

Nutrition and interference competition have interactive effects on the behavior and performance of Argentine ants

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Abstract. Food availability often influences competitive outcomes through effects on consumer growth. Although it has received less attention, food availability may also affect competition through nutritional effects on behavior. One hypothesis linking nutrition and competition in ants posits that increased access to carbohydrates favors greater investment in worker traits that underlie behavioral dominance. We tested this hypothesis by varying dietary protein:carbohydrate (P:C) ratios and levels of interspecific interference for Argentine ants (*Linepithema humile*), a widespread invasive species. As predicted, colonies facing interference increased patrolling more when reared on low P:C diets; this result is the first demonstration of an interactive effect of nutrition and interference on ant colonies. Several results suggest that this dietary effect on patrolling was due primarily to changes in colony size rather than worker behavior. Colonies on lower P:C diets had lower worker mortality and larger final colony sizes. Diet had little effect on per capita patrolling, and worker behavior in performance assays depended more on previous exposure to interference than on diet. Our findings indicate that dietary P:C ratios can influence Argentine ant performance in a competitive environment and suggest a mechanism by which monopolization of carbohydrate-rich resources can help invasive ants displace native ant competitors.

Key words: aggression; behavioral dominance; carbohydrates; defense; foraging; invasive species; *Linepithema humile*; macronutrients; metabolic fuel hypothesis (MFH); nutrient imbalance; protein; resource allocation.

INTRODUCTION

Food resources represent an essential component of the ecological niches of heterotrophic organisms. Individual growth and reproduction are often constrained by food quantity, but can also depend strongly on food chemical composition and its associated effects on nutritional physiology (Raubenheimer and Simpson 1997). One key aspect of nutrition is the relative abundance of macronutrients (protein, carbohydrates, lipids) in the diet. Because macronutrients have different biochemical properties, scarcity or excess of any one nutrient can have distinct phenotypic consequences (Kay et al. 2005). Quantifying the consequences of macronutrient deficiencies will thus help clarify how food quality shapes niches and influences outcomes of ecological interactions.

Variation in food quality is particularly important for omnivores that collect macronutrients from distinct resources. One such group is the ants, many species of which obtain protein from animal tissue and carbohydrates from nectars and insect exudates (Blüthgen and Feldhaar 2009). Because availabilities of these resources

can vary independently (Kay 2002), colonies may often face variation in the relative cost of acquiring different macronutrients. In addition, nutrient demand differs among life stages within colonies, as workers shunt protein to queens and larvae but retain carbohydrates (Weeks et al. 2004). As a result, variation in macronutrient access may differentially affect traits that influence ecological interactions.

How macronutrient availability affects the success of an individual may depend on the nature of the ecological interactions it faces (e.g., Behmer et al. 2002, Lee et al. 2006). One potentially diet-mediated interaction for ant colonies involves interference competition (Hölldobler and Wilson 1990, Davidson 1997). Interference is widespread in ants, and can strongly influence the local abundance and distribution of ant species (Hölldobler and Wilson 1990, Rowles and O'Dowd 2007). Several authors have suggested that macronutrient balance may influence prowess in competitive interactions (Davidson 1997, Blüthgen et al. 2000, Helms and Vinson 2002). One hypothesis, first outlined in Davidson (1997), predicts that colonies with access to more carbohydrates (and less protein) will invest to a greater extent in worker traits (such as activity and aggression) that underlie behavioral dominance. Increased allocation of resources to workers is predicted because carbohydrates can fuel worker activity but cannot support growth without

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protein and other nutrients. Colonies with access to abundant sources of carbohydrates thus face lower growth opportunity costs when resources are allocated to worker activities. We call this idea the metabolic fuel hypothesis (hereafter MFH). Positive associations among carbohydrate availability, worker aggressiveness, and behavioral and ecological dominance have been reported in several studies (Davidson et al. 2003, Palmer et al. 2008), and these results support the MFH. Recently, Grover et al. (2007) showed that worker activity and aggression were diminished by complete carbohydrate deprivation but remained unaffected by prey availability. Such results are consistent with those from studies linking macronutrient access and longevity in nonsocial insects (Lee et al. 2008, Maklakov et al. 2008).

