Applying Optimal Foraging Theory to Assess Nutrient Availability Ratios for Ants
Author(s): Adam Kay
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APPLYING OPTIMAL FORAGING THEORY TO ASSESS NUTRIENT AVAILABILITY RATIOS FOR ANTS

ADAM KAY

Department of Biology, University of Utah, Salt Lake City, Utah 84112 USA

Abstract. Although the availability of food resources affects a wide range of ecological and evolutionary processes, its role in generating patterns in natural systems remains largely unresolved. Elucidating the importance of resource availability should be made easier by the development of techniques that can measure the amount of resources that are accessible to a consumer, rather than simply the abundance of resources in the environment. In this study, I develop a behavioral assay for inferring the ratio of nutrients available to organisms in the field. The assay involves measuring the responses of foragers to nutrient solutions. These responses are used to determine the mean effective concentration, or ED$_{50}$, of a nutrient, defined as the concentration that is rejected in 50% of trials. Because ED$_{50}$ provides a measure of the quality of a depletable patch at which a consumer would quit foraging, it is analogous to the giving-up density (GUD), a common tool in ecological research. Here, I use ED$_{50}$s to estimate the ratio of carbohydrates: protein available to ant colonies. Using supplementation experiments, I show that ED$_{50}$s of sucrose and casein (a source of amino acids) reveal the net rates at which a colony expects to acquire each resource elsewhere in the environment. These results demonstrate that differences in ED$_{50}$s will reveal differences in the availabilities of nutrients when other factors affecting the costs and benefits of foraging are controlled. To control these factors, I measured a colony's ED$_{50}$s of sucrose and casein at the same time and location. Using this technique, I found that ratios of carbohydrate: protein availability differed significantly among 10 species of ants in southeastern Arizona, USA. Ratios were highest for species that are known to collect liquids from extrafloral nectaries and phloem-feeding insects. Carbohydrate: protein ratios may be especially low for three granivorous species, *Pogonomyrmex barbatus*, *Pogonomyrmex occidentalis*, and *Aphaenogaster cockerelli*, which accepted sucrose solutions but rejected even highly concentrated casein solutions. Because ratios of carbohydrate: protein availability differed substantially among species in the same habitat, the results of this study suggest that measures of resource abundance may poorly predict habitat quality for consumers.

Key words: ants; Arizona; carbohydrates; ED$_{50}$; effective concentration; giving-up density; nutritional composition; optimal foraging; protein; resource availability.

INTRODUCTION

The availability of food influences virtually every ecological and evolutionary process, including the foraging behavior and life history strategies of individuals, the structure and dynamics of populations, and the organization of communities. Although many studies focus on the role of quantitative differences in food availability (e.g., Bautista et al. 1998, Sherman and Eason 1998), there is a growing awareness that differences in the nutritional composition of foods can have an important influence on a variety of phenomena (Sterner and Hessen 1994, Simpson and Raubenheimer 2001). All animals require multiple nutrients (e.g., protein, carbohydrates, and fats), and the dietary balance of these nutrients can influence survival and reproduction (Raubenheimer and Simpson 1997). Because nutrient balance affects performance, ratios of available nutrients can influence diet choice (Pennings et al. 1993), feeding behavior (Simpson and Simpson 1990), and food assimilation efficiency (Stockhoff 1992). These ratios can also affect interspecific interactions and the structure of communities, because optimal diet mixtures differ among species (Tilman 1982, Sterner et al. 1997).

Despite the putative impact of resource access on biological patterns, its role remains widely unresolved because of difficulties associated with measuring natural variation in resource availability (Hutto 1990). As with food availability, in general, the relative availabilities of nutrients are probably quite variable in nature: foods such as animal tissue, fruits, seeds, pollen, and nectar differ substantially in nutrient composition (Begon et al. 1996), and the relative abundances of food types can vary in space and time (e.g., Haslett 1989, Blake and Loiselle 1991). However, the abundance of a resource may often reveal little about its
availability, that is, the amount accessible to a consumer (Johnson 1980). Because prey features, the feeding constraints of consumers, and the activities of competitors and predators can also limit foraging opportunities (Wiens 1984), techniques that sample abundance will often provide only crude estimates of availability (Myers et al. 1980). Yet, because it is a consumer’s access to resources that determines its potential for resource use (Wiens 1984), measures of availability may provide important insight into the effects of resources on individual, population, and community features.

