

The Economics of Optimal Foraging by the Red Imported Fire Ant

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Abstract

For social organisms, foraging is often a complicated behavior where tasks are divided among numerous individuals. Here, we ask how one species, the red imported fire ant (*Solenopsis invicta* Buren) (Hymenoptera: Formicidae), collectively manages this behavior. We tested the Diminishing Returns Hypothesis, which posits that for social insects 1) foraging investment levels increase until diminishing gains result in a decelerating slope of return and 2) the level of investment is a function of the size of the collective group. We compared how different metrics of foraging (e.g., number of foragers, mass of foragers, and body size of foragers) are correlated and how these metrics change over time. We then tested the prediction that as fire ant colonies increase in size, both discovery time and the inflection point (i.e., the time point where colonial investment toward resources slows) should decrease while a colony's maximum foraging mass should increase. In congruence with our predictions, we found that fire ants recruited en masse toward baits, allocating 486 workers and 148 mg of biomass, on average, after 60 min: amounts that were not different 30 min prior. There was incredible variation across colonies with discovery time, the inflection point, and the maximum biomass of foragers all being significantly correlated with colony size. We suggest that biomass is a solid indicator of how social taxa invest their workforce toward resources and hypothesize ways that invasive fire ants are able to leverage their enormous workforce to dominate novel ecosystems by comparing their foraging and colony mass with co-occurring native species.

Key words: biomass, collective behavior, colony size, invasive species, social insect

The act of searching for and acquiring food, or foraging, is one of the most quintessential behaviors that animals partake in to acquire the necessary nutrients that fuel their survival, growth, and reproduction (Stephens and Krebs 1986, Behmer et al. 2002, Simpson and Raubenheimer 2012). Foraging, however, often involves exploring spatially and temporally patchy environments where critical choices must be consistently made in order to maximize fitness—a task that can be both energetically costly (Fewell 1988, Rytter and Shik 2016) and potentially dangerous (Schmitz and Suttle 2001, Hermann and Thaler 2014). To predict and test how such foraging decisions are made, behavioral ecologists have often used optimality models where the costs and benefits of specific actions are contrasted to determine the point at which a currency like energy is maximized (MacArthur and Pianka 1966, Pyke et al. 1977, Stephens and Krebs 1986).

Since the mid-1960s (Emlen 1966, MacArthur and Pianka 1966), the body of literature covering optimality models, often under the umbrella of optimal foraging theory, has significantly expanded to

test different metrics of foraging behavior across a variety of taxonomic groups (Cowie 1977, Waddington and Holden 1979, Werner and Mittelbach 1981, Stephens and Krebs 1986, Perry and Pianka 1997, Brown et al. 1999, Simpson et al. 2004, Costa et al. 2008, Doniol-Valcroze 2011). One optimality model that garnered significant attention during this time was the marginal value theorem (MVT) as it posits how animals move through patchy environments in search of resources (Charnov 1967). The MVT focuses on predicting the optimal amount of time to spend in a patch before the ratio of energy gained (benefit) to energy used (cost) decreases to the overall average net intake for the entire habitat. That is, the MVT predicts when diminishing and accordingly marginal returns on an investment start to occur. Pyke (1978) tested the MVT with hummingbirds, finding that the optimal decision to stay or leave an inflorescence was predictable and a function of the number of flowers visited, the number of flowers available, and the amount of nectar obtained from the last flower. While the MVT has been useful in

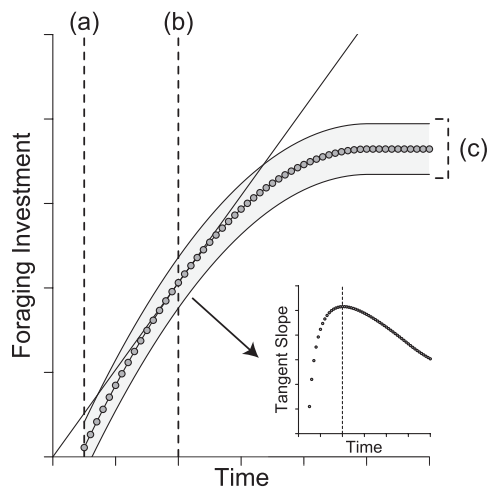


Fig. 1. Hypothetical plot of the Diminishing Returns Hypothesis which predicts that as time progresses, ant colonies should invest more workers until diminishing gains result in a decelerating slope of return. Vertical dashed lines represent two time periods, discovery time (a) and the inflection point (b), that are predicted to decrease with colony size while the amount of foraging investment is predicted to vary with colony size (c). The inflection point (b) represents the hypothetical time when colonial investment toward resources slows. We visualize the inflection point here as the time along the predicted logarithmic curve where the slope of the tangent line to the origin (0,0) no longer increases (inset plot; see Materials and Methods). Points along the curve represent hypothetical foraging investment (either foragers or biomass) as a function of time with a gray polygon signifying variation that may occur across colonies (c).