Little is known, however, about how macronutrient access affects ant colony performance in a competitive environment. The MFH posits interactive effects of diet composition and interference competition, as interference should be particularly costly for colonies with less access to carbohydrates because such colonies will have fewer resources for fueling territorial defense. Previous presentations of the MFH have not considered whether predicted diet-related changes in colony-level behavior result from shifts in individual worker behavior or from nutritional effects on colony size. Identifying which mechanism is most important is critical for determining how rapidly nutritional conditions will affect competitive interactions.

Here, we use a controlled feeding study to test whether colonies on diets with lower protein:carbohydrate (P:C) ratios invest more in food defense and in turn exhibit improved success when facing interference competition. Our study species is the Argentine ant, *Linepithema humile*, a widespread and competitively dominant invasive species (Holway et al. 2002). This species is well suited for our study because it interacts aggressively with other ant species (Holway 1999) and relies heavily on carbohydrate-rich resources (Markin 1970).

METHODS

We collected material for experimental colonies of Argentine ants from 10 sites in San Diego County, California, USA in May 2008. Collecting sites were separated by at least 1 km. For each site, we used the material collected to make 10 experimental colonies (1 colony per treatment, as described below). Each colony consisted of 4 queens, ~1000 workers (456 ± 0.408 mg [mean \pm SE]), and 45 ± 0.852 mg of brood. We reared colonies in circular containers (18×8 cm) connected to arenas ($32 \times 18 \times 11$ cm) with tubing. We lined containers with Fluon (Northern Products, Woonsocket, Rhode Island, USA) to prevent escape. In each circular container, we placed three nest chambers (glass test tubes: 10×100 mm) half full of water and stopped

with cotton. We reared colonies on a 12:12 hour light:dark cycle at 22°C.

We randomly assigned colonies to one of five chemically distinct diets ($n = 20$ colonies per diet group). Each diet contained a unique P:C ratio (after Lee et al. 2008). Dietary P:C ratios (6:1, 3:1, 1:1, 1:3, 1:6) spanned the P:C ratio (1:2) shown recently to promote maximal growth in ants (Dussutour and Simpson 2008a). The main component of the diet was an agar gel consisting of sucrose and ground crickets (hereafter, mixed gel). We manipulated the P:C ratio by modifying the relative amounts of sucrose and crickets in the diet while standardizing food density (100 g/L). We estimated P:C ratio by assuming crickets were 0.6 g protein/g dry mass (Finke 2002). We provided each colony with 1.25 g of agar gel for 6 days per week for 12 weeks. Most colonies produced only small amounts of brood during the first 3 weeks of the experiment. In order to increase brood production, we began at week 4 to provide colonies with freeze-killed fruit flies and a sucrose gel on the seventh day of each week; these additional resources gave workers a protein source (flies) that could be carried to the nest for provisioning brood. We provided flies and sucrose gel simultaneously; each colony received the same amount of resource (7 mg dry mass per feeding); relative amounts reflected treatment P:C ratios. Throughout, we removed any remaining materials after 3 hours. Water was available ad libitum throughout the experiment.

Within each diet treatment, we randomly assigned half of the colonies ($n = 10$) to an interference competition treatment; the other half ($n = 10$) served as controls. For interference, we introduced 5 workers of the pavement ant *Tetramorium caespitum* during three feeding periods per week; introductions were made every second day in the 6-day period that colonies received the mixed gel. In preliminary work, we found that adding pavement ant workers invoked a sustained aggressive response from Argentine ant colonies. We introduced pavement ants 5 min after food was provided and colonies had begun recruiting to the food. We removed pavement ants after 3 hours; new pavement ants were used for each bout of feeding. Upon removal of pavement ants, we classified their injury state into one of four categories: (1) no obvious injuries, (2) missing limbs but able to walk, (3) unable to walk, but alive, and (4) dead. During the first and last week of the experiment, we recorded the number of Argentine ant workers gathering food and patrolling on two consecutive days when colonies received the mixed gel. For the interference treatment, gathering food and patrolling were thus recorded on one day with and one day without pavement ant introductions (order randomized). We classified workers as gathering food if their mandibles were in contact with food, and as patrolling if they were in the foraging arena but were not gathering food; these two categories adequately captured the main behaviors of ants observed during feeding trials. We recorded

gathering and patrolling activity 30, 45, and 60 min after food was provided (when recruitment levels peaked). We ended diet treatments after 12 weeks.

