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Author(s): Peter Nonacs and Lawrence M. Dill

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## MORTALITY RISK VS. FOOD QUALITY TRADE-OFFS IN A COMMON CURRENCY: ANT PATCH PREFERENCES<sup>1</sup>

PETER NONACS<sup>2</sup> AND LAWRENCE M. DILL

*Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University,  
Burnaby, British Columbia, Canada V5A 1S6*

**Abstract.** Many studies have shown that predation risk affects foraging behavior, but quantitative predictions are rare because of the lack of a common currency for energy intake and mortality. This problem is soluble in ants. We gave 12 *Lasius pallitarsis* colonies the choice between foraging in two patches that differed both in food quality and in associated mortality risk. We independently measured the growth that colonies could achieve on the diets offered in those patches. With no risk at either patch, colonies always preferred the higher food quality patch. When mortality risk (a large *Formica subnuda* ant) was associated with the trail to the higher food quality patch, the use of that patch depended on the magnitude of the growth differential between feeding in risky or safe patches: the greater the benefit of feeding in the risky patch, the greater was its relative usage. Colonies valued risky patches equally to safe patches at the point where forager mortality rates were approximately offset by colony growth gain. This ability to reduce mortality risk while foraging may be a factor that favors insect sociality, in general.

**Key words:** *ants; colony growth; Lasius pallitarsis; optimal foraging; patch choice; predation risk; social insects; trade-off.*

### INTRODUCTION

Natural selection should produce animals that are efficient food gatherers, and from this basic premise arises optimal foraging theory (OFT). OFT predictions have generally been supported when animals face simple decisions, such as choosing the prey items that maximize net energy returns (Stephens and Krebs 1986). In nature, however, foragers encounter complex situations whose solutions may demand the sacrifice of some amount of foraging success in order to achieve other goals as well.

The most common example of behavioral compromise is with the often conflicting goals of simultaneously foraging and avoiding predators. The responses to predation risk can be placed in four general categories (Fraser and Huntingford 1986). Animals can ignore the hazard entirely and continue behaving as if the risk were absent (risk-reckless). They can alter their behavior in ways that absolutely minimize their risk (risk-avoiding). They can change their behavior proportional to the increase in risk (risk-adjusting), or they can take proportionally greater risks in situations of high gain and proportionally less risks where gain is low (risk-balancing).

These categories can describe the range of predation risk trade-offs, but neither this classification scheme nor most studies of predation risk explicitly address the question of whether observed responses to risk are

optimal or even adaptive. Animals could certainly react inappropriately to risk, but they usually have been assumed to trade off adaptively between food intake rate and avoidance of predators. Showing this to be true empirically has been difficult because of the lack of a common currency. Without accurate estimates in a common currency of the fitness consequences of food intake and the probability of being eaten, only qualitative predictions can be made (e.g., animals should forage more cautiously in the presence of predators).

To decide whether behavioral trade-offs substantially increase fitness, one needs to study a species with the following characteristics. First, the value of food to individuals must be known in terms of how the food is converted into growth and/or translated into offspring. Second, the population must be susceptible to real and accurately measurable levels of predation. Third, the level of predation risk for the animal must be, at least in part, dependent upon the animal's foraging decisions. With these three conditions, the fitness consequences of all possible foraging decisions can be determined.

Social insects fulfill these requirements. Colony growth depends on the amount of food brought back by the forager workers, and growth is very important for survival and eventually for reproduction (Michener 1964, Oster and Wilson 1978). Small colonies are very vulnerable to destruction by larger colonies of conspecifics and competitor species (Pontin 1961). Therefore, there are great survival benefits for colonies in growing quickly (Oster and Wilson 1978).