predicting when solitary animals should abandon low resource areas (Pyke 1978, Giraldeau and Kramer 1982, Parker 1992, Wajnberg et al. 2000), can optimality models like the MVT be leveraged to predict foraging behavior in social insect taxa?

Social insects such as ants, bees, termites, and wasps are well known for their complex societies and the important ecological functions they provide to many ecosystems (e.g., decomposition, pollination, and predation). Compared to solitary organisms, social insect groups are comprised of often specialized individuals that collectively work together while performing different tasks—brood care, defense, egg production, foraging, nest maintenance, scouting, etc.—as a ‘superorganism’ (Wheeler 1991, Hölldobler and Wilson 2009, Dornhaus et al. 2012). Groups, like individuals, can also have behavioral differences in aggressiveness, communication, foraging, and learning that promote unique personalities (Wray et al. 2011, Pinter-Wollman 2012, Jandt et al. 2014, Marting et al. 2017). Moreover, these behaviors are often modified by the overall size of the group (reviewed in Dornhaus et al. 2012). For example, foraging efficiency has been positively associated with group size, both theoretically and empirically, in Pharaoh ants (Beekman et al. 2001). In social insects, tests of optimality models have been successful in understanding foraging behavior [e.g., bumble bee departure decisions (Cibula and Zimmerman 1984), giving-up time variation in ants (Breed et al. 1996), and predation risk in termites (Korb and Linsenmair 2002)]. We posit, however, that optimality models like the MVT may not be well equipped to deal with the scenario of a continuous investment response in foraging that is unique to recruitment by social insects. Acknowledging the importance of size and sociality, we propose an analog to the MVT called the Diminishing Returns Hypothesis (see Fig. 1) which posits that for social insects 1) foraging investment levels increase until diminishing gains result in a decelerating slope of return and 2) this investment level is a function of the size of the collective group.

Here, we test the Diminishing Returns Hypothesis by exploring how colonies of the red imported fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae) (hereafter RIFA), apportion their workforce toward resources over time. RIFA is a model system to explore how collective foraging decisions are made by a social insect. From small incipient colonies to mature colonies containing over 250,000 individuals, RIFA ‘superorganisms’ can vary over five orders of magnitude in size within a given population (Tschinkel 2006). Additionally, RIFA’s worker caste is continuously polymorphic, facilitating the species’ ability to monopolize resources of varying size and nutritional quality (Greenberg et al. 1985, Hooper-Büi et al. 2002, Cook et al. 2010, Roeder and Kaspari 2017). To test the Diminishing Returns Hypothesis, we first compared how different metrics of RIFA’s foraging biology (e.g., number of foragers, mass of foragers, and average body size of foragers) are correlated and how these metrics change over time, suggesting mass as an alternative to the commonly used method of counting individuals. In a follow-up experiment, we then assessed parts 1) and 2) of the Diminishing Returns Hypothesis by quantifying the time it took RIFA colonies—varying 22-fold in size—to discover resources (Fig. 1a), the point at which colonies reduced the mass of foragers they were investing toward resources (hereafter the inflection point, Fig. 1b), and the maximum mass of foragers that colonies invested toward resources (Fig. 1c). We predicted that as RIFA colonies increase in size, both discovery time and the inflection point should decrease while a colony’s maximum foraging mass should increase. Such behavioral traits have undoubtedly aided RIFA in dominating disturbed landscapes (Lofgren et al. 1975, Porter and Savignano 1990, Wilder et al. 2011, LeBrun et al. 2012, Resasco et al. 2014), and we thus extrapolated our results to compare the foraging and colony mass of this invasive species to other native ant species as a potential mechanism for its dominance.