Although direct measurement of all of the factors that affect resource availability will often be difficult, availability can instead be inferred using behavioral assays founded upon optimal foraging theory. Foraging theory can serve as the basis for tests that reveal an individual’s view of its environment (Rosenzweig and Abramsky 1997). This approach involves establishing experimentally the predicted links between foraging behavior and environmental conditions, then using behavioral variation to infer a forager’s perception of environmental differences. Such assays have been used to measure key determinants of habitat quality such as predation risk (Nonacs and Dill 1990, Brown et al. 1992), which are otherwise difficult to quantify.

The marginal value theorem can be especially useful for studying habitat quality (Brown 1988, Bowers and Brelan 1996). This model predicts that a forager will leave a patch when the marginal rate of gain equals its expected gain rate in the environment (Charnov 1976a). This prediction suggests that an optimal forager’s rate of gain when it quits a patch will reveal its perceived global access to resources, and thus is an indirect measure of resource availability.

The quitting gain rate is determined by factors that influence the marginal cost and benefit of exploiting a patch (Brown 1988). The marginal cost is a function of metabolic expenses and predation risk, whereas the marginal benefit depends on the rate of resource harvest. Harvest rates are a function of travel time to the patch, the forager’s harvesting ability, and resource density in the patch (the “giving-up density” or GUD).

GUDs can serve as indicators of resource availability if other factors that affect quitting gain rates can be controlled. It may often be difficult to control factors such as predation risk and harvesting ability when GUDs for different individuals are compared. However, GUDs are ideal for assessing ratios of nutrients available to an individual. If GUDs of different nutrients are measured for an individual at the same time and place, then metabolic cost, risk, travel time to patches, and harvesting ability will all be controlled. Thus, comparing nutrient GUDs for an individual should reveal its perception of the relative availabilities of those nutrients.

In this study, I use GUDs to infer the relative availabilities of carbohydrates and protein for ant colonies. Davidson (1997) suggested that ratios of carbohydrate:protein availability play a key role in ant communities. Because the cost of traits depends on the availability of their required substrates, high ratios of carbohydrate:protein availability may make affordable the high foraging tempo, territorial defense, and other energetically expensive activities seen in many ecologically dominant species. Quantifying variation in carbohydrate:protein availability should provide a foundation for tests of this hypothesis and should elucidate its potential importance, while also revealing the potential for nutritional considerations to explain interspecific differences in foraging behavior.

Dietary differences suggest that carbohydrate:protein availability may differ considerably among ant species. Although all ants collect some form of proteinaceous food, many also collect sugary exudates from plants and Homoptera (Hölldobler and Wilson 1990). Differential access to these liquids could produce substantial variation in carbohydrate:protein availability ratios. Because investment in liquid collection can differ even among closely related species (Tennant and Porter 1991), differences in carbohydrate:protein availability may be common in ants.

This study has three parts. First, I test whether ant responses agree quantitatively with central predictions of optimal foraging theory: environmental conditions for ants can be inferred from foraging decisions only if the theory quantitatively predicts their behavior. Second, I determine whether ants view carbohydrates and protein as distinct resources. If carbohydrates and protein provide ants with the same resource (e.g., energy), then their GUDs will provide only separate estimates of the expected rate of gain of that resource in the environment. However, if ants view these nutrients as distinct resources and their behavior agrees with predictions from foraging theory, then differences in GUDs of the nutrients measured under standardized conditions will reflect differences in the expected gain rates of the nutrients. In the third part of this study, I measure GUDs of carbohydrates and protein for colonies of 10 ant species and then compare the ratio of these measures to test for interspecific differences in carbohydrate:protein availability.

**Methods**

To estimate GUDs for ant colonies, I measured worker responses to nutrient solutions of various concentrations. From these responses, I estimated a colony’s median effective concentration (ED90) of the nutrient, which is the concentration that 50% of the workers reject (Sudd and Sudd 1985). Although this approach measures responses to discrete items and not patch depletion, I assume that ED90s are analogous to GUDs because the resource density rejected by the average worker of a colony should equal the density remaining in a depletable patch when a colony ceases foraging.

