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Functional traits and trophic ecology of Santa Cruz Island native ants

A thesis submitted in partial satisfaction of the requirements for the degree of Master's of  
Science

in

Biology

by

Jillian Kristine Schat

Committee in Charge:

Professor David Holway, Chair  
Professor Elsa Cleland  
Professor Carolyn Kurle

2018

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Chair

University of California, San Diego

2018

## DEDICATION

I would like to express my gratitude to the past and present members of the Holway Lab for their comradery and advice, to my friends and family for their compassion and wisdom, and to my best friend and partner Ryan Golden for his unwavering support and love; this thesis is dedicated to them.

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I would like to thank Dr. David Holway, my committee chair, and Ph.D. candidate Ida Naughton for their support, advice, and contributions to this work.

Chapter 1 is currently being prepared for submission for publication of the material. Dr. David Holway was the primary investigator, and co-author of this material along with Ida Naughton.

## ABSTRACT OF THE THESIS

Functional traits and trophic ecology of Santa Cruz Island native ants

by

Jillian Kristine Schat

Master's of Science in Biology

University of California, San Diego 2018

Professor David Holway, Chair

Functional traits are popular tool to assess functional ecology. Functional traits determine how an organism interacts with its community. The utility of functional traits has been well documented in plant and vertebrate systems but has not been as thoroughly applied to invertebrate systems. Morphology is a common functional trait used to predict ecology in vertebrate and plant models. This study tested the ability of morphology to predict trophic ecology of native ants from Santa Cruz Island. Trophic interactions represent a large portion of inter- and intraspecific

interactions within a community. Analyzing these interactions is key to understanding ecosystem functioning. To assess trophic ecology, I used stable isotope analysis of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  as well as predation and scavenging assays. To assess morphology, I measured 27 morphological traits from eight species of ant. The 10 most cited measurements were analyzed using linear regressions to assess the relationships between morphology and trophic ecology. Significant relationships exist between morphology and stable isotope values but not between morphology and predation or scavenging ability. The lack of relationship between morphology and predation or scavenging ability could be due to environmental conditions or due to morphology's inability to predict predation or scavenging behavior. In future works, I would perform phylogenetic corrections to account for relatedness between ant species and apply similar observational studies to other ant community assemblages.

## CHAPTER 1

### Introduction

Using functional traits to assess niche partitioning and community assembly has become increasingly popular (McGill et al. 2006; Liu et al. 2018). A functional trait is a characteristic that predicts a species' functional niche (McGill et al. 2006). Quantifying the relationship between functional traits and functional niches allows one to assess ecosystem functioning across species and habitats (McGill et al. 2006, Lawton 1999). The same species may occupy alternative functional niches depending on the local community structure, but the establishment of relationships between functional traits and functional niche will allow for the prediction of these alternative functional niches (Bello et al. 2010). While the relationships between functional traits and functional ecology have begun to be assessed in animals (Cornelissen et al. 2003), it is still not as widely used as called upon by the functional ecology community (Kraft, Valencia & Ackerly 2008). Morphology is a commonly cited functional trait (Kraft, Valencia & Ackerly 2008), capable of predicting functional ecology in plants (Cornelissen et al. 2003) and vertebrates (Norberg & Rayner 1987). This study aims to assess morphology's ability to predict trophic ecology, a crucial aspect of a species' functional niche.

Ants are an excellent model taxon to test morphology as a predictor of trophic ecology given their diverse diets (Kaspari 1996; Harrison & Breed 1987; Floren, Biun & Linsenmair 2002; Anderson & VanLaehoven 1996) and variation in morphological traits (Weiser & Kaspari 2006). Morphological traits of ants have been tested as functional traits (Gotwald 1978, Weiser & Kaspari 2006) and are examined here as presumed predictors of different aspects of trophic ecology. The physical constraints that morphology imposes on an organism act as an initial filter in trophic niche acquisition (Weiser & Kaspari 2006, Gibb & Parr 2013). Morphology can influence the type of

food an organism consumes (Gotwald 1978) and its relative effectiveness in obtaining that resource (Kaspari 1996).

Trophic interactions are one of the most common ecological interactions, making trophic position a particularly useful functional niche to examine. The trophic ecology of ants has been well studied (Fedlhaar, Gerhard & Bluethgen 2009; Hanna et al. 2016; Smith & Suarez 2010), but there is still a need to examine trophic ecology from a functional traits perspective (McGill et al. 2006). This venture has been initiated by some authors (Gibb & Parr 2013; Kaspari 1993; Donoso 2014 among others), and this study will build upon their work in the hopes of further determining the functional basis of morphological traits. I aim to accomplish this by testing for associations between morphological traits and ecological function (trophic position and foraging behavior). Because morphology influences ants' efficiency in obtaining food (Pearce-Duvet et al. 2011, Kaspari 1996), I predict that leg length will negatively correlate with trophic position (Weiser & Kaspari 2006), that cranial features – e.g., eye size, scape length, mandible length – will negatively correlate with trophic position (Gibb et al. 2015), and that overall size – body length & Weber's length – will negatively correlate with trophic position (Weiser & Kaspari 2006, Gibb et al. 2015) due to the need to compensate for relatively less efficient foraging. I test these predictions using an assemblage of native ants in California.

## Methods

### *Study System*

I conducted this study on Santa Cruz Island, Santa Barbara County, California. I conducted field work from June – August 2017. All study plots (n = 10) are centered in island scrub oak (*Quercus pacifica*) woodland and are circular with a radius of 10 m (314 m<sup>2</sup>). Plots were matched with respect to percent vegetation cover, number of mature *Q. pacifica* individuals, and the

composition of perennial vascular plants, which (aside from *Q. pacifica*) include the following: *Cercocarpus betuloides*, *Eriogonum arborescens*, *Heteromeles arbutifolia*, *Q. agrifolia*, and *Rhus integrifolia* (Hanna et al. 2015). Plots are separated from one another by > 500 m. Seven of the ten plots were established in 2010 as control plots for a long-term study examining the recovery of native ants following island-wide removal of the non-native Argentine ant (*Linepithema humile*) (Hanna et al. 2015). These seven plots support similar native ant assemblages to one another, with an average of 11 native ant species per plot, and no introduced ant species (Hanna et al. 2015). I added three plots in June 2017 that match the criteria of previously established plots above. GPS coordinates for all ten plots are listed in Appendix 1.1.

The island supports at least 32 native species of ant (Hanna et al. 2015, Naughton et al. 2014, Wetterer et al. 2000). Ant species collected on the plots in the present study include *Camponotus clarithorax*, *C. hyatti*, *C. maritimus*, *Crematogaster marioni*, *Formica moki*, *Monomorium ergatogyna*, *Pheidole hyatti*, *Polyergus vinosus*, *Solenopsis molesta*, and *Tapinoma sessile* (Table 1). *Camponotus clarithorax* was only collected on plot 7, and so excluded from analysis. *Polyergus vinosus* was also excluded from analysis because it is a social parasite of *F. moki* (Topoff & Zimmerli 1993). I collected ants by beating vegetation (Hanna et al. 2015), opening senescent oak apple galls (Araujo et al. 1995), searching along branches (Davidson 1997), and by examining leaf litter by hand (Donoso 2014).

#### *Stable Isotope Analysis*

I used an aspirator to collect specimens for isotope analysis and immediately placed them in plastic vials and then in a cooler with ice packs. All specimens were placed in a 0°C freezer within one hour after collection. I kept specimens frozen for at least 4 hours prior to further processing. In dimorphic species (e.g., *P. hyatti*), only individuals of the minor worker caste were

collected (Gibb & Parr 2013); majors in dimorphic species usually do not contribute to foraging (Mertl & Traniello 2009). In polymorphic species (e.g., *Camponotus* spp.), all worker castes were collected (Gibb & Parr 2013). While collecting ants, I also collected arthropod herbivores (e.g., sawfly and Lepidopteran larvae), arthropod predators (e.g. spiders and scorpions) from each plot.

To process samples for isotope analysis, herbivores and predators were left whole. For all ants I removed the petiole, post-petiole, and gaster because these body parts contain most of its digestive tract and thus recently consumed food; therefore, inclusion of the gaster could obscure the actual stable isotope ratio of the ant (Tillberg et al. 2006). I dried all arthropod specimens for 3 hours 70°C, homogenized material from dried specimen samples with respect to plot and ant species or consumer type (i.e., herbivore or predator) and stored each sample in 55 x 91 mm Bioquip End-Opening Glassine Envelopes in sealed glass jars with ¼ cup of Bioquip Products Indicating Silica Gel as desiccant until further processing (Smith & Suarez 2010). A homogenized mass of 0.5 – 1.5 mg of each sample was packed into Costech 5 x 9 mm tin capsules and sent to the University of California Davis Stable Isotope Facility where samples were analyzed with a Europa-Hydra 20/20 continuous flow IRMS (UC Davis Stable Isotope Facility).

