THE PONERINE PARADOX: FORAGING INEFFICIENCIES IN THE GIANT TROPICAL ANT, *PARAPONERA CLAVATA* (HYMENOPTERA: FORMICIDAE: PONERINAE)

CHAD S. GORBATKIN, SARAH C. ISBEY,
ZACHARY A. MAYER, AND ALLISON M. CITRO

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Abstract: Bullet ants, *Paraponera clavata* (Formicidae: Ponerinae), are one of the oldest phylogenetic groups of ants and display the primitive trait of solitary foraging. When a prey item is too large for a single ant to carry, *P. clavata* will recruit other workers to segment pieces for transportation back to the colony. Our study examined how a primitive, eusocial ant responds to varying prey biomass. We predicted that the time required to segment and carry insect prey to the nest would increase as prey biomass increased and that single bullet ants would have higher biomass movement rates than groups. We measured ant responses to insect prey presence, including time to take the prey item into the nest, number of prey segments, and total ant recruitment. Our results supported our predictions, showing that total processing time increased with mass and that prey biomass movement rates (g/min and g/min/ant) were faster for individuals than for groups. Our findings suggest solitary foraging in *P. clavata* is much more efficient than group foraging because *P. clavata* has not evolved efficient social foraging methods for larger prey items.

Key Words: bullet ant, social insects, foraging efficiency

INTRODUCTION

The bullet ant, *Paraponera clavata* (Hymenoptera: Formicidae: Ponerinae), is a primitive ant species that acts as a top-down regulator in some neotropical ecosystems (Dyer 2002; Janzen 1983). Bullet ants build subterranean nests at the base of trees, though they have also been shown to nest arboreally (Thurber et al. 1991). Sources of mortality include parasitic phorid flies (Brown and Feener 1991) and competing conspecifics from nearby nests (Breed et al. 1991). *P. clavata* have also been shown to be over-dispersed, indicating strong competition between colonies (Thurber et al. 1991).

P. clavata use both visual cues and pheromones to map trails to food sources (Ehmer 1999), which include nectar, arthropods, and occasionally small vertebrates (Fewell et al. 1996). High contrast areas (e.g., light gaps) are key to bullet ant vision (Ehmer 1999), and may be more important than pheromone trails in guiding bullet ants. Although they are capable solitary foragers, *P. clavata* will recruit others from its colony to nectar or food sources depending on the amount available and the distance from the colony (Breed et al. 1996). When prey is too large for a single

ant to carry back, multiple ants will segment the prey outside the nest, carrying it to the colony in pieces.

Although one of the most widespread and oldest living phylogentic assemblages (Wilson and Holldobler 2005), ponerine ants remained socially primitive. Because bullet ants are a primitive, eusocial species with only basic social capacities, their communications (e.g., pheromone trails) are relatively undeveloped (Wilson and Holldobler 2005). Confused and disoriented ants are seen frequently once a prey item is located by a forager (*personal observation*). Unlike other more socially developed ants, such as the subfamily Ecitoninae, they are unable to synchronize their efforts to bring prey back to the nest (Wilson and Holldobler 2005).

Despite these primitive characteristics and apparent foraging limitations, bullet ants maintain important effects on arthropod populations. For example, bullet ants prey upon leaf-cutter ants (Dyer 2002), one of the dominant herbivores in the neotropics (Hölldobler and Wilson 1990). Because they have the ability to indirectly influence plant biomass, understanding their foraging behaviors is important to understanding forest dynamics (Dyer 2002). Although many previous studies have looked at foraging rates, recruitment, and behaviors (e.g. Nelson et al 1991; Breed et al. 1996; Baader 1996), none have looked specifically at prey segmentation, subsequent movement, or foraging efficiency of both individual and groups of bullet ants.

Our study investigates patterns of prey biomass processing in *P. clavata*. We hypothesized prey processing and movement rates would vary depending on the mass of the prey item and recruitment. We predicted segmentation and overall processing time would increase with prey biomass. Because of the primitive foraging characteristics described above, we also predicted that single bullet ants would have higher prey biomass movement rates than both groups and individual ants within groups (both grams/min and grams/min/ant).

METHODS

Study System:

We collected data throughout the day on 13 and 14 February, 2007, at the La Selva Biological Station, Costa Rica. All but two trials were performed during daylight hours. We used one *P. clavata* colony located approximately 450 m into the Sendero de Arboleda trail, approximately 25 m east of marker 550, 900 on the trail map.

Field Methods:

We collected 19 *P. clavata* prey items (eight grasshoppers, five katydids, five crickets, and one praying mantis) from the grassy area

surrounding La Selva Biological Station. We used one massed prey item per trial. We severed the prey's muscles, preventing it from flying away. The prey item was placed at the base of the *P. clavata* colony, *c.* 10 cm from a colony entrance. We presented one ant from the colony with the prey item. Timing began when the ant first stung the prey item. We recorded the total number of segments into which the prey was divided, the number of segments that were taken to the nest, the time at which each segment was brought into the nest, and the total time until all of the segments had been brought into the nest. Every two minutes we counted the number of *P. clavata* on the prey item and the total number of ants outside of the colony (i.e., on the prey item, ground, and tree) in order to determine maximum number of ants on the prey item and maximum number of ants out of the colony at any one time during the trial. Once all the segments had been brought to the nest, we continued to count the number of ants every two minutes until all ants had returned to the colony. We waited at least five minutes between trials.