To assay worker responses in ED90 trials, I put drops
of nutrient solution on sheets of wax paper in front of outbound foragers. I scored foragers that touched a drop with their mandibles as accepting the solution if their mandibles remained in the drop for 5 s, or rejecting it if they moved quickly away. After 5 s, it became clear (in most species) that a worker had been drinking because its gaster began to swell. Ants that never touched the drop were not included in either category. I tested responses of ≥10 ants at each of a number of dilutions. I measured responses to solutions presented in haphazard order until I found a concentration that all or almost all workers accepted, one that was almost universally rejected, and at least one to which responses were mixed. I conducted assays with solutions of either sucrose or soluble casein, a source of amino acids derived from cow milk. To control for interspecific differences in the value of water, I measured ED
\text{so}_{50}\text{ only when } > 90\% \text{ of workers rejected water drops.}

Although GUDs can provide information about the economics of foraging under natural conditions, the presence of artificial resource patches may distort a forager’s perception of the environment’s quality (Brown 1988). To avoid this distortion, I removed acceptable drops from workers after 5 s (which minimized recruitment) and tried not to sample workers more than once. I placed wax paper 0.5 m from nest entrances to avoid measuring the responses of maintenance workers that, in some species, regularly wandered around the area surrounding the nest. In preliminary observations, ants that ventured 0.5 m from the nest were usually beginning foraging trips and often continued to travel away from the nest after being tested. Finally, to prevent the residue of drops from affecting subsequent assays, I frequently replaced wax paper sheets.

To calculate ED
\text{so}_{50}, I used logistic regression to fit the response data to the function

\text{worker acceptance} \quad = \frac{1}{1 + e^{(\beta + \gamma \log(\text{concentration of solution}))}} \times 100\%

where \(\beta\) and \(\gamma\) are location and slope parameters. The ED
\text{so}_{50} equals exp(–\(\beta/\gamma\)). I used SYSTAT 10 (SYSTAT 1996) to estimate parameters with an iterative process and then to calculate ED
\text{so}_{50}s and their 95\% confidence intervals.

**Supplementation experiments**

I conducted a series of supplementation experiments to test whether the responses of ants to nutrient solutions is consistent with central predictions of optimal foraging theory and whether ants view carbohydrates and protein as distinct resources. These experiments measured the effects of sucrose or casein supplementation on colonies of *Dorymyrmex smithi* in oak woodland habitat near Portal, Arizona, USA. To supplement a colony, I gave it access to a solution during daylight hours (about 0500–1900 hours) throughout a 24-h period. I filled 0.65-mL eppendorf tubes with solution and placed them in racks 0.5 m from the nest entrance. In all cases, workers discovered the tubes within minutes of placement. I replaced tubes every 2–3 h with tubes containing fresh solution and provided colonies with enough tubes to ensure unlimited access to a solution during supplementation periods. No colony was used in more than one experiment.

Using supplemented colonies, I tested two central predictions of optimal foraging theory: (1) the abundance of low-quality resources does not affect selectivity (Charnov 1976b), and (2) foragers attack prey items only if the rate of gain from those items exceeds the expected gain rate in the environment as a whole (Stephens et al. 1986). The latter prediction is a discrete version of the marginal value theorem. I used mixed-factorial designs in both experiments. In the first test, I measured “baseline” ED
\text{so}_{50}s of sucrose for eight *D. smithi* colonies, then provided four of the colonies with a low-quality sucrose supplement (1% mass/volume, m/v) for 24 h. I considered 1% sucrose to be of low quality because workers frequently rejected it in preliminary tests. I supplemented four control colonies with water. After one day, I removed the supplements and immediately measured sucrose ED
\text{so}_{50}s. In all supplementation experiments, I conducted ED
\text{so}_{50} trials at least 90° from the location of the supplement to ensure that subjects were not recruits to the supplement.