We estimated worker mortality in the final week by counting dead workers in containers. We removed all dead workers and food remnants from containers one week before this survey. We determined per capita mortality by dividing counts by final worker population size.

We also assayed individual worker activity and interspecific aggressiveness at the end of the final week. We quantified colony activity as in Grover et al. (2007). Briefly, we measured colony-level exploration of a novel structure placed in each nest container. Structures consisted of three 30 cm long bamboo skewers arranged as a tripod with cards attached to the tips. We counted workers on a structure after 5, 10, and 15 min. We divided time-averaged activity scores by the number of workers present in each colony to generate a per capita activity score. We measured interspecific aggression using a titration assay. For each trial, we took 10 ants from an experimental colony and matched them against 2 pavement ants. Each match took place in an 11 cm diameter plastic container that had 5-cm edges lined with Fluon. If a fight occurred, the Argentine ant–pavement ant pair was removed and placed in a smaller container (the pavement ant was immediately replaced; the Argentine ant was not). We assessed the fate (uninjured, moribund, dead) of the Argentine ant in each pair 5 min after removal. We continued each match for 10 min, at which time we recorded the number of Argentine ants that had been removed from the 11-cm container. Because Argentine ants became less likely to attack pavement ants as more of their nestmates were removed, this assay provided a simple way of quantifying aggression on a continuous scale. Observers were blind to the experimental group during all trials.

We sacrificed all colonies after 12 weeks and measured the number of surviving workers, brood wet mass, and per worker lipid content. For lipid analysis, we randomly selected 50 workers from each colony and dried them to a constant mass. We determined total lipid content using a phosphovanillin reagent as in Grover et al. (2007). We used a 70:30 mixture of glycerol trioleate:glycerol tripalmitate as a standard.

We used ANOVA to test how dietary P:C ratio and interference affected each dependent variable. We treated dietary P:C ratio as a fixed factor because ratios used were a nonrandom subset of those likely found in nature and were set by us at the start of the experiment. For gathering and patrolling activity, we included diet, interference, whether or not colonies in the interference treatment faced pavement ants on that day (hereafter introduction), and all interaction terms. For all other dependent variables, models included diet, interference, and the diet \times interference interaction. Colony of origin was also included in each model as a random factor. We

used Brown-Forsythe tests to assess homogeneity of variances. Prior to analysis, we log-transformed data that violated this assumption. Following each ANOVA, we used Tukey tests to compare means across experimental groups.

RESULTS

Argentine ant colonies substantially increased patrolling activity after pavement ants were introduced to foraging arenas, but the extent of the response depended on diet treatment (Fig. 1A–D; Appendix A). During the first week of the experiment, patrolling activity per colony (Fig. 1A) and per capita (Fig. 1C) were significantly higher after pavement ant introduction for colonies in the interference treatment (interference \times introduction interaction; $P < 0.001$), and this increase was consistent across diets (interference \times introduction \times diet interaction; $P = 0.974$). In contrast, at the experiment's end, per colony patrolling in the interference treatment depended significantly on diet composition (interference \times introduction \times diet interaction; $P = 0.006$), with particularly high increases for colonies on protein-poor, carbohydrate-rich (low P:C) diets (Fig. 1B). Diet did not significantly affect patrolling activity on a per capita basis (Fig. 1D; interference \times introduction \times diet interaction; $P = 0.132$). Argentine ants consistently attacked pavement ants during the experiment. Mean pavement ant injury score was 2.34 ± 0.06 in the first week and 2.60 ± 0.06 in the last week of the experiment, indicating moderate to major injuries for the average ant. This score did not differ significantly among diets ($F_{4,81} = 0.993$, $P = 0.417$).

Colony food gathering depended on both interference and diet, but the effects of these treatments varied over time (Fig. 1E–H; Appendix A). Initially, the interference treatment resulted in a small (but significant) decrease in per colony (Fig. 1E) and per capita (Fig. 1G) food gathering (main effect of interference; $P = 0.021$), and this effect did not vary significantly among diets (interference \times diet interaction; $P = 0.470$). At the experiment's end, this decrease in per colony food gathering was substantial (main effect of interference; $P < 0.001$) and colonies on protein-poor, carbohydrate-rich (low P:C) diets fed more than did colonies on higher P:C diets (Fig. 1F). Per capita food gathering was also lower for colonies in the interference treatment (main effect of interference; $P < 0.001$), but it was not significantly affected by diet treatment (main effect of diet; $P = 0.073$).

