can be argued that RFF should have also had the greater effect for the same reason with communication. How-

ever, RFF having less of an effect than RTF (as seen in Fig. 2B) is inconsistent with individual experience alone, but is possible if communication is involved.

Second, the RBW condition did not consistently have a more pronounced inhibitory effect on foraging, either immediately after risk addition or cumulatively (Figs 2B & C), although all the foraging workers should have encountered mortality risk sooner and more often than in the other conditions.

Finally, in the 1/16 diet strength experiment any risk addition reduced recruitment. However, if returning foragers did not communicate risk to their nestmates, the rate of ants *leaving* for the food source after the *F. subnuda* was released should have been less affected by the addition of risk in the RFF condition than in the RTF or RBW conditions. This is because the naive foragers leaving the colony for the food would not have immediately encountered the *F. subnuda* in the RFF condition (*i.e.*, they would have passed through the arena and crossed the teeter-totter and been counted rather than retreating back to the colony). The average number of ants leaving the colony across all conditions in the last 15 min of the pretreatment phase was 3.78 per 5 min. In the first 5 min of the treatment phase the average number of ants leaving for the food source was 1.3% greater in the NR condition. The numbers of ants in the RFF, RTF and RBW conditions, however, were 33.9%, 38.4% and 7.4% less, respectively. That the reaction in the RFF condition is more similar to RTF and RBW than to NR argues against the alternative hypothesis but is consistent with communication between workers.

Discussion

Ants can communicate danger via a wide variety of chemical alarm signals (PARRY & MORGAN, 1979). Often the alarm reaction is a generalized response to many different threats (HÖLLDOBLER, 1978). However in some cases, such as *Pheidole dentata* colonies responding to contacting *Solenopsis* spp. workers, the reaction is specific to that ant genus. *P. dentata* foragers rapidly recruit many soldiers to attack the *Solenopsis* workers and colonies do not show as pronounced a reaction to workers of other, less threatening species (WILSON, 1975 & 1976). Furthermore, over repeated encounters, *P. dentata* can also learn to respond similarly to an allopatric species (CARLIN & JOHNSTON, 1984). Clearly then, *P. dentata* workers can communicate a message that has a specific meaning about the type of danger and the action required to their nestmates.

This study presented *Lasius pallitarsis* foragers with mortality risks in such ways that inferences about mortality risk communication could be made based on subsequent colony behaviour. It is not known whether the change in behaviour of *L. pallitarsis* is species-specific to *F. subnuda* or to the risk, *per se*. The ecological interactions of the two species and reactions of *L. pallitarsis* to the presence of *F. subnuda* are discussed elsewhere (NONACS, 1988; NONACS & DILL, 1988). Nevertheless, the experiments support the hypothesis that mortality risk, like food presence and quality, is a piece of information that can be communicated between foragers and is used in deciding a specific course of action.

Evidence for communication of mortality risk is the lack of recruitment responses when the initial returning foragers encountered a poor food patch and danger on the trail. Recruitment did occur when there was no risk. Likewise in the divided trail experiment, the addition of risk to a situation where ants are actively foraging at a poor patch rapidly reduces the rate at which food loads are collected. This occurs even in situations where the risk is located such that foragers can encounter it only after feeding. An alternative hypothesis that ants do not communicate risk and must personally encounter danger to react to it, is not consistent with several results, such as the lack of a recruitment response in reaction to successful foragers from a poor food patch with associated risk in the first experiment. Ants were observed exchanging the collected liquid food, but this stimulates foraging only if risk is not present. Furthermore, in the divided trail experiment, the responses of colonies to the various locations of risk are not explicable by individual experience alone. Particularly striking is the rapid decline in the rate of ants leaving the colony with RFF, the condition in which risk cannot be experienced until well after departure from the colony.

If risk information is communicated in all food level conditions, then foragers' response to this information depends on what they perceive about food quality. In both experiments, when food is good, risk is ignored or at least tolerated, probably because potential colony growth gains offset the loss of a few foragers (NONACS & DILL, 1990). The observed reductions in load return rate in the divided trail experiment are consistent with the *F. subnuda* increasing the travel time of foragers through interactions in the risk arenas. NONACS & DILL (1988) showed under similar experimental conditions that, although colonies recruit to good food patches, agonistic interactions reduce load return rates by about 30%. When food quality is moderate (colonies can maintain them-

selves but not grow), ants in the RFF condition may “take a chance” that risk is gone (in nature, the *F. subnuda* could have moved elsewhere). Returning foragers either do not communicate their risk experience, or if they do communicate it, the other ants ignore it and go to the food anyway. However in the RTF and RBW conditions, foragers are reluctant to pass by the *F. subnuda* to reach the food patch, reducing return rates. Apparently the perceived risk to self is not offset by the potential food reward to the colony. Finally, when the food is very poor, it does not pay foragers even to take a chance that the risk is gone, and they therefore remain within the nest even in treatments where only successful foragers return to the colony.