Materials and Methods

Study Site

All experiments were run at the University of Oklahoma Biological Station (Kingston, OK, 33.88°N, 96.80°W, 204-m elevation) during the summer months of June to August when RIFA is most active (Roeder et al. 2018). Data were collected in 2016 (experiment 1) and 2018 (experiment 2) on colonies that were at least 5 m apart. Yearly air temperatures range from -16.1°C to 44.4°C with a mean annual rainfall of 1027.94 mm (Oklahoma Climatological Survey). This location, while undergoing secondary succession after decades of row crop agriculture, is dominated by the monogyne form of RIFA (Roeder and Kaspari 2017).

Experiment 1: Determining the Best Metric for Quantifying RIFA’s Foraging Behavior

For 20 RIFA colonies, we assessed if the number of foraging individuals was correlated with the mass of those individuals to test if counts and mass could be used interchangeably when quantifying foraging behavior in ants. We did this by placing pieces of Bar-S hotdog (wet mass = 3.55 ± 0.05 g) into 50-ml centrifuge bait tubes. We positioned four of these bait tubes 0.5 m from the edge of each nest at the cardinal points, and retrieved one vial after 10, 20, 30, and 60 min. All bait vials were run at 25°C , a temperature that has been correlated with high RIFA activity at this location (Roeder et al. 2018). Ants were counted, dried at 60°C for 48 h, and weighed to the nearest 0.01 mg using an R 200D electronic semimicrobalance (Sartorius Research, Göttingen, Germany). We also determined if larger workers recruited to resources as time progressed by calculating the average body size of ants from each vial by dividing the foraging mass by the number of foragers. To test whether foraging behavior was consistent over time,

we used a different set of 10 RIFA colonies and placed one bait tube 0.5 m North of each colony, which was retrieved after 60 min. We repeated this single bait tube behavioral assay for five consecutive days, drying and weighing ants as described above.

Experiment 2: Testing the Diminishing Returns Hypothesis

Hypothesis

Using 24 different RIFA colonies, we tested the two predictions of the Diminishing Returns Hypothesis. First, we assessed if foraging investment, here reported as the mass of foragers, increased and then plateaued with time from when a resource became available. We did this by positioning six bait tubes that were identical to those used in experiment 1 (see description above), 0.5 m from the edge of each nest, collecting one vial at 10, 20, 30, 40, 50, and 60 min. All bait trials were run concurrently at 25°C. Collected ants were dried at 60°C for 48 h and weighed to the nearest 0.01 mg.

Second, we assessed whether colony size was a good predictor of three components of ant foraging behavior: the time required to first discover a bait tube, the point at which colonies reduced the mass of foragers they were investing toward resources (i.e., the inflection point), and the maximum mass of foragers on a bait at any given sample point. We estimated colony size by calculating mound volume in liters—which is highly correlated with a colony's biomass and can accordingly be used as a proxy for colony size (Tschinkel 2006, Roeder and Kaspari 2017)—using the equation for a prolate spheroid and then converting that value to mg using an equation from Tschinkel (1993). We quantified discovery time by placing a single bait tube 0.5 m directly North of each of the 24 colonies and recording the time at which the first ant forager appeared inside. These discovery ants were also dried and weighed as above. We estimated the inflection point for each colony using 7 time points and masses (i.e., the initial discovery point and the subsequent six 10-min sample intervals). Values were fitted to a logarithmic curve representing the prediction of a decelerating investment level (Fig. 1) and the logarithmic equation for each colony was used to calculate predicted values for each second from 1 to 3600, representing our 60-min trial period. A tangent line was created between the origin (0,0) and each predicted point to determine the time at which the slope no longer increased (Fig. 1b). The inflection point, in essence, represents the predicted time at which RIFA colonies slow the rate at which they allocate workers to a resource. Finally, we used the largest mass of foragers at any sample point to represent the maximum investment level by a colony.

Statistical Analyses

All analyses were run in R, version 3.5.3 (R Core Team 2019). Variables were checked for normality using the Shapiro–Wilk's test and log-transformed when non-normal. In experiment 1, the scaling exponent (hereafter b) of a log–log standardized major axis (SMA) regression was used to compare the number of foragers to their dry mass. Deviation from isometry was determined by comparing 95% CIs around the calculated slope to the predicted scaling exponent ($b = 1$). We next tested if the body size of foragers increased over time and whether the foraging behavior of RIFA was consistent across days using the nonparametric Friedman test with Nemenyi post-hoc comparisons controlling for colony identity. In experiment 2, we compared the mass of foragers across the six 10-min time intervals using the Friedman test with Nemenyi post-hoc comparisons controlling for colony identity. Ordinary least squares regressions were used to compare log-transformed variables (i.e., discovery time, inflection point, and the maximum mass of foragers) to estimates of colony size.