I used  $\delta^{15}\text{N}$  to estimate relative trophic position of arthropods collected from study plots (Boecklen et al. 2011) but also considered  $\delta^{13}\text{C}$ .  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  are calculated as shown in Equation 1, Appendix 1.2. Because storage of arthropod samples in ethanol can corrupt  $\delta^{13}\text{C}$  data (Kaehler & Pakhomov 2001), samples used for isotope analysis were not stored in ethanol at any time.  $\delta^{13}\text{C}$  data have accompanied  $\delta^{15}\text{N}$  as a tool to gain information about trophic niche (Tillberg et al. 2006). In some cases,  $\delta^{13}\text{C}$  has been indicated to covary with  $\delta^{15}\text{N}$  and so possibly be indicative of trophic position (Smith & Suarez 2010). More commonly,  $\delta^{13}\text{C}$  is used to discern the type of primary resource – C3 or C4 plants – consumed by the organism (Heinrich, Weaver & Bell 2010). I also

estimated relative trophic position (TP) using Equation 2, Appendix 1.2. I calculated trophic position because it allows for the comparison of  $\delta^{15}\text{N}$  across study site by standardizing  $\delta^{15}\text{N}$  values according to the primary resources present at the study site (Post 2002). I test the relationship of  $\delta^{15}\text{N}$  and trophic position to see if this standardization is necessary for the ants collected in this study. Appendix 1.3 summarizes mean values for  $\delta^{15}\text{N}$ , trophic position,  $\delta^{13}\text{C}$  values, and trophic position of each ant species across study plots, as well as  $\delta^{15}\text{N}$  values and trophic position at each plot.

### *Morphometric analysis*

To measure morphometric traits of the common ant species on the island scrub oak woodlands plots, I collected ants from each plot in July 2017 and immediately placed them in 95% ethanol. These specimens were later point mounted to facilitate measurement. I used a dissecting microscope with a mounted micrometer accurate to 0.01 mm to estimate the size of 27 morphological traits (Appendix 1.4). To measure the eye length and eye width of *M. ergatogyna* and *S. molesta*, both ant species with minute workers, I used a mounted micrometer accurate to 1 nm. One to three workers of each species from each plot were measured. I calculated means of each measurement for each species, then averaged means across plots to achieve a species-wide estimate for each morphological trait (Appendix 1.4). In dimorphic species (e.g., *Pheidole hyatti*), I only measured minor workers (Gibb & Parr 2013); in polymorphic species (e.g., *Camponotus* spp.). A total of 223 ant workers were collected and measured.

Measurements were made relative to the ants' length by dividing each measurement by Weber's length from the same ant (Gibb & Parr 2013). Weber's length is the linear distance from the anterior edge of the pronotum to the posterior edge of the propodeum (Weiser & Kaspari 2006). Relativizing measurements was done prior to taking the means of measurements. Aside from



Weber's length, exceptions to this include the following: number of petiolar nodes, eye length and mandible length (which I divided by head length, not Weber's length), and eye width and mandible width (which I divided by head width, not Weber's length) (Kaspari 1993; Gibb & Parr 2013).

I examined recent publications on ants ( $n = 22$  studies) for the 10 most commonly used morphological traits. These traits include Weber's length, femur length, head width, head length, scape length, mandible length, leg length, eye length, polymorphism, and tibia length. In this way, my analysis tests whether or not morphological traits of presumed functional importance actually reflect ecological function (Burne, Hayward & Lester 2015). In addition to referencing literature, I performed a principle components analysis (Gibb & Parr 2013) and independent components analysis (both in R v 3.4.3) to determine which 10 traits contributed the most to variation in morphology (Appendix 1.5). Neither of these statistical methods produced multiple axes of variation given the high degree of correlation between morphological traits (Appendix 1.6).

#### *Predation and Scavenging Assays*

I used behavioral assays to assess the ability of each ant species to prey upon depredate and scavenge termites, a resource commonly consumed by ants. Individual baits used in these assays consisted of a plastic petri dish containing three termites (Oliviera et al. 1987), a damp paper towel, and a small amount of leaf litter collected from the plot being observed. Prior to the assays being performed, I collected termites from stands of mulefat (*Baccharis salicifolia*) adjacent to study plots. Termites used in predation baits were left alive, whereas termites used in the scavenging assays were freeze killed but thawed prior to use.

I prepared twenty predation baits and twenty scavenging baits for each assay. I evenly dispersed fifteen of each bait type on the ground in the plot, marked them with pin flags, and set them level with the top layer of the leaf litter. I fastened the remaining baits to the top surface of

the main branches of shrubs and trees in the plot 1 – 2 m from the ground. I observed ants walking easily on the tape; the tape provided a bridge to the baits and allowed for the inclusion of arboreal foragers (Davidson 1997). I monitored all baits continuously for 80 minutes. In my preliminary observations, ant activity peaked at or before 80 minutes, and no new interactions were seen at the baits after the peak in activity.

The ability of each ant species to prey upon and scavenge was estimated using the proportion of baits of each type discovered by different ant species. Discovery occurred when an ant made physical contact with a termite including but not limited to the following: touching the termite with antennae, or biting, chasing, or carrying the termite. Ants almost always consumed or removed the termite subsequent to discovery. Each plot received two rounds of behavioral assays because ants often exhibit bi-modal peaks of activity during the day (Briese & Macauley 1980). To capture both peaks of activity for each plot, I performed one behavioral assay in the morning and one in the afternoon. During the first round of assays, each plot received an assay either in the morning or in the evening with the time determined at random. During the second round of assays, whichever plots previously received assays in the mornings, now received assays in the evening, and vice versa. Morning and afternoon data were averaged for each plot. For the analysis of these data, I calculated the proportions of baits discovered by each ant species in each assay type (predation or scavenging) averaged across the two sampling periods on each plot.

The proportion of baits discovered in the predation or scavenging trials depends in part on the abundance of each ant species. Using colony count data collected from March - June 2017, I corrected for abundance by dividing each discovery proportion by the number of colonies of a given species on a given plot. Colony abundance on each plot was estimated by placing crumbs from Pecan Sandies (Keebler<sup>®</sup>) cookies in small piles 1 m apart throughout the entire plot. Cookie

baits with *S. molesta* present were representative of a nearby, singular *S. molesta* colony. I followed all other ant species that recruited to cookie baits back to their colony entrance to verify that the entrance was on the plot. I considered each colony entrance a separate colony. Because colony count data was only available for 7 of the 10 plots, only 7 plots were used for all analyses except paired *t*-tests to examine differences in predation and scavenging ability within each species. When conducting these comparisons between predation and scavenging ability, only species present during assays on five or more plots were used: *C. maritimus*, *F. moki*, *M. ergatogyna*, and *P. hyatti*.

### *Statistical Analysis*

The relationships between morphology and  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , and between morphology and predation and scavenging abilities are indicative of morphology's ability to predict trophic ecology. To assess morphology's reliability as a functional trait, I used simple linear regressions to test for associations between a putative functional trait and a measured ecological function ( $\delta^{15}\text{N}$ ,  $\delta^{13}\text{C}$ , predation ability, discovery ability). Most morphological traits measured were highly correlated with one another. A correlation matrix, with a Bonferroni correction for 10 comparisons, can be found in Appendix 1.6. Because morphological traits were so highly correlated, neither a principal components analysis nor an independent components analysis was appropriate to assist in variable reduction (Appendix 1.5).

I conducted additional analyses on different aspects of the stable isotope data. I used separate one-way ANOVAs to test for differences in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  among herbivores, predators and each ant species. A Tukey HSD was used as a multiple comparison procedure after each one-way ANOVA. I used a correlation to test the relationship between  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . Lastly, I used a linear regression to test the relationship between  $\delta^{15}\text{N}$  (predictor variable) and trophic position (response variable).

## Results

### *Stable Isotope Analysis*

$\delta^{15}\text{N}$  values differed among ants, herbivores, and predators (Fig. 1; one-way ANOVA:  $F_{9,73} = 29.32$ ,  $P < 0.00001$ ). Most ant species had  $\delta^{15}\text{N}$  values that were intermediate between herbivores and predators. Both *Camponotus* species had  $\delta^{15}\text{N}$  values not different from herbivores, whereas the  $\delta^{15}\text{N}$  value of *Solenopsis molesta* exceeded that of the predators (Fig. 1).  $\delta^{13}\text{C}$  values also differed among ants, herbivores, and predators (Fig. 2; one-way ANOVA:  $F_{9,73} = 17.27$ ,  $P < 0.00001$ ). Ants, herbivores, and predators exhibited a range  $\delta^{13}\text{C}$  values (-23 to -28) that would be expected for consumers occupying a plant community dominated by C3 plants (O'Leary 1988).  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of ants, herbivores and predators were uncorrelated ( $r^2 = -0.0063$ ,  $P = 0.48$ ). Trophic position increased linearly with  $\delta^{15}\text{N}$  values (Fig. 3; simple linear regression:  $F_{1,81} = 286.7$ ,  $P < 0.00001$ ,  $R^2 = 0.78$ ).

### *Morphometric Analysis*

Linear regressions showed significant relationships between almost all morphological traits (except worker polymorphism) and  $\delta^{13}\text{C}$  values (Table 2). Linear regressions showed significant relationships between several morphological traits (all but femur length, polymorphism, and tibia length) and  $\delta^{15}\text{N}$  and trophic positions (Table 3). Figure 4 summarizes the relationships between morphological traits and  $\delta^{15}\text{N}$  values for each species of ant. Figure 5 summarizes the relationships between morphological traits and  $\delta^{13}\text{C}$  values for each species of ant.