Final colony size, worker mortality rates, and worker condition depended much more on diet than on exposure to pavement ant workers. Final colony size (= number of living workers) was higher for colonies on protein-poor, carbohydrate-rich (low P:C) diets (Fig. 2; main effect of diet; $F_{4,80} = 80.584$, $P < 0.001$). Final colony size was also significantly affected by interference ($F_{1,80} = 12.676$, $P < 0.001$), although interference only reduced colony size for colonies on low P:C diets

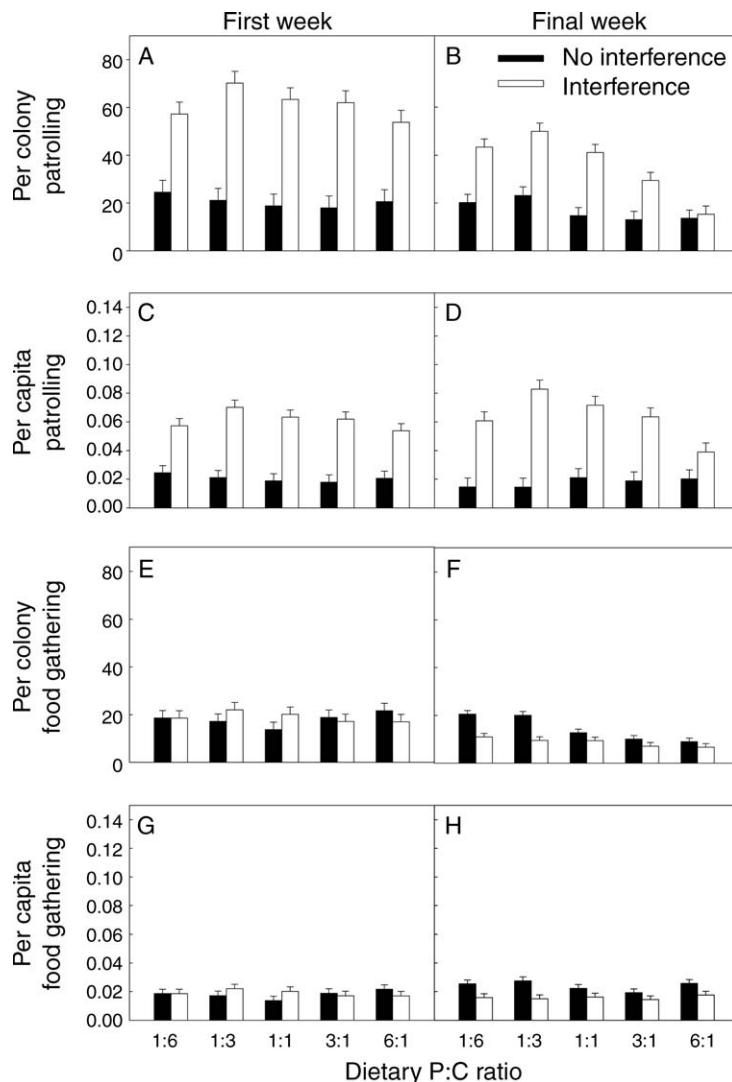


FIG. 1. The effect of dietary protein : carbohydrate (P:C) ratio and exposure to interference competition on patrolling activity and food-gathering activity of Argentine ant colonies. Results are for days in which Argentine ants were exposed to pavement ants during the first week (panels A, C, E, G) and during the final week (panels B, D, F, H) of the experiment. The bars show least-square means (\pm SE). Factors in the ANOVA were diet, interference treatment, whether pavement ants were introduced that day, and all interactions. Colony of origin was also included in the model. Interference substantially increased patrolling activity (left panels). Colonies on carbohydrate-rich (low P:C) diets had higher interference-related patrolling activity in the final week of the experiment on a per colony basis (panel B), but not on a per capita basis (panel D), suggesting that diet-related changes in patrolling were determined by changes in colony size during the experiment.