Nonacs and Dill (1988) demonstrated that *Lasius pallitarsis* (Provancher) ant colonies can simultaneous-

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<sup>2</sup> Present address: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138 USA.

ly forage and avoid mortality risk. Colonies were given access to two patches containing food of identical quality, but with one patch having an associated mortality risk. This risk was located in an area along the foraging trail where the *L. pallitarsis* foragers could physically encounter (and be killed by) a much larger *Formica subnuda* Emery worker. Under these conditions colonies abandoned the risky patch, but continued to use the safe one. This result did not require the ants to make a behavioral trade-off because colonies did not suffer any reduction in food intake by using only the safe patch. We now quantify the colony growth benefits ant colonies get from various food sources and report the ants' behavior in a situation in which a safer patch has poorer food quality, so that avoiding risk requires a trade-off in lost colony growth.

## METHODS

### *Diet level and colony growth*

Estimating the value of a food source to an ant colony requires measuring the conversion of a known amount of food to biomass. To do this we fed 14 colonies (biomass range of 65.5–226.7 mg, each with a queen, 20–50 workers, larvae, and eggs) on five liquid diets of different concentration. The best diet was an undiluted (=full strength) solution of sugar, proteins, vitamins, and nutrients (for details of diet composition, see Nonacs and Dill 1988). The other four diets were sequential twofold dilutions such that they were  $\frac{1}{2}$ ,  $\frac{1}{4}$ ,  $\frac{1}{8}$ , and  $\frac{1}{16}$  the concentration of the original recipe.

Every colony experienced each diet level once. The protocol was a cycle of 1 wk on the full strength diet (the "recovery period") followed by 2 wk on one of the five diets (a randomly chosen "experimental treatment"). Food of the appropriate concentration was available ad libitum. The amount taken was measured once a day, and corrected for evaporation. Cycles were repeated until every colony experienced all five diet levels. The colonies were kept in Tygon tube containers (10 cm length, 1.2 cm interior diameter) with moistened cotton plugs at one end. The biomass of the colonies was measured between the two diet levels at each transition by placing the colony under a bright light, stimulating the colonies to move within a few hours to a new, shaded tube, which was weighed before and after the move. For six colonies, errors during a cycle in measurement of biomass (because the colonies took > 1 d to move), or of food eaten, required an extra cycle. The errors were randomly distributed across the diet levels. When they were not being moved, the colonies were kept on a 16:8 light:dark schedule at 19°–23°C.

### *Patch choice experiments*

Twelve other laboratory colonies were given access to two patches in an apparatus and under conditions detailed in Nonacs and Dill (1988). The patches con-

tained the liquid ant diets of either full strength, or  $\frac{1}{2}$ ,  $\frac{1}{4}$ ,  $\frac{1}{8}$ , or  $\frac{1}{16}$  concentration, for which we had measured colony growth per load (see above, *Diet level and colony growth*). In a given trial, each patch contained a different diet concentration so that the nutritive values of the two patches were never equal. With the five diets this resulted in 10 patch pairings, with either 2-, 4-, 8-, or 16-fold differences in relative concentration.

Trials began by collecting foraging individuals near the nest and placing equal numbers (2–5 individuals) in the two food patches. 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 food that replenished itself as the ants fed. After the foragers became satiated, the patches were connected via Tygon tubing (3.5 mm interior diameter) to the home area; the ants returned (a distance of 50 cm) 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 the initial foragers was discontinued.

The initial foragers did not encounter danger or risk as they returned to the colony. Risk, in the form of a *F. subnuda* worker, was added only to the side with the higher concentration (henceforth referred to as the "risky" side), in approximately half the trials. This larger ant was restricted to one 5 cm area along the trail to and from the patch by constructing a tube-within-a-tube pathway. The inner tube was Tygon with openings large enough to allow free passage of *L. pallitarsis* foragers, but too small for the *F. subnuda* to escape from the larger, outer tube. Therefore, physical contact between individuals of the two species within this "arena" was possible. In trials designated as risky, we placed into the arena (right or left trail, randomly chosen) a large *F. subnuda* worker after the initial foragers had passed on their inward trip to the colony, but before they or new recruits could return. Therefore, the foragers could either choose between the two patches based only on nutritive difference, or make trade-offs between food and safety. Twofold dilutions ensured that the differences between any pair of diets would be greater than the 30% reduction in load retrieval rate (delay) caused by a *F. subnuda* along the trail to the food patch (Nonacs and Dill 1988). Therefore, if foragers preferred a safe patch over one containing a more concentrated diet but with associated risk it would not be because the safe patch had a higher net energy return rate.