### *Predation and Scavenging Assays*

Discovery of termite baits in the predation assay increased with the number of colonies present plots (simple linear regression:  $F_{1,5} = 14.44$ ,  $P = 0.01$ ,  $R^2 = 0.69$ ), but no such relationship existed for the discovery of baits in the scavenging assay ( $F_{1,5} = 0.0072$ ,  $P > 0.05$ ). Predation and

scavenging abilities for each species are listed in Appendix 1.7. Neither predation nor scavenging ability varied with  $\delta^{15}\text{N}$  or trophic position (Table 3), and no morphological trait was associated with predation or scavenging (Table 4). Figure 6 shows the proportions of termite baits discovered by different ant species in the predation assay. Figure 7 shows the proportions of termite baits discovered by different ant species in the scavenging assay.

## Discussion

Isotope data (especially  $\delta^{15}\text{N}$  values) indicated the potential for trophic niche partitioning for at least some of the ants that occupy island scrub oak woodland. Some species (*C. maritimus* and *C. hyatti*) had  $\delta^{15}\text{N}$  values that were not different from herbivores, while others appear more carnivorous (*M. ergatogyna*, *T. sessile*, *P. hyatti* and *S. molesta*). The close relationship between trophic position and  $\delta^{15}\text{N}$  was expected given the similar habitat and spatial proximity of study plots. It seems evident from  $\delta^{13}\text{C}$  values that herbivores, ants and predators obtained resources from C3 based plants (O’Leary 1988), which is consistent with the notion that all ants foraged predominantly within island scrub oak habitat, a plant assemblage numerically dominated by C3 plants. Most morphological traits assessed predicted  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values, supporting the notion that these traits reflect function (Burne et al. 2015; Weiser & Kaspari 2006; Gibb et al. 2015). Morphology did not predict the number of baits discovered in the predation and scavenging assays, nor did the results of the predation or scavenging assays predict  $\delta^{15}\text{N}$  or  $\delta^{13}\text{C}$  values.

Variation in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  both depend on diet (DeNiro & Epstein 1980; O’Leary 1988), and studies on ants report interspecific variation with respect to stable isotope ratios (Tillberg et al, 2007; Menke et al. 2010; Feldhaar, Gebaur & Bluethgen 2010). The isotope ratios observed in this study revealed interspecific differences in  $\delta^{15}\text{N}$  that presumably reflect differences in diet. While arthropods also differed with respect to  $\delta^{13}\text{C}$ , all arthropods were foraging within C3

(presumably island scrub oak) habitat.  $\delta^{13}\text{C}$  values may be more useful as a tool to estimate foraging range than a tool to estimate trophic position. Other studies have used isotope values similarly (Lott, Meehan & Heath 2003) to estimate migratory patterns in birds. While ants are not known for migrating, a similar approach could be useful in patchy habitats.

Both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were predictable using morphological traits. This set of results supports the hypothesis that morphological traits reflect function (Gibb et al. 2015; Retana, Arnan & Cerda 2015; Silva & Brandao 2010) and can be used to predict trophic ecology. Smaller bodies, relatively smaller heads, relatively larger antennal scapes, mandibles, and legs all seem to contribute to higher  $\delta^{15}\text{N}$  values. This conjures the image of a small ant with larger cranial features, similar to *M. ergatogyna* or *P. hyatti*, both genera that are known for their predatory tendencies (Dowd & Kok 1981; Wilson 2005). Further studies of these morphological trends should include a more detailed analysis of foraging behavior associated with this body type. Morphological traits showed very high correlation with one another. While the trends above were significant, the strong relationships between morphological traits may indicate that the use of multiple morphological traits to predict trophic ecology may be unnecessary.

Behavior is often cited as a functional trait (Bihn, Gebaur & Brandl 2010), especially with respect to foraging strategy (Kaspari 1996; Gotwald 1978). The results of the predation and scavenging assays, however, indicated broad overlap among ant species with respect to their ability to discover termite baits. Saturating plots with termite baits might obscure interspecific differences in competitive ability (Savolainen & Vepsäläinen 1988). In light of the lack of interspecific differences in predation and scavenging ability, and that these behaviors did not vary with trophic position, it seems unsurprising that morphology was not predictive of foraging behavior.

Morphological traits often correlate with one another (Weiser & Kaspari 2006) as also seen in this study. It would be beneficial to continue searching for a diverse set of functional traits capable of predicting trophic ecology. Data such as caste polymorphism (Feener, Lighton & Bartholomew 1988), colony size, or dispersal ability (Noordwijk et al. 2015) could be additional traits to consider when predicting trophic ecology. One of the benefits of using functional traits to make predictions about functional niches concerns the ability to apply these predictions in unexamined systems (Lawton 1999; Bello et al. 2010). As the relationship between morphology and trophic ecology becomes better understood, the nuances of this association can be further analyzed. Adjusting for phylogeny, for example (Liu et al. 2016) could explain some of the trophic groupings found in Santa Cruz Island native ants. The ant species with the lowest  $\delta^{15}\text{N}$  values (*C. maritimus* and *C. hyatti*) are congeners, and other studies have found low values for these species as well (Tillberg et al. 2006). Analyzing relationships between functional traits and evolutionary history would deepen understanding of functional traits as well as provide valuable information about their ontogeny from an evolutionary perspective.

I would like to thank Dr. David Holway, my committee chair, and Ph.D. candidate Ida Naughton for their support, advice, and contributions to this work.

Chapter 1 is currently being prepared for submission for publication of the material. Dr. David Holway was the primary investigator, and co-author of this material along with Ida Naughton.

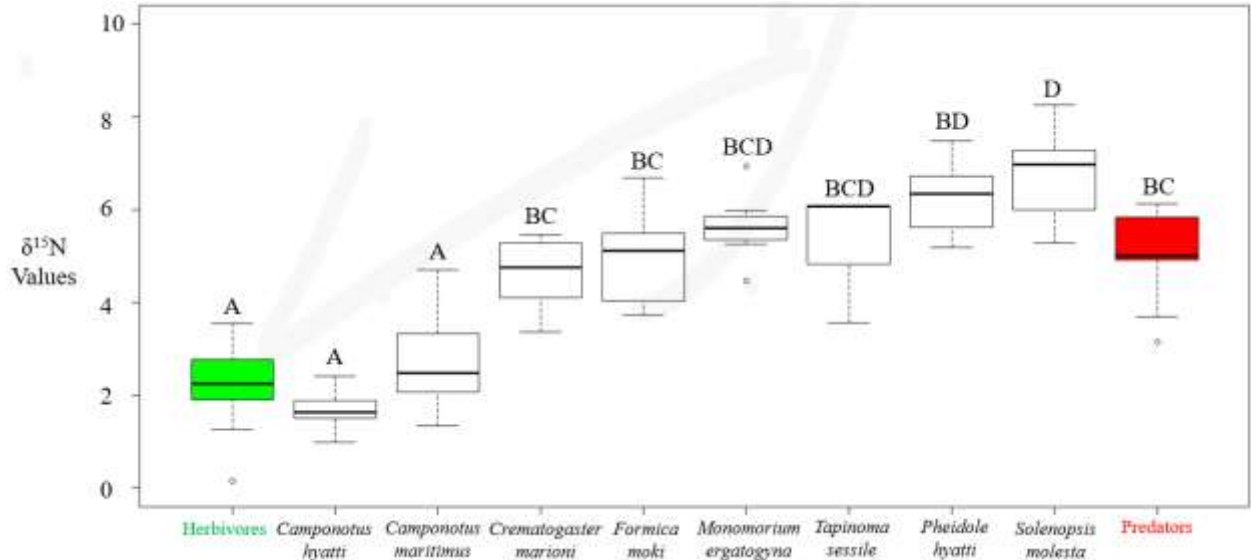


Figure 1  $\delta^{15}\text{N}$  values for ants, herbivores, and predators. Species with the same letter above boxplots represent statistically similar groups from Tukey HSD following one-way ANOVA.

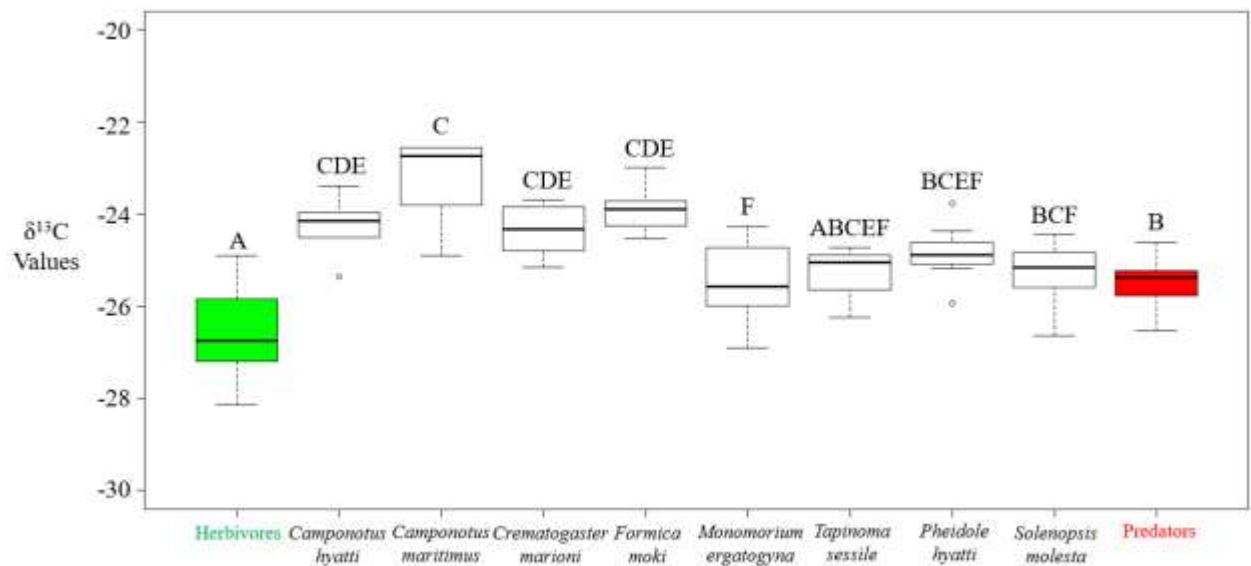


Figure 2  $\delta^{13}\text{C}$  values for ants, herbivores, and predators. Species with the same letter above boxplots represent statistically similar groups from Tukey HSD following one-way ANOVA.