In the second experiment, I compared worker responses to expected environmental gain rates of sucrose or casein. I manipulated environmental gain rates by providing experimental colonies with high-quality supplements (10% m/v sucrose or 3% and 6% m/v casein). I assumed that these supplements were of high quality because workers readily accepted drops of these solutions in preliminary trials. The concentration of these supplements provided a surrogate for expected environmental gain rates in ED
\text{so}_{50} trials; ants frequently visited these rich supplements and had unlimited access to them throughout the supplementation period, and travel times to supplements and trials were similar because supplements and trials were at the same distance from nest entrances. For the sucrose test, I measured and compared ED
\text{so}_{50}s of sucrose before and 24 h after supplementing four *D. smithi* colonies with 10% sucrose and four control colonies with water. For the casein test, I measured and compared ED
\text{so}_{50}s of casein before and 24 h after supplementing six colonies with 3% casein and three control colonies with water. I then gave experimental colonies even higher quality casein (6%) for 24 h and measured ED
\text{so}_{50} again.

I also used the casein-supplemented colonies to determine whether ants view protein and carbohydrates as distinct resources. To test this hypothesis, I measured and compared ED
\text{so}_{50}s of sucrose before and after supplementing colonies with either casein (3% or 6%) or water. If these nutrients provide ants with the same
resource, then supplementation with high-quality casein will decrease the marginal value of that resource, resulting in a higher ED$_{50}$ of sucrose. If they are distinct, then sucrose ED$_{50}$ will not increase after casein supplementation.

**Carbohydrate : protein availability ratios**

To estimate carbohydrate : protein availability ratios, I measured sucrose and casein ED$_{50}$s for 10 species of ants. I tested six species (D. smithi, Forelius sp. 2, Myrmecocystus mendax, Pheidole diversipilosa, Pogonomyrmex occidentalis, and Trachymyrmex arizonensis) in oak woodland habitat (elevation 1700 m) and four species (Aphae nogaster cockerelli, Forelius sp. 1, Formica perpilosa, and Pogonomyrmex barbatus) in desert thornscrub near Portal (elevation 1400 m). The *Forelius* species are apparently undescribed (S. Cover, personal communication). The diets of these species are diverse: *T. arizonensis* cultivate fungus (Creighton 1950); *P. occidentalis* and *P. barbatus* harvest seeds (Cole 1968); *P. diversipilosa* and *A. cockerelli* collect arthropods and seeds (Whitford et al. 1980); and *D. smithi*, *F. sp. 1*, *F. sp. 2*, *M. mendax*, and *F. perpilosa* collect insects and various exudates (Schumacher and Whitford 1974, Snelling 1976, Hölldobler 1982; personal observation).

To control factors other than resource densities that affect foraging decisions, I measured a colony's ED$_{50}$ of each nutrient consecutively at the same location. I controlled metabolic costs and risk by testing responses at the same distance from a nest under similar conditions. Both ED$_{50}$s for a colony could be measured in 1–3 h; to control for any climatic changes during this period, I alternated the order of trials across colonies. Alternating trial order also controlled for any risk that workers might associate with a trial. In addition, I controlled travel times by conducting trials at a fixed distance from a nest, and I controlled for harvesting abilities by offering each nutrient in solution.

**RESULTS**

The logistic model accurately described worker responses to solutions in all trials (see the example in Fig. 1). In the supplementation experiments, the average $r^2$ was 0.988 ($n = 59$ trials) for worker responses to sucrose and 0.989 ($n = 27$ trials) for responses to casein. For the interspecific comparison, the average $r^2$ was 0.982 ($n = 60$ trials) for sucrose and 0.990 ($n = 43$ trials) for casein.

Greater access to low-quality resources did not affect worker responses, as indicated by the lack of interaction between day of measurement (before vs. after supplementation) and supplement type (water vs. 1% sucrose) (Table 1, Fig. 2). Prior to supplementation, ED$_{50}$s ranged from 2.21% to 3.82% (mean = 3.11%, $n = 4$), well above the 1% sucrose in the supplement.

Supplementation with high-quality sucrose (10%) or casein (3%, 6%) increased selectivities significantly more than did supplementation with water (Table 1). The response to the nutrient supplements also resulted in significant main effects of day of measurement and supplement type. Prior to supplementation, ED$_{50}$s were well below the concentrations of the supplements (sucrose ED$_{50}$, mean = 2.24%, range = 1.86–2.43%, $n = 4$; casein ED$_{50}$, mean = 1.17%, range = 0.92–1.48%, $n = 6$). After supplementation, sucrose ED$_{50}$ did not differ significantly from 10% (Fig. 3) and casein ED$_{50}$