(interference \times diet interaction; $F_{4,80} = 2.954$, $P = 0.025$). Diet also had a marginally significant effect on per capita brood mass ($F_{4,80} = 2.469$, $P = 0.051$) and this measure was lowest for colonies on the lowest P:C diet (Appendix B). Per capita worker mortality at the end of the experiment was much higher for colonies on high P:C diets, but was not significantly affected by interference (Appendix C). Treatment differences in worker lipid content at the end of the experiment reflected differences in worker mortality and colony size (Fig. 2), with lowest values for workers in the low P:C treatments (diet; $F_{4,80} = 25.818$, $P < 0.001$).

In contrast to the results on colony size, individual worker behavior depended primarily on interference rather than diet treatment (Fig. 3). Colonies that had not experienced interference had more workers explore a novel structure than did colonies in the interference treatment (Fig. 3; main effect of interference; $F_{1,80} = 73.723$, $P < 0.001$). This measure of per colony activity was particularly high for control colonies on protein-poor, carbohydrate-rich (low P:C) diets (main effect of diet; $F_{4,80} = 7.454$, $P < 0.001$; interference \times diet interaction; $F_{4,80} = 9.513$, $P < 0.001$). Per capita activity was also significantly higher for control colonies (Fig. 3;

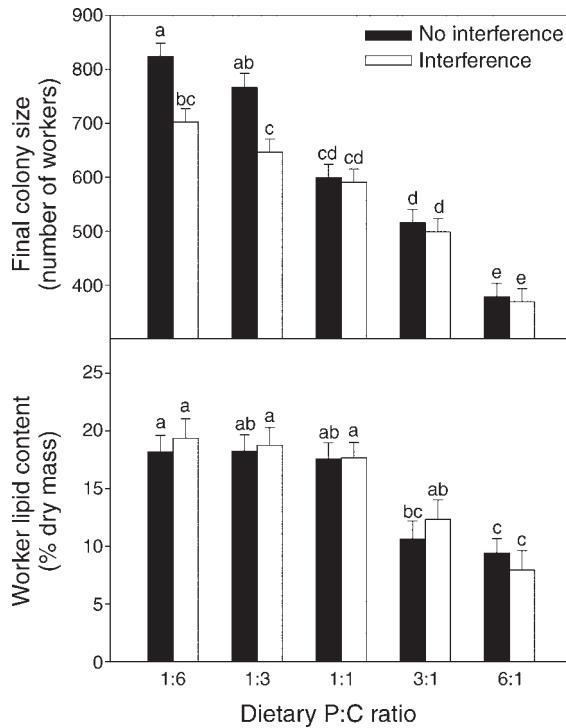


FIG. 2. The effect of dietary protein:carbohydrate (P:C) ratio and exposure to interference competition on colony size (number of living workers) and worker lipid content. The bars show least-square means (\pm SE). Factors in each ANOVA were diet, interference treatment, and the diet \times interference interaction. The colony of origin was also included in the model (colony size, $F_{9,80} = 13.066$, $P < 0.001$; worker lipid, $F_{9,80} = 0.501$, $P = 0.869$). Different lowercase letters indicate significant differences ($P < 0.05$) in pairwise comparisons.

$F_{1,80} = 35.039$, $P < 0.001$), and there was a significant interference \times diet interaction ($F_{4,80} = 3.749$, $P = 0.008$), as the effect of interference on per capita activity was more pronounced for colonies on low P:C diets. Aggression was also significantly affected by the interference treatment ($F_{1,80} = 58.766$, $P < 0.001$), as workers from control colonies were much more likely to fight with pavement ants in staged interactions than were workers from colonies that had been regularly exposed to pavement ants during the 12-week experiment (Fig. 3). There was no significant diet effect ($F_{4,80} = 1.508$, $P = 0.208$) or diet \times interference interaction ($F_{4,80} = 1.304$, $P = 0.276$) on worker aggression. More than a third ($146/368 = 39.7\%$) of interspecific fights in these assays resulted in the death of the Argentine ant within 5 min; this percentage was not significantly affected by diet ($F_{4,63} = 1.655$, $P = 0.172$) or by interference treatment ($F_{1,63} = 0.109$, $P = 0.742$).

