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FORAGING RESPONSE OF THE ANT *LASIUS PALLITARSIS* TO FOOD SOURCES WITH ASSOCIATED MORTALITY RISK

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SUMMARY

Lasius pallitarsis (Provancher) ant colonies were offered a choice between two food patches of equal nutritive quality but with one of the patches having associated with it one of several types of mortality risk indicators. Foraging decisions appeared to be affected only when the *L. pallitarsis* foragers could actually physically encounter a potential mortality agent (a larger *Formica subnuda* Emery). Odors of either crushed conspecifics, a *F. subnuda*, or a *F. subnuda* in conflict with *L. pallitarsis* workers, were sensed by *L. pallitarsis* workers but did not affect patch choice.

RESUME

Réponses de la fourmi *Lasius pallitarsis* à des sources de nourriture associées à des risques de mortalité

On a offert à des colonies de fourmis *Lasius pallitarsis* (Provancher) le choix entre deux sources de nourriture d'égale valeur nutritive mais différant quant au risque perçu de mortalité, une des sources étant associée avec plusieurs indices de risque de mortalité. Les décisions relatives à la recherche de nourriture ne semblent être affectées que quand les ouvrières *L. pallitarsis* entrent en contact physique avec un risque concret de mortalité (une grosse *Formica subnuda* Emery, en l'occurrence). Les ouvrières de *L. pallitarsis* perçoivent les odeurs de conspécifiques broyées, de *F. subnuda* ou de *F. subnuda* en combat avec d'autres ouvrières de *L. pallitarsis*, mais leur choix de source de nourriture n'en est pas affecté.

INTRODUCTION

An ant colony forages in a complex environment. Food may appear unpredictably in time and location and if multiple food sources are available at the time, the colony may have to decide whether to recruit simultaneously

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to several food sources, exploit them sequentially, or use only the most profitable. Moreover, a colony's habitat certainly must be heterogeneous in ways other than just energetic reward. Foragers can fall victim to both predators and competitors from other ant colonies, and risk of mortality could alter foraging behavior. Simulated predation of workers from the area surrounding nest entrances results in the cessation of foraging activity by *Pogonomyrmex* species (GENTRY, 1974; WHITFORD and BRYANT, 1979). Natural predation by spiders at nest entrances also halts foraging (MACKEY, 1982). Extreme rates of predation at nest entrances may limit the range of colony responses to only such drastic measures as total cessation of above ground activity. If only certain areas of the territory are dangerous, however, then the colony need not stop foraging entirely, but instead concentrate its activity in safer regions.

An ant colony has the potential to communicate complex information about both food and risk. Numerous studies have demonstrated the nature and effectiveness of alarm and recruitment pheromones in the Formicidae (for a review, see PARRY and MORGAN, 1979). However, to our knowledge, no study has examined behavior in which both recruitment to food and alarm occur simultaneously. Because in most species different glands and different chemicals are used in these two behaviors, colonies may exhibit a wide range of responses to simultaneous stimuli. A continuum of reaction is possible, from total cessation of foraging to a complete ignoring of the alarm.

The goal of this study is to examine the interaction between alarm and food recruitment in an ecologically relevant situation. To do this, we gave captive *Lasius pallitarsis* (Provancher) colonies a choice between two food sources of equal nutritive value but with different levels of risk in their acquisition. *L. pallitarsis* appears to possess the behavioral complexity needed to handle competing stimuli of food and alarm. Species of the genus *Lasius* have sophisticated means of communication in both chemically recruiting foragers via trail pheromones from the hindgut (ATTYGALLE and MORGAN, 1985), and producing alarm substances from Dufour and mandibular glands (PARRY and MORGAN, 1979). Moreover, dealing with mortality risk is likely to be an integral part of foraging for *L. pallitarsis*. This species forms large colonies in moist woodlands of the pacific northwest of North America, and has areas within its territories where foragers encounter colonies of both conspecifics and other species. In an ecologically similar species, *L. neoniger*, TRANIELLO (1983) hypothesized that aggressive interactions with numerous other species exerted selection pressure on foraging behavior.

