

Mechanisms of carbohydrate-fuelled ecological dominance in a tropical rainforest canopy-foraging ant

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Abstract. 1. Canopy-foraging ants have carbohydrate-rich diets and the stoichiometric excess of carbon may result in energetic allocation decisions that facilitate ecological dominance.

2. If dietary carbohydrates facilitate ecological dominance in canopy ants, then the mechanism for this relationship is unknown.

3. Four hypotheses were posit that may explain how a carbohydrate-rich diet might facilitate ecological dominance in canopy ants: Aggressive Defense, Metabolic Fuel, Foraging Success, and Prey Acquisition.

4. To assess these hypotheses, experiments were conducted on the canopy-foraging bullet ant, *Paraponera clavata* (Fabricius), an omnivorous species that demonstrates high variability in the relative contribution of carbohydrates to the diets of colonies.

5. No support was found for the Aggressive Defense, Metabolic Fuel and Prey Acquisition hypotheses.

6. The Foraging Success hypothesis was supported, as the proportion of nectar in the diet predicted the overall foraging success.

7. It was argued that there is no explicit advantage in the exploitation of nectar over other food resources, other than the fact that it is the most accessible food resource in the rainforest canopy.

Key words. Aggression, competition, density, foraging, nectar, omnivory, *Paraponera*, predation, tempo.

Introduction

Organisms become ecologically dominant by accessing resources more readily than competing species. In animals, behavioural mechanisms of resource acquisition and use may explain how some species become more ecologically dominant, which means that they are highly abundant where they occur (Arnan *et al.*, 2011). In relatively simple environments, such as agroecosystems, the mechanisms that facilitate ecological dominance may be overt, and readily tested (Philpott & Foster, 2005; Vandermeer *et al.*, 2008). However, in a more biologically and structurally complex environment, the ways that species become ecologically dominant can remain enigmatic despite persistent investigation (Armbrecht *et al.*, 2004; Philpott *et al.*, 2006). In a rainforest canopy, it is difficult to detect which resources enable the emergence of dominance, or how these resources result in increased population sizes indicative of

ecological dominance. Understanding the mechanisms of ecological success in abundant organisms remains a foundational issue.

The ants that forage in the canopies of tropical rainforests are typically presented as an archetype of ecological dominance (Richard *et al.*, 2001; Sanders *et al.*, 2007; Dejean *et al.*, 2010). It is commonly accepted, and may even be true, that canopy-foraging ants have become ecologically dominant by shifting to a herbivorous diet (Davidson *et al.*, 2003; Russell *et al.*, 2009). Whereas terrestrial ants have a Nitrogen (N)-rich and Carbon (C)-poor diet, the converse is the case for ants that collect their food from the canopies (Yanoviak & Kaspari, 2000; Weiser *et al.*, 2010). Canopy-foraging ants, which principally collect sugary solutions for their diet, collect scant quantities of N from honeydew and experience a stoichiometric excess of C.

Notwithstanding copious evidence that a high-carbohydrate diet is associated with ecologically dominant canopy-foraging ants of tropical rainforests, we do not know how – or even if – a carbohydrate diet facilitates ecological dominance of species in this guild. Ant colonies do not necessarily collect all of

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the energy-bearing carbohydrates that they can, and colonies can modulate carbohydrate intake relative to energetic demands of colony growth (Dussutour & Simpson, 2008). However, workers do require carbohydrates as fuel to survive (Dussutour & Simpson, 2012), and the more fuel that workers take in, the longer workers are able to survive and forage (Lach *et al.*, 2009). While it has been proposed that the success of arboreal ants is their exploitation of nectar (Davidson *et al.*, 2003; Russell *et al.*, 2009), there has not been an evaluation of how nectar might be used by arboreal ants to become successful. The purpose of the present study is to propose and evaluate the potential mechanisms that can account for an association between high C diets and ecological dominance in rainforest canopy ants.

