

Foraging Ecology of the Tropical Giant Hunting Ant *Dinoponera australis* (Hymenoptera: Formicidae)—Evaluating Mechanisms for High Abundance

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ABSTRACT

A central goal of ecology is to understand the mechanisms behind variation in the abundance of species. Food web theory predicts higher biomass for animals at lower trophic levels. However, some high trophic level species may reach great abundance via highly efficient foraging behaviors. We evaluated ecological and behavioral traits of the giant tropical ant *Dinoponera australis* related to these mechanisms. We determined its distribution and abundance, documented its foraging behavior, and measured its trophic position in a population at P.N. Iguazú, Argentina. We report that *D. australis* colonies are overdispersed, and the species reaches a wet biomass of more than 2.5 kg/ha at this site. *Dinoponera australis* foraging behavior is characterized by route fidelity of individual workers, with different individuals specializing on different areas around the nest. Finally, stable isotopic evidence and direct observation suggest these ants are among the top predators in this terrestrial invertebrate community. We interpret our findings in the context of how the behavior of an abundant top predator creates an exception to the usual trade-off between biomass and trophic level. Together these data provide insight into the biology of one of the world's largest ants and why they may be able to attain such high densities where they occur.

Abstract in Spanish is available in the online version of this article.

Key words: ant abundance; route fidelity; stable isotope; trophic position.

A LONG-STANDING GOAL OF ECOLOGY IS TO UNDERSTAND PATTERNS OF INTRA- AND INTER-SPECIFIC VARIATION IN ABUNDANCE (MacArthur 1957, Preston 1962, Levey 1988, Hubble 2001). Ants, which can make up one quarter of insect biomass in tropical ecosystems (Hölldobler & Wilson 1990, Schultz 2000), have been the subjects of extensive research in this area (Kaspari *et al.* 2000, 2004, Dunn *et al.* 2009, McGlynn *et al.* 2010, Weiser *et al.* 2010, Longino & Colwell 2011). Despite this research, the mechanisms that allow certain ant species to attain high abundance often remain elusive. A potential mechanism for success that has received a lot of attention is the role of foraging and recruitment behavior on the ability of ants to monopolize resources (Carroll & Janzen 1973, Traniello 1989, Hölldobler & Wilson 1990, Dornhaus & Powell 2010).

One hypothesis for achieving high abundance and numerical dominance in tropical ant communities is the monopolization of

plant-based carbohydrate resources (*e.g.*, nectar or honeydew exudates from hemipterans) (Davidson 1998, Blüthgen *et al.* 2003, Davidson *et al.* 2003). Originally proposed for the success of tropical arboreal ants (Blüthgen *et al.* 2003, Davidson *et al.* 2003), this theory suggests by reducing their relative trophic position, colonies can use plant-based carbohydrates to fuel larger, more active colonies. This mechanism has also been proposed to explain the success of some invasive ants (Tillberg *et al.* 2007, Helms & Vinson 2008, Wilder *et al.* 2011).

Despite theoretical and empirical support for this hypothesis, some of the most abundant ants in the tropics are top predators, most notably the army ants (O'Donnell *et al.* 2007). While many army ants are dietary specialists (*e.g.*, that primarily prey on other ants; Franks & Bossert 1983, Rettenmeyer *et al.* 1983, Powell & Clark 2004), the most conspicuous are swarm-raiding species that are famous for their large colonies capable of capturing much of the invertebrate and small vertebrate biomass in areas they raid (Rettenmeyer 1963, Hölldobler & Wilson 1990, Kaspari *et al.* 2011). In contrast to the ‘carbohydrate

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for fuel' hypothesis, the success of army ants likely arises from their efficient mass recruitment and foraging behavior. Army ant foragers exhibit considerable variation in body size and behavioral specialization including subcastes that specialize on handling particular prey sizes (Powell & Franks 2005). Moreover, colonies send out workers in only a subset of the area around their bivouac each time they forage, resulting in colonies avoiding locations where prey has already been reduced (Franks & Fletcher 1983).

Route fidelity by individual foragers may be another mechanism by which predatory ants increase foraging efficiency. Wehner *et al.* (2004) found increasing levels of route fidelity during *Cataglyphis bicolor* forager ontogeny; they propose that route fidelity may reduce foraging time by exploiting resources in landscapes with familiar navigational cues. Heuristic modeling by Buchkramer and Reinhold (2008) predicts increasing foraging efficiency when ants remain faithful to previously successful foraging routes in this solitary foraging species. Finally, Elizalde and Farji-Berner (2012) also found that route fidelity played a role in the decision making behavior of trail-following *Acromyrmex lobicornis*, a mass-recruiting, leaf-cutting ant.

The ant subfamily Ponerinae contains over 900 described species that exhibit an amazing array of variation in size, diet, abundance, and foraging strategies (Bolton *et al.* 2006, Schmidt 2009). While most ponerines are generalist predators, many specialize on one prey type (*e.g.*, termites—*Pachycondyla marginata*, millipedes—*Tbaumatomyrmex* spp., or isopods—*Leptogenys* spp.) (Peeters & Crewe 1987, Hölldobler & Wilson 1990, Brandão *et al.* 1991, Leal & Oliveira 1995, Dejean & Evraerts 1997). Similarly, members of this subfamily vary substantially in colony size and foraging strategy; some species have large colonies (> 50,000 workers) that exhibit army ant-like foraging behaviors, while others have colonies of less than 20 individuals and are solitary foragers (Peeters & Crewe 1987, Maschwitz *et al.* 1989, Brandão *et al.* 1991, Paiva & Brandão 1995). While most species are rare, a few are among the most common and abundant ants in tropical forests.

We examined the foraging ecology and nesting biology of the giant hunting ant, *Dinoponera australis* (subfamily Ponerinae) in northeastern Argentina (locally known as 'hormiga Tigre'). In addition to being one of the world's largest ants, it can be among the most abundant ants in areas where it occurs (authors' pers. obs.). We test two potential, non-competing, hypotheses to explain this ant's numerical abundance: (1) in addition to insects, it forages extensively on plant-based resources and subsequently has a relatively low trophic position; and (2) over dispersion of nests coupled with individual route fidelity allows it forage efficiently. First, we use data of colony size and dispersion, coupled with capture data from pitfall traps, to estimate the relative abundance and biomass of *D. australis* at our field site. Then, to support or reject each hypothesis, we addressed the following questions: what is the diet and relative trophic position of this species relative to other ants in their community? What are the foraging patterns of individual workers and do they exhibit route fidelity?