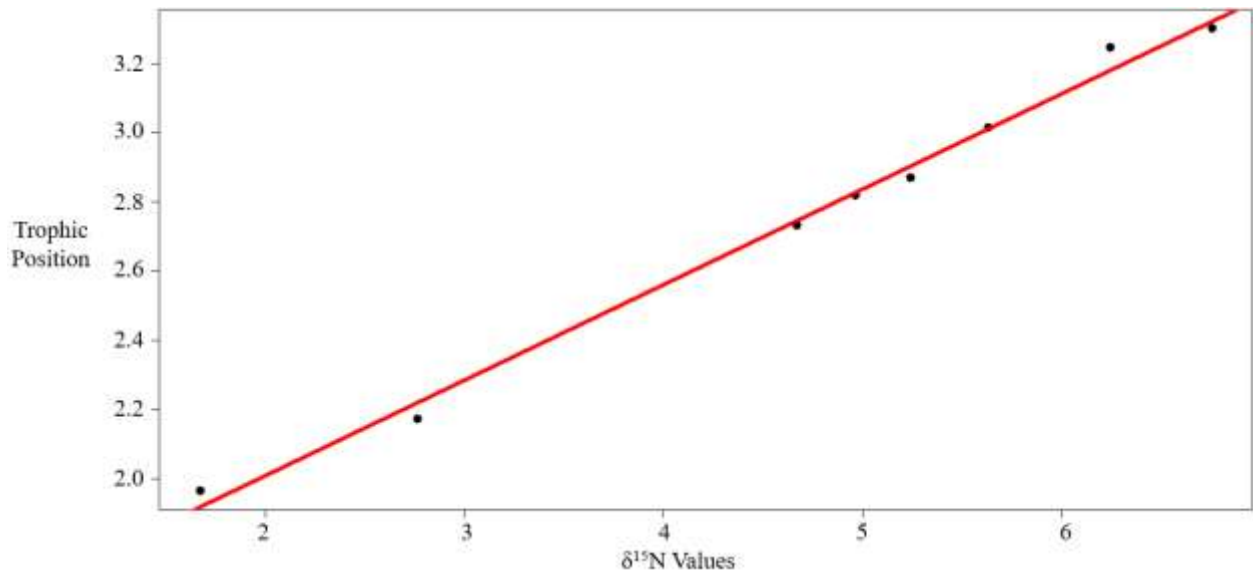


Figure 3 The relationship between  $\delta^{15}\text{N}$  and trophic position for the eight ant species in this study. Line is the least squares regression. Data points are means of individual ant species.

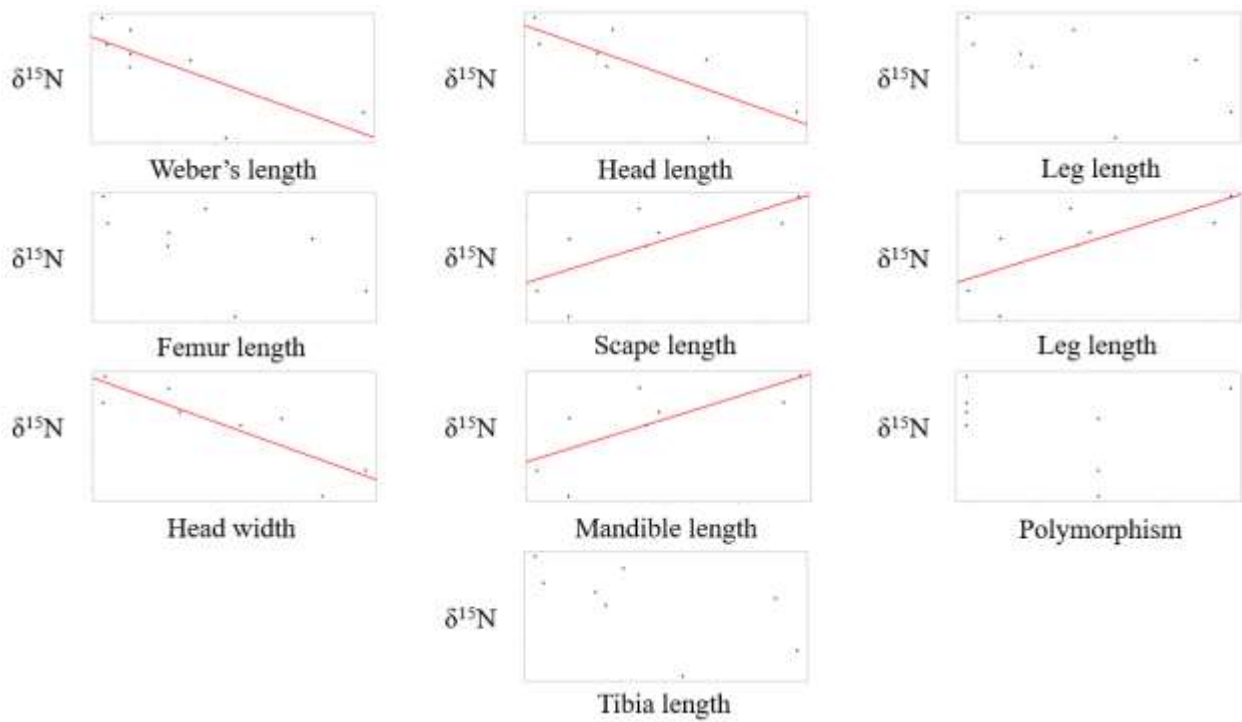


Figure 4 Linear regressions of  $\delta^{15}\text{N}$  and morphological traits. Lines show significant least square regressions. Data points are mean values of individual ant species.

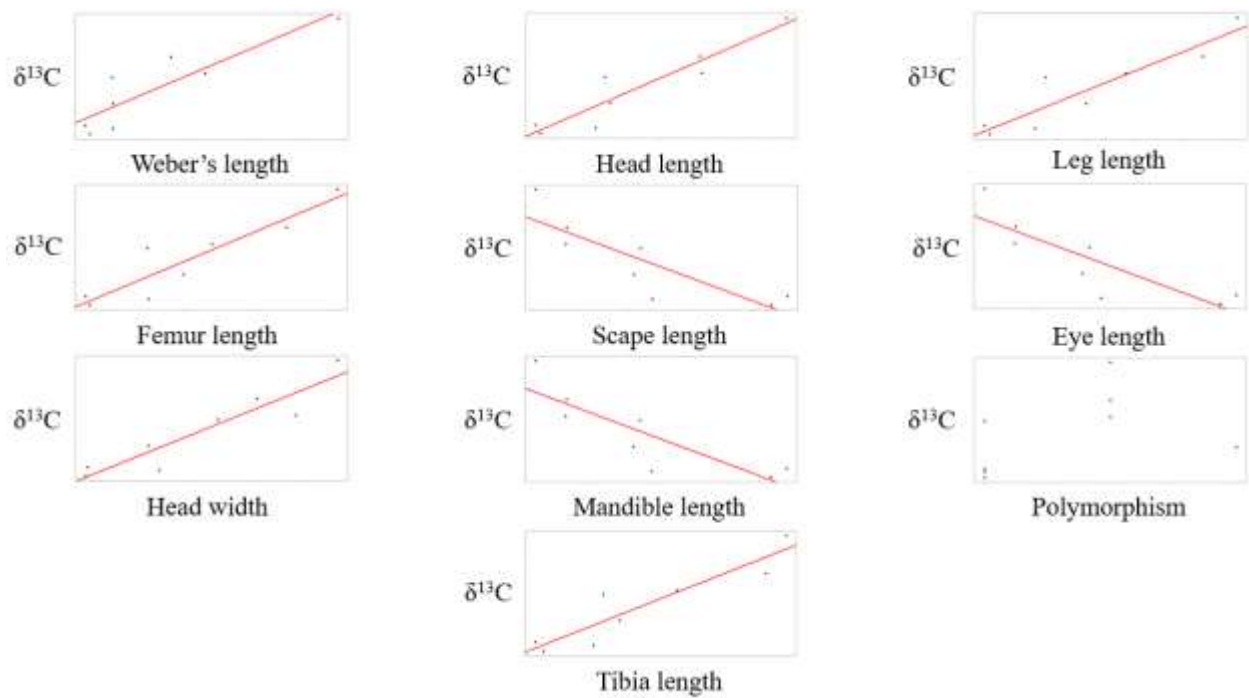


Figure 5 Linear regressions of  $\delta^{13}\text{C}$  and morphological traits. Lines show significant least square regressions. Data points are mean values of individual ant species.