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>1% sucrose (ED$_{50}$ of sucrose)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Supplement type†</td>
<td>1, 6</td>
<td>0.336</td>
<td>0.583</td>
</tr>
<tr>
<td>Day‡</td>
<td>1, 6</td>
<td>1.241</td>
<td>0.308</td>
</tr>
<tr>
<td>Type × day</td>
<td>1, 6</td>
<td>0.462</td>
<td>0.522</td>
</tr>
<tr>
<td>10% sucrose (ED$_{50}$ of sucrose)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Supplement type†</td>
<td>1, 6</td>
<td>185.315</td>
<td>&lt;0.0005</td>
</tr>
<tr>
<td>Day‡</td>
<td>1, 6</td>
<td>91.664</td>
<td>&lt;0.0005</td>
</tr>
<tr>
<td>Type × day</td>
<td>1, 6</td>
<td>206.451</td>
<td>&lt;0.0005</td>
</tr>
<tr>
<td>3%, 6% casein (ED$_{50}$ of casein)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Supplement type†</td>
<td>1, 7</td>
<td>255.577</td>
<td>&lt;0.0005</td>
</tr>
<tr>
<td>Day§</td>
<td>2, 14</td>
<td>78.388</td>
<td>&lt;0.0005</td>
</tr>
<tr>
<td>Type × day</td>
<td>2, 14</td>
<td>71.194</td>
<td>&lt;0.0005</td>
</tr>
<tr>
<td>3%, 6% casein (ED$_{50}$ of sucrose)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Supplement type†</td>
<td>1, 7</td>
<td>6.249</td>
<td>0.041</td>
</tr>
<tr>
<td>Day§</td>
<td>2, 14</td>
<td>0.496</td>
<td>0.619</td>
</tr>
<tr>
<td>Type × day</td>
<td>2, 14</td>
<td>0.955</td>
<td>0.408</td>
</tr>
</tbody>
</table>

† Water vs. nutrient solution.
‡ Before vs. after supplementation.
§ Before vs. after supplementation with 3% casein or water vs. after supplementation with 6% casein or water.
were statistically indistinguishable from 3% or 6% in 11 of 12 cases (Fig. 4; sign test, \(P = 0.006\)).

Access to high-quality casein had no affect on the \(ED_{50}\)s of sucrose (Table 1, Fig. 5). Colonies that received casein did have significantly higher \(ED_{50}\)s of sucrose than did water-supplemented colonies, but this difference existed before supplementation occurred.

Among species, there were significant differences in \(ED_{50}\)s of sucrose and casein (Table 2; for sucrose, \(F_{9,99} = 13.126, P < 0.0005\); for casein, \(F_{6,36} = 34.910, P < 0.0005\)) and in ratios of sucrose \(ED_{50}:\) casein \(ED_{50}\) (\(F_{6,36} = 6.768, P < 0.0005\)). Casein \(ED_{50}\)s and \(ED_{50}\) ratios could not be determined for *Aphaenogaster cockerelli*, *Pogonomyrmex barbatus*, and *Pogonomyrmex occidentalis* because these species did not accept even concentrated (30%) casein. Species that collect carbohydrate-rich exudates (*Forelius* sp. 1, *Forelius* sp. 2, *Myrmecocystus mendax*, *Formica perpilosa*, and *Dorymyrmex smithi*) had higher \(ED_{50}\) ratios than those that do not, indicating that differences in \(ED_{50}\) ratios generally agree with differences in diet composition. \(ED_{50}\) ratios also differed significantly among species in the same habitat, both in the oak woodlands (\(F_{4,24} = 5.553, P = 0.003\)) and in the desert (\(t\) test, \(t = 3.612, df = 8.5, P = 0.006\)).

**DISCUSSION**

This study indicates that foraging behavior can be used to assay nutrient availability ratios. I will first discuss the tests of the assay’s key assumptions and then consider the results of its application to ants in southeastern Arizona.

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**FIG. 2.** Mean effective concentrations (\(ED_{50}\)) of sucrose for *Dorymyrmex smithi* colonies before and after receiving (A) water supplements or (B) 1% sucrose supplements. Data are means and 95% CI estimates.