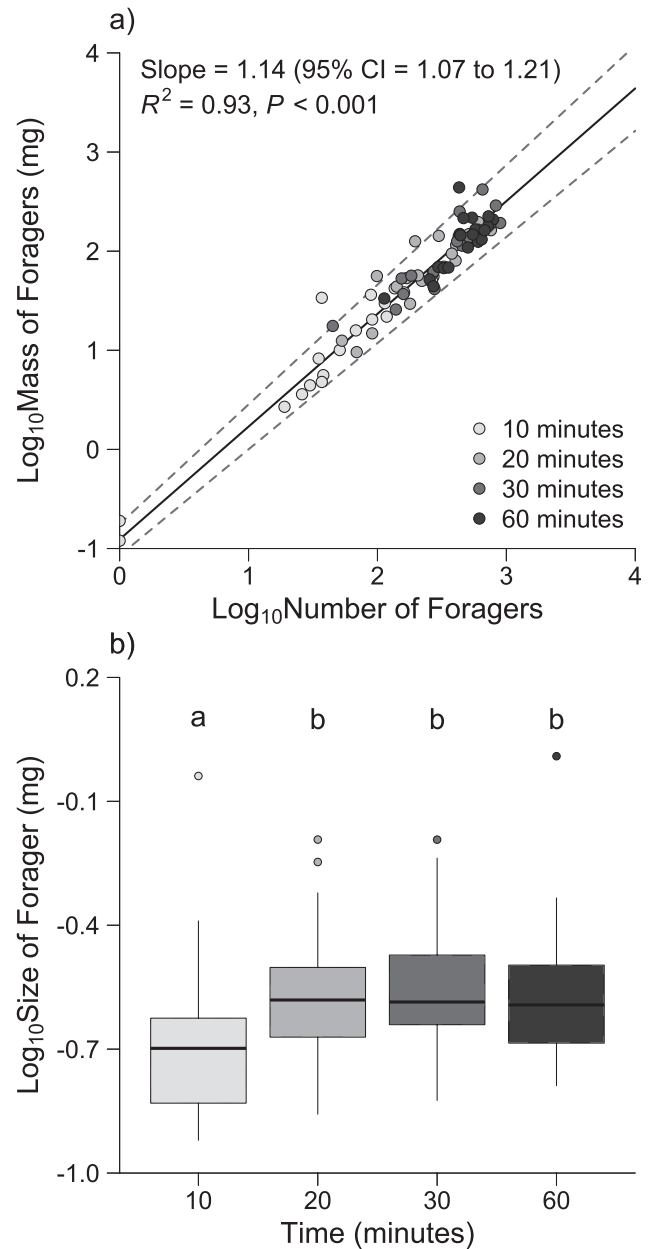


Fig. 2. Foraging metrics of the red imported fire ant (*Solenopsis invicta*; RIFA). Panel (a) shows the allometric relationship between the number of foragers and the biomass of those foragers while panel (b) shows the average body size of foragers across four time periods. Points in panel (a) are color coded to match the time period of collection. Box plots in panel (b) display the median, 25th and 75th percentiles with whiskers representing 1.5 times above or below the interquartile range. Letters above boxes indicate significant differences between time periods from Nemenyi post-hoc comparisons ($P < 0.05$).

Results

Experiment 1: Determining the Best Metric for Quantifying RIFA's Foraging Behavior

The number and mass of foragers RIFA colonies invested toward resources increased on average 428 and 578%, respectively, from 10 to 60 min (Fig. 2a). However, the exponent between these two variables was allometric ($b = 1.14$) as 95% CIs around the calculated slope did not overlap the predicted exponent of $b = 1$ (slope range = 1.07–1.21). That is to say, as time progressed, the mass of foragers became