We posit four non-exclusive hypotheses that may explain how canopy ants may use the energy of a C-rich diet to become ecologically dominant. The *Aggressive Defense Hypothesis* is that colonies of ants use the energy from carbohydrates to mount a higher defensive response against nest disturbance. In colloquial settings, it is common to hear that arboreal ants are aggressive on account of their access carbohydrates, even although this idea has not received much scrutiny within the literature. The use of carbohydrates to increase aggression is known to occur during intraspecific interactions (Grover *et al.*, 2007) and may be critical for species that are nest-space limited (Philpott & Foster, 2005). If the *Aggressive Defense Hypothesis* is acting, then we predict that colonies with a higher concentration of nectar or greater number of ants collecting nectar will be more aggressive to external perturbations.

The *Metabolic Fuel Hypothesis* argues that colonies with a higher energy intake send a greater number of individuals to forage and patrol home ranges; this hypothesis was coined by Kay *et al.* (2010). In colonies of the non-arboreal thieving ant *Ectatomma ruidum* (Roger), an experimental test of the Metabolic Fuel Hypothesis in laboratory colonies shows that whole-colony metabolic rates are not altered by the relative proportion of carbohydrates in the diet. However, Kaspari *et al.* (2012) found that field supplementation of carbohydrates increased ant foraging activity at the community level, concomitant with changes in species composition. In the present study, the *Metabolic Rate Hypothesis* will be tested by making available substantial ambient variation in the concentration of nectar in the field. If this hypothesis is correct, then we predict that a higher proportion of ants collecting nectar, and the concentration of nectar that ants collect, will be associated with the foraging activity level.

The *Foraging Success Hypothesis* proposes that colonies with a higher carbohydrate intake will also experience a greater rate of success in foraging. Unlike the *Metabolic Rate Hypothesis*, which proposes a connection between foraging activity levels and carbohydrate intake, the *Foraging Success Hypothesis* addresses the rate of success of foragers regardless of foraging activity levels. This hypothesis predicts that when colonies have access to more carbohydrates, workers that leave the colony to forage are more likely to return to the colony with food resources. The *Foraging Success Hypothesis* does not indicate that there is any particular behavioural or physiological benefit from carbohydrates that enhances competitive ability, and merely is that colonies collect sugar because it is there, perhaps

making the best of an otherwise unproductive foraging bout. If this hypothesis is correct, then we predict the proportion of ants collecting nectar, and the concentration of nectar they are collecting will be associated with the proportion of foragers returning home with a food item of any kind.

Last, the *Prey Acquisition Hypothesis* may be considered as a subset of the *Foraging Success Hypothesis*. According to the *Prey Acquisition Hypothesis*, colonies with a high C diet are more able to collect prey. This might seem counterintuitive, but there is not necessarily a tradeoff between the total amount of sugar collected and the proportion of prey in the diet. This could happen if the energy from carbohydrates is used for longer foraging bouts to increase the chance of encountering suitable prey, or by providing energy that may increase the success in subduing a prey item. As arboreal ants are N limited, then it is reasonable to test the possibility that excess carbohydrate consumption might be allocated towards an increased rate of prey capture. If this hypothesis is correct, we predict the number of foragers collecting nectar, and the concentration of nectar they carry, is associated with the proportion of foragers returning with a prey item; more nectar may be associated with a higher relative trophic position, estimated by $\delta^{15}\text{N}$.

The success of ants in the rainforest canopy is coupled with their exploitation of the carbohydrates in this environment (Russell *et al.*, 2009). Does the exploitation of this resource facilitate their ecological dominance? Here we evaluate these four hypotheses, using the canopy-foraging bullet ant *Paraponera clavata* (Fabricius) as a model organism.