METHODS

STUDY GENUS.—The genus *Dinoponera* consists of seven species of large, queenless ants that occur from Amazonian Peru and Brazil to northeastern Argentina (Paiva & Brandão 1995, Lenhart *et al.* 2013). *Dinoponera* workers are among the largest ants in the world (Fig. 1A) and colonies can range from less than 20 workers in *D. australis* to over 140 in *D. quadriceps* (Paiva & Brandão 1995, Monnin & Peeters 1999, Monnin *et al.* 2003). Colony densities are also variable and can reach up to 80 nests per ha (Paiva & Brandão 1995, Lenhart *et al.* 2013). Workers forage solitarily for prey in all species examined (Fowler 1985, Fourcassié *et al.* 1999, Fourcassié & Oliveira 2002, Araujo & Rodrigues 2006). Quantitative information on diet is restricted to two studies, one of *D. quadriceps* (Araujo & Rodrigues 2006) and a second on *D. gigantea* (Fourcassié & Oliveira 2002), both of which found workers returning with arthropods and occasionally seeds and fruits. All species nest in the soil, and two studies on nest dispersion found colonies to be either distributed randomly (*D. australis*, Paiva & Brandão 1995) or overdispersed (*D. quadriceps*, Vasconcellos *et al.* 2004).

FIELD SITE.—Our research was conducted at three sites within Iguazú National Park, Misiones Province, in northeastern Argentina (Fig. 1B). The habitat consists of subtropical rain forest, receiving approximately 1800 mm of rain/yr. Our field sites were primarily located in the forest along the Macuco Trail near the Centro de Investigaciones Ecológicas Subtropicales field station. The work was conducted over four primary time periods: December 2005, January 2008, January 2009, and August 2011.

NEST DISTRIBUTION AND ESTIMATE OF BIOMASS.—We marked the entrance of all *D. australis* nests in three separate plots measuring 0.03 ha, 0.31 ha, and 0.07 ha in 2005, 2009, and 2011, respectively. All plots were in the same habitat type (secondary forest) and had similar topography. Plots were chosen based on first locating foraging ants away from the park trail, following the ants back to the nest, and then looking for more nests outward from this nest. The final size of the plot was determined by accessibility of the habitat. Using a compass and measuring tape, we mapped the location of each nest on a Cartesian grid. We determined the identity and distance from each *D. australis* nest to the closest conspecific nest and calculated the mean of these distances for each plot. Using ImageJ (Rasband 1997), we determined the area and perimeter of the searched plots. From these geometric parameters we calculated the expected mean \pm standard deviation nearest neighbor distance accounting for the number of nests discovered in each plot. Nearest neighbor analysis yields a Z-score which is compared to a standard normal distribution; a score ≤ -1.96 indicates clustering while a score ≥ 1.96 indicates overdispersion ($\alpha = 0.05$).

To estimate *D. australis* biomass in this area, we combined the colony densities from our surveys of nest distribution with estimates of colony size from excavated colonies at this same site.

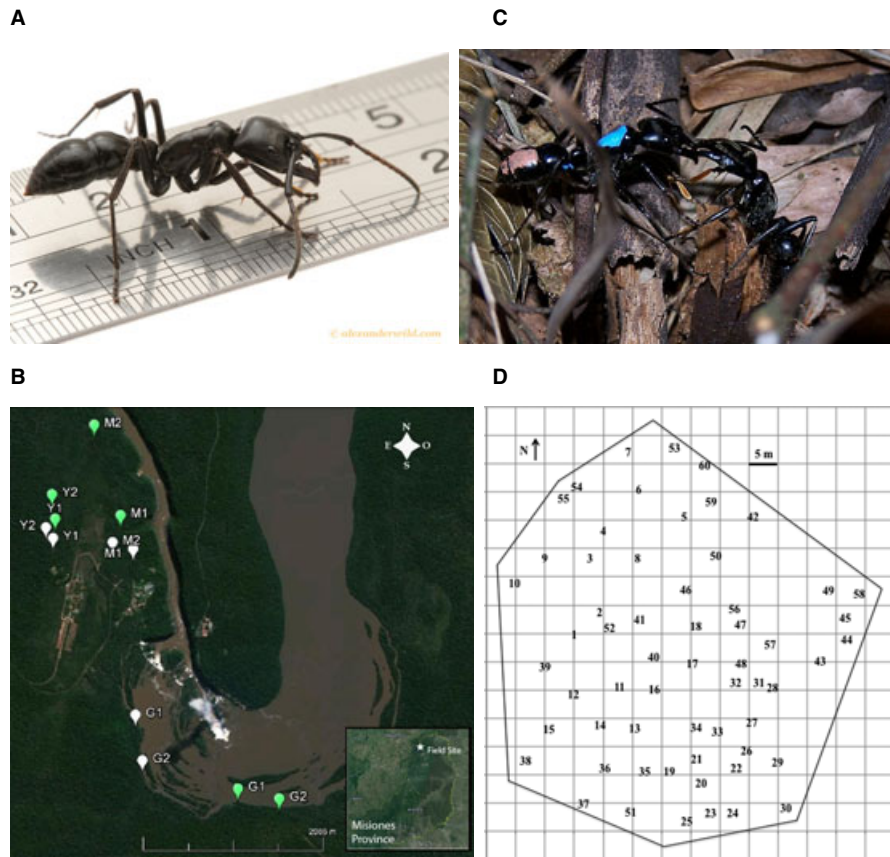


FIGURE 1. A) A worker of *Dinoponera australis* with ruler for scale. Photo © Alex Wild (www.alexanderwild.com), used by permission. B) Aerial photograph of Iguazú National Park in Argentina with the location of the pitfall transects. The plots used to estimate nest dispersion and for examination of foraging and diet were located in the vicinity of white markers M1 and M2. The transects were separated for analysis based upon the trail systems they ran along: Macuco trail - transects M1 and M2, Garganta - transects G1 and G2, and Yacaratiá - transects Y1 and Y2. The white markers signify transects run in 2008 and the green in 2009. C) Two marked workers from different nests engaged in a “ritualized” aggressive encounter that lasted for over 15 minutes. Photo by Chad Tillberg. D) A sample nest plot from 2009 at Iguazú National Park showing the over-dispersed distribution of *D. australis* nests. Each number represents a different colony.

We only used the two largest plots for this analysis (2005 and 2009) as the third plot had a much higher estimate of colony density likely reflecting the small area surveyed (Table 2). The number of workers per colony was estimated from a total of nine excavated colonies; five are reported in Smith *et al.* (2011) and an additional four were excavated during this study (three in 2008 and one in 2011).