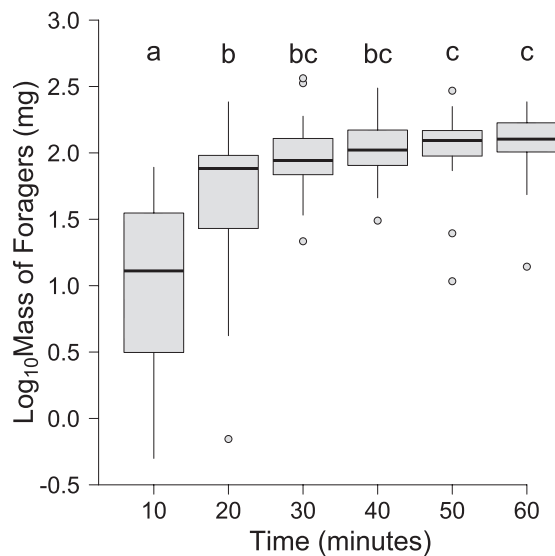


Fig. 3. Testing the Diminishing Returns Hypothesis by comparing the relationship between foraging biomass and time. The box plot displays the median, 25th and 75th percentiles with whiskers representing 1.5 times above or below the interquartile range. Letters above boxes indicate significant differences between time periods from Nemenyi post-hoc comparisons ($P < 0.05$).

greater than what was predicted given the number of workers collected. Indeed, the average body size of foragers increased 0.06 mg after the first 10 min ($\chi^2 = 25.62$, $df = 3$, $P < 0.001$) but remained relatively constant thereafter (Fig. 2b). Despite this variance, RIFA colonies apportioned similar amounts of foraging mass after 60 min across repeated sampling days ($\chi^2 = 5.92$, $df = 4$, $P = 0.205$).

Experiment 2: Testing the Diminishing Returns Hypothesis

Over 60 min, the average mass of foragers that colonies invested toward resources increased from 21.8 to 130.7 mg (Fig. 3; $\chi^2 = 63.55$, $df = 5$, $P < 0.001$). In congruence with the Diminishing Returns Hypothesis, this 500% increase primarily occurred within the first 30 min after which investment levels plateaued and only increased ca. 5% during consecutive sample periods (Fig. 3). There was, however, considerable intercolonial variation in foraging mass at 60 min (range = 13.9–242.4 mg) as colonies varied up to 22-fold in estimated size.

Each foraging metric was a function of colony size as predicted by the Diminishing Returns Hypothesis (Fig. 4). Discovery time and the inflection point decreased with colony size as the largest colony located baits 1.8 min faster ($R^2 = 0.14$, $P = 0.040$; Fig. 4a) and reached the inflection point 6.5 min faster ($R^2 = 0.15$, $P = 0.037$; Fig. 4b) than the smallest colony. The largest colony also invested 2.6-fold more biomass (+203.7 mg) toward baits across the 60-min trial ($R^2 = 0.30$, $P = 0.004$; Fig. 4c).

Discussion

Here, we tested the Diminishing Returns Hypothesis by demonstrating how ant colonies, varying 22-fold in size, optimize their foraging behavior by apportioning their workforce to resources over time. In doing so, we document an intriguing pattern: the foraging biomass of RIFA colonies 1) approached an asymptote within 30 min, 2) was consistent across multiple days, and 3) scaled with the size of the colony. Colony size—a potential analog to body size—may thus be

one of the most important biological traits shaping an organism's life-history and ecology for social taxa like ants (Kaspari and Vargo 1995, Shik 2008, Dornhaus et al. 2012, Burchill and Moreau 2016).

Optimal Foraging and Behavior in Ants

Most ant species are central place foragers that locate, recruit and collect resources within a given area (Traniello 1993, Lanan 2014). To test how colonies behave as a collective group, foraging studies have often focused on counting individuals that are visiting a bait or resource as a metric of recruitment (Human and Gordon 1996, LeBrun 2005, Lach et al. 2010, Bockoven et al. 2015). Yet, we posit that using counts of workers in isolation may be overlooking one important fact that is additionally useful for disentangling complex behavioral hierarchies in assemblages—biomass. As an example, imagine a *Camponotus pennsylvanicus* worker, a large bodied carpenter ant weighing 9.0 mg, compared to a single RIFA worker weighing 0.2 mg. It would take ~45 RIFA foragers to equal this single *Camponotus* worker in mass, yet in most behavioral studies that use counts these individuals would be considered equal. Counts of workers may also be confounded by polymorphic species like RIFA which recruit larger individuals over time for the defense and retrieval of food (Wills et al. 2018), a result we observed in our population that occurs after 10 min (Fig. 2b). We thus suggest that future behavioral studies on ants should at least consider biomass as one alternative to worker counts to better understand the foraging ecology of colonies or species.