All colonies experienced at least one trial with risk and one trial without risk for each of the four possible relative differences in patch concentrations (but not all of the 10 possible pairings of absolute patch value). One trial (either 4 or 24 h long) was run every 2nd d. With respect to the goals of this study, trial length was not a significant factor and the pattern of patch use over time is considered elsewhere (Nonacs and Dill 1990).

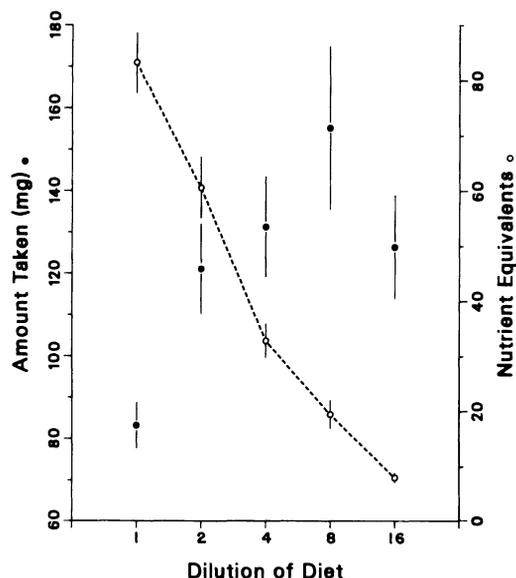


FIG. 1. Amount and nutrient value of the food taken in a 2-wk period on various diets (means  $\pm$  SE). The total amounts of food taken (●) by 14 colonies over the 2-wk experimental treatment period are given for each of the five diet levels. The number of nutrient equivalents taken (○) for the same period is calculated by dividing the total amount taken by the diet dilution.

At the end of the trial, the state of the *F. subnuda* and the number of dead *L. pallitarsis* workers in the arena were recorded. The food tubes were weighed before and after a trial, and the change in mass corrected for evaporative loss. Patch preference was measured as the proportion of all the food taken that came from the higher concentration patch. Results were discarded for trials in which  $<5.0$  mg (4 h) or 10.0 mg (24 h) of food in total was taken because variability in evaporative loss made estimates of lesser amounts unreliable.

All colonies had larvae, but only four colonies had queens. In previous foraging experiments, queen presence did not influence patch preference or response to risk (Nonacs and Dill 1988). A further complication here was that the queened colonies were all smaller than the nonqueened ones ( $<75$  workers as compared to  $>150$ ). Of colony size and queen state, increasing colony size appeared more likely to influence patch use (possibly by increasing activity), but neither factor significantly influenced response to mortality risk (Nonacs 1988).

## RESULTS

### *Diet level and colony growth*

The colonies took more food at the poorer diet levels (Fig. 1). In principle, the colonies could have entirely offset poorer food quality by taking a greater volume of food (e.g., 4 mg of one-quarter strength has the same nutrient content as 1 mg of full strength). Dividing the

amount taken on each diet by their dilution factors gives the intake in nutrient equivalents. It is clear that even though colonies increased intake in volume, for each progressive dilution significantly (all means are  $>2$  SE apart) fewer nutrient equivalents were brought back to the colonies (Fig. 1).

This reduced nutrient intake should be reflected in colony growth, which was initially intended to be measured as the change in biomass over the 2-wk experimental period. However, the mass obtained at the beginning of an experimental period slightly overestimates true colony biomass. When colonies were switched from the experimental diet to the full strength recovery diet, they generally immediately "binged," since the recovery period provided a higher quality food than four of the five prior experimental treatments. It is not surprising that colonies reacted in this manner to what they may well have perceived as a transient bonanza. The effect of this binging was still evident after the week of recovery, giving the appearance of colony growth when ant repletes were simply storing larger amounts of food (Nonacs 1988).