To determine if *Dinoponera* densities at our plots were indicative of general patterns at other sites in the National Park, we placed two transects of pitfall traps in each of three trail systems in the park (Macuco, Garganta and Yacaratiá) (Fig. 1B). Pitfall trapping consisted of burying unbaited plastic containers (8 cm diam, 10 cm deep) partially filled with water, ethanol, and detergent with their lip flush with the surface. Traps were placed 20 m apart (2008) or 10 m apart (2009) and left out for either 3 d (2008) or 2 d (2009) before collection. All traps were left closed for 2 d before opening to avoid ‘digging in’ effects (Greenslade 1973). In January 2008, we set out six transects of five traps each, and in March of 2009, we set out six transects of 20 traps each, for a total of 150 traps. Transects 1 and 2 at Mac-

uco overlapped with the plots used to map individual *Dinoponera* colonies. We used an ANOVA to compare the number of *Dinoponera* caught/trap/d across the three areas.

DIET ANALYSIS.—In 2005, we collected all prey items carried by returning foragers from seven colonies during a 4-h observation period. To compliment these direct observations, we collected the returning workers, workers of other ant species, arthropods of known trophic position (*e.g.*, herbivores, predators), and plant material from the site immediately surrounding the seven colonies. We performed stable isotope analysis on these samples to estimate the relative trophic level of *D. australis*. We defined trophic levels (TL) based on $\delta^{15}\text{N}$ data for primary producers (*i.e.*, plants, TL = 1), primary consumers (*i.e.*, herbivores, TL = 2), and secondary consumers (*i.e.*, primary predators, TL = 3). Then, we compared $\delta^{15}\text{N}$ measurements of the ant community, including *D. australis*, to these values. Other studies of terrestrial arthropod communities have shown that enrichment in $\delta^{15}\text{N}$ of 2–3‰ (permil) approximates a trophic level (DeNiro & Epstein 1981, Mooney & Tillberg 2005, Feldhaar *et al.* 2009). Animals exhibit-

TABLE 1. Geometric properties of surveyed plots and results of nearest neighbor analysis for *Dinoponera australis* nest distribution.

Year	Survey area m ² (ha)	Perimeter (m)	N nests	Expected nearest neighbor mean ± SD	Observed mean nearest neighbor (m)	Z	P
2005	300 (0.03)	67	10	2.9 ± 0.5	4.9	3.7	< 0.001
2009	3613 (0.36)	208	60	3.8 ± 0.3	5.3	5.4	< 0.001
2011	730 (0.07)	124	13	4.0 ± 0.7	5.9	3.0	< 0.01

ing trophic omnivory may have non-integer TLs. All samples were prepared and analyzed following the methods of Tillberg *et al.* (2006).

FORAGING BEHAVIOR.—We captured and marked foragers from seven *D. australis* colonies (three in 2005 and four in 2009). The trajectory of all worker foraging trips was recorded when ants were 1 m away from the nest to determine a departure vector for each foraging trip. Mean trip vector (\bar{r}) was calculated for ants that completed at least five foraging trips. Mean vector length indicates the degree of overlap of repeated departures ranging from 1.0 (perfect overlap among all departure vectors) to 0.0 (perfect symmetrical dispersion of departure vectors). Colonies were observed for 4–6 h per day over four consecutive days. A Rayleigh test was performed to determine if foraging route distribution was random for those individuals making five or more trips and for each colony as a whole.

RESULTS

NEST DISTRIBUTION AND ESTIMATE OF BIOMASS.—The average nearest neighbor distance did not differ among our three plots (Kruskal–Wallis test: $df = 2$, $H = 1.9$, $P > 0.05$). Nearest neighbor analysis revealed that nests in all three plots were significantly overdispersed (Table 1, Fig. 1D).

We discovered 83 nests in the 0.46 total hectares we searched, for an extrapolated abundance of 180 nests per hectare. The excavated colonies had between 18–86 adult individuals, with a mean (\pm SD) of 44.6 (\pm 21.4) adults per nest. The estimated number of nests for the two largest plots surveyed (in 2009 and 2011) was 166 and 185 nests/ha. This scales to \sim 7827 *D. australis* workers/ha. Mean dry mass of individual *D. australis* workers is 104.8 ± 22.7 mg (Smith *et al.* 2011). We also weighed ten live nestmates together and calculated a wet mass of 323 mg per individual. This equates to an estimated dry biomass of 820.3 ± 177.7 g/ha and a wet biomass of 2528.1 g/ha for this species.

The number of workers caught per day of pitfall trapping varied across the three trapping locations ($df = 2$, $F = 5.078$, $P = 0.007$). Fisher's PLSD *post-hoc* tests revealed that mean (\pm SD) capture rates of traps from transects along Macuco (1.7 ± 1.3) and Garganta (1.5 ± 1.0) were similar ($P = 0.37$), but both had higher capture rates than Yacaratiá (1.0 ± 0.7) (Macuco v. Yacaratiá, $P = 0.002$; Garganta v. Yacaratiá, $P = 0.034$).

TABLE 2. Mean $\delta^{15}\text{N}$ and number (N) of prey items from different taxonomic groups retrieved from *Dinoponera australis* foragers.

Prey	N	Mean $\delta^{15}\text{N} \pm \text{SE}$
Arachnida		
Araneae	2	8.89 ± 0.12
Insecta		
Blattodea	2	3.53 ± 0.59
Coleoptera, Curculionidae	2	4.52 ± 1.72
Diptera, Asilidae	1	3.95
Hemiptera	3	2.30 ± 0.33
Hymenoptera, Formicidae	2	6.28 ± 1.76
Hymenoptera, Vespidae	1	8.14
Lepidoptera	12	5.27 ± 0.45
Mantodea	1	4.7
Orthoptera	11	4.91 ± 0.423
Phasmatodea	1	4.02
Unidentified plant material	2	2.46, 2.06
Unidentified insect material	1	6.47

DIET ANALYSIS.—Collections of *D. australis* prey yielded a mixture of arthropods from the second (*i.e.*, herbivores) and third (*i.e.*, primary predators) trophic levels, as well as some unidentifiable objects that were likely plant material (Table 2). Plants, known herbivores, and known predators had $\delta^{15}\text{N}$ values reflecting a 3‰ fractionation between trophic levels (Fig. 2). Mean (\pm SE) *D. australis* $\delta^{15}\text{N}$ was 10.0 (\pm 0.1) ‰; this is 2.2‰ higher than mean $\delta^{15}\text{N}$ of primary predator arthropods (7.8 ± 1.0) and similar to other predacious ant species at the site (Fig. 2).

The $\delta^{15}\text{N}$ of prey varied widely both within and among colonies (Fig. 3), reflecting the diversity of prey retrieved (Table 2). Comparisons of $\delta^{15}\text{N}$ values among *Dinoponera* workers reveal only small amounts of within-colony variation ($< 0.5\text{‰}$). Among-colony $\delta^{15}\text{N}$ variation was also relatively small ranging from 9.4 to 10.4 ‰ (Fig. 3). Across all colonies, the relative trophic position of *D. australis* at this site is 3.7.