In our study, RIFA performed as predicted by the Diminishing Returns Hypothesis. Colonies recruited quickly and in large numbers, reaching optimal investment levels within 30 min and maintaining that level of investment for the entirety of the observed period (Fig. 3). Such foraging patterns have been observed in other studies on RIFA, yet one novel aspect to our work is that we found the magnitude of the observed positive decelerating relationship was governed by colony size in a predictable manner across our measured population. However, the effect of colony size on discovery time and the inflection point, while significant, accounted for only 14 and 15% of the variation, respectively. One possibility for this discrepancy is that forager density may not positively scale with colony size. Previous work from Tschinkel (2011a) has shown that the density of foragers in a m^2 area actually decreases with colony size in the spring and there is no relationship between forager density and colony size in the fall. Discovery time and the inflection point may be decoupled from colony size if the density of RIFA scouts does not increase with the size of the colony. Alternatively, the relationship between discovery time/inflection point and colony size may have become more evident in our experiments than in Tschinkel's as we used bait stations that were close (0.5 m) to the mound instead of sampling forager density throughout a colony's territory. Nonetheless, we discuss three other factors likely to contribute to colony-level differences in foraging.

First, differential gene expression may occur that can be linked to foraging and other behaviors (Lucas and Sokolowski 2009, Ingram et al. 2016). For example, RIFA colonies with higher expression of the gene *sifor* have recently been shown to forage, explore, and recruit more to nectar than colonies with lower *sifor* expression (Bockoven et al. 2017). If *sifor* expression is variable across colonies in our population, it could be one reason why large amounts of variation in discovery time and the inflection point were observed for medium sized colonies (Fig. 4a and b). Second, nutrition may vary across colonies. In natural populations where RIFA have discrete territorial boundaries, certain nutrients may not be readily available

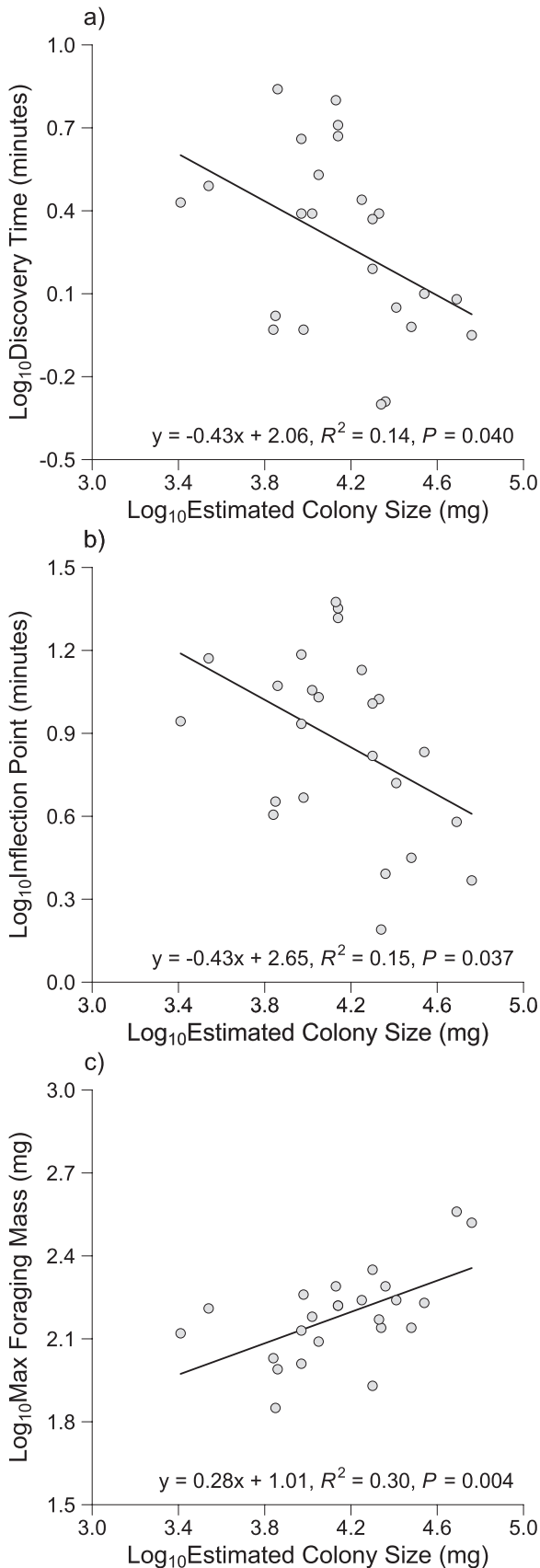


Fig. 4. Relationship between fire ant colony size and discovery time (a), the inflection point (b), and the maximum invested foraging biomass (c). Figures have inset linear equations and R^2 values. All regressions were significant at $P < 0.05$.