DISCUSSION

Our results are the first to show an interactive effect of nutrition and interference competition on the growth and performance of ant colonies. As predicted by the

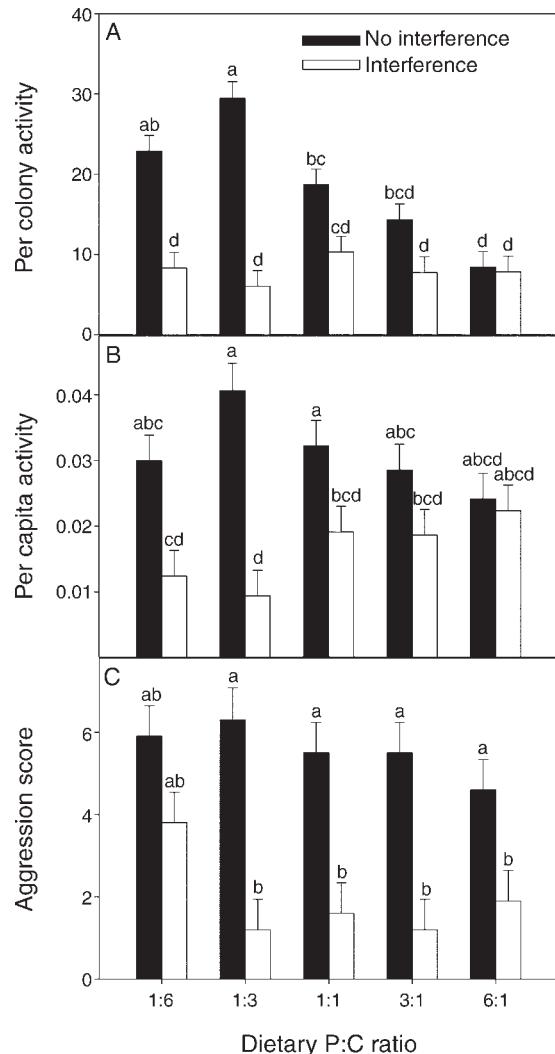


FIG. 3. The effect of dietary protein:carbohydrate (P:C) ratio and exposure to interference competition on worker behavior measured using performance assays. (A) Per colony activity is the time-averaged number of workers on a novel structure. (B) Per capita activity is per colony activity/colony size. (C) The aggression score is the number of Argentine ants (out of 10) that engaged in fights with pavement ants during staged encounters. The bars show least-square means (\pm SE). Factors in each ANOVA were colony of origin, diet, interference treatment, and the diet \times interference interaction. Colony of origin was significant for per colony activity ($F_{9,80} = 7.092$, $P < 0.001$) and per capita activity ($F_{9,80} = 7.250$, $P < 0.001$), but not for aggression ($F_{9,80} = 0.479$, $P = 0.885$). Different lowercase letters indicate significant differences ($P < 0.05$) in pairwise comparisons.

metabolic fuel hypothesis (MFH), colonies reared on carbohydrate-rich (low P:C) diets patrolled foraging areas substantially more when facing interference than did colonies reared on high P:C diets. However, contrary to prediction, interference more negatively impacted final colony size for colonies on lower P:C diets. Importantly, diet had little effect on per capita

patrolling, suggesting that dietary effects were due primarily to the large reduction in colony size in high P:C treatments. Moreover, diet composition had little effect on individual worker activity and interspecific aggression in performance assays; instead, variation in these traits depended primarily on previous exposure to interference. These results suggest a mechanistic link between diet and competitive prowess in ant colonies, and show at least in principle how access to carbohydrates could enhance behavioral dominance in invasive ants such as the Argentine ant.

Diet composition had a large effect on colony growth: colonies on protein-rich, carbohydrate-poor (high P:C) diets had higher worker mortality and smaller final colony sizes than did colonies on lower P:C diets. Studies on solitary insects also demonstrate increased mortality rates on high P:C diets because of costs of processing excess protein (Lee et al. 2008, Malkolov et al. 2008). Recently, Dussutour and Simpson (2009) found a qualitatively similar result in a species of *Rhytidoponera* ants. By quantifying food intake, they showed that colonies on high P:C diets increased food gathering to maintain carbohydrate levels (see also Dussutour and Simpson 2008b), but greater food intake resulted in excess protein accumulation that was in turn associated with increased worker mortality. It remains unclear how high P:C diets increase mortality rates, although it could be related to costs associated with eliminating nitrogenous waste products (Lee et al. 2008).

