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Towards a nutritional ecology of invasive establishment: aphid mutualists provide better fuel for incipient Argentine ant colonies than insect prey

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Abstract Many potential species invasions fail before establishment. This is likely especially true for invasive Argentine ants that must overcome a severe founding bottleneck and transition from propagules that rely on protein-rich prey to massive supercolonies that dominate by consuming carbohydrate-rich honeydew from hemipteran mutualists. While this dietary shift supports the classic idea that protein fuels early colony development and carbohydrates maintain adult workers, recent evidence suggests that carbohydrates can govern initial colony establishment. In this study, we use lab experiments to show that resources from aphid mutualists had greater benefits for Argentine ant propagule survival, maintenance, growth, and worker activity rates than did prey items. These effects persisted at low aphid densities, and when colonies were otherwise starved. Moreover, prey-starved colonies did not appear to consume aphids, suggesting that carbohydrate-rich honeydew is a mechanism that facilitates colony establishment. Combined, these results support a hypothesis that the dietary shift from prey to honeydew is driven more by increased access to hemipterans after establishment, than by specific benefits of prey early in colony development. The results highlight the important role of nutritional ecology for studying invasive establishment, linking propagule success not only to the supply of food resources, but also to their quality.

Keywords Dietary plasticity · Colony demography · *Linepithema humile* · Invasive species · Nutritional ecology

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Introduction

Many potential species invasions fail before establishment, during a period when propagules face severe demographic and ecological challenges (Simberloff 2009). Invasive ants exemplify this trend. While established colonies are some of the most dominant of all invasive organisms (Holway et al. 2002), ants are exceptionally vulnerable during the founding stage, when the loss of even a few workers can be fatal (Pontin 1960; Oster and Wilson 1978; Tschinkel 1992; Vogt et al. 2000; Johnson and Gibbs 2004; Frederickson 2006). However, some invasive colonies do overcome this founding bottleneck and proceed towards dominance over native taxa. And yet, because this establishment typically occurs hidden from view, much remains unknown about the underlying mechanisms.

The Argentine ant (*Linepithema humile*) is one of the most ubiquitous and destructive invasive ants

(Holway et al. 2002) and provides a model for studying the ecology of species invasions (Markin 1970; Bond and Slingsby 1984; Holway 1999; Christian 2001; Suarez et al. 2002; Sanders et al. 2003; Rodriguez-Cabal et al. 2009). Once established, they often form supercolonies with millions of queens and workers that lack nest boundaries (Holway et al. 1998; Giraud et al. 2002; Tsutsui et al. 2003). However, in contrast to the ecological dominance of supercolonies, small propagules perform poorly when facing resource limitation (Hee et al. 2000) and competition (Walters and MacKay 2005; Sagata and Lester 2009).

Newly arriving Argentine ants also feed at different trophic levels than established supercolonies, shifting over time, from protein-rich prey items to carbohydrate-rich honeydew provided by hemipteran mutualists (e.g. aphids, scale, mealybugs) (Tillberg et al. 2007). Indeed, established invasive ant populations are often most dense and ecologically destructive when fueled by hemipteran mutualists (Helms and Vinson 2002; O'Dowd et al. 2003; Abbot and Green 2007; Brightwell and Silverman 2011). However, experimentally provided carbohydrate-based resources are also sufficient to support the invasive spread of Argentine ants (Rowles and Silverman 2009). To understand this dietary plasticity, we develop hypotheses examining whether the early consumption of prey by arriving Argentine ants reflects dietary preference or limited access to hemipteran mutualists.