(Wilder et al. 2011, Roeder and Kaspari 2017). Colonies may thus invest a larger proportion of their workforce toward securing limiting resources (Dussutour and Simpson 2009, Wills et al. 2015, Prather et al. 2018). In our experiments, we used hot dog baits that were comprised primarily of lipids and proteins, but few carbohydrates. And although RIFA has been shown to aggressively forage on many different bait types (e.g., candy, cat food, cookies, crickets, hot dogs, sucrose solution, tuna fish; Morrison et al. 2000; Tschinkel 2006, Calixto et al. 2007; Wilder et al. 2013; Bockoven et al. 2015; Wills et al. 2015, Roeder et al. 2018), we cannot dismiss the fact that baseline nutritional status may be an important factor modulating foraging behavior. Third, colonies may exhibit distinct behaviors or behavioral syndromes. Species often have behavioral types where some individuals are consistently more aggressive across a variety of contests and tasks (Jandt et al. 2014). In ants, such types may result in colony-level personalities that are linked to different amounts of activity (Bengston and Dornhaus 2014, Marting et al. 2017), perhaps contributing to differences in foraging investment. These hypotheses are not mutually exclusive but suggest alternative mechanisms that could be considered for future research.

An additional aspect we have yet to discuss is that we focused here on a colony's response to baits that were consistent in size, consistent in quality, and that were placed close to the nest. However, in the giant tropical ant, *Paraponera clavata*, distance and resource amount are incredibly important factors determining recruitment (Fewell et al. 1992, Breed et al. 1996). Thus, while our study aimed to control these factors, both the amount of resources and the distance of those resources from the nest may impact not only our predictions and metrics of foraging but could likewise change how ants behave (e.g., cooperative food transfer occurring far from the nest but not nearby; Fewell et al. 1992).

Comparing RIFA Foraging and Colony Mass to Native Ant Species

To visualize what our results may mean for the local ant assemblage, we opportunistically collected 22 native ant species from the area surrounding the Oklahoma Biological Station (Supp Table 1 [online only]). This sample is equal to about half of the known species from Marshall County, Oklahoma where this study took place (Roeder and Roeder 2016). For each species, we aimed to weigh at least 25 workers and then collated colony sizes (i.e., number of ants per colony) from literature sources to create an estimate of colony mass for each species by multiplying the average individual worker mass by the colony size (Supp Table 1 [online only]). We then compared these estimated colony mass values to the average foraging and colony mass of RIFA. The results are shown in Fig. 5 and suggest that RIFA's foraging mass is greater than the estimated colony mass for 45% of the co-occurring native ant species (10 of 22), many of which are small myrmecines from the genera *Monomorium*, *Myrmecina*, *Pheidole*, *Strumigenys*, and *Temnothorax*. This foraging mass estimate for RIFA is also likely an underestimate of the total workforce as it represents only ca. 1% of a colony's total mass at a single resource (Roeder et al. 2018). The estimated average colony mass of RIFA, on the other hand, was greater than 95% of the co-occurring species (21 of 22)—the lone exception being the red harvester ant, *Pogonomyrmex barbatus*, whose workers are often 20-fold larger than RIFA. Taken as a whole, this result suggests that substantial biomass differences between invasive and native ants are likely one of the key reasons that species like RIFA are able to dominate novel environments (Porter and Savignano 1990, Wilder et al.