One species that is likely to have an impact on *L. pallitarsis* behavior is *Formica subnuda* Emery, which is a much larger ant and a facultative slave-maker. Although *L. pallitarsis* workers are not enslaved, they tend to do poorly in agonistic encounters with *F. subnuda*. This species is commonly found in the same habitats as *L. pallitarsis* and has a high overlap in diet.

and nest site preference (pers. obs.). Furthermore, CZECHOWSKI (1975) reported *F. sanguinea* raiding *L. niger* colonies. These species are closely related and similar in habit to *F. subnuda* and *L. pallitarsis*, respectively.

METHODS

The colonies were housed in moistened sawdust in $13 \times 13 \times 4.5$ cm plastic containers within larger $21 \times 21 \times 7$ cm plastic containers (A in *fig. 1*) and given unlimited access (from a side port on the larger container) to an artificial diet. This was similar to that of ETTERSHANK (1967), except that we replaced specific amino acids with 1.75 g of casein, used only 15 g of sucrose as sugar, and added 0.1 g of NaCl, one B complex vitamin and one multi-mineral tablet. All food was removed one day prior to an experimental trial and because the liquid diet could not be stored, such deprivation assured that the colony was not satiated and would actively recruit to new food sources.

Trials began by collecting foraging individuals in the large container and placing equal numbers (2-5 individuals) in two food patches (C in *fig. 1*). Food was available from a coil of Tygon tubing (1.5 mm interior diameter) with both ends blocked with cotton batting so that there was a constant droplet of which replenished itself as the ants fed. After the foragers became completely satiated, the patches were connected via Tygon tubing (3.5 mm interior diameter) to the home area (*fig. 1*); the ants returned from both food patches in roughly the same numbers and at the same time. Any trial in which there was not an approximately symmetrical return of foragers was abandoned.

The initial foragers never encountered danger or risk. Risk was added to only one side (henceforth referred to as "risky"), in one of four ways. In one method we crushed 1-4 of the new recruits (or returning foragers) as they were heading toward the food source to test whether foraging decisions could be affected by the presence of freshly killed nestmates alone. A second method was to construct a tube-within-a-tube pathway (B in *fig. 1*). The inner tube was of mesh that allowed the passage of *L. pallitarsis* foragers to and from the food source but prevented their passage into the outer tube. Within the outer tube, on the risky side, we placed a large *F. subnuda* worker after initial foragers had passed on their inward trip to the colony, but before they or new recruits could return. In these trials, there was no physical contact between *L. pallitarsis* and the *F. subnuda* worker. The third method was identical to the second except that 1-3 *L. pallitarsis* nestmates were placed in the outer tube at the same time as the *F. subnuda* worker. The ants fought, with the *L. pallitarsis* workers generally being killed over several hours, so that foraging decisions could be affected by the odor of the *F. subnuda* worker and/or the nestmate alarm and defense chemicals. Finally, the fourth method was similar to the previous two except that the fine mesh tubing was replaced with a Tygon tube with openings large enough to allow free passage for *L. pallitarsis* foragers, but too small for the *F. subnuda* to escape the larger tube. Therefore, physical contact between individuals of the two species was possible. The side designated to be risky was chosen randomly prior to each trial for all methods.

Trials began after the return of the initial foragers and were of two lengths, short (3-4 hours) and long (18-24 hours), to test for time-dependent changes in foraging behavior (e.g. learning). Where foragers were crushed, we did only short trials. The food tubes were weighed immediately before and after each trial. Relative side preference was measured as the weight loss of the safe side divided by the total weight loss of both sides. The data were arcsine transformed before statistical analysis. Tubes without