Materials and methods

Work was conducted from May to August 2012 at La Selva Biological Station, Sarapiquí Canton, Heredia Province, Costa Rica ($84^{\circ}00'12.92''\text{W}$; $10^{\circ}25'52.61''\text{N}$). La Selva is located in a lowland tropical rainforest that receives c. 4 m of rainfall annually. Most colonies of *P. clavata* nest at the base of canopy trees but forage almost exclusively in rainforest canopies (Breed & Harrison, 1989). Ants foraging for both prey and liquid food carry these items back to the nest between their mandibles, and the size of individuals is large enough that the observer is capable of determining if a forager is carrying liquid or prey, or is returning to the nest with nothing between her mandibles. This species was selected because its nesting habit and body size, as well as its external liquid transport behaviour, facilitated this study which would be difficult or impossible to conduct in most other ecologically dominant rainforest canopy-foraging ants. Experiments were conducted with 31 actively foraging colonies of *P. clavata*. All fieldwork was conducted between 19:00 and 03:00 hours, the apparent peak foraging time of *P. clavata* during the time of the experiment. Colonies were selected as a subset of colonies that we located for a sample population representing the geographic extent of the area and a variety of forest ages, including old growth forests and secondary growth forests between 10 and 70 years of age, presenting a range of trophic conditions for *P. clavata* colonies. This is designed to capture a broad ambient range of carbohydrate abundance and concentration in the canopy so that behavioural differences among colonies with different resource environments may be assessed.

Each colony was subjected to the following experimental regimen twice, with at least 14 days separating each sampling period. Analyses were conducted on the mean values of these observation periods, with each mean value as a single observation. The fluid was removed from mandibles of 10 returning foragers who were carrying a fluid between their mandibles. The concentration of this sugar in nectar was assayed in the field using a brix refractometer (BTX-1, VEE GEE Scientific, Inc., Kirkland, Washington). After this nectar sampling procedure, the foraging activity and diet of the colony were observed for 0.5 h. The number of foragers returning to the nest was counted, and their loads were categorised as follows: empty, liquid, and prey. A haphazardly selected subset of 22 colonies were subjected to a nest defence aggression bioassay, in which colony entrances were physically disturbed with three pokes of a stick with a diameter of c. 5 cm, and the number of individuals emerging from the nest entrance in the subsequent 10 s was counted as an estimate of the nest defense response. This assay was conducted by the same investigator, three times on separate days, with each assay separated by at least 2 weeks, with all of the colonies tested in a single day, and the mean value for each colony was used in the analysis.

From a subset of 22 colonies (the same as the aggression bioassay), three workers were collected for stable isotope analysis. Samples of legs were weighed into tin capsules in an analytical balance to the nearest μg , with c. 1 mg ant tissue per capsule. Ratios of stable isotopes in the ant tissue were measured with a PDZ Europa 20/–20 isotope ratio mass spectrometer at the UC Davis Stable Isotope Facility. Values of $\delta^{15}\text{N}$ were calibrated using values from established laboratory standards, run every 12 samples, and calibrated against NIST Standard Reference Materials. The $\delta^{15}\text{N}$ of animal tissue offers a rough estimate of relative trophic position, with the assumption that the $\delta^{15}\text{N}$ of dietary sources among the compared colonies are equivalent (Tillberg *et al.*, 2006).

After conducting basic descriptive statistics, hypotheses were evaluated using conducting statistical tests to evaluate the predictions. All tests were conducted in JMP 10 (SAS Institute, Cary, North Carolina), using generalised linear models to test whether the independent dietary variables were associated with the response variables for each hypothesis. Proportional variables were square-root transformed prior to analysis.

Results

The proportions of prey and nectar in the diets of colonies were highly variable. The mean proportion of nectar among food items ranged from 34% to 90% among colonies, with a median of 68%. The mean nectar concentrations were also variable among colonies, ranging from 8.5% to 19.7%, with a median of 13.2. For each colony, the mean number of foragers returning to the nest per 30-min observation period was 72.2 ± 31.8 SD, ranging from 9.0 to 143.5.

The *Aggressive Defense Hypothesis* was not supported, as the mean number of ants collecting nectar and the concentration of sugar in nectar did not predict the mean number of individuals responding to nest disturbance [5.8 ± 3.2 SD; $N = 22$; generalised linear model (GLM) $\chi^2_2 = 0.362$, $P = 0.835$].