FORAGING BEHAVIOR.—We witnessed a total of 351 unique foraging trips made by individuals from seven different colonies. Twenty-five individual ants were seen to depart from their nests five or more times during our observations, accounting for 181—about 52 percent—of all trips observed. The remainder of the

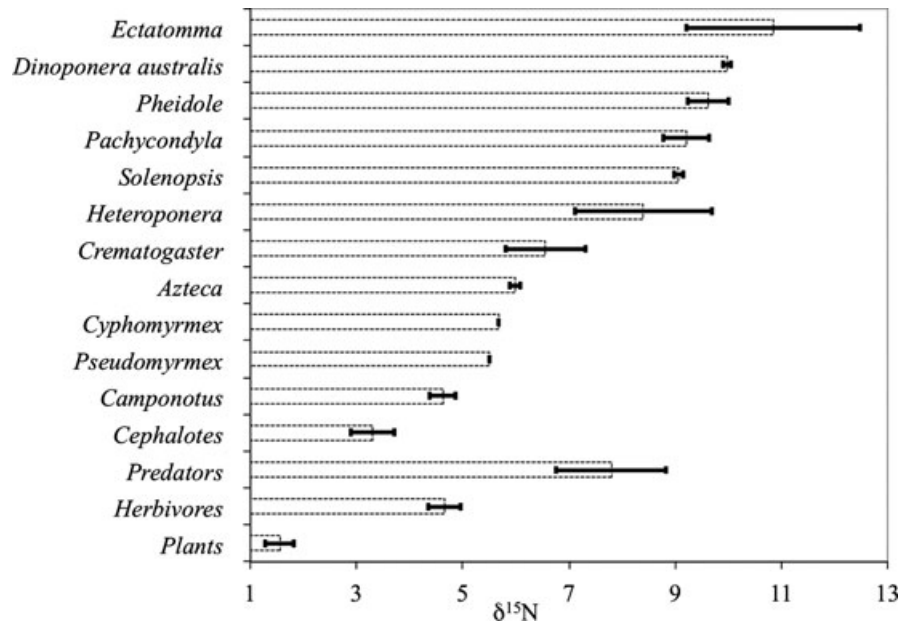


FIGURE 2. $\delta^{15}\text{N} \pm \text{SE}$ values for several ant genera, known predatory and herbivorous arthropod taxa, and plant material from the *Dinoponera* plot in 2005.

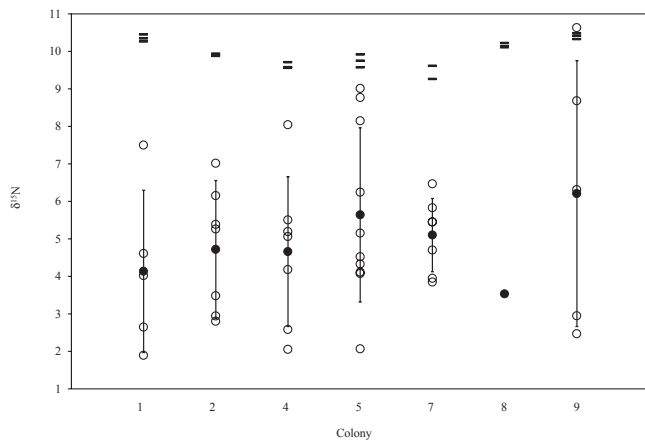


FIGURE 3. $\delta^{15}\text{N}$ of each *Dinoponera australis* worker (—), all prey (○), and prey mean \pm standard deviation (●) from seven colonies. Note the small within colony variation for *D. australis* relative to its prey, except for Colony 8 where prey $N = 1$.

foraging trips was performed by ants seen four or fewer times. Of these 25 foragers, 21 exhibited a significant degree of route fidelity (departed in the same direction and foraged in the same area) (Fig. 4). Two nests showed no whole-colony foraging bias, while five nests did show significant foraging bias; however, the mean colony foraging vector never exceeded $r = 0.3$ except in one case (Fig. 4).

DISCUSSION

Unlike that of many tropical arboreal ants, the remarkable abundance *D. australis* in the forest surrounding Iguazu Falls is not

fueled by a low trophic position diet. Instead, these predaceous ants may attain their remarkably high biomass through behaviors that increase the efficiency of foragers.

NEST DISTRIBUTION AND ESTIMATE OF BIOMASS.—We found strong evidence for an overdispersed pattern of nest locations suggesting strong territorial interactions among colonies. In total, we found 83 nests in the 0.46 ha we searched (Table 1) for a mean nest density of 180 nests/ha. Our distribution results are similar to those reported for *D. quadricaps* (Vasconcellos *et al.* 2004). However, a previous study on *D. australis* in southern Brazil found 37 nests to be randomly dispersed in a 0.25 ha plot (Paiva & Brandão 1995). This difference from our finding may result from differences in the density of the nests in each location. Nest density in our focal population (180/ha) was higher than that encountered by Paiva and Brandão (1995) in southern Brazil (148/ha). Perhaps the lower density of this population in Brazil relaxed inter-colony competitive interactions, resulting in a less-structured nest distribution pattern. Our data are consistent with many other studies that find that ant colonies are overdispersed in nature suggesting competition for resources and territoriality may shape their distribution (Levings & Traniello 1982, Ryti & Case 1984, 1986, Cushman *et al.* 1988, Adams & Tschinkel 2001).

Fourcassié and Oliveira (2002) observed “ritualized territorial contests” between individuals of *D. gigantea* when they met at territorial borders that could last up to 30 min. We observed similar behaviors when marked individuals from two different colonies would meet (Fig. 1C). The ants would lock mandibles, and each would raise its body as high as possible. However, no injurious aggression was witnessed. In one case, the ants remained together for over 15 min until we disturbed them by taking a photograph.