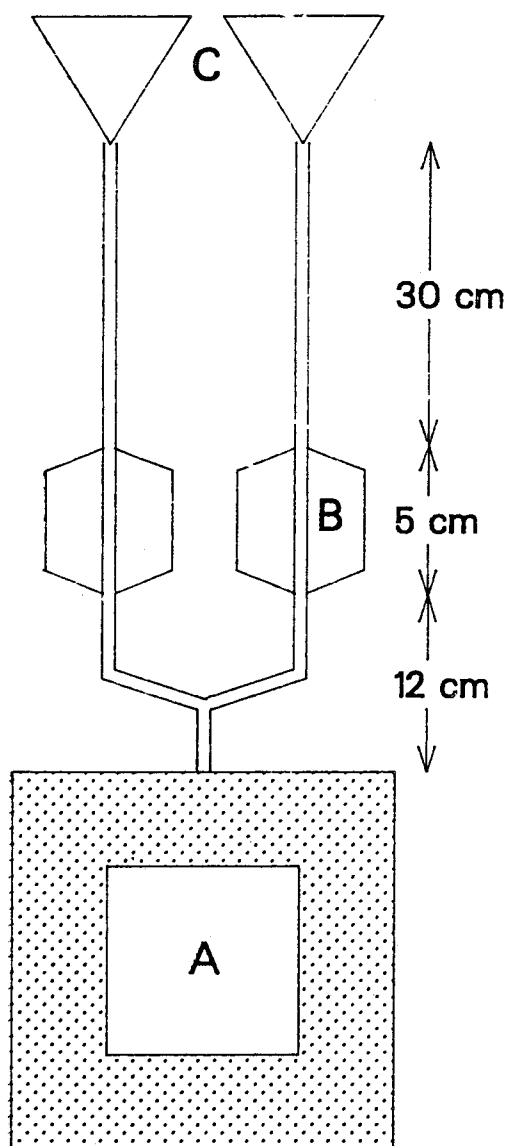


Fig. 1. — Schematic diagram of the colony and experimental design. A. Nest container. The large *Formica subnuda* could be placed in one of the outer tubes (B) after the initial foragers had returned from the food patches (C). Depending upon the experimental protocol, *Lasius pallitarsis* foragers may or may not be able to contact the large ant physically. In trials where foragers were crushed, the risk tubes were replaced with a single tube of the same length, in which a few recruiting foragers were killed. See text for further explanation.

Fig. 1. — Schéma d'une colonie et plan de l'expérience. A. Nid. La grosse *Formica subnuda* pouvait être placée dans l'un des tubes extérieurs (B) après que les premières ouvrières soient revenues des sources de nourriture (C). Les ouvrières de *Lasius pallitarsis* ont la possibilité ou non d'entrer en contact physique avec la grosse fourmi selon le protocole expérimental utilisé. Pour les essais où les ouvrières étaient broyées, les tubes indicateurs de danger étaient remplacés par un tube de même longueur dans lequel quelques ouvrières revenant de la source de nourriture étaient détruites. Se référer au texte pour de plus amples détails.

access to them by ants were kept during trials to measure evaporative loss, which was subtracted as a correction factor.

We used 13 colonies, of which 4 were reared from mated alates and thus had fertile queens. The remainder were unqueened colonies, collected from the field, in which queens were either not found or had died in the laboratory. All colonies had larvae and anywhere from about 20 to several hundred adult workers. Some colonies experienced

more than one treatment, but no colony experienced every treatment. The queened colonies, being generally smaller, fed enough only in long trials to give results measurably different from the evaporative loss and could not be used in short trial protocols.

With the first three experimental protocols there was a possibility that the treatments would have no effect because the ants were incapable of detecting chemical stimuli. To test for this possibility, we placed three queenright *L. pallitarsis* colonies in a Tygon tube container (10 cm length, 1.2 cm interior diameter) and created a continuous slow airflow from an aquarium air pump. After the colonies had settled, we injected into the tube connecting the colony to the pump, 3 cc of room air (the control), or air from a vial containing either freshly crushed conspecifics, a single *F. subnuda* worker, or a single *F. subnuda* worker in conflict with two *L. pallitarsis*. Workers rapidly jerk their bodies up and down when excited. To measure the responses to the various odors we counted the total number of bobs/minute by all ants on a colony for three minutes both before and after injection. Each treatment was presented twice to every colony.