For the full strength experimental treatment, the above problem was easily dealt with: growth was simply measured over the entire 3-wk cycle of recovery and experimental treatment. Binging was not a prob-

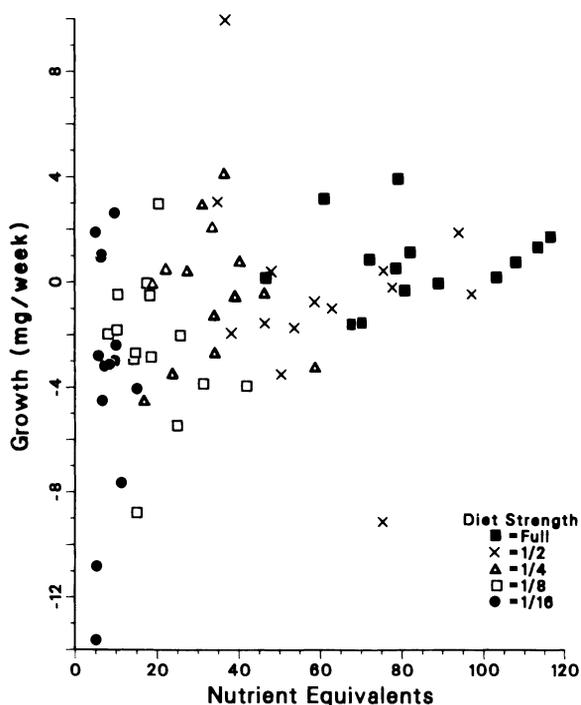


FIG. 2. Growth per week as a function of nutrient equivalent intake. The growth experienced by 14 colonies on the five diets is plotted as the change in colony biomass, in milligrams per week. Nutrient equivalents are calculated as the total amount of diet taken divided by diet dilution. The growth estimates have been corrected (see *Results: Diet level and colony growth*).

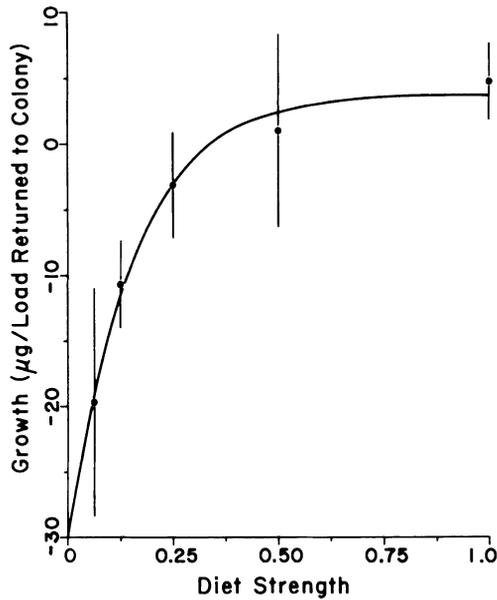


FIG. 3. Growth consequences per load returned to the colony. The average growth by colonies per load of food returned by workers (●, means  $\pm$  SE) is shown for each of the five diets under ad libitum conditions. Growth was calculated using corrected estimates of biomass (see *Results: Diet level and colony growth*). The number of loads was the total amount of food taken divided by the average amount of food carried by a forager on one trip (0.3 mg). A load of full strength diet was assigned a value of one, and the values for the other diets were in accordance with their dilution levels. The line,  $y = 3.800 - 34.416e^{-6.449x}$  is estimated from the data.

lem in the recovery periods following full strength treatments. Therefore, masses at the start of experimental treatments that followed a full strength cycle were taken to be accurate. For the remaining 60% of the experimental treatments, however, the masses of colonies at the beginning of the experimental periods appeared to be overestimated by 1.5% (Nonacs 1988) and were adjusted slightly downward by an equivalent amount.