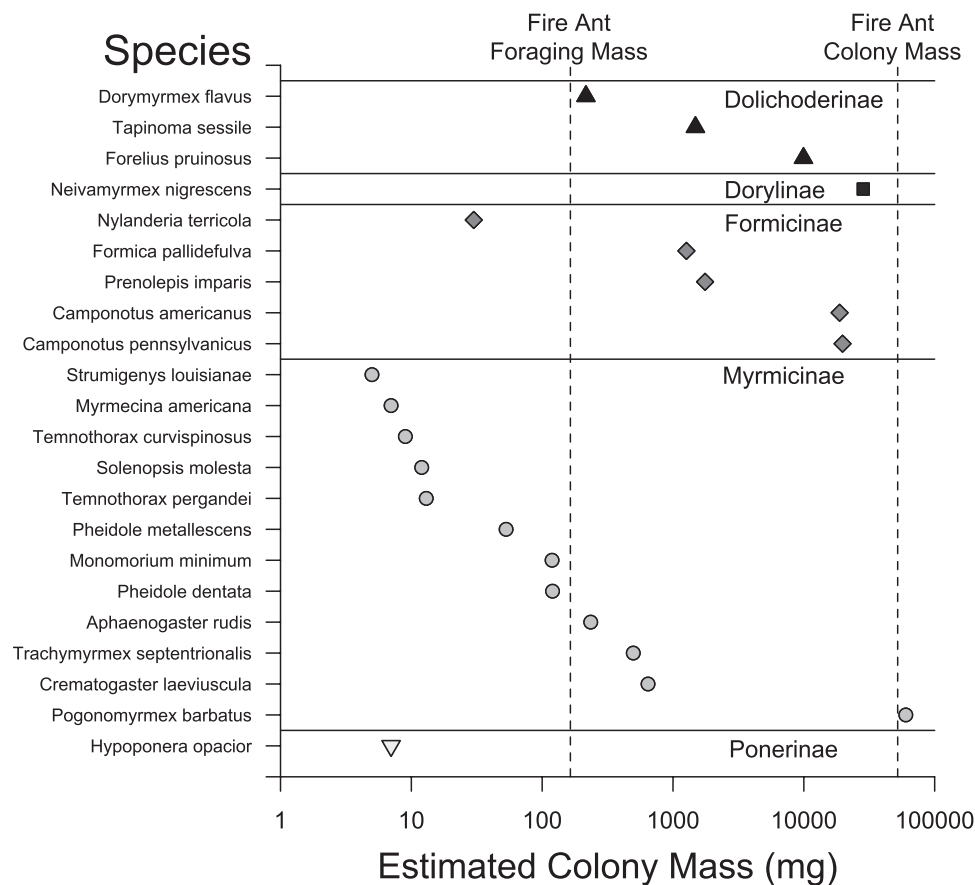


Fig. 5. Comparisons between red imported fire ants (*Solenopsis invicta*; RIFA) and native ant species in Oklahoma. Species are arranged top to bottom by estimated colony biomass within ant subfamilies [Dolichoderinae (upward facing triangle), Dorylinae (square), Formicinae (diamond), Myrmicinae (circle), and Ponerinae (downward facing triangle)]. The x-axis is on a \log_{10} scale. Dashed vertical lines represent either the average foraging biomass of RIFA from this study or the estimated colony biomass of RIFA. Values for worker masses and colony sizes are found in Supp Table 1 (online only).

2011, Resasco et al. 2014). When combined with bait discoveries under 3 min and peak investments in mass around 30 min, it should not be surprising that RIFA has thrived in human modified habitat across the southeastern United States (Vinson 1997, Eubanks et al. 2002, King and Tschinkel 2008, Bockoven et al. 2015, Roeder et al. 2018).

Conclusions and Future Directions

Social insects make up a large proportion of the animal biomass in many ecosystems (Hölldobler and Wilson 1990, King et al. 2013, Griffiths et al. 2018). Yet information on how, and how much, of that biomass is allocated toward behaviors like foraging is lacking for most species. We focused here on a well-known, dominant invasive as previous studies have created an extensive body of literature on fire ant natural history, enabling us to estimate important metrics like colony size (reviewed in Tschinkel 2006). In doing so, we have uncovered that RIFA, as a species, forages in a predictable way that is often determined by the size of the collective group. However, information on the natural history of most co-occurring ants that we found at our study site (Supp Table 1 [online only]) is lacking and thus it would be quite difficult to test our hypothesis for many of the native species. Previous commentaries have suggested a greater emphasis should be placed on the basic biology of social insects (Tschinkel 1991, Tschinkel 2011b), a sentiment that we echo. With more detailed information on the biology of ants, future research

could focus on quantifying intra- and interspecific differences in behavior to test if the observed foraging patterns here are consistent within and across species.

Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

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