**FIG. 3.** Mean effective concentrations (\(ED_{50}\)) of sucrose for *Dorymyrmex smithi* colonies before and after receiving (A) water supplements or (B) 10% sucrose supplements. Data are means and 95% CI estimates. The dashed horizontal line in panel (B) represents the concentration of the sucrose supplement.
Supplementation experiments

Results of the first two supplementation experiments support central predictions of optimal foraging theory. Supplementation of colonies with low-quality resources did not affect selectivity in \( ED_{50} \) trials (Fig. 2); selectivity has also been found to be independent of the abundance of low-ranking prey in many other systems (Stephens and Krebs 1986). In the second experiment, \( ED_{50} \) did not differ significantly from the concentration of solutions in high-quality supplements (Figs. 3B and 4B), results that agree quantitatively with the central prediction of the discrete marginal value theorem. Although ants have been shown to respond to food patches in ways consistent with the marginal value theorem (Nonacs and Dill 1990, Bonser et al. 1998), this experiment is the first quantitative test of a version of the theorem using ants. The response of colonies to high-quality supplements indicates that ants can form and use estimates of environmental gain rates and can make these estimates for both carbohydrates and protein.

Sucrose \( ED_{50} \) did not increase after casein supplementation (Fig. 5), indicating that sucrose and casein are distinct resources. Other evidence also suggests that these nutrients provide ants with distinct resources. Carbohydrates and protein meet different colony needs (Wheeler 1994) and colonies spend more effort foraging for each nutrient when they are scarce, indicating that ants can recognize and separately regulate their intake (A. Kay, unpublished manuscript).

Although sucrose and casein are distinct resources, they are nutritionally interdependent, or complementary, sensu Tilman (1982). Colonies fed an intermediate mixture of carbohydrates and protein produce more brood than do colonies fed mixtures that contain pro-

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**Fig. 4.** Mean effective concentrations (\( ED_{50} \)) of casein for *Dorymyrmex smithi* colonies before and after receiving (A) water supplements or (B) high-quality (3% or 6%) casein supplements. Data are means and 95% CI estimates. The dashed horizontal lines in panel (B) represent the concentrations of the casein supplements.

**Fig. 5.** Mean effective concentrations (\( ED_{50} \)) of sucrose for *Dorymyrmex smithi* colonies before and after receiving (A) water supplements or (B) 3% or 6% casein supplements. Data are means and 95% CI estimates.
Table 2. Median effective concentrations (ED50s) of sucrose and casein, and ratios of ED50 sucrose to ED50 casein for 10 species of ants in southeastern Arizona, USA.

<table>
<thead>
<tr>
<th>Species (no. colonies sampled)</th>
<th>ED50 sucrose</th>
<th>ED50 casein</th>
<th>ED50 sucrose: ED50 casein</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean ± 1 SE</td>
<td>95% CI</td>
<td>Mean ± 1 SE</td>
</tr>
<tr>
<td>Forelius sp. 1 (8)</td>
<td>5.91 ± 0.51</td>
<td>±1.30</td>
<td>0.77 ± 0.14</td>
</tr>
<tr>
<td>Forelius sp. 2 (6)</td>
<td>5.17 ± 0.67</td>
<td>±0.67</td>
<td>1.03 ± 0.39</td>
</tr>
<tr>
<td>Myrmecocystus mendax (6)</td>
<td>3.71 ± 0.38</td>
<td>±0.85</td>
<td>1.10 ± 0.21</td>
</tr>
<tr>
<td>Formica perpilosa (7)</td>
<td>2.64 ± 0.41</td>
<td>±0.88</td>
<td>1.10 ± 0.19</td>
</tr>
<tr>
<td>Dorymyrmex smithi (8)</td>
<td>2.46 ± 0.18</td>
<td>±0.38</td>
<td>1.01 ± 0.13</td>
</tr>
<tr>
<td>Pheidole diversipilosa (6)</td>
<td>1.35 ± 0.15</td>
<td>±0.41</td>
<td>1.18 ± 0.19</td>
</tr>
<tr>
<td>Trachymyrmex arizonensis (3)</td>
<td>2.59 ± 0.43</td>
<td>±0.85</td>
<td>6.13 ± 0.59</td>
</tr>
<tr>
<td>Aphaenogaster cockerelli (5)</td>
<td>2.72 ± 0.25</td>
<td>±0.74</td>
<td>not accepted</td>
</tr>
<tr>
<td>Pogonomyrmex occidentalis (6)</td>
<td>3.99 ± 0.68</td>
<td>±0.97</td>
<td>not accepted</td>
</tr>
<tr>
<td>Pogonomyrmex barbatus (6)</td>
<td>8.60 ± 1.46</td>
<td>±1.51</td>
<td>not accepted</td>
</tr>
</tbody>
</table>

Notes: Ratios of ED50 sucrose to ED50 casein were calculated for each colony and were then averaged to find species means. ED50 casein could not be calculated for P. barbatus, P. occidentalis, or A. cockerelli because these ants never accepted casein solutions.