Colony growth (as mass change in milligrams per week) increased with diet concentration and with measured nutrient intake (Fig. 2). For the purpose of examining foraging decisions, it is necessary to know the value of the load of food a forager returns to the colony with a given diet. Thus, in a separate experiment, 39 *L. palliarsis* workers were measured to bring back 11.8 mg of food, giving an average load size of 0.3 mg. Dividing the overall change in biomass by the number of loads taken (total amount of food taken divided by load size) gives the growth (in micrograms per load) for colonies under ad libitum conditions for each of the diet levels (Fig. 3). The relationship of growth per load ( $y$ ) to diet level ( $x$ ) is best described by an exponential regression of the form  $y = 3.800 - 34.416e^{-6.449x}$ . From this equation, the value to a forager of getting one load of food from a patch containing a given diet can be expressed in terms of resultant

TABLE 1. Patch differences. The difference in patch quality for each of the 10 diet pairings is calculated as the gain in growth per load (from Fig. 3) if a load were to be gathered at the higher concentration patch rather than the lower one. (1 = full strength patch.)

| Diet concentration pairing       | Growth differential ( $\mu\text{g}/\text{load}$ ) |
|----------------------------------|---|
| 1 vs. $\frac{1}{2}$              | 1.32  |
| $\frac{1}{2}$ vs. $\frac{1}{4}$  | 5.50  |
| 1 vs. $\frac{1}{4}$              | 6.81  |
| $\frac{1}{4}$ vs. $\frac{1}{16}$ | 7.62  |
| $\frac{1}{4}$ vs. $\frac{1}{8}$  | 8.52  |
| $\frac{1}{2}$ vs. $\frac{1}{8}$  | 14.01   |
| 1 vs. $\frac{1}{8}$              | 15.32   |
| $\frac{1}{4}$ vs. $\frac{1}{16}$ | 16.14   |
| $\frac{1}{2}$ vs. $\frac{1}{16}$ | 21.63   |
| 1 vs. $\frac{1}{16}$             | 22.94   |

colony growth. The 95% confidence intervals for growth per load on full,  $\frac{1}{2}$ , and  $\frac{1}{4}$  strength diets included zero growth, indicating that, on average, colonies could at least maintain themselves if they fed in patches containing these diets. The 95% confidence intervals for growth on  $\frac{1}{8}$  and  $\frac{1}{16}$  strength diets did not include zero, indicating that, on average, colony maintenance was not possible.

Positive growth could indicate gains both in larval biomass and from new egg production. Loss in colony biomass could indicate both loss in individual larval biomasses and cannibalism of some eggs and larvae to maintain the other colony members. Destruction of larvae could explain why the slope of the growth curve is steeper under conditions of negative growth.

From the regression equation in Fig. 3, we estimated the growth differentials between single loads at all possible diet pairings (Table 1). For example, loads gathered at full and  $\frac{1}{16}$  patches result at 3.74 and  $-19.20 \mu\text{g}$  of growth, respectively. The growth differential resulting from taking a full strength rather than a  $\frac{1}{16}$  strength load is, therefore,  $22.94 \mu\text{g}$ . If ants evaluate patches based on their potential for producing colony growth (or minimizing biomass loss), then their use of risky but high food quality patches should increase with increases in growth differential between the risky and safe patches. In trials without risk, patch choice should be relatively unaffected by growth differential because the higher concentration patch should always be preferred.

#### Patch choice experiment

In this experiment there existed a real danger for ants in foraging at the patch with the *F. subnuda*. Using the load size estimate of 0.3 mg, 8370 loads of food were gathered from the risky patch. In gaining this food, 146 workers were killed by *F. subnuda*.