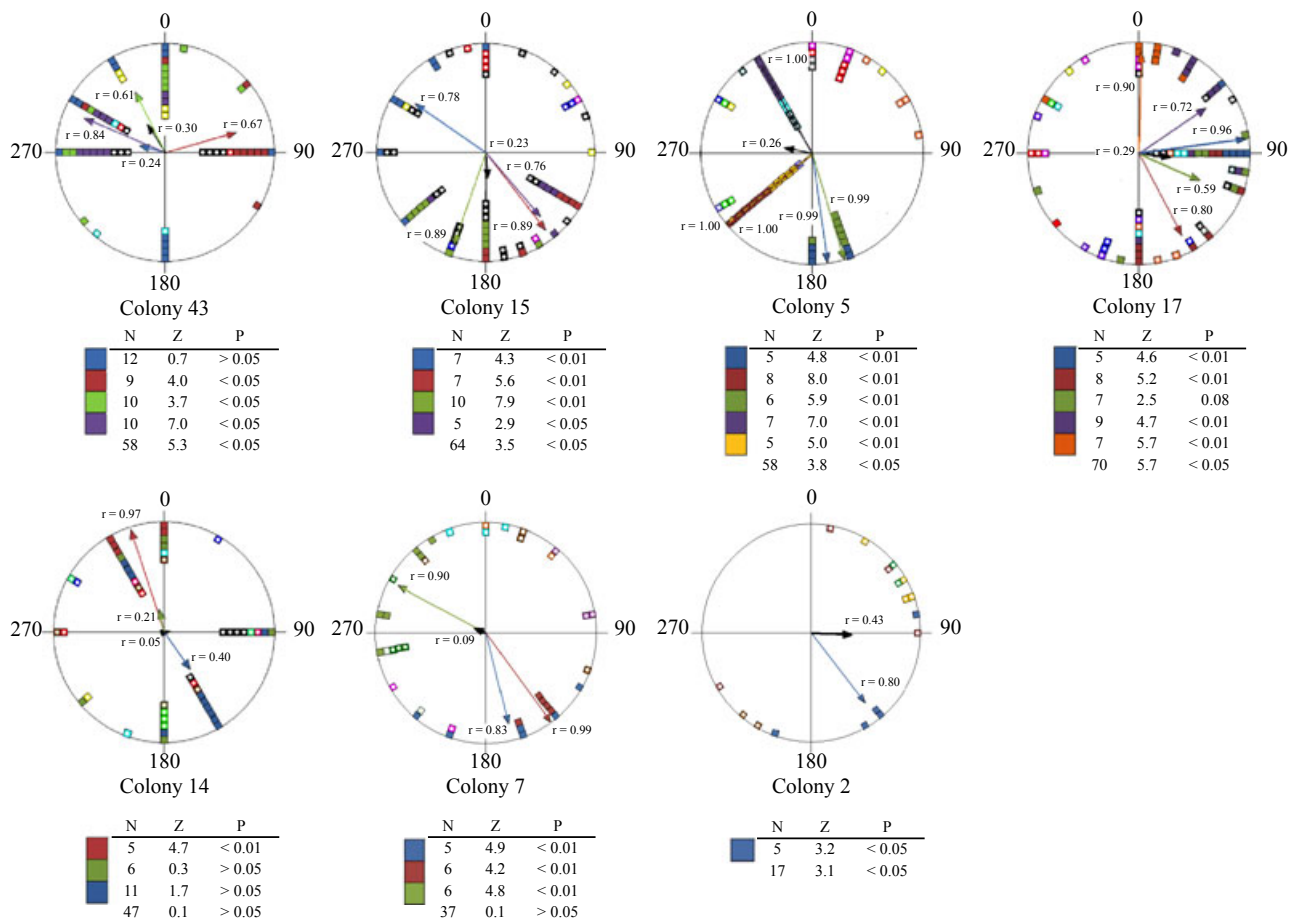


FIGURE 4. Foraging trajectories from seven *Dinoponera australis* colonies. Each square represents the departure direction of one trip; different colors correspond to different marked individuals. Solid symbols are foragers observed to make five or more foraging trips. Colored arrows indicate mean departure vector (r) for these individuals. The black arrow is the colony mean vector for all observed foraging trips by all individuals. Rayleigh test results for workers with five or more trips and for the whole colony are in tables below each figure. Colonies 2, 5, and 7 were observed in 2005, the remainder in 2009.

Some encounters probably do escalate to injurious aggression as we frequently observed foragers missing one or more legs or antennae.

The biomass estimates of *D. australis* at our sites within P.N. Iguazú are high for a single species, even when compared to other omnivorous/insectivorous ants or other organisms in tropical systems. For example, *D. quadriceps* was estimated to have a wet biomass of 461 g/ha in Atlantic rain forest in Brazil (Vasconcellos *et al.* 2004). Other insectivorous tropical ant species such as the bullet ant *Paraponera clavata* (wet biomass: 266 g/ha at La Selva Biological Station in Costa Rica, Tillberg & Breed 2004) and *Eciton burcbelli* (wet biomass of 480 g/ha at BCI Panama, Franks 1996) have one quarter or less the estimated biomass of *D. australis*. The high estimates of biomass for *D. australis* at Iguazú may reflect a lack of many other highly insectivorous ant species that could compete for resources. However, army ants (including *Eciton vagans* and *Labidus praedator*) and other large, predatory ponerine ants (*e.g.*, *Odontomachus* and *Pachycondyla*) also occur at this site (authors' unpubl. data). This population of

D. australis appears similar in biomass to tropical insectivorous mammals such as rodents (Eisenberg 1990, Glanz 1990). It should be noted that while our data are high for a single ant species, the total dry biomass for ants collectively was reported at near 50,000 g/ha for a forest in Florida in the Southeastern United States (King *et al.* 2013).

Pitfall trapping data suggest that the density (and/or activity) of *D. australis* is not uniform throughout the park so our estimates of biomass may only be relevant to the high density areas where our plots were located. Much of the park consists of secondary forest including the area where we estimated nest density. The high density and biomass of *D. australis* may be an artifact of their ability to persist in disturbed forest where other insectivores (including other ants and small mammals) are not able to maintain abundant populations. This possible mechanism needs to be examined with future surveys of a wide variety of insectivorous taxa. In addition, more surveys are needed throughout the range of *D. australis* to determine, if the biomass we estimated is really an outlier relative to other populations.

DIET ANALYSIS.—Many ants thought to be largely predatory have been found to incorporate significant amounts of plant-based material into their diet (e.g., Passos & Oliveira 2004, Tillberg & Breed 2004). Isotopic and observational data indicate that *D. australis* is a top predator in the invertebrate food web. Foragers returned to the nest primarily with arthropod prey. Only two of 41 prey items were likely plant material (Table 2). Half of the prey items were from two families of largely herbivorous insect, Lepidoptera (larvae) and Orthoptera. The stable isotope results confirm that colonies are incorporating prey from a variety of trophic levels with the end result being that *D. australis* colonies at this site are closer to secondary predators than primary predators in the invertebrate food web.

The total range in $\delta^{15}\text{N}$ among the seven colonies was only 1.0‰, which is relatively small compared to intraspecific variation reported in some other ant species (Blüthgen *et al.* 2003, Tillberg *et al.* 2006, Fieder *et al.* 2007). Another large and abundant Neotropical ant, *Paraponera clavata*, had a $\delta^{15}\text{N}$ range among colonies of 2.2‰ (Tillberg & Breed 2004). However, the more omnivorous *P. clavata* forage in tree canopies where they collect both animal prey and plant-based exudates—nectar, honeydew—and this larger dietary breadth may account for the larger among-colony $\delta^{15}\text{N}$ range of this species. *Dinoponera gigantea* has been observed to bring back similar types of prey compared to *D. australis* (Table 2); however, 22 percent of all food items collected from *D. gigantea* were plant material such as seeds and fruit (Fourcassie & Oliveira 2002). Our enumeration of items collected from the mandibles of returning *D. australis* foragers found only two of the 41 items (*i.e.*, 7%) were potentially plant material. No isotope data are presently available for *D. gigantea*, but if this species incorporates more plant-based resources in its diet than *D. australis*, then it may also have a larger intraspecific range in $\delta^{15}\text{N}$ values, similar to *P. clavata*.