Portionally more carbohydrates or protein (A. Kay, in preparation). Because they are complementary, the marginal value of either nutrient should increase when the other becomes more available (Abrams 1987).

Although nutrient value depends on the availability of complementary resources, the absence of a decrease in sucrose ED50s after casein supplementation suggest that this value has no direct effect on rejection densities. The marginal value of food can affect the allocation of time to foraging (McNamara and Houston 1986) and a forager’s sensitivity to risk (Dill and Fraser 1984). These changes in behavior can indirectly lead to lower GUDs if foraging depletes resource abundance across a forager’s range (Brown 1988). However, resource value should not directly lead to lower rejection densities because foragers should never continue to exploit a patch if leaving it would allow them to find richer sources elsewhere, even if that resource is in high demand. Thus, despite an increase in sucrose value after casein supplementation, workers may have continued to reject dilute sucrose in ED50 trials because they still expected to obtain richer sources elsewhere in the environment. These results do not agree with the conclusion of Kotler et al. (1998), who suggested that bowls of water next to feeding trays lowered the GUD of seeds because water sources increased the seeds’ marginal value.

**Carbohydrate : protein availability**

ED50s of both sucrose and casein differed significantly among species. These differences, however, are difficult to interpret because it is likely that there is interspecific variation in multiple factors that affect the marginal costs and benefits of foraging.

Conversely, a comparison of ED50 ratios for colonies clearly revealed that carbohydrate : protein availability differ significantly among ant species. Ratios were high (2.73–9.47) for species that regularly collect sugary exudates and lower (0.42–1.18) for species that do not. Carbohydrate : protein availability ratios may also be low for Aphaenogaster cockerelli, Pogonomyrmex barbatus, and Pogonomyrmex occidentalis, three species that do not collect exudates and that consistently rejected even highly concentrated casein solutions. Workers might have rejected these solutions because they were unable to sense casein or found it unpalatable, but anecdotal evidence suggests that neither explanation is likely. For two A. cockerelli colonies and one P. occidentalis colony, I offered workers drops of a 2% sucrose solution and mixtures with 2% sucrose plus casein. Although 2% sucrose was usually rejected, workers frequently accepted 2% sucrose with added casein (Fig. 6) and acceptance increased with the casein concentration in the mixed solutions.

Alternatively, Aphaenogaster and Pogonomyrmex workers may have rejected casein solutions because they expected to harvest protein more quickly from other sources. Ants in the subfamily Myrmicinae, such as Aphaenogaster and Pogonomyrmex, possess only a simple proventriculus, a digestive organ that controls the flow of liquid between the crop and the midgut (Eisner 1957). This simplicity may prevent these ants from effectively collecting, transporting, and storing liquids (see Davidson 1997). At the same time, Aphaenogaster and Pogonomyrmex workers efficiently locate and capture solid sources of protein such as seeds and arthropods (Hölldobler et al. 1978, Fewell 1988). As a result, the expected rate of protein harvest from solid foods in the environment may be higher than the rate that workers could harvest protein from even concentrated casein solutions. If workers rejected casein solutions because harvest rates were too low, then their ED50s of casein should be very high. Because these species did not accept sucrose solutions, their carbohydrate : protein availability ratios may thus be much less than 1.0.

Differences in the ability to harvest liquids may provide a general explanation for interspecific differences in carbohydrate : protein availability ratios. Ants in the Dolichoderinae (Forelius, Dorymyrmex) and Formici-
nae (*Formica, Myrmecocystus*) have a modified proventriculus that facilitates the collection and storage of liquids (Eisner 1957). Because the dry mass of most nectar and exudates consists almost entirely of carbohydrates (Hölldobler and Wilson 1990), drinking ability should increase carbohydrate but not protein availability.