A multiple regression analysis of the patch choice data showed that the proportional use of the higher concentration (=risky) patch was not significantly affected by the total amount of food taken in a trial, the number of foragers killed per hour, the amount of food

TABLE 2. Standard partial regression coefficients and their significance levels. The dependent variable is the proportion of the total food taken in a trial that was taken from the risky patch.

| Independent variable*               | Coefficient | <i>t</i> | <i>P</i> |
|-------------------------------------|-------------|----------|----------|
| No. killed/trial                    | 0.2964      | 2.23     | .028     |
| No. killed/h                        | 0.1161      | 0.95     | NS       |
| Total food taken in a trial         | -0.0124     | -0.11    | NS       |
| Take in previous 48 h:<br>amount    | 0.0225      | 0.10     | NS       |
| Take in previous 48 h:<br>nutrients | 0.1401      | 0.66     | NS       |
| Average temperature during<br>trial | -0.0616     | -0.63    | NS       |

\* The dependent variable was regressed against the number of *L. pallitarsis* foragers killed per trial, the number killed per hour, the total amount of the food taken in that trial, the amount of food (by mass) taken in the previous 48 h, the nutrients taken in the previous 48 h (amount multiplied by dilution factor), and the average temperature during the trial.

(either mass or nutritive content) collected in the previous 48 h, or room temperature. Only the number of foragers killed per trial was significantly correlated with increased use of the risky patch (Table 2). It is likely that as traffic to the risky patch increased, so did the number of fatal encounters with the large ant. These regression results indicate that the patch preferences analyzed below were unlikely to be affected by variables not explicitly included or controlled for in the experimental design.

The mean proportion of food taken from the higher concentration patch for each of the 10 diet pairings was regressed against the estimated growth differential for these pairings (Fig. 4). There was a highly significant relationship between expected growth differential and relative patch use (Fig. 4, solid line;  $R^2 = 0.819$ ,  $F = 36.171$ ,  $df = 1, 8$ ,  $P = .0003$ ). (The preceding analysis used corrected mass values. If uncorrected values are used, there is still a significant relationship:  $R^2 = 0.662$ ,  $F = 15.665$ ,  $df = 1, 8$ ,  $P = .0042$ .) In trials without mortality risk, the use of the higher concentration patch also increased with the magnitude of the expected growth differential, but the slope of the line was not significant (Fig. 4, dashed line;  $R^2 = 0.315$ ,  $F = 3.683$ ,  $df = 1, 8$ ,  $P > .05$ ).

Two results shown in Fig. 4 invite special notice. First, differences in growth did not always reflect the relative differences in concentration of food. For example, a pairing between full and one-quarter strength patches represented a fourfold difference in concentration, but choices between twofold dilutions in  $\frac{1}{4}$  and  $\frac{1}{8}$ , or  $\frac{1}{4}$  and  $\frac{1}{16}$  strength pairings had the greater estimated growth differentials (6.81 compared to 8.52 and 7.62  $\mu\text{g}/\text{load}$  respectively). As predicted by these growth differentials, foragers used the safe patch to a greater extent in the former pairing than in the latter two. Likewise, the pairing of  $\frac{1}{4}$  and  $\frac{1}{16}$  strength patches was both predicted and observed to produce more use of the risky patch than the greater relative concentration