The capacity for rapid population growth following introduction is a trait shared by many successful invasive species. For a founding ant colony, this means rapidly producing new workers. We thus propose the resource preference hypothesis (RPH), based on the classic paradigm that protein fuels colony growth (brood production) and carbohydrates fuel colony maintenance (worker survival) (Sorensen and Vinson 1981). The RPH predicts that the delayed shift to carbohydrates reflects demographic shifts within colonies, from rapid production of brood after arriving, to maintaining adult workers once established. Alternatively, the dietary shift may reflect extrinsic ecological constraints. The resource limitation hypothesis (RLH) holds that arriving Argentine ants consume prey because they lack access to hemipteran mutualists that are either rare or guarded by resident ants. Indeed, carbohydrates appear to be important for early colony development in another hemipteran tending invasive ant, *Solenopsis invicta* (Macom and

Porter 1995; Helms and Vinson 2008; Wilder et al. 2011).

We test these hypotheses using controlled lab experiments on Argentine ant propagules. We examine how consuming insect prey and hemipteran-derived resources shape the following traits governing invasive establishment: survival, maintenance, growth, and activity rates. We further measure the strength of hemipteran-derived benefits by manipulating aphid densities. The resource preference hypothesis (RPH) would be supported if prey consumption maximizes performance—indicating that prey consumption helps newly arrived Argentine ants meet the nutritional demands of rapid brood production. In contrast, higher performance with access to aphid mutualists would support a basic prediction of the resource limitation hypothesis (RLH)—that newly arrived Argentine ants would rely on hemipterans if they had access.

Methods

Experimental setup

We collected Argentine ants from Research Triangle Park (NC, 35°51′N, 78°49′W) on June 4, 2011. Ants were extracted from leaf litter and maintained in the lab in fluon-coated containers with plaster nests and fed 25 % sucrose-water and German cockroaches, *Blattella germanica*. On July 7, 2011 we set up 60 incipient colonies, each with 1 queen, 50 workers and no brood, and allowed them to colonize plastic cups filled with potting soil and a 2 week old cotton plant (*Gossypium hirsutum*) inside a 19.4 L bucket lined with fluon®, and covered with a lid of fine mesh. While cotton plants have extra floral nectaries, they are present in low densities, such that nectary use by ants is minimal relative to aphid-derived honeydew (Powell and Silverman 2010; Wilder et al. 2011). After 3 days of acclimation, we inspected colonies for worker mortality and began the experiment (Day 1). All nests were stored in a climate controlled lab at 12:12 L:D, 26 °C, and 65 % RH.

We crossed three aphid densities (none, low, high) with presence/absence of ad lib prey items (freshly killed German cockroaches) using 10 colony replicates for each of the 6 aphid/cockroach combinations (N = 60). On Day 1, cotton plants in the low and high

aphid treatments were inoculated with 100 cotton aphids (*Aphis gossypii*). Cotton aphids are widespread plant generalists and known mutualists of Argentine ants (Mondor et al. 2008; Powell and Silverman 2010). Every third day, we (1) inspected Control plants to verify they lacked aphids, (2) culled all but 100 aphids from Low Aphid plants, and (3) counted all aphids on High Aphid plants to monitor population growth rates. During these checks, we also added 30 ml dH$_2$O to the soil of all plant cups, and 3 freshly killed cockroaches in a petri dish to nests in the +cockroach treatment.

Every 2 weeks, we planted three seeds of *G. hirsutum* in the soil of each cup to ensure aphids had ad lib plant material on which to expand their populations. We trimmed any plants that grew too large for nest chambers.

Insect prey, aphid mutualists, and colony establishment

We examined the effects of prey availability and aphid density on colony *survival* (queen mortality), *maintenance* (number and mass of surviving original workers), and *growth* (brood production). Mortality estimates were possible because workers removed dead ants to trash middens at the bottom of nesting buckets which we collected weekly and inspected for dead workers and/or the queen. After 40 days, we made a final check of the middens and then harvested all colonies by carefully spreading out the soil in a large fluoned tray. We collected and counted all workers, larvae, pupae, and queens and then weighed each colony component to the nearest 1 μg after drying at 65 °C for 24 h.