FORAGING BEHAVIOR.—Most foragers examined exhibited significant route fidelity; of the 25 workers observed to make five or more foraging trips, 21 repeatedly foraged in a non-random direction from the nest. This finding suggests that individual *D. australis* foragers tend to specialize in certain areas around the nest, a behavior that may increase foraging efficiency in solitary foraging species that do not recruit nest mates when resources are found. Fourcassie and Oliveira (2002) found evidence for significant route fidelity in the congener *D. gigantea*. Like *D. australis*, *D. gigantea* nests underground and solitary foragers search the leaf litter in the area surrounding the nest. Fresneau (1985) also reported regional foraging specialization in the ponerine *Neoponera apicalis*.

The whole-colony foraging effort is more dispersed; five of the seven colonies had significant overall foraging vectors, but even these had *r*-values of 0.3 or less with exception of colony 2 (Fig. 4). During observation, foragers departed toward all quadrants surrounding each colony, and there were no gaps between departure vectors exceeding 90° for six of the seven colonies (Fig. 4). As with individual foraging behavior, our whole-colony findings are also comparable to Fourcassie and Oliveira (2002)

who found a significant whole-colony foraging vector in just one of the three *D. gigantea* colonies they observed.

Taken together, these findings suggest that selection may shape foraging behavior at two levels—that of the individual and of the colony. First, route fidelity may increase the efficiency of the individual worker. Specialized foraging in a subset of the surrounding habitat could increase familiarity of an individual: (1) with likely sources of food, increasing the probability of success; and (2) with navigational cues, thereby decreasing the foraging time. Both of these propositions are amenable to testing in this system. Second, distributed foraging routes among nestmates would result in foraging coverage of the total surrounding habitat by the colony. Hence, a colony explores its surroundings in all directions, but it does so by the actions of numerous individuals specialized to efficiently exploit a subset of the total habitat. Heterogeneous resource distribution, intraspecific competition, and unintentional observational bias may explain the cases where we did discover a slight, but significant, whole-colony foraging bias. It would also be worth examining if colony level route fidelity is determined by the direction of nearest neighbor and the size of neighboring colonies. As with the findings of Wehner *et al.* (2004) and Buchkremer and Reinhold (2008), route fidelity may be a common way for solitary foraging ants to increase foraging efficiency especially for taxa with small colonies that do not use chemical trails when foraging.

Araujo and Rodrigues (2006) measured a short return time relative to the time spent foraging in *D. quadriceps*, which led the authors to suggest that the ants are using visual cues for orientation. Two observations made during this study provide fuel for future work and suggest a strong visual component to the orientation system of this ant. First, when we removed food from a returning worker, the worker ran into the nest for a few minutes then emerged and immediately returned to the exact spot where the prey was taken away and started walking in circles as if looking for it. Second, when we placed a worker that consistently foraged in one direction from the nest in a location we had never seen it forage, the ant was still able to immediately return to the nest entrance. These incidental observations suggest the ants may have a spatial map (or cognitive equivalent) of landscape or canopy features around their nest allowing them to keep track of where they are relative to the nest opening (Hölldobler 1980). Future studies would benefit from experimentally manipulating the landmarks around the colony to determine if foragers are using visual cues to set foraging direction and the area searched.

In conclusion, we found evidence for route fidelity in foraging at the individual and colony level in a large, highly predacious, and abundant Neotropical ant species. Local distribution of this species appears to be governed by negative inter-colony interactions as indicated by nest site spatial distribution and behavioral interactions between non-nestmates. Together, our data suggest that the high biomass of this species is not likely a result of incorporating large amounts of plant-based resources as seen in other abundant tropical ants (Blüthgen *et al.* 2003, Davidson *et al.* 2003, Tillberg & Breed 2004). Instead, their large size and individual foraging behavior may allow them to efficiently gather

insect resources in a manner distinct to the mass recruiting seen in army ants. Future work is still needed to test other potential mechanisms for the high biomass of *D. australis* at this site including an examination of the abundance of other insectivorous ground foraging taxa. Finally, not all species with workers that exhibit individual route fidelity occur at high density. More research is needed to examine how this behavior is tied to foraging success, colony growth, and the nature and persistence of the food resources in the community.