A relationship between P:C availability and colony size is also suggested from ecological studies that have associated ant abundance with nectar and honeydew availability in tropical rainforest canopies (Davidson 1997, Blüthgen et al. 2003). Previous authors have noted that nectar and honeydew exploitation may support larger ant populations because of efficiency gains from feeding at a lower trophic level compared to that consumed by ants that are highly carnivorous (Tobin 1994, Davidson 1997, Tillberg et al. 2007). The relationship between dietary P:C and worker mortality shown here indicates that nutrition may also contribute to the relationship between access to plant-based resources and colony growth. Given that numerical dominance often underlies competitive prowess in ants (Palmer 2004), the link between diet composition and worker maintenance may be an important general mechanism by which resource quality influences the composition of ant assemblages.

Our results show mixed support for the MFH. As predicted, colonies on protein-poor, carbohydrate-rich (low P:C) diets patrolled more than did colonies on higher P:C diets. However, contrary to prediction, the negative effect of interference on colony size was larger for colonies on low P:C diets. This result likely reflects a specific aspect of our design; the interference treatment remained constant throughout the experiment. In nature, investment in defense can deter neighbor intrusions and secure more exclusive access to food

finds. Consistent introduction of competitors, while experimentally tractable, prevented colonies that invested more in patrolling from accruing benefits available under field conditions. In fact, consistent introduction of pavement ants, which frequently killed Argentine ants in staged fights, likely increased risk exposure for colonies with high patrolling rates. Further insight into the role of metabolic fuel on ant colony interactions could be gained if experimental designs allow for the accrual of realistic benefits from defense.

Although patrolling was higher for colonies on protein-poor, carbohydrate-rich (low P:C) diets, this difference was not associated with changes in individual worker behavior. Studies have suggested that increased carbohydrate access favors higher worker tempo (i.e., activity rates) (Davidson 1997, Kay and Adler 2003, Grover et al. 2007), but we found instead that diet did not significantly affect either per capita patrolling or individual worker activity and aggression in performance assays. However, activity and aggression did depend strongly on whether colonies had been exposed to interference during the experiment. Many studies have shown that ants facing risk can modify patch-use behavior (Nonacs and Dill 1990) or overall foraging effort (Kay and Rissing 2005). These studies have generally focused on responses to short-term variation in risk (but see Thomas et al. 2007), so less is known about how long-term exposure to aggressive competitors affects ant behavior. Our performance assays showed that exposure to interference for 12 weeks significantly reduced a colony's tendency to explore a novel structure, indicating that long-term risk can affect worker behavior even in the absence of that risk. This result is consistent with the habituation to neighbors (the "dear-enemy phenomenon") that has been documented in other systems (Langen et al. 2000).

The lack of a diet effect on individual activity and aggression levels contrasts somewhat with recent results presented in Grover et al. (2007). In that study, access to sucrose (but not prey) significantly affected individual worker activity and intraspecific aggression in Argentine ants. A key difference between the two studies was that Grover et al. (2007) included treatments in which colonies had no access to sucrose and treatments in which colonies had access to much higher levels of sucrose than those used in the present study. In addition, colonies in Grover et al. (2007) were not exposed to competition throughout the experiment, and the aggression assay tested responses to conspecifics. Taken together, the results of both studies suggest that individual worker activity and aggression may only be affected if carbohydrate deprivation is extreme and prolonged (i.e., if colonies receive no sucrose for 12 weeks). Moreover, our results illustrate that care should be taken in assessing how diet affects aggressive contacts with other ants; how such interactions play out can be sensitive to the species involved (Holway 1999).

Interactions between nutrition and interference competition may be especially important for invasive ants, such as the Argentine ant (Davidson 1998). Invasive ants are conspicuous consumers of nectars and honeydew (Helms and Vinson 2002), and their competitive success has often been linked to high worker densities (Holway et al. 1998, Abbott 2005). Our results, along with those from previous studies (Grover et al. 2007, Helms and Vinson 2008), reveal a functional link between nutrient access and elevated worker densities and suggest a mechanism by which monopolization of carbohydrate-rich resources may help invasive ants displace native ant competitors.

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APPENDIX A

ANOVA results for observations of Argentine ant patrolling and food gathering (*Ecological Archives* E091-007-A1).

APPENDIX B

A figure showing the effects of diet composition and interference on per capita worker mortality in Argentine ants (*Ecological Archives* E091-007-A2).

APPENDIX C

A figure showing the effects of diet composition and interference on brood production in Argentine ants (*Ecological Archives* E091-007-A3).