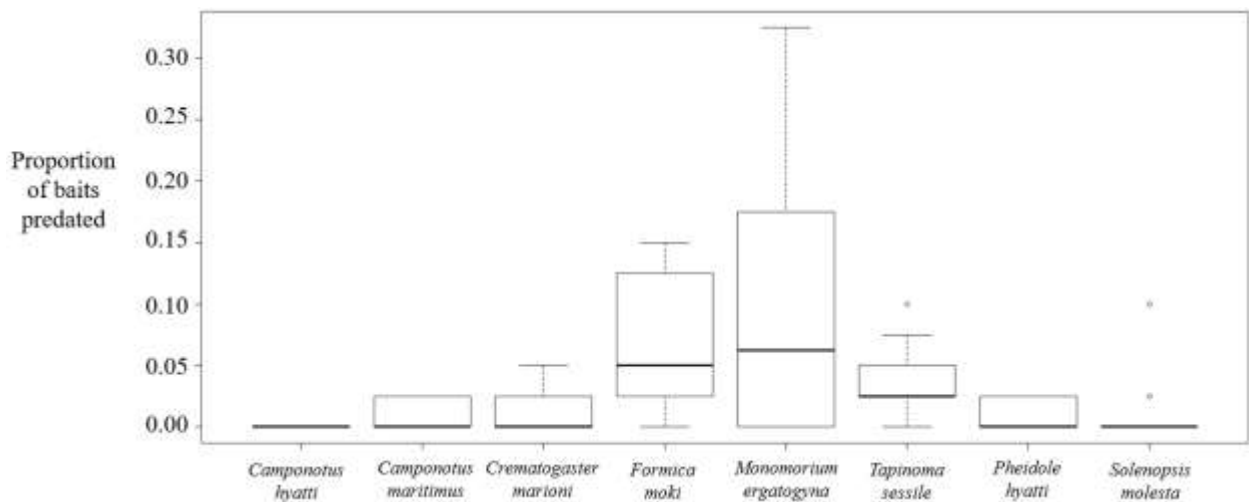


Figure 6 Proportion of baits discovered in the predation assay by each ant species across study plots.

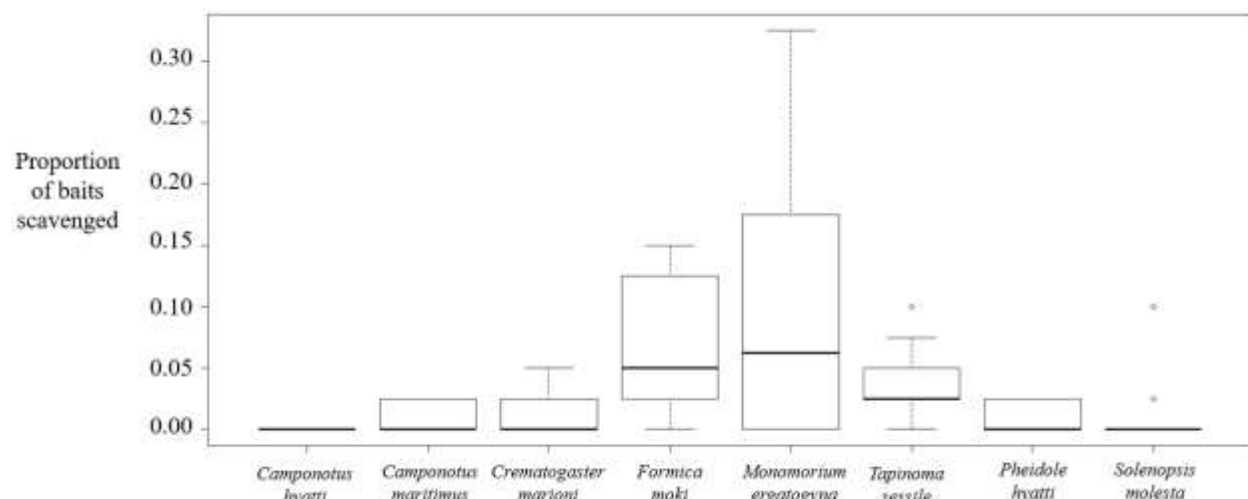


Figure 7 Proportion of baits discovered in the scavenging assay by each ant species across study plots.

Table 1 Species of ants collected in each study plot.

Species	Plot										Number of plots with a given ant species
	1	2	3	4	5	6	7	8	9	10	
<i>Camponotus maritimus</i>	X	X	X	X	X	X	X	X	X	X	10
<i>Crematogaster marioni</i>	X	X	X	X	X	X	X	X	X	X	10
<i>Formica moki</i>	X	X	X	X	X	X	X	X	X	X	10
<i>Monomorium ergatogyna</i>	X	X	X	X	X	X	X	X	X	X	10
<i>Pheidole hyatti</i>	X	X	0	X	X	0	X	0	0	X	6
<i>Solenopsis molesta</i>	0	X	X	X	X	X	X	X	0	X	8
<i>Tapinoma sessile</i>	0	X	0	0	0	0	X	0	0	X	3
Plot-level ant richness	5	7	5	6	6	5	7	5	4	9	

Table 2 Linear regressions between  $\delta^{13}\text{C}$  (response variable) and either morphometric traits or foraging behavior (predictor variables); (-) denotes unobtained values.

Morphometric	$\delta^{13}\text{C}$				
	F	df	P	R <sup>2</sup>	Slope
Weber's length	22.3	1,6	0.0033*	0.75	4.62
Femur length	33.9	1,6	0.0011*	0.82	1.20
Head width	39.9	1,6	0.00073*	0.85	2.17
Head length	43.5	1,6	0.00058*	0.86	1.56
Scape length	15.9	1,6	0.0072*	0.68	-4.55
Mandible length	15.9	1,6	0.0072*	0.68	-10.5
Leg length	34.7	1,6	0.0011*	0.83	0.390
Eye length	15.9	1,6	0.0072*	0.68	-344
Polymorphism	1.43	1,6	0.28	0.057	0.47
Tibia length	34.8	1,6	0.0011*	0.83	1.24
Foraging Behavior	F	df	P	R <sup>2</sup>	Slope
Frequency of predation	0.890	1,6	0.38	-0.016	0.12
Frequency of scavenging	0.430	1,6	0.54	-0.088	0.061

Table 3 Linear regressions between  $\delta^{15}\text{N}$  or trophic position (response variables) and morphometric traits or foraging behavior (predictor variables); (-) denotes unobtained values.

<i>Morphometric</i>	$\delta^{15}\text{N}$					Trophic Position				
	<i>F</i>	<i>df</i>	<i>P</i>	$\text{R}^2$	slope	<i>F</i>	<i>df</i>	<i>P</i>	$\text{R}^2$	slope
Weber's length	8.8	1,6	0.025*	0.53	-8.6	10	1,6	0.019*	0.56	-2.5
Femur length	3.7	1,6	0.10	0.28	-1.7	3.9	1,6	0.096	0.29	-0.49
Head width	18	1,6	0.0053*	0.71	-4.3	19	1,6	0.0045*	0.72	-1.2
Head length	9.7	1,6	0.021*	0.56	-2.8	10	1,6	0.019*	0.57	-0.79
Scape length	7.1	1,6	0.037*	0.47	8.5	6.9	1,6	0.039*	0.46	2.3
Mandible length	7.1	1,6	0.037*	0.47	20	6.9	1,6	0.039*	0.46	5.4
Leg length	3.8	1,6	0.098	0.29	-0.56	4.0	1,6	0.094	0.30	-0.16
Eye length	7.1	1,6	0.037*	0.47	640	6.9	1,6	0.039*	0.46	180
Polymorphism	0.26	1,6	0.63	-0.11	-0.47	0.14	1,6	0.72	-0.14	-0.10
Tibia length	4.0	1,6	0.092	0.30	-1.8	4.2	1,6	0.085	0.32	-0.51
<i>Foraging Behavior</i>	<i>F</i>	<i>df</i>	<i>P</i>	$\text{R}^2$	slope	<i>F</i>	<i>df</i>	<i>P</i>	$\text{R}^2$	slope
Frequency of predation	0.046	1,6	0.84	-0.16	0.014	0.041	1,6	0.85	-0.16	0.046
Frequency of scavenging	0.040	1,6	0.85	-0.16	0.0089	0.035	1,6	0.86	-0.16	0.030

Table 4 Linear regressions between predation and scavenging (response variables) and morphometric traits (predictor variables); (-) denotes unobtained values.