We performed a correlation between prey mass (log-transformed) and total segments (log-transformed). Because these were highly correlated (r^2=0.79, $F_{1,16}$=61.70, P<0.0001), we chose to analyze the effect of mass in order to focus on biomass movement rates. We performed a simple linear regression to test the effect of prey mass (log-transformed) on total processing time (log-transformed). T-tests assuming unequal variances were used to compare rates of biomass movement by a single ant with rates of biomass movement by a group (i.e. ≥2 ants) for both g/min and g/min/ant. Using g/min and g/min/ant allowed us to analyze group prey biomass movement at both group and individual levels.

A Levene's test was used to analyze the variance in total biomass movement (g/min) between individuals and a group. One outlier was excluded from all statistical analyses because the single ant displayed a prey biomass movement rate (1.77 g/min) that was 984% greater than the mean prey biomass movement rate for a single ant. The mass of this prey item (0.85 g) was also the maximum processed by an individual ant. Data were analyzed using JMP 6.0.

RESULTS

Total processing time increased with prey mass (Log (time) = 2.9568519 + 1.3264649 Log (mass); r^2=0.88, $F_{1,16}$=118.80, P<0.0001; Fig. 1).

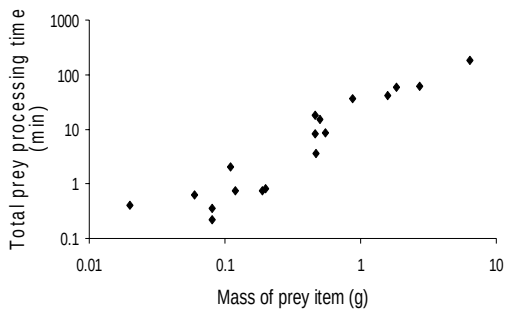

Figure 1. Total prey processing time (time from initial sting until all prey pieces arrived in the colony) increased with prey mass during 18 feeding trials of *Paraponera clavata*. *P. clavata* from a single colony were sampled 13-14 February at La Selva Biological Station, Costa Rica.

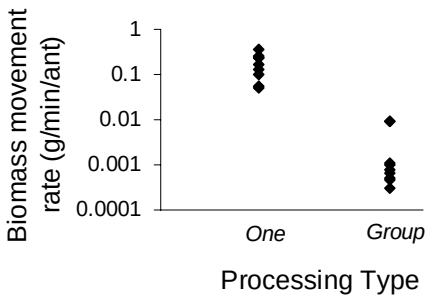

Figure 2. Mean prey biomass movement rate (g/min/ant) for processing by one bullet ant (*Paraponera clavata)* was approximately 7020% higher than mean prey biomass movement rate for ants in a group. N=9 for one ant (single ant moving prey item), N=9 for group (two or more ants working to move prey item). Prey was massed before each feeding trial, and time of movement was defined as time from first sting until final prey pieces arrived in the colony. Total number of ants in a group was the maximum number of ants processing the prey item at any given moment. Mean and SE are not shown due to distortion of these values when using a log scale. *P. clavata* from a single colony were sampled 13-14 February at La Selva Biological Station, Costa Rica.

The mean prey biomass movement rate (non-transformed) into the colony by a single ant (mean ± SD = 0.18 ± 0.10 g/min) was 447% greater than the total mean prey biomass movement rate by an ant group (0.04 ± 0.01 g/min; $t_{11.43}$=5.28, P=0.0002 for log-transformed data). The mean prey biomass movement rate per individual (non-transformed) for a single ant (0.18 ± 0.10 g/min/ant) was 7020% greater than the mean prey biomass movement rate per ant individual within a group (0.0026± 0.0038 g/min/ant; $t_{12.54}$=10.16, P<0.0001 for log-transformed data; Fig. 2). The variance of prey biomass movement rate (log-transformed; g/min) for a single ant was significantly higher than for a group ($F_{1,16}$=5.25, P=0.0358).

All whole prey items under 0.46 g were handled by a single ant. Between 0.46 and 0.85 g, processing type (i.e. single ant or group) varied. Above 0.85 g, all prey items were handled by a group and broken into segments.

DISCUSSION

Our data support our two predictions, (1) that *P. clavata* segmentation of prey and total prey processing time would increase with biomass and (2) that individual ants would have higher per ant biomass movement rates than groups of ants.

Prey processing time:

As prey size increased, the total processing time necessary to cut up a prey item and bring it into the nest also increased (Fig. 2). Although large prey items require both more workers for transport and more time to cut and transport prey, these larger prey items may be necessary to support the energy demands of the colony.