In the first three protocols, the negative stimulus could not physically hamper passage of *L. pallitarsis* foragers, but in the fourth, the large ant could potentially block the food trail as well as kill individual foragers. This could affect the rate at which food could be delivered to the colony. To measure the magnitude of this effect we tested three colonies presented with only one patch, which either was without risk or had a *F. subnuda* along the trail. As in previous experiments trials were initiated by placing a few foragers in the food patch. After the first recruits began arriving, we recorded the number of foragers that returned to the colony with full food loads (easily identified by distended abdomens) in each 5 minute interval for one hour.

RESULTS

The *L. pallitarsis* workers were clearly capable of detecting conspecific and *F. subnuda* worker odors (table I). The activity rate was significantly increased over pre-injection levels and by comparison to the control injection for all potential risk stimuli (table II). However, there were no significant differences between the reactions to the various risk stimuli. Although the colony counts, particularly in the first minute, may have errors associated with them because of the high rate of response, they were conservative and probably somewhat underestimate the activity levels of the colony.

The results from the food choice experiments indicate that only when foragers could physically contact the large ant were colony foraging decisions affected. In all cases, where contact was possible, the colonies strongly preferred the safe side. With all other experimental protocols, no preference was shown for either the safe or risky choice (fig. 2). A Tukey test (SOKAL and ROHLF, 1981; $\alpha = 0.05$) divided the results into two significantly distinct groupings. There were no significant differences between any treatment groups in which contact with the *F. subnuda* worker was possible, but all these groups were significantly different from all the treatment groups in which contact was not possible.

The experiments used both queened and queenless colonies. In no set of treatments, however, did the two groups display significantly different reac-

Table I. — Number of bobs per minute by all *L. pallitarsis* workers in a colony in response to odor presentations. The minute 0 figure is the average level of activity per minute for the three minutes before the injection of test odors. All three colonies in the experiment experienced each treatment twice; the data reported are the means per treatment ($n = 6$) $\pm$ S.E. The number of workers per colony ranged from 20-30.

Tableau I. — Nombre de sautilllements par minute pour toutes les ouvrières d'une colonie de *L. pallitarsis* en réponse aux présentations d'odeurs. Le chiffre à la minute 0 est le niveau d'activité moyen par minute pour les trois minutes précédant l'injection des odeurs testées. Les trois colonies utilisées dans l'expérience ont reçu chaque traitement deux fois. Les données indiquées sont les moyennes par traitement ($n = 6$) $\pm$ E.S. Le nombre d'ouvrières variait entre 20 et 30 par colonie.

Minute	Control (Room air)	Formica Alone	Crushed <i>Lasius</i>	Formica + <i>Lasius</i>
0	0.00 $\pm$ 0.00	1.11 $\pm$ 0.19	0.56 $\pm$ 0.31	0.17 $\pm$ 0.11
1	4.83 $\pm$ 2.77	27.17 $\pm$ 6.80	41.00 $\pm$ 12.93	45.33 $\pm$ 7.97
2	1.83 $\pm$ 0.68	5.00 $\pm$ 4.41	16.00 $\pm$ 8.97	14.33 $\pm$ 3.53
3	0.50 $\pm$ 0.48	0.67 $\pm$ 0.47	8.17 $\pm$ 5.02	6.17 $\pm$ 2.97

Table II. — F values (and their levels of significance) for ANOVA comparisons of reactions between odor presentation treatments. Time and interaction effects have been partialled out.

Tableau II. — Valeurs du F (et leurs niveaux de signification statistique) provenant d'analyses de variance sur les réactions des fourmis entre les traitements d'odeurs. L'influence du temps et des interactions a été partiellement neutralisée.