<i>Morphometric</i>	Predation					Scavenging				
	<i>F</i>	<i>df</i>	<i>P</i>	$\text{R}^2$	slope	<i>F</i>	<i>df</i>	<i>P</i>	$\text{R}^2$	slope
Weber's length	0.23	1,6	0.65	-0.12	0.34	0.12	1,6	0.74	-0.14	0.17
Femur length	2.0	1,6	0.21	0.13	0.22	1.4	1,6	0.27	0.060	0.14
Head width	0.25	1,6	0.64	-0.12	0.16	0.13	1,6	0.73	-0.14	0.081
Head length	0.73	1,6	0.43	-0.040	0.18	0.46	1,6	0.51	-0.078	0.11
Scape length	0.51	1,6	0.50	-0.075	-0.50	0.37	1,6	0.56	-0.099	-0.30
Mandible length	0.51	1,6	0.50	-0.075	-1.16	0.37	1,6	0.56	-0.099	-0.70
Leg length	2.41	1,6	0.17	0.17	0.075	1.7	1,6	0.24	0.092	0.046
Eye length	0.51	1,6	0.50	-0.075	-38	0.37	1,6	0.56	-0.099	-23
Polymorphism	0.69	1,6	0.44	-0.047	0.12	0.37	1,6	0.57	-0.099	0.061
Tibia length	2.7	1,6	0.15	0.19	0.25	2.0	1,6	0.21	0.12	0.16

## APPENDIX

### Appendix 1.1 GPS coordinates of study plots.

Plot	Latitude	Longitude
1	33°99'32.22" N	-119°69'43.68" W
2	33°99'31.77" N	-119°68'59.98" W
3	33°99'61.10" N	-119°63'99.74" W
4	33°98'86.69" N	-119°68'42.59" W
5	33°59'57.12" N	-199°43'30.31" W
6	33°59'43.87" N	-119°38'12.89" W
7	33°59'52.94" N	-119°43'12.83" W
8	33°98'96.93" N	-199°71'10.97" W
9	34°00'03.78" N	-119°73'51.10" W
10	33°99'27.48" N	-119°68'64.54" W

### Appendix 1.2

Equation 1  $R_{\text{sample}}$  is the ratio of heavy to light isotopes present in the sample.  $R_{\text{standard}}$  represents an internationally used standard of heavy to light isotope ratio (Deniro & Epstein 1980; O'Leary 1988).

$$\delta = \left( \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right) * 1000$$

Equation 2 TP is an estimation of carnivory in an organism's diet. A relatively higher trophic position indicates a larger portion of the organism's diet is carnivorous (Roeder & Kaspari 2017).  $\lambda$  denotes the trophic position of the lowest trophic level (e.g. autotrophs = 1) (Post 2002). In this analysis, the lowest trophic position is occupied by herbivores, so  $\lambda = 2$ .  $\Delta N$  is the standard assumed  $^{15}\text{N}/^{14}\text{N}$  enrichment per trophic level of 3.4‰ (Post 2002).

$$TP = \lambda + \frac{\delta^{15}\text{N}(\text{ant}) - \delta^{15}\text{N}(\text{base})}{\Delta N}$$

Appendix 1.3 Arithmetic means  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  for herbivores, predators, and ants, and mean relative trophic positions and  $\delta^{15}\text{N}$  across study plots and at each plot. Empty spaces (-) represent unobtained data.

Species	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	Average TP	Trophic Position at Each Plot									
				1	2	3	4	5	6	7	8	9	10
Known herbivores	-26.59	2.18	2	2	2	2	2	2	2	2	2	2	2
Known predators	-25.48	4.97	2.84	3.04	3.04	2.84	-	3.07	2.84	3.03	2.68	2.64	2.37
<i>Camponotus maritimus</i>	-23.17	2.77	2.17	2.71	1.95	2.07	1.79	2.11	2.68	2.69	1.94	1.51	2.27
<i>Crematogaster marioni</i>	-24.34	4.67	2.73	3.16	2.43	2.71	2.79	2.93	2.85	2.85	2.52	2.67	2.42
<i>Formica moki</i>	-23.93	4.97	2.82	3.46	2.34	3.36	2.69	2.82	2.94	2.95	2.57	2.22	2.85
<i>Monomorium ergatogyna</i>	-25.45	5.63	3.02	3.61	2.89	2.94	2.87	2.94	2.97	3.35	2.68	2.88	3.01
<i>Pheidole hyatti</i>	-24.85	6.24	3.25	3.48	2.96	-	3.05	3.83	-	3.38	-	3.00	3.03
<i>Solenopsis molesta</i>	-25.28	6.75	3.30	-	2.87	3.53	3.19	3.18	3.47	3.74	3.10	-	3.34
<i>Tapinoma sessile</i>	-25.34	5.24	2.87	-	3.03	-	-	-	-	3.10	-	-	2.49
Species	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	Average TP	$\delta^{15}\text{N}$ at Each Plot									
				1	2	3	4	5	6	7	8	9	10
Known herbivores	-26.59	2.18	2	0.15	2.56	2.07	2.77	1.27	2.16	2.34	3.54	3.00	1.91
Known predators	-25.48	4.97	2.84	3.69	6.13	4.94	-	4.92	5.01	5.83	5.86	5.19	3.15
<i>Camponotus maritimus</i>	-23.17	2.77	2.17	2.57	2.41	2.32	2.06	1.65	4.46	4.70	3.23	1.35	2.81
<i>Crematogaster marioni</i>	-24.34	4.67	2.73	4.10	4.03	4.49	5.45	4.42	5.04	5.23	5.31	5.28	3.36
<i>Formica moki</i>	-23.93	4.97	2.82	5.12	3.72	6.69	5.13	4.03	5.35	5.56	5.49	3.74	4.80
<i>Monomorium ergatogyna</i>	-25.45	5.63	3.02	5.61	5.60	5.27	5.78	4.47	5.44	6.94	5.86	5.98	5.35
<i>Pheidole hyatti</i>	-24.85	6.24	3.25	5.19	5.83	-	6.34	7.47	-	7.05	-	6.41	5.42
<i>Solenopsis molesta</i>	-25.28	6.75	3.30	-	5.54	7.26	6.81	5.28	7.14	8.26	7.30	-	6.45
<i>Tapinoma sessile</i>	-25.34	5.24	2.87	-	6.08	-	-	-	-	6.07	-	-	3.57

Appendix 1.4 Arithmetic means of each morphological trait measured for each species in millimeters. All measurements were taken at the widest point of the morphological feature. Polymorphism was measured such that 1 = monomorphic, 2 = dimorphic, 3 = polymorphic. Eye position is calculated as the distance from the mandible to the beginning of the eye divided by the head length (Kaspary 1993). Eye separation is calculated as the distance between eyes at the nearest point divided by head width (Bihn, Gebaur & Brandl 2010). Traits used in this study are indicated with \*.

Morphometric	<i>Camponotus hyatti</i>	<i>Camponotus maritimus</i>	<i>Crematogaster marioni</i>	<i>Formica moki</i>	<i>Monomorium ergatogyna</i>	<i>Pheidole hyatti</i>	<i>Solenopsis molesta</i>	<i>Tapinoma sessile</i>	Example from literature
Body length	1.43	1.16	1.72	1.52	1.80	1.72	1.82	1.72	Donoso 2014
Weber's length*	1.02	1.26	0.85	0.96	0.81	0.85	0.8	0.85	Arnan, Cerda & Retana 2014
Pronotum width	0.20	0.16	0.24	0.21	0.25	0.24	0.26	0.24	Silva & Brandao 2010
Pronotum length	0.23	0.18	0.27	0.24	0.29	0.27	0.29	0.27	Kaspary 1993
First gaster segment length	0.33	0.27	0.40	0.36	0.42	0.40	0.42	0.40	Gibb et al. 2015
Petiole length	0.20	0.17	0.25	0.22	0.26	0.25	0.26	0.25	Gibb et al. 2015
Petiole width	0.12	0.09	0.14	0.12	0.15	0.14	0.15	0.14	Silva & Brandao 2010
Petiole height	0.13	0.10	0.15	0.14	0.16	0.15	0.16	0.15	Silva & Brandao 2010
Number of petiole nodes	1	1	2	1	2	2	2	1	Burne et al. 2015
Femur length*	1.16	1.63	0.87	1.77	0.42	1.16	0.39	0.88	Bihn, Gebaur & Brandl 2010
Tibia length*	1.09	1.43	0.76	1.75	0.33	0.88	0.27	0.69	Liu et al. 2016
Tarsus length	1.50	1.78	0.94	2.13	0.53	1.49	0.50	0.75	Gibb et al. 2013
Total leg length*	3.76	4.84	2.57	5.65	1.28	3.53	1.15	2.31	Gotwald 1978
Head width*	1.17	1.33	0.89	1.03	0.40	0.63	0.41	0.67	Gibb et al. 2015
Clypeal length	0.053	0.04	0.08	0.05	0.14	0.08	0.15	0.09	Pierce-duvet, Elemans & Feener 2011
Head length*	1.42	1.89	0.89	1.41	0.54	0.92	0.51	0.84	Feener, Lighton & Bartholomew 1988
Scape length*	0.20	0.15	0.32	0.2	0.53	0.31	0.56	0.34	Liu et al. 2016

Appendix 1.4 Arithmetic means of each morphological trait measured for each species in millimeters. All measurements were taken at the widest point of the morphological feature. Polymorphism was measured such that 1 = monomorphic, 2 = dimorphic, 3 = polymorphic. Eye position is calculated as the distance from the mandible to the beginning of the eye divided by the head length (Kaspari 1993). Eye separation is calculated as the distance between eyes at the nearest point divided by head width (Bihn, Gebaur & Brandl 2010). Traits used in this study are indicated with \*.