Unanswered by this study is the mechanism by which distant danger is communicated. Ants may use their alarm pheromones in conjunction with food recruitment signals to give a single, mixed message of both food and danger. Many species have at least several chemicals that have been shown to affect behaviour when presented alone (PARRY & MORGAN, 1979). Using them in combination may produce a chemical language that can communicate more complex information, such as the opposing stimuli of food and danger, in a single message. Such use of multiple compounds is present in individual identification where combinations of chemicals provide cues for kin, nestmate, conspecific and species-specific discrimination (HÖLLDOBLER & CARLIN, 1987).

Alternatively, ants could modulate food recruitment signals to indicate that the food source is less valuable than suggested by its nutritive quality alone (*i.e.*, foragers could exchange food with nestmates, but fail to perform the behaviours necessary to elicit recruitment). For example, MÖGLICH & HÖLLDOBLER (1975) in *F. fusca* and VAN VORHIS KEY & BAKER (1986) in *Iridomyrmex humilis* show that tactile interaction between foragers significantly enhances food recruitment.

Individual behaviours of workers in response to specific combinations of stimuli need to be observed to elaborate how risk and food are communicated simultaneously. However, although the mechanism by which risk is communicated is unknown, it does appear that *L. pallitarsis* workers characterize their environment in terms of both food and risk distributions. The colony's ability to allocate foragers in a manner that efficiently exploits food resources has long been considered to be a major advantage for the social insects. The ability to communicate mortality risk must likewise be viewed as an additional benefit to all colony members and therefore a factor which favors sociality.

Summary

Ant foragers are known to communicate food presence in distant patches, but do they also communicate information about distant mortality risk? Recruitment to a food source in a laboratory *Lasius pallitarsis* colony depended upon whether the initial returning foragers had encountered mortality risk (a larger *Formica subnuda*) and the quality of the food they found. When food quality was high, risk appeared to not affect recruitment; when quality was low, risk inhibited foraging. In a second experiment, *L. pallitarsis* colonies had access to food of several qualities through a divided trail, which forced foragers to take different routes to and from the food patch. Danger was either entirely absent, present only on the way to the patch, present only on the way from the patch, or along both routes. When food quality was poor colonies recruited to food when risk was absent, but risk anywhere significantly reduced the level of foraging. This included the situation where only returning foragers could encounter danger, which strongly suggests that their behaviour was a critical factor in whether nestmates would continue foraging. When food quality was moderate, only treatments with risk on the way to the food significantly inhibited foraging. When food quality was good, colonies continued to forage at a high rate, irrespective of presence or location or risk. In total, *L. pallitarsis* foragers appear to communicate and use information about both food and mortality risk in deciding whether to exploit patches.

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Resumen

Es sabido que las hormigas buscadoras de alimento comunican la presencia de fuentes de alimento distantes, pero, ¿acaso comunican también información sobre posibles riesgos de muerte distantes? El reclutamiento a una fuente de alimento por parte de una colonia de *Lasius pallitarsis* en el laboratorio dependía de si las primeras buscadoras de alimento retornaban a la colonia habiéndose tropezado con riesgos mortales (obreras de *Formica subnuda*) y de la calidad del alimento que encontraban. Cuando la calidad del alimento era alta, el riesgo parecía no afectar al reclutamiento; cuando la calidad era baja, el riesgo parecía inhibir la obtención del alimento. En un segundo experimento, colonias de *L. pallitarsis* tenían acceso a alimento de varias calidades diferentes a través de un camino dividido, el cual obligaba a las buscadoras de alimento a tomar diferentes rutas para ir y para regresar de la fuente de alimento. El riesgo era o inexistente, o presente sólo en el camino de ida, o sólo en el camino de regreso, o presente tanto en el de ida como en el de regreso. Cuando la calidad del alimento era baja las colonias reclutaban a la fuente de alimento sólo cuando el riesgo era inexistente, pero riesgo en cualquier lugar reducía el nivel de obtención de alimento. Esto incluía la situación en que las obreras sólo encontraban el riesgo en el camino de regreso, lo cual sugiere que su comportamiento es un factor de importancia crítica en determinar si miembros de la misma colonia continuarían la obtención del alimento. Cuando la calidad del alimento era mediana, sólo el riesgo en el camino de ida a la fuente de alimento inhibía la obtención significativamente. Cuando la calidad del alimento era alta, las colonias continuaban su obtención a un alto nivel, sin tener en cuenta la presencia o posición del riesgo. En resumen, parece ser que, al decidir si una fuente de alimento va a ser explotada, las obreras de *L. pallitarsis* comunican y usan información tanto sobre el alimento como sobre el riesgo de su obtención.