Treatment	Compared to			
	Control (Room air)	Formica Alone	Crushed <i>Lasius</i>	Formica + <i>Lasius</i>
Pre-exposure	9.36 (0.028)	16.10 (0.010)	12.65 (0.016)	76.54 (0.000)
Formica + <i>Lasius</i>	52.43 (0.001)	5.74 (> 0.05)	0.00 (> 0.95)	—
Crushed <i>Lasius</i>	11.89 (0.018)	1.79 (> 0.2)	—	—
Formica Alone	8.75 (0.032)	—	—	—

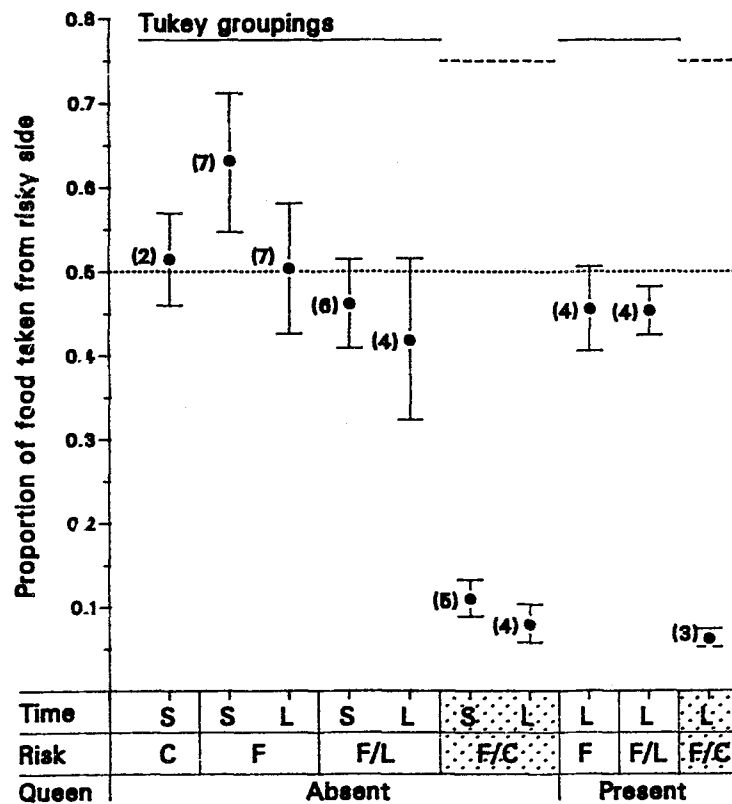


Fig. 2. — Foraging decisions in response to different types of risk. Preference is measured as the proportion of food taken from the side with the associated risk. Means ($\pm$ one standard error) are plotted for each treatment group. In parentheses are the number of colonies under each protocol, from which the means are calculated. S and L are short and long trials, respectively. C means recruiting foragers are crushed. F means *Formica subnuda* present, but no contact with foragers possible. F/L means *Lasius pallitarsis* workers in the tube with a *F. subnuda*, but no contact with foragers possible. F/C means *F. subnuda* can contact foragers. See text for further clarification. The solid and dashed lines represent homogeneous groups whose means did not differ significantly by Tukey analysis at $p = 0.05$.

Fig. 2. — Décisions alimentaire en réponse à différents types de risques. La préférence est mesurée par la proportion de nourriture prise du côté auquel un risque est associé. Les moyennes $\pm$ une erreur standard sont tracées pour chaque traitement. Le nombre de colonies à partir desquelles ces moyennes sont calculées est entre parenthèses sous chaque protocole expérimental. S et L désignent les essais courts et longs, respectivement. C désigne les ouvrières pourvoyeuses broyées. F représente la présence de *Formica subnuda*, mais sans possibilité de contact avec les ouvrières. F/L représente les ouvrières *Lasius pallitarsis* présentes dans le tube avec *F. subnuda*, mais sans contact avec les ouvrières revenant de la source de nourriture, tandis que F/C représente *F. subnuda* pouvant entrer en contact avec les ouvrières. Voir le texte pour de plus amples détails. Les lignes en trait plein et en trait interrompu représentent des groupes homogènes dont les moyennes ne diffèrent pas de façon significative d'après une analyse de Tukey à $p = 0.05$.