The *Metabolic Fuel Hypothesis* was not supported as the proportion of ants collecting nectar and the concentration of nectar did not predict the mean number of all ants that returned from foraging trips ($N = 31$ GLM $\chi^2_2 = 0.286$, $P = 0.867$).

The statistical model for the *Foraging Success Hypothesis* was supported, as the proportion of ants collecting nectar and the concentration of the nectar did predict the proportion of ants that foraged successfully ($N = 31$ GLM $\chi^2_2 = 27.33$, $P < 0.0001$). The effect tests of this GLM indicate that the proportion of successfully foraging ants was predicted by the proportion of ants bringing home a nectar solution ($\chi^2_1 = 26.59$, $P < 0.0001$; Fig. 1a; $r^2 = 0.53$) and the concentration of nectar ($\chi^2_1 = 4.51$, $P = 0.034$). This effect of nectar on overall foraging success is placed into context considering that the proportion of ants successfully foraging was not predicted by foraging activity level (Fig. 1b; $r^2 = 0.01$), nor the proportion of ants returning with prey items (Fig. 1c; $r^2 = 0.003$).

The *Prey Acquisition Hypothesis* was not supported as the proportion of foragers returning with prey items was independent of the number of foragers carrying nectar and the concentration of nectar (mean = 13.4 ± 3.1 SD); ($N = 31$; $\chi^2_2 = 3.482$; $P = 0.180$), as was the mean $\delta^{15}\text{N}$ of colonies (mean = 6.2 ± 0.7 SD; $F_{2,19} = 0.540$, $P = 0.592$).

Discussion

Our results favour the *Foraging Success Hypothesis* as a possible explanation for carbohydrate-fuelled ecological dominance in rainforest canopy ants. We found that the proportion of workers collecting nectar was associated with the overall food collection rate, even although the amount of prey collected by colonies was not tied to nectar consumption. *P. clavata* colonies are adept at adjusting foraging effort to respond to differences in nectar availability (Breed *et al.*, 1987; Fewell *et al.*, 1992). We found that across the entire home range throughout the canopy, the overall success of foraging was tied to the fraction of ants bringing nectar back to the nest. This relationship was independent of the number of foragers. This result is not a major surprise, but in the absence of support for the other models then it appears that the only reason that these canopy ants forage for nectar not because it is particularly advantageous, but because it is available. When a forager returns to the colony without a food item, this is more of a failure to collect nectar than it is a failure to hunt for prey. As nectar availability goes, so does foraging efficiency.

The reliance on nectar as a food source is particularly surprising – and presumably an indicator of major energetic constraints – considering the marginal benefit of foraging for nectar. When *P. clavata* workers forage for nectar, they experience only a small energetic benefit compared to the amount of work that it takes to retrieve the resource. A foraging bout resulting in prey capture results in over 17 times greater net energetic benefit than those trips that gathering nectar (Fewell *et al.*, 1996). If less than 25% of the workers collecting nectar are successful, then the effort invested into collecting nectar is a net energetic loss for *P. clavata* workers (Fewell *et al.*, 1996). Nonetheless, we found that the successful collection of nectar does not increase the rate of collection of more energetically favorable prey items.