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LITERATURE CITED

- ADAMS, E. S., AND W. R. TSCHINKEL. 2001. Mechanisms of population regulation in the fire ant *Solenopsis invicta*: An experimental study. *J. Anim. Ecol.* 70: 355–369.
- ARAUJO, A., AND Z. RODRIGUES. 2006. Foraging behavior of the queenless ant *Dinoponera quadricaps* Santschi (Hymenoptera: Formicidae). *Neotrop. Entomol.* 35: 159–164.
- BLÜTHGEN, N., G. GEBAUER, AND K. FIEDLER. 2003. Disentangling a rainforest food web using stable isotopes: Dietary diversity in a species-rich ant community. *Oecologia* 137: 426–435.
- BOLTON, B., G. ALPERT, P. S. WARD, AND P. NASKRECKI. 2006. *Bolton's Catalogue of Ants of the World: 1758–2005*. CDROM. Cambridge, Massachusetts: Harvard University Press.
- BRANDÃO, C. R. F., J. L. M. DINIZ, AND E. M. TOMOTAKE. 1991. *Thaumatomyrmex* strips millipedes for prey: A novel predatory behavior in ants, and the first case of sympatry in the genus (Hymenoptera: Formicidae). *Insectes Soc.* 38: 335–344.
- BUCHKREMER, E. M., AND K. REINHOLD. 2008. Sector fidelity—An advantageous foraging behavior resulting from a heuristic search strategy. *Behav. Ecol.* 19: 984–989.
- CARROLL, C. R., AND D. H. JANZEN. 1973. Ecology of foraging by ants. *Annu. Rev. Ecol. Syst.* 4: 231–257.
- CUSHMAN, J. H., G. D. MARTINSEN, AND A. I. MAZEROLL. 1988. Density- and size-dependent spacing of ant nests: Evidence for intraspecific competition. *Oecologia* 77: 522–525.
- DAVIDSON, D. W. 1998. Resource discovery versus resource domination in ants: A functional mechanism for breaking the trade-off. *Ecol. Entomol.* 23: 484–490.
- DAVIDSON, D. W., S. C. COOK, R. R. SNELLING, AND T. H. CHUA. 2003. Explaining the abundance of ants in lowland tropical rainforest canopies. *Science* 300: 969–972.
- DEJEAN, A., AND C. EVRAERTS. 1997. Predatory behavior in the genus *Leptogenys*: A comparative study. *J. Insect Behav.* 10: 177–191.
- DENIRO, M. J., AND S. EPSTEIN. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. *Geochim. Cosmochim. Acta* 45: 341–351.
- DORNHAUS, A., AND S. POWELL. 2010. Foraging and defense strategies. In L. Lach, C.L. Parr, and K.L. Abbott (Eds.) *Ant ecology*. pp. 210–230. Oxford University Press, New York, New York.
- DUNN, R. R., N. J. SANDERS, B. GUÉNARD, AND M. D. WEISER. 2009. Geographic gradients. In L. Lach, C. L. Parr, and K. L. Abbott (Eds.) *Ant ecology*. pp. 38–58. Oxford University Press, New York, New York.
- EISENBERG, J. F. 1990. Neotropical mammal communities. In A. Gentry (Ed.). *Four neotropical rain forests*, pp. 358–368. Yale University Press, New Haven, Connecticut.
- ELIZALDE, L., AND A. FARJI-BERNER. 2012. To be or not to be faithful: Flexible fidelity to foraging trails in the leaf-cutting ant *Acromyrmex lobicornis*. *Ecol. Entomol.* 37: 370–376.
- FELDHAAR, H., G. GEBAUER, AND N. BLÜTHGEN. 2009. Stable isotopes: Past and future in exposing secrets of ant nutrition (Hymenoptera: Formicidae). *Myrmecol. News* 12: 3–13.
- FIEDER, K., F. KUHLMANN, B. C. SCHLICK-STEINER, F. M. STEINER, AND G. GEBAUER. 2007. Stable N-isotope signatures of central European ants—Assessing positions in a trophic gradient. *Insectes Soc.* 54: 393–402.
- FOURCASSIÉ, V., A. HENRIQUES, AND C. FONTELLA. 1999. Route fidelity and spatial orientation in the ant *Dinoponera gigantea* (Hymenoptera, Formicidae) in a primary forest: A preliminary study. *Sociobiology* 34: 505–524.
- FOURCASSIÉ, V., AND P. S. OLIVEIRA. 2002. Foraging ecology of the giant Amazonian ant *Dinoponera gigantea* (Hymenoptera, Formicidae, Ponerinae): Activity schedule, diet and spatial foraging patterns. *J. Nat. Hist.* 36: 2211–2227.
- FOWLER, H. G. 1985. Population foraging and territoriality in *Dinoponera australis* (Hymenoptera: Formicidae). *Rev. Bras. Entomol.* 3–4: 443–447.
- FRANKS, N. 1996. Ecology and population regulation in the army ant *Eciton burchelli*. In E.G. Leigh, Jr., A.S. Rnad, and D.M. Windson (Eds.) *The ecology of a tropical forest*, 2nd edition, pp. 389–395. Smithsonian Institution, Washington, DC
- FRANKS, N. R., AND W. H. BOSSERT. 1983. The influence of swarm raiding army ants on the patchiness and diversity of a tropical leaf litter ant community. In E. L. Sutton, T. C. Whitmore, and A. C. Chadwick (Eds.). *Tropical rain forest: Ecology and management*, pp. 151–163. Blackwell, Oxford.
- FRANKS, N. R., AND C. R. FLETCHER. 1983. Spatial patterns in army ant foraging and migration: *Eciton burchelli* on Barro Colorado Island, Panama. *Behav. Ecol. Sociobiol.* 12: 261–270.
- FRESNEAU, D. 1985. Individual foraging and path fidelity in a ponerine ant. *Insectes Soc.* 32: 109–116.
- GLANZ, W. E. 1990. Neotropical mammal densities: How unusual is the community on Barro Colorado Island, Panama. In A. Gentry (Ed.). *Four neotropical rain forests*, pp. 287–313. Yale University Press, New Haven, Connecticut.
- GREENSLADE, P. J. M. 1973. Sampling ants with pitfall traps: Digging-in effects. *Insectes Soc.* 20: 343–53.
- HELMS, K. R., AND S. B. VINSON. 2008. Plant resources and colony growth in an invasive ant: The importance of honeydew-producing Hemiptera in carbohydrate transfer across trophic levels. *Environ. Entomol.* 37: 487–493.
- HÖLLDOBLER, B. 1980. Canopy orientation: A new kind of orientation in ants. *Science* 210: 86–88.
- HÖLLDOBLER, B., AND E. O. WILSON. 1990. *The ants*. Belknap Press of Harvard University Press, Cambridge, Massachusetts.
- HUBBLE, S. P. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, New Jersey.
- KASPARI, M., S. O'DONNELL, AND L. ALONSO. 2000. Three energy variables predict ant abundance at a geographic scale. *Proc. R. Soc. B* 267: 485–490.
- KASPARI, M., S. O'DONNELL, J. LAITKE, AND S. POWELL. 2011. Predation and patchiness in the tropical litter: Do swarm-raiding army ants skim the cream or drain the bottle? *J. Anim. Ecol.* 80: 818–823.
- KASPARI, M., P. WARD, AND M. YUAN. 2004. Energy gradients and the geographic distribution of local ant diversity. *Oecologia* 140: 407–414.
- KING, J. R., R. J. WARREN, AND M. A. BRADFORD. 2013. Social insects dominate eastern US temperate hardwood forest macroinvertebrate communities in warmer regions. *PLoS ONE* 8(10): e75843.