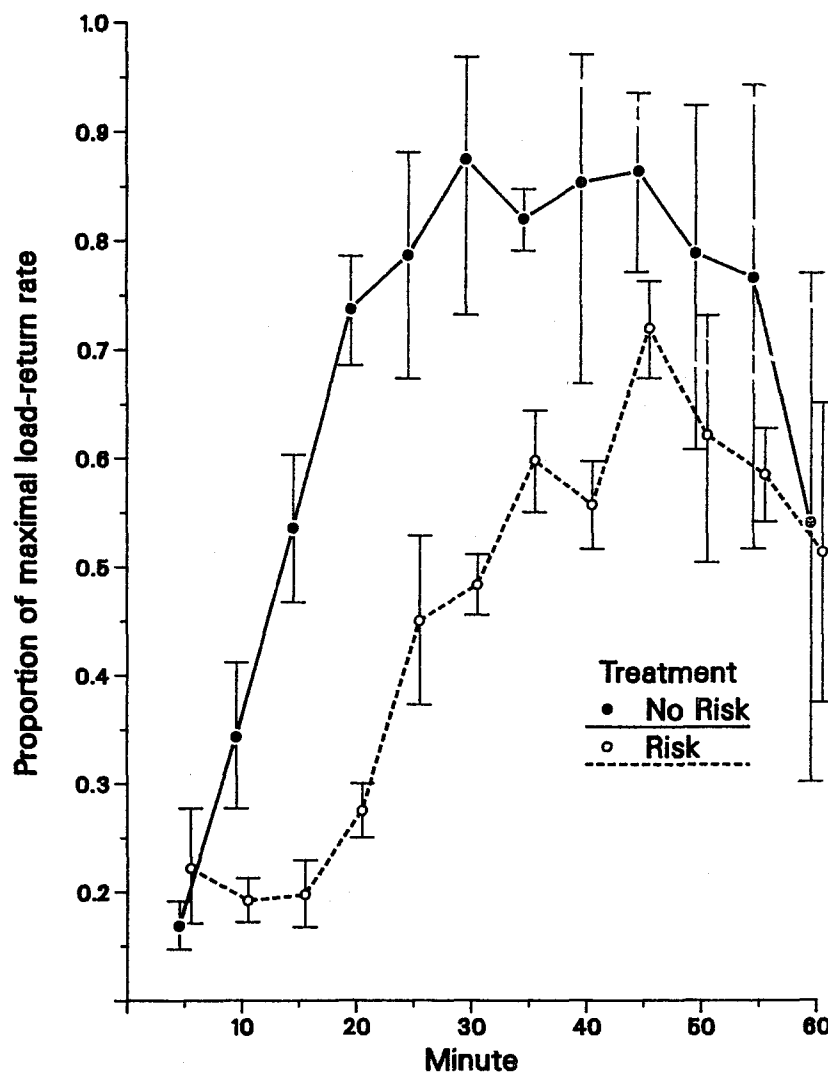


Fig. 3. — The average rate of food gathering by colonies with and without risk. The rate ($\pm$ S.E.) of each colony is calculated as the number of foragers returning with full loads in each 5 minute interval divided by the maximum number of loaded foragers ever observed to return in any 5 minute interval for each colony.

Fig. 3. — Le taux moyen de récolte de nourriture par les colonies en présence et en absence de risques. Le taux ($\pm$ E.S.) de chaque colonie est calculé comme étant le nombre d'ouvrières retournant avec une charge maximale dans chacun des intervalles de 5 minutes, divisé par le plus grand nombre d'ouvrières observées revenant avec une charge parmi tous les intervalles de 5 minutes, pour chaque colonie.

tions to risk (fig. 2). There were also no differences between short or long trials. *L. pallitarsis* apparently did not learn over a day to associate one food source with the presence of *F. subnuda* odor and avoid it as potentially dangerous.

When the large ant could contact the foragers, it significantly ($F = 35.05$; $df = 1.2$; $p < 0.03$) reduced the rate at which food loads were returned to the colony—on average about 30 % (fig. 3). In this experiment, only one food source was available at a time.