Extrinsic factors such as the relative abundances of liquid and solid foods may also cause differences in carbohydrate : protein availability ratios. In the desert near Portal, Arizona, extrafloral nectaries and ant-tended Homoptera are common only on plants such as mesquite (*Prosopis juliflora*) and tar bush (*Fluorencia cernua*) that differ in size and are patchily distributed. Spatial variation also exists in the abundance of proteinaceous foods such as seeds (Gordon 1993) and termites. Thus, there may be local variation in the relative abundances of carbohydrate and protein sources that produce differences in carbohydrate : protein availability.

In addition, carbohydrate : protein availability may also be skewed by differences in the intensity of competition. For example, *Forelius* spp. can control persistent resources (Hölldobler 1982) and rarely co-occur with other ants on nectar-producing shrubs (Van Zee et al. 1997). The presence of dominant ants such as *Forelius* could thus restrict access to carbohydrates and reduce carbohydrate : protein availability for other species in the community.

The results of the ED$_{50}$ assays suggest a number of novel predictions concerning the behavior and ecology of these species. First, the nutritional composition of food items should influence the foraging decisions of these ants, and the relative importance of components should differ among species. Most studies of ant foraging have assumed that energy content is a suitable measure of food value (Traniello 1989); thus, little is known about the nutritional basis of food choice in ants (but see Crist and MacMahon 1992). The ED$_{50}$ results suggest that food choice will be affected by both protein and carbohydrate content, and protein content may influence food choice more for species that collect exudates, whereas carbohydrate content may be more important for species that do not collect liquids. Second, ED$_{50}$ values should indicate the quality of reward needed for plants, Homoptera, and other symbionts to attract the services of ants. High ED$_{50}$s of sucrose for species that collect exudates suggest that symbionts producing dilute carbohydrate solutions are likely to be ignored, and low ED$_{50}$s of casein for these species suggest that the amino acid content of rewards may be particularly important for attracting ants. Third, because carbohydrate : protein availability ratios appear to be low for granivorous species, seeds rich in carbohydrates may be especially vulnerable to predation. Because *Pogonomyrmex* and *Aphaenogaster* spp. are important desert granivores (Brown et al. 1979), ant predation may select against higher carbohydrate contents in seeds and may increase investment in defensive structure and chemicals in carbohydrate-rich seeds. In addition, the ED$_{50}$ results suggest that carbohydrate : protein availability ratios may impact the resource-use strategies of these species. Although investment in foraging tempo and other energetically expensive activities has not been quantified, it may be higher for species with relatively greater access to sources of metabolic fuel: *Forelius* have been described as “seeth[ing] with rapid motion” (Hölldobler and Wilson 1990) whereas *A. cockerelli* are “remarkably deliberate in their movements” (Creighton 1950).

**Comparison to abundance measures**

Behavioral assays can provide more information about a consumer’s access to a resource than abundance measures. Using GUDs or ED$_{50}$s to indicate the rate at which a consumer expects to acquire a resource provides an integrated measure of resource access that incorporates all of the factors that influence this ex-

**FIG. 6.** The percentage of worker ants accepting solutions containing casein (dm/v = dry mass/volume) added to 2% sucrose solution. Results are for (A) one *Pogonomyrmex occidentalis* colony and (B) two *Aphaenogaster cockerelli* colonies.
pectation. In addition, these measures reveal resource availability at the spatial scale that is relevant to the consumer, obviating the need for researchers to assume the appropriate scale of measurement. In this study, ED50 ratios differed among species within the same habitat, suggesting that measures of abundance would have provided little information about resource availability.

Using ED50s, the GUD technique can be applied to social insects with diverse feeding habits. Because their calculation requires multiple responses to a variety of foods, ED50s may often require more time and effort to collect than GUD measurements, and they may be more difficult to determine for solitary organisms or for social insects with small worker forces. However, unlike GUDs, measuring ED50s does not alter a colony's nutritional state or its perception of environment quality. Thus this technique can be applied repeatedly to an individual colony. In this study, I used this advantage to infer the relative availabilities of two nutrients. This technique should also allow for investigations of individual variation, including individual responses to experimental manipulation of foraging constraints. Such investigations could provide novel insight into the mechanisms organizing the populations and communities of social insects.

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