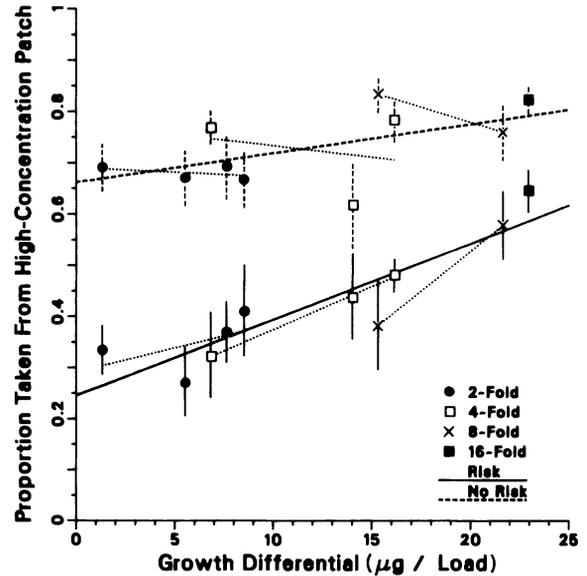


FIG. 4. Patch use as a function of growth differential between the patches. The proportion of food taken from the higher concentration patch (means  $\pm$  SE) is plotted against the growth differential for loads from the pair of patches available (from Table 1). There were 10 pairings that fell into four groups of equal relative concentration differences, ranging from 2- to 16-fold. The long solid and dashed lines are the linear regressions of all 10 pairings when mortality risk was either present or absent, respectively. The shorter dotted lines are regressions within the groupings of equal relative concentration where there was more than one diet pairing.

difference between full and  $\frac{1}{8}$  strength patches. Therefore, the ants' patch choices were more sensitive to growth consequences than they were to the relative concentrations of the diet.

This is also shown by the fact that although the 10 possible diet pairings fall into four groups based on relative concentration differences (from 2- to 16-fold), within each group all pairings did not result in equal trade-offs of colony growth for safety. Within every group where  $>1$  pairing of equal relative difference (two- to eightfold) was possible, use of the risky patch increased with the absolute difference in resultant colony growth, just as in the relationship across all 10 pairings (slopes of the dotted lines in Fig. 4, lower set, are very similar to the overall regression shown by the solid line). Therefore, the overall relationship of risk taking to relative patch quality (measured as colony growth) is internally consistent. In trials without risk, the relationships within groups of equal relative concentration difference differ from the overall relationship (negative slopes for the upper set of dotted lines in Fig. 4 and slightly positive slope of the dashed line).

The data in Fig. 4 can also be considered a "behavioral titration" for the cost of risk. When two patches have equal value to the colony, foragers should use both equally. Therefore, the cost of risk can be estimated from the amount of growth colonies are willing

to sacrifice for safety from mortality risk. From the regression equation ( $y = 0.245 + 0.0149x$ ) for the data in Fig. 4 (lower set), it appears that safety had a value of  $\approx 17.1 \mu\text{g}$  of reduced colony growth per load returned to the colony. At that point foragers were indifferent to the risky and safe patches.

#### DISCUSSION

*Lasius pallitarsis* ants evaluate food patches based on both nutritive quality and associated mortality risk. They trade off between colony growth and forager survival. These results have implications for the study of ant and social insect behavior and for optimal foraging theory in general.

Several ant species are sensitive to differences in food quality and show discrimination during food collection. Taylor (1977) found that foraging behavior in *Solenopsis geminata* and *Pogonomyrmex occidentalis* is consistent with a hypothesis of maximizing net rate of energy intake. He found that foragers consistently recruit more to patches that are closer to the colony, have higher reward rates, or have less potential for delays from interference between workers. *S. geminata* also preferentially collect large rather than small seeds. Davidson (1978) found that *P. rugosus* foragers rank seeds based on their profitabilities, and Holder Bailey and Polis (1987) found that *P. californicus* preferentially collect seed sizes with the highest energy return rates. Likewise, several studies have shown that increasing aboveground mortality rate affects foraging behavior (Gentry 1974, Whitford and Bryant 1979, Shaffer and Whitford 1981, MacKay 1982, Munger 1984, Gordon 1986). The work presented here and similar behavioral trade-offs shown by *Myrmica incompleta* (Nonacs and Dill 1990) are evidence that ants can respond to both risk and food quality simultaneously.

The ability to cooperatively exploit their habitat is a defining characteristic of many eusocial insect species and undoubtedly is a factor in why highly social insects, as a group, are so successful ecologically. Forager communication of the location, quality, and quantity of food sources allows colonies to track their environment and effectively allocate the work force to the collection process. In doing so, returning *L. pallitarsis* foragers can communicate not only food quality, but the presence of mortality risk along the trail as well (Nonacs 1990). *L. pallitarsis* colony use of food patches is also sensitive to short-term changes in risk (Nonacs and Dill 1990). The ability to respond dynamically to two simultaneous variables (food and mortality risk) should result in a substantial competitive advantage. Therefore, the evolution of sociality and its subsequent success may have been favored by increased efficiency in both finding food and reducing forager mortality rates.