DISCUSSION

Lasius pallitarsis colonies appeared to avoid food sources only where there was physical contact or interference between the foragers and the large, potentially lethal competitor, *Formica subnuda*. Although *L. pallitarsis* workers did react to the presence of *F. subnuda*, dead conspecifics, and the alarm pheromones of nestmates, they did not avoid food sources associated with such cues. It is not clear from our study whether the responses of *L. pallitarsis* foragers to contacting *F. subnuda* were specific to that particular species or whether they were a general response to potentially lethal encounters. It is significant, however, that in response to an ecologically relevant threat situation, foraging behavior was altered.

Patch preferences could have been determined partly by energetic return rates. In trials where the foragers never physically encountered the large ant, the travel time differences between the safe and risky patches were probably negligible. Where physical contact was possible, however, the *F. subnuda* significantly reduced the rate at which food loads were brought to the colony (fig. 3). If this were due to physical blocking (rather than to a behavioral decision to not forage), then this could explain the patch preferences in the present experiment. However, when colonies face decisions about patches that vary both in risk and nutritive value, they avoid risk to a greater extent than would be predicted solely by energetic return rates (NONACS, 1988). This suggests that ants avoid risk *per se*.

It was therefore likely that physical contact not only reduced energetic return but also critically altered the nature of the information the colony received, perhaps through changes in the motivational state of the foragers. Contact with the large ant may have caused an outbound forager to abandon its attempt to reach food, and a satiated, nest-bound forager to return rapidly to the colony, with reduced or no trail marking. Although each successful individual forager may have evaluated the food sources equally in nutritive net return, the cumulative effect the colony's standpoint could have been relatively more trail deposition to the safe food source than to the risky one. Therefore, over time recruitment became biased toward the safe side.

A forager may also alter its tactile excitatory behavior. MÖGLICH and HÖLLDOBLER (1975) in *Formica fusca* and VAN VORHIS KEY and BAKER (1986) in *Iridomyrmex humilis* show that tactile interaction between foragers significantly enhances recruitment to food sources. In *L. pallitarsis* foragers, contact with the *F. subnuda* worker may have changed the rate, intensity, or context of their tactile communication and therefore also biased foraging responses toward the safe side.

The above experiments cannot conclusively distinguish the mechanism by which *L. pallitarsis* communicates about and responds to risk. To fully understand the decision process on the colony level, specific responses by individuals to encountered stimuli will have to be investigated. Furthermore, these experiments involved changes in only one variable, the type of risk. In nature, food sources are likely to vary in nutritive as well as in associated risk, and colonies may have to make more complicated decisions which involve trade-offs between risk and nutritive return (NONACS, 1988).

It seems logical for colonies to have avoided dangerous encounters when equally valuable, but safer, alternative food sources were available. However, why did interactions which were less severe than physical interference fail to alter foraging preferences? It may be related to the information (or lack thereof) transmitted to foragers by these less intense stimuli.

The crushing of foragers is probably not analogous to competition or predation effects. It may more closely resemble the random consequences to an ant colony of a world inhabited by large, mobile, vertebrates. Death on a trail from being stepped on may have low predictive power regarding whether repeat occurrences are more or less likely than on other trails. Therefore, crushing may have little inhibitory effect because it gives foragers no information about future risk. *L. pallitarsis* colonies live in environments where contact with competitors is also inevitable. To exploit only food sources without any associated risk may restrict colonies to an impossibly small set of food items. Therefore, the presence of other ants may have effects only when they directly interfere with foragers, as in the last set of experiments. It is interesting to note that the length of trials had no effect on foraging preferences: *L. pallitarsis* colonies did not eventually abandon food sources associated with competitors.

Finally, it is significant that in *L. pallitarsis*, foraging behavior was not noticeably altered by queenlessness. This may be due in part to mature colonies of this species being very large (to the range of about 100,000 individuals) with groups of workers and larvae often being physically separated from the main nest. Adaptive foraging behavior requires rapid and flexible responses which may be impossible to dynamically coordinate with queen state. Therefore, unlike brood rearing (see BRIAN 1983, for a review), foraging behavior may be largely independent of queen influence in *L. pallitarsis*.

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