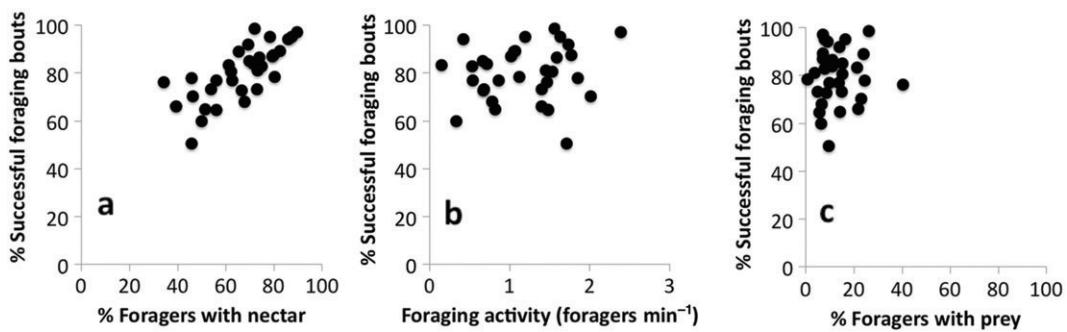


Fig. 1. The % of returning foragers bearing nectar predicts the overall frequency of successful foraging (panel a), although unaffected by the level of foraging activity (panel b) or the proportion of prey collected (panel c). These relationships are consistent with the Foraging Success Hypothesis.

We surmise that the collection of nectar does not help colonies endow surplus activities that increase behavioral dominance. In a previous study by our laboratory group, Larson *et al.* (2014) found that colonies collecting solutions with less than 10% sugar content shifted foraging efforts towards prey acquisition. Thus, there is a threshold in which the marginal benefits of nectar collection lose their value. While other ant species might still be using carbohydrates to amplify activity rates to engage in activities to facilitate behavioral dominance, *P. clavata* does not seem to be using nectar in this fashion. Our working hypothesis, which is open for future testing, is nectar collection provides a consistent source of energy that is primarily allocated to colony maintenance.

The emergence of ecologically dominant canopy ants has been facilitated by mutualisms with gut microbes that enable colonies to persist on a low-N diet (Eilmus & Heil, 2009; Russell *et al.*, 2009; Anderson *et al.*, 2012). *Paraponera clavata* colonies are highly variable in the amount of prey found in their diet (Tillberg & Breed, 2004), probably more so than other canopy-foraging ants (Blüthgen *et al.*, 2003), and do not appear to have a consistent gut microbiome as other canopy specialists (Kautz *et al.*, 2013). Nonetheless, a symbiotic Rhizobiales bacterium, which is likely to play a role in N recycling, is positively associated with a carbohydrate-biased diet of *P. clavata*, and increases in prevalence along with the experimental addition of sugar water to the diet of the ants (Larson *et al.*, 2014).

With the evolution of tighter microbe–ant symbioses in other clades of canopy-foraging ants, a carbohydrate-rich diet may more readily fuel behaviors that increase behavioural dominance in a fashion that does not occur in *P. clavata*. As *P. clavata* are facultatively associated with an N-cycling bacterium, mediated by the quantity of nectar in the diet, then our understanding of the associations among diet, microbes, foraging behaviour and competitive interactions in *P. clavata* may inform our understanding of the initial emergence of carbohydrate specialisation in arboreal ants.

There are a number of caveats that we share to prevent inappropriate extensions of the present findings. This study was conducted only in a single species. While clearly a dominant species in the canopy, *P. clavata* differs from other canopy-foraging ants in its terrestrial nesting habit, huge body size, and phylogenetic uniqueness as the sole member of the subfamily Paraponerinae. The present experiment did not directly test the physiological

or interspecific mechanisms tied to each hypothesis but instead evaluated whether predicted patterns tied to each hypothesis were observed. Investigation of the comparative metabolic physiology of canopy-foraging ants may be a critical companion to the current approach incorporating ecological, phylogenetic, and coevolutionary studies.

Carbohydrate-rich diets that are limited in N are both typical and necessary for ants to become abundant in the canopies of tropical rainforests. The present findings indicate that in *P. clavata*, ambient variance in the collection of carbohydrates is only associated with elevated means to achieve ecological dominance insofar as nectar collection results in the more successful foraging effort. This result is consistent with work indicating that elevated dietary carbohydrates do not affect the worker activity rate of ant colonies (Kay *et al.*, 2012). The generally accepted notion that carbohydrates fuel behavioural activities that result in ecological dominance should benefit from more detailed reevaluation in other environments, and across the ant phylogeny.

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