In terms of optimal foraging theory, this study is one of the first in which trade-offs can be evaluated quantitatively. Several recent studies on the effects of pre-

dation risk have examined more than qualitative changes in behavior. Gilliam (1982) used a dynamic model to predict that juvenile bluegill sunfish (*Lepomis macrochirus*) should always minimize  $\mu/g$ , which is their mortality rate ( $\mu$  = rate of being eaten by bass) divided by their growth rate ( $g$ ). Fish altered habitat use in the presence of bass (Werner et al. 1983), but predation rate could not be measured with sufficient precision across the habitats to test whether  $\mu/g$  (mortality per unit growth) was minimized.

Gilliam and Fraser (1987) presented juvenile creek chub (*Semotilus atromaculatus*) with combinations of habitats with empirically measured feeding and mortality rates. They found that the fish significantly preferred the habitat that minimized  $\mu/f$ , where  $f$  is gross foraging rate. Although the study did not relate foraging rate to actual growth or realized reproductive potential, it did show that simple "rules of thumb" can suffice to solve a multiple goal problem.

Abrahams (1987) quantified the growth benefits of certain diets for male and female guppies (*Poecilia reticulata*). Only females grow indeterminantly and their rate of reproduction is energy limited, making food more valuable to females. Therefore, they take more risks than males to gain food, and show quantitatively predictable shifts to risky patches in response to changes in reward rates (Abrahams and Dill 1989). However, whether these trade-offs maximize fitness remains unknown.

Foraging in ants can involve maximizing energy brought back to the colony and/or minimizing mortality risk experienced. In situations with a single goal, worker behavior in *L. pallitarsis* is straightforward and obviously adaptive. When two patches differ in mortality risk but not in nutritive value, foragers prefer the safe patch (Nonacs and Dill 1988). Conversely, when two patches differ only in nutritive value (neither patch with associated risk), foragers always prefer the higher quality patch (upper line in Fig. 4). When both food quality and mortality risk vary, the foragers risk-balance (Fraser and Huntingford 1986) in that they take proportionally more risks as potential colony gains increase (lower line in Fig. 4). Knowing both the value of the food and the mortality rate allows the effectiveness of the trade-offs to be quantitatively assessed.

A forager's value to the colony is measured as the amount of food she gains through her actions over her foraging lifetime. An average worker weighs  $1.37 \pm 0.11 \text{ mg}$  (an average of 15 unfed, randomly selected foragers from three colonies; size range = 0.90–2.20 mg). For every forager killed in the course of exploiting risky patches, on average 57.3 loads of food were brought back. Therefore, at the indifference point, where risky and safe patches are valued equally, the colony grows 0.98 mg in biomass for every forager killed ( $57.3 \times 17.1 \mu\text{g}$ ). Although this gain does not offset the loss of average-sized workers, colonies can raise smaller new workers and suffer no numerical decline in colony

size with little reduction in ergonomic efficiency. Average worker size fluctuates in natural colonies across both stages of development and times of year, and the lack of larger sized individuals affects mostly defense and retrieval of large, discrete prey items (Hölldobler and Wilson 1990). With respect to retrieval of liquid foods, as in these experiments, size is of lesser importance. Thus, risky and safe patches were approximately equivalent in value to the colony at the apparent indifference point and foragers could not have substantially improved the colony energy budget by taking either more or less mortality risk.

In conclusion, our results from ants and those of Gilliam (1982), Gilliam and Fraser (1987), and Abrahams and Dill (1989) from fish suggest that it is possible to examine predation risk trade-offs both qualitatively and quantitatively. Therefore, the focus for future research must be not only on whether animals make trade-offs, but on how well they do so and what that implies about their evolutionary history and present day ecology.

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