Morphometric	<i>Camponotus hyatti</i>	<i>Camponotus maritimus</i>	<i>Crematogaster marioni</i>	<i>Formica moki</i>	<i>Monomorium ergatogyna</i>	<i>Pheidole hyatti</i>	<i>Solenopsis molesta</i>	<i>Tapinoma sessile</i>	Example from literature
Mandible length*	0.09	0.06	0.14	0.09	0.23	0.13	0.24	0.15	Parr et al. 2017
Mandible width	0.25	0.22	0.33	0.29	0.73	0.47		0.44	Silva & Brandao 2010
Eye position	0.34	0.39	0.33	0.31	0.30	0.15	0.39	0.20	Kaspari 1993
Eye separation	0.63	0.64	0.73	0.62	0.75	0.65	0.84	0.58	Bihn, Gebaur & Brandl 2010
Distance between eyes	0.73	0.83	0.65	0.63	0.30	0.41	0.34	0.39	Gibb & Parr 2013
Polymorphism*	2	2	1	2	1	3	1	1	Burne et al. 2015
Eye length*	0.002	0.002	0.004	0.003	0.007	0.004	0.007	0.004	Weiser & Kaspari 2006
Eye width	0.002	0.002	0.003	0.003	0.007	0.004	0.007	0.004	Weiser & Kaspari 2006
Petiole volume (mm <sup>3</sup> )	0.03	0.10	0.02	0.05	0.005	0.007	0.003	0.002	
Eye area (mm <sup>2</sup> )	0.07	0.13	0.03	0.11	4.79E-05	0.02	1.04E-5	0.02	



Appendix 1.5 Principal components analysis of all morphological traits from all species of ant.

	Principal Component 1	Principal Component 2	Principal Component 3
<i>Eigenvalues</i>	24.2	5.29	0.99
<i>Eigenvectors</i>			
Body length	0.90	-0.42	-0.04
Weber's length	-0.77	0.61	0.04
Pronotum width	0.90	-0.42	-0.04
Pronotum length	0.90	-0.42	-0.04
First gaster segment length	0.90	-0.42	-0.04
Petiole length	0.90	-0.42	-0.04
Petiole width	0.90	-0.42	-0.04
Petiole height	0.90	-0.42	-0.04
Number of petiolar nodes	0.77	0.14	0.38
Femur length	-0.97	-0.15	0.13

Appendix 1.6 Correlation matrix of the 10 morphological traits used for analysis following a Bonferroni correction ( $\alpha_0 = 0.05/10$  traits =  $\alpha = 0.005$ ).

	Weber's length	Femur length	Head width	Head length	Scape length	Mandible length	Leg length	Eye length	Poly-morphism	Tibia length
Weber's length	N/A	0.13	0.05	0.1	0.05	0.16	0.15	0.07	0.5	0.12
Femur length	0.13	N/A	2.5E-4*	6.6E-6*	8.7E-6*	1E-7*	2.2E-4*	1.4E-5*	0.071	7.7E-9*
Head width	0.05	2.5E-4*	N/A	1.3E-7*	2E-3*	1.9E-4*	2.2E-4*	3E-5*	0.22	1.1E-4*
Head length	0.1	6.6E-6*	1.3E-7*	N/A	4.9E-4*	2.6E-6*	4.7E-6*	2.9E-5*	0.013	3.3E-6*
Scape length	0.05	8.7E-6*	2E-3*	4.9E-4*	N/A	4.2E-4*	3.1E-5*	9.3E-5*	0.054	3.7E-4*
Mandible length	0.16	1E-7*	1.9E-4*	2.6E-6*	4.2E-4*	N/A	3.8E-7*	1.2E-4*	0.06	1.1E-6*
Leg length	0.15	2.2E-4*	2.2E-4*	4.7E-6*	3.1E-5*	3.8E-7*	N/A	1.6E-5*	0.06	7.5E-10*
Eye length	0.07	1.4E-5*	3E-5*	2.9E-5*	9.3E-5*	1.2E-4*	1.6E-5*	N/A	0.14	3.6E-6*
Poly-morphism	0.5	0.071	0.22	0.013	0.054	0.06	0.06	0.14	N/A	0.1
Tibia length	0.12	7.7E-9*	1.1E-4*	3.3E-6*	3.7E-4*	1.1E-6*	7.5E-10*	3.6E-6*	0.1	N/A

Appendix 1.7 Proportion of predation and scavenging baits visited by each species of ant with and without controlling abundance.

Species	Predation	Scavenging	t	df	P
Raw proportions					
<i>Camponotus maritimus</i>	0.075	0.025	-0.36	9	0.73
<i>Crematogaster marioni</i>	0.050	0.025	-	-	-
<i>Formica moki</i>	0.35	0.33	0.72	9	0.49
<i>Monomorium ergatogyna</i>	0.50	0.45	0.32	9	0.76
<i>Pheidole hyatti</i>	0.23	0.15	2.25	9	0.05*
<i>Solenopsis molesta</i>	0.075	0.025	-	-	-
<i>Tapinoma sessile</i>	0	0.025	-	-	-
Per colony proportions					
<i>Camponotus maritimus</i>	0.26	0.17	-0.36	9	0.73
<i>Crematogaster marioni</i>	0.031	0.016	-	-	-
<i>Formica moki</i>	0.79	0.57	1.00	9	0.34
<i>Monomorium ergatogyna</i>	0.31	0.28	0.68	9	0.51
<i>Pheidole hyatti</i>	0.21	0.14	2.25	9	0.051
<i>Solenopsis molesta</i>	0.017	0.0060	-	-	-
<i>Tapinoma sessile</i>	0	0.086	-	-	-

## REFERENCES

- Anderson, G.; VanLaehoven, S. "Initial studies on insect succession on carrion in southwestern British Columbia." *Journal of Forensic Sciences*, JFSCA, Vol. 41, No. 4, July 1996, pp. 617-625.
- Araujo, L. M.; Lara, A. C. F.; Fernandes, G. W. "Utilization of *Apion* sp. (Coleoptera Apionidae) galls by an ant community in southeastern Brazil." *Tropical Zoology*, Vol. 8:2, 1995, pp. 319-324.
- Arnan, X; Cerda, X; Retana, J. "Ant functional responses along environmental gradients." *Journal of Animal Ecology*, Vol. 83, 2014, pp. 1398-1408.
- de Bello, F; Lavorel, S.; Diaz, S.; Harrington, R.; Cornelissen, J.; Bardgett, R.; Berg, M.; Cipriotti, Pablo; F., Christian; H., Daniel; Martins da silva, P.; Potts, S. G.; Sandin, L.; Sousa, J. P.; Storkey, J.; Wardle, D. A.; Harrison, P. A. "Towards an assessment of multiple ecosystem processes and services via functional traits." *Biodiversity Conservation*, Vol. 19, 2010, pp. 2873-2893.
- Boecklen, W. J.; Yarnes, C. T.; Cook, B. A.; Avis, J. C. "On the use of stable isotopes in trophic ecology." *Annual Review Ecol. Evol. Syst.* Vol. 42, 2011, pp. 411-440.
- Bihn, J. H.; Gebaur, G.; Brandl, R. "Loss of functional diversity of ant assemblages in secondary tropical forests." *Ecology*, Vol. 91(3), 2010, pp. 782-792.
- Burne, A. R.; Hayward, J.; Lester, P. J. "Density-dependent effects of an invasive wasp on the morphology of an endemic New Zealand ant." *Biological Invasions*, Vol. 17, 2015, pp. 327-335.
- Briese, D. T.; Macauley, B. J. "Temporal structure of an ant community in semi-arid Australia." *Australian Journal of Ecology*, Vol. 5, 1980, pp. 121-134.
- Cornelissen, J. H. C.; Lavorel, S.; Garnier, E.; Diaz, S.; Buchmann, N.; Gurvich, D. E.; Reich, P. B.; Steege, H. ter; Morgan, H. D.; van der Heijden, M. G. A.; Pausas, J. G.; Poorter, H. "A handbook of protocols for standardized and easy measurement of plant functional traits worldwide." *Australian Journal of Botany*, Vol. 51, 2003, p. 335-380.

Davidson, DW. "The role of resource imbalances in the evolutionary ecology of tropical arboreal ants." *Biological Journal of the Linnean Society*, Vol. 61, 1997, pp. 153-181.

Davidson, DW; Cook, SC.; Snelling, RR. "Liquid-feeding performances of ants (Formicidae): ecological and evolutionary implications." *Oecologia*, Vol. 139, 2004, 255-266.

DeNiro, M. J.; Epstein, S. "Influence of diet on the distribution of nitrogen isotopes in animals." *Geochimica et Cosmochimica*, Vol. 45, 1980, pp. 341-351.

Donoso, D. A. "Assembly mechanisms shaping tropical litter ant communities." *Ecography*, Vol. 37, 2014, pp. 490-499.

Dowd, P. F.; Kok, L. T. "Predators of *Rhinocyllus conicus* (Coleoptera: Curculionidae) in Virginia." *Environmental Entomology*, Vol. 10, Issue 1, 1981, pp. 136-138.

Feldhaar, H.; Gebauer, G.; Bluethgen, N. "Stable isotopes: past and future in exposing secrets of ant nutrition (Hymenoptera: Formicidae)." *Myrmecological News*, Vol. 13, 2009, pp. 3-13.

Feener Jr., D. H.; Lighton, J. R. B.; Bartholomew, G. A. "Curvilinear allometry, energetics and foraging Ecology: a comparison of leaf-cutting ants and army ants." *British Ecological Society*, Vol. 2, No. 4, 1988, pp. 509-520.