Biomass movement rate:

An important aspect in the survival of any ant colony is the rate at which its foraging workers can transport prey. Solitary ants were faster on average (0.14 g/min faster) at moving biomass into the nest than an entire group of ants (Fig. 2). A single worker was extremely efficient at moving prey biomass (0.18 grams/minute/ant faster) compared to ants foraging in groups. This much lower per-ant group foraging rate was due to four major social foraging inefficiencies. When foraging in groups, recruited ants (1) fought over prey items and (2) failed to locate prey accurately using pheromone trails of the recruiting ant. (3) *P. clavata* tended to over-recruit ants for prey processing and transport, leaving many ants without prey processing tasks. (4) In many cases, ants cut and transported leaves back to the colony. Ants apparently discovered later that the leaves were not food items and dropped them. More derived species have overcome these inefficiencies through complex pheromones, associated sensory systems, and divisions of labor (Brady 2003). The relative chaos of *P. clavata* social foraging is in stark contrast to the highly organized social foraging of many eusocial ant species.

Wilson and Hölldobler (2005) describe the "ponerine paradox" as "globally successful yet socially primitive." *Paraponera clavata* is a perfect example of this paradox: it is evolutionarily less derived and lacks the complicated social foraging strategies (e.g., complex pheromone communication, cooperative transport of prey) of other more developed ant lineages, such as the subfamily Ecitoninae (army ants; Wilson and Hölldobler 2005). Yet the high efficiency of *P. clavata* as solitary foragers may explain why they have persisted relatively unchanged for 100 million years (Wilson and Holldobler 2005). The long term availability and stability of the ecological niche occupied by *P. clavata* has allowed *P. clavata* to remain successful while other ants with more complex behaviors have diversified. Thus, *Paraponera clavata* may not have experienced strong natural selection for more complex foraging organization.

LITERATURE CITED

Baader A. P. 1996. The significance of visual landmarks for navigation of the

giant tropical ant, *Paraponera clavata* (Formicidae, Ponerinae). Insectes Sociaux 43: 435-450.

Bolton, B. 1995. A taxonomic and zoogeographical census of the extant ant taxa (Hymenoptera: Formicidae). Journal of Natural History. 1037-1056.

Brady, S.G. 2003. Evolution of the army ant syndrome: the origin and long-term evolutionary stasis of a complex of behavioral and reproductive adaptations. Proceedings of the National Academy of Sciences USA 100: 6575-6579.

Breed, M. D., T. M. Stiller, J. H. Fewell, and J. M. Harrison. 1991. Intercolonial interactions and nestmate discrimination in the giant tropical ant, *Paraponera clavata*. Biotropica 23: 301-306.

Breed, M. D., R. M. Bowden, M. F. Garry, and A. L. Weicker. 1996. Giving-up time variation in response to differences in nectar volume and concentration in the giant tropical ant, *Paraponera clavata* (Hymenoptera: Formicidae). Journal of Insect Behavior 9: 659-672.

Brown, B. V. and D. H. Feener. 1991. Behavior and host location cues of *Apocephalus paraponerae* (Diptera: Phoridae), a parasitoid of the giant tropical ant, *Paraponera clavata* (Hymenoptera: Formicidae). Biotropica 23: 182-187.

Dyer, L. 2002. A quantification of predation rates, indirect positive effects on plants, and foraging variation of the giant tropical ant, *Paraponera clavata*. Journal of Insect Science 2: 1-7.

Ehmer, B. 1999. Orientation in the Ant *Paraponera clavata*. Journal of Insect Behavior 12: 711-722.

Elahi, R. 2005. The effect of water on the ground nesting habits of the giant tropical ant, *Paraponera clavata*. Journal of Insect Science 5: 1-7.

Fewell, J. H., J. F. Harrison, J. R. B. Lighton, and M. D. Breed. 1996. Foraging energetics of the ant, *Paraponera clavata*. Oecologia 105: 419-427.

Hölldobler, B. and E. O. Wilson. 1990. The Ants. Harvard University Press.

Janzen, D. H, editor. 1983. Costa Rican Natural History. Chicago: The University of Chicago Press.

Nelson, C. R., C. D. Jorgensen, H. L. Black, and J. Whiting. 1991. Maintenance of foraging trails by the giant tropical ant *Paraponera clavata* (Insecta, Formicidae, Ponerinae). Insectes Sociaux 38: 221-228.

Thurber, D. K., M. C. Belk, H. L. Black, C. D. Jorgensen, S. P. Hubbell, and R. B. Foster. 1993. Dispersion and mortality of colonies of the tropical ant *Paraponera clavata*. Biotropica 25: 215-221.

Wilson, E. O. and B. Hölldobler. 2005. The rise of the ants: a phylogenetic and ecological explanation. Proceedings of the National Academy of Science USA 102: 7411-7414.