- LEAL, I. R., AND P. S. OLIVEIRA. 1995. Behavioral ecology of the neotropical termite-hunting ant *Pachycondyla marginata*: Colony founding, group-raiding and migratory patterns. *Behav. Ecol. Sociobiol.* 37: 373–383.
- LENHART, P. A., S. T. DASH, AND W. P. MACKAY. 2013. Revision of the giant Amazonian ants of the genus *Dinoponera* (Hymenoptera, Formicidae). *J. Hymenopt. Res.* 31: 119–164.
- LEVEY, D. J. 1988. Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. *Ecol. Monogr.* 58: 251–269.
- LEVINGS, S. C., AND J. F. A. TRANIELLO. 1982. Territoriality, nest dispersion, and community structure in ants. *Psyche* 88: 265–319.
- LONGINO, J. T., AND R. K. COLWELL. 2011. Density compensation, species composition, and richness of ants on a neotropical elevational gradient. *Ecosphere* 2(3): 000–000:art29, doi:10.1890/ES10-00200.1
- MACARTHUR, R. H. 1957. On the relative abundance of bird species. *Proc. Natl Acad. Sci. USA* 43: 293–295.
- MASCHWITZ, U., S. STEGHAUS-KOVAC, R. GAUBE, AND H. HANEL. 1989. A South East Asian ponerine ant of the genus *Leptogenys* (Hym., Form.) with army ant life habits. *Behav. Ecol. Sociobiol.* 24: 305–316.
- MCGLYNN, T. P., M. D. WEISER, AND R. R. DUNN. 2010. More individuals but fewer species—tests of the more individuals hypothesis from experiments on a diverse tropical fauna. *Biol. Lett.* 6: 490–493.
- MONNIN, T., AND C. PEETERS. 1999. Dominance hierarchy and reproductive conflicts among subordinates in a monogynous queenless ant. *Behav. Ecol.* 10: 323–332.
- MONNIN, T., F. L. W. RATNIEKS, AND C. R. F. BRANDÃO. 2003. Reproductive conflict in animal societies: Hierarchy length increases with colony size in queenless ponerine ants. *Behav. Ecol. Sociobiol.* 54: 71–79.
- MOONEY, K. A., AND C. V. TILLBERG. 2005. Temporal and spatial variation to ant omnivory in pine forests. *Ecology* 86: 1225–1235.
- O'DONNELL, S., J. LATTKE, S. POWELL, AND M. KASPARI. 2007. Army ants in four forests: Geographic variation in raid rates and species composition. *J. Anim. Ecol.* 76: 580–589.
- PAIVA, R. V. S., AND C. R. F. BRANDÃO. 1995. Nests, worker population, and reproductive status of workers, in the giant queenless ponerine ant *Dinoponera Roger* (Hymenoptera: Formicidae). *Ethol. Ecol. Evol.* 7: 297–312.
- PASSOS, L., AND P. S. OLIVEIRA. 2004. Interaction between ants and fruits of *Guaipira opposita* (Nyctaginaceae) in a Brazilian sandy plain rainforest: Ant effects on seeds and seedlings. *Oecologia* 139: 376–382.
- PEETERS, C., AND R. CREWE. 1987. Foraging and recruitment in Ponerine ants: Solitary hunting in the queenless *Ophthalmopone berthoudi* (Hymenoptera: Formicidae). *Psyche* 94: 201–214.
- POWELL, S., AND E. CLARK. 2004. Combat between large derived societies: A subterranean army ant established as a predator of mature leaf-cutting ant colonies. *Insectes Soc.* 51: 342–351.
- POWELL, S., AND N. R. FRANKS. 2005. Caste evolution and ecology: A special worker for novel prey. *Proc. R. Soc. Lond. B* 272: 2173–2180.
- PRESTON, F. W. 1962. The canonical distribution of commonness and rarity. *Ecology* 43(185–215): 410–432.
- RASBAND, W. S. 1997. IMAGEJ, U. S. National Institutes of Health, Bethesda, Maryland, <http://imagej.nih.gov/ij/>, 1997–2012.
- RETTEMEYER, C. W. 1963. Behavioral studies of army ants. *Univ. Kans. Sci. Bull.* 44: 281–465.
- RETTEMEYER, C. W., R. CHADAB CREPET, M. G. NAUMANN, AND L. MORALES. 1983. Comparative foraging by Neotropical army ants. In P. Jaisson (Ed.). *Social insects in the tropics*, pp. 59–73. Université Paris-Nord, Paris.
- RYTI, R. T., AND T. J. CASE. 1984. Spatial arrangement and diet overlap between colonies of desert ants. *Oecologia* 62: 401–404.
- RYTI, R. T., AND T. J. CASE. 1986. Overdispersion of ant colonies: A test of hypotheses. *Oecologia* 69: 446–453.
- SCHMIDT, C. A. 2009. Molecular phylogenetics and taxonomic revision of Ponerine ants (Hymenoptera: Formicidae: Ponerinae). PhD Thesis, University of Arizona.
- SCHULTZ, T. R. 2000. In search of ant ancestors. *Proc. Natl Acad. Sci. USA* 97: 14028–14029.
- SMITH, C. R., A. V. SUAREZ, N. D. TSUTSUI, S. E. WITTMAN, B. EDMONDS, A. FREAUFE, AND C. V. TILLBERG. 2011. Nutritional asymmetries are related to division of labor in a queenless ant. *PLoS ONE* 6: e24011. doi:10.1371/journal.pone.0024011
- TILLBERG, C. V., AND M. D. BREED. 2004. Placing and omnivore in a complex food web: Dietary contributions to adult biomass of an ant. *Biotropica* 36: 266–271.
- TILLBERG, C. V., D. A. HOLWAY, E. G. LEBRUN, AND A. V. SUAREZ. 2007. Trophic ecology of invasive Argentine ants in their native and introduced ranges. *Proc. Natl Acad. Sci. USA* 104: 20856–20861.
- TILLBERG, C. V., D. P. MCCARTHY, A. G. DOLEZAL, AND A. V. SUAREZ. 2006. Measuring the trophic ecology of ants using stable isotopes. *Insectes Soc.* 53: 65–69.
- TRANIELLO, J. F. A. 1989. Foraging strategies of ants. *Annu. Rev. Entomol.* 34: 191–20.
- VASCONCELLOS, A., G. G. SANTANA, AND A. K. SOUZA. 2004. Nest spacing and architecture, and swarming of males of *Dinoponera quadriceps* (Hymenoptera, Formicidae) in a remnant of the Atlantic forest in Northeast Brazil. *Braz. J. Biol.* 64: 357–362.
- WEHNER, R., C. MEIER, AND C. ZOLLIKOFER. 2004. The ontogeny of foraging behavior in desert ants, *Cataglyphis bicolor*. *Ecol. Entomol.* 29: 240–250.
- WEISER, M. D., N. J. SANDERS, D. AGOSTI, A. N. ANDERSEN, X. ARNAN, C. A. BRUHL, X. CERDA, A. M. ELLISON, B. L. FISHER, M. C. FITZPATRICK, H. GIBB, N. J. GOTELLI, A. D. GOVE, B. GUENARD, M. JANDA, M. KASPARI, E. J. LAURENT, J.-P. LESSARD, J. T. LONGINO, J. D. MAJER, S. M. MENKE, T. P. MCGLYNN, C. L. PARR, S. M. PHILPOTT, M. PFEIFFER, J. RETANA, A. SUAREZ, H. VASCONCELOS, S. P. YANOVIAK, AND R. R. DUNN. 2010. Canopy and litter ant assemblages share similar climate-species density relationships. *Biol. Lett.* 6: 769–772.
- WILDER, S. M., D. A. HOLWAY, A. V. SUAREZ, E. G. LEBRUN, AND M. D. EUBANKS. 2011. Intercontinental differences in resource use reveal the importance of mutualisms in fire ant invasions. *Proc. Natl Acad. Sci. USA* 108: 20639–20644.