Floren, A.; Biun, A.; Linsenmair, K. E.. "Arboreal ants as key predators in tropical lowland rainforest trees." *Oecologia*, Vol. 131, 2002, pp. 137-144.

Gibb, H.; Stoklosa, J.; Warton, D. I.; Brown, A. M.; Andrew, N. R.; Cunningham, S. A. "Does morphology predict trophic position and habitat use of ant species and assemblages?" *Oecologia*, Vol. 177, 2015, pp. 519-531.

Gibb, H.; Parr, C. L. "Does structural complexity determine the morphology of assemblages? An experimental test on three continents." *PLOS One*, Vol. 8(5), 2013.

Gotwald Jr., W. H. "Trophic ecology and adaptation in tropical old world ants of the subfamily dorylinae (Hymenoptera: Formicidae)." *Biotropica*, Vol. 10, No. 3, 1978, pp. 161-169.

Harrison, J. M.; Breed, M. D. “Temporal learning in the giant tropical ant, *Paraponera clavate*.” *Physiological Entomology*, Vol. 12, 1987, pp. 317-320.

Hanna, C.; Naughton, I.; Boser, C.; Holway, David. “Testing the effects of ant invasions on non-ant arthropods with high-resolution taxonomic data.” *Ecological Application*. Vol. 25, No. 7, 2015, 1841-1850.

Hanna, C.; Naughton, I.; Boser, C.; Holway, D. “Aphid-tending ants on introduced fennel: can resources derived from non-native plants alter the trophic position of higher-order consumers?” *Ecological Entomology*, 2016.

Heinrich, K.; Weaver, R. J.; Bell, H. A. “Determining the source of house flies (*Musca domestica*) using stable isotope analysis.” *Pest Management Science*, Vol. 68, 2010, pp. 31-37.

Kaehler, S.; Pakhomov, E. A. “Effects of storage and preservation on the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures of selected marine organisms.” *Marine Ecology Progress Series*, Vol. 219, 2001, pp. 299-304.

Kaspari, M. “Body size and microclimate use in Neotropical granivorous ants.” *Oecologia*, Vol. 96, 1993, pp. 500-507.

Kaspari, M. “Worker size and seed size selection by harvester ants in a Neotropical forest.” *Oecologia*, Vol. 105, 1996, pp. 397-404

Kraft, N. J. B.; Valencia, R.; Ackerly, D. D. “Functional traits and niche-based tree community assembly in an amazonian forest.” *Science*, Vol. 322, 2008 pp. 580-582.

Lawton, J. H. “Are there general laws in ecology.” *Oikos*, Vol. 84, No. 2, 1999, pp. 177-192.

Liu, C.; Guenard, B.; Blanchard, B.; Peng, Y.; Economo, E. P. “Reorganization of taxonomic, functional, and phylogenetic ant biodiversity after conversion to rubber plantation.” *Ecological Monographs*, Vol. 86(2), 2016, pp. 215-227.

Liu, J.; Wilson, M.; Hu, G.; Liu, J.; Wu, J.; Yu, M. “How does habitat fragmentation affect the biodiversity and ecosystem functioning relationship?” *Landscape Ecology*, Vol. 33, 2018, pp. 341-352.

Lott, C. A.; Meehan, T., D.; Heath, J. A. “Estimating the latitudinal origins of migratory birds using hydrogen and sulfur stable isotopes in feathers: influence of marine prey base.” *Oecologia*, Vol. 134, 2003, pp. 505-510.

McGill, B. J.; Enquist, B. J.; Weiher, E.; Westoby, M. “Rebuilding community ecology from functional traits.” *TRENDS in Ecology and Evolution*, Vol. 21, No. 4, 2006, pp. 178-185.

Menke, S. B.; Suarez, A. V.; Tillberg, C. V.; Chou, C. T.; Holway, D. A. “Trophic ecology of the invasive argentine ant: spatio-temporal variation in resource assimilation and isotopic enrichment.” *Oecologia*, Vol. 164, 2010, pp. 763-771.

Mertl, A. L.; Traniello, J. F. A.; “Behavioral evolution in the major worker subcaste of twig-nesting pheidole.” *Behavioral Ecology and Sociobiology*, Vol. 63, No. 10, 2009, pp. 1411-1426.

Naughton, I.; Caterino, M. S.; Hanna, C.; Holway, D. “Contributions to an arthropod inventory of Santa Cruz Island, California.” *Monographs of the Western North American Naturalist*, Vol. 7(1), 2014, pp. 297-305.

van Noordwijk, C. G. E. (Toos); Verberk, W. C. E. P.; Turin, H.; Heijerman, T.; Alders, K.; Dekoninck, W.; Hannig, K.; Regan, E.; McCormack, S.; Brown, M. J. F.; Remke, E.; Siepel, H.; Berg, M. P.; Bonte, D.. “Species-area relationships are modulated by trophic rank, habitat affinity, and dispersal ability.” *Ecology*, Vol. 96(2), 2015, pp. 518-531.

O’Leary, M. “Carbon isotopes in photosynthesis.” *BioScience*, Vol. 38, No. 5, 1988, pp. 328-336.

Oliveira, P. S.; Oliveira-Filho, A. T.; Cintra, R. “Ant foraging on ant-inhabited *Triplaris* (Polygonaceae) in western Brazil: a field experiment using live termite-baits.” *Journal of Tropical Ecology*, Vol. 3, 1987, pp. 193-200.

Parr, C. L.; Dunn, R. R.; Sanders, N. J.; Weiser, M.I D.; Photakis, M.; Bishop, T. R.; Fitzpatrick, M. C.; Arnan, X.; Baccaro, F.; Brandao, C. R. F.; Chick, L.; Donoso, D. A.; Fayle, T. M.; Gomez, C.; Grossman, B.; Munyai, T. C.; Pacheco, R.; Retana, J.; Robinson, A.; Sagata, K.; Silva, R. R.; Tista, M.e; Vasconcelos, H.; Yates, M.; Gibb, H. “*GlobalAnts*: a new database on the geography of ant traits (Hymenoptera: Formicidae).” *Insect Conservation and Diversity*, Vol. 10, 2017, pp. 5-20.

Pearce-Duvet, J. M. C.; Elemans, C. P. H.; Feener Jr., D. H. "Walking the line: search behavior and foraging success in ant species." *Behavioral Ecology*, 2011.

Post, D. M. "Using stable isotopes to estimate trophic position: models, methods, and assumptions.." *Ecology*. Vol. 83(3), 2002, pp. 703-718.

Retana, J.; Arnan, X.; Cerda, X. "A multidimensional functional trait analysis of resource exploitation in European ants." *Ecology*, Vol. 96(10), 2015, pp. 2781-2793.

Roeder, K. A.; Kaspari, M.. "From cryptic herbivore to predator: stable isotopes reveal consistent variability in trophic levels in an ant population." *Ecology*, Vol. 98(2), 2017, pp. 297-303.

Savolainen, R.; Vepsäläinen, K.. "A competition hierarchy among boreal ants: impact of resource partitioning and community structure." *Oikos*, Vol. 51, No. 2, 1988, pp. 135-155.

Silva, R. R.; Brandao, C. R. F. "Morphological patterns and community organization in leaf-litter ant assemblages." *Ecological Monographs*, Vol. 80(1), 2010, pp. 107-124.

Smith, C. R.; Suarez, A. V. "The trophic ecology of castes in harvester ant colonies." *Functional Ecology*, Vol. 24, No. 1, 2010, pp. 122-130.

Solida, L.; Grasso, D. A.; Testi, A.; Fanelli, G.; Scalisi, M.; Bartolino, V.; Mori, A.; Fanfani, A. "Differences in the nesting sites microhabitat characteristics of two syntopic species of *Messor* harvester ants in a phytosociological homogeneous grassland area." *Ethology Ecology & Evolution*, Vol. 23, Issue 3, 2011.

Tillberg, C. V.; McCarthy, D. P.; Dolezal, A. G.; Suarez, A. V. "Measuring the trophic ecology of ants using stable isotopes." *Insectes Sociaux*, Vol. 53, 2006, pp. 65-69.

Tillberg, C.V., D.A. Holway, E.G. LeBrun & A.V. Suarez. 2007. Trophic ecology of Argentine ants in their native and introduced ranges. *Proceedings of the National Academy of Sciences* 104:20856-20861.

Weischer, P. T.; Pearce-Duvet, J. M. C.; Feener, D. H. "Assembling an ant community: species functional traits reflect environmental filtering." *Oecologia*, Vol. 169, 2012, pp. 1063-1074.

Weiser, M. D.; Kaspari, M.. "Ecological morphospace of New World ants." *Ecological Entomology*, Vol. 31, 2006, pp. 131-142.

Wetterer, J. K.; Ward, Philip S.; Wetterer, Andrea L.; Longino, John T.; Trager, James C.; Miller, Scott E. "Ants (Hymenoptera: Formicidae) of Santa Cruz Island, California." *Bulletin of Southern California Academy of Sciences*, Vol. 99(1), 2000, pp. 25-31.

Wilson, E. O. "Oribatid mite predation by small ants of the genus *Pheidole*." *Insectes Sociaux*, Vol. 52, 2005, pp. 263-265.