We assumed that dead workers in middens were initial colony members for two reasons. First, they were not produced during the experiment because each colony began without brood as in Hee et al. (2000), and development from egg to adult is ca. 40 days at 26 °C (Newell and Barber 1913). Second, some new workers were present on Day 40, but these were lightly colored 'callow' workers under 3 days old (Newell and Barber 1913) that we combined with pupae and larvae for estimates of brood production.

We used survival analyses (SAS Inst. V. 9.2, LIFETEST procedure) to analyze colony mortality because the data were right-censored (i.e. many queens remained alive on day 40). In this test, we computed nonparametric estimates of survival distributions and used log-rank tests to compare homogeneity of distributions across aphid/cockroach treatments. We used two-way ANOVAs to examine the effects of aphid and cockroach treatments on colony *maintenance* (mass of surviving workers on Day 40) and *growth*, estimating total brood production by summing the highly correlated dry masses of larvae, pupae and callow workers. In both ANOVAs, we dropped non-significant interactions from the model. We used post hoc Tukey tests to further examine treatment effects.

We also examined colony maintenance by analyzing the effects of aphid and cockroach treatments on weekly measures of worker survival using a two-way repeated measures ANOVA. The important terms in the analysis were the time by treatment interactions. A Mauchly's sphericity test was significant ($p < 0.0001$), so we used Huynh–Feldt adjusted probabilities when interpreting results. All means reported in text are followed by ±1 SD.

Aphid derived resources and behavioral tempo

Because carbohydrates in synthetic diets are known to increase Argentine ant aggression and activity levels (Grover et al. 2007; Kay et al. 2010), we tested how aphid derived resources, rich in carbohydrates, influence foraging activity, another behavior critical for colony establishment. On Day 1, we inserted a 30 cm long wooden dowel marked at 10 cm intervals and topped by a 2 cm × 2 cm foam platform into the soil of each nesting cup. After the first week and during the last week of the experiment (Day 8 and 36), we pinned a freshly killed cockroach to each platform and recorded the number of workers recruiting after 10 min (colony foraging), and then divided this by the number of workers alive in each colony (per capita foraging) as per Kay et al. (2010). Recruited workers were those above the 20 cm line on the dowel. We removed cockroaches immediately after trials to prevent workers from returning insect parts to the nest.

Within each of the 6 aphid/cockroach treatments, half the colonies received a pinned cockroach prey item (n = 5), and half (n = 5) an empty control pin. In this way, we tested whether recruiting workers were responding aggressively to the physical disturbance of inserting a pin in the platform (e.g. Grover et al. 2007), or whether workers actively foraged for the pinned prey item. We used a three way ANOVA to test for interacting effects of aphid treatment, cockroach

treatment and pin treatment on colony and per capita foraging activity.

Prey availability and the outcome of a conditional mutualism

We examined how prey limitation affects whether incipient colonies consume aphid honeydew or body tissue. Focusing on the High Aphid treatment, we used repeated measures ANOVA to compare aphid population growth rates when colonies were provided prey (+cockroach) and when they were otherwise starved of protein (−cockroach), interpreting the time by cockroach treatment interaction. The assumption of sphericity was rejected (Mauchly's test $p < 0.0001$), so we used Huynh–Feldt adjusted probabilities.

Results

Our results support the RLH. Aphid mutualists fueled colony establishment better than insect prey—even at low aphid densities, and when colonies were otherwise starved. First, access to aphids significantly increased colony survival at both High and Low densities relative to control (log-rank test, $p < 0.0001$), but prey items increased colony survival only in the absence of aphids (log-rank test, $p = 0.05$). This was because while 100 % of colonies survived with high aphid densities, and 95 % survived with low aphid densities (1 colony died in the low aphid, no cockroach treatment), only 60 % of colonies survived when deprived of aphids (2 colonies died with cockroaches and 6 without).

Second, colonies maintained significantly more of their initial worker biomass when provided aphids ($F_{2,55} = 66.16$, $p < 0.0001$), at both low (4.31 ± 1.49 mg) and high aphid densities (4.71 ± 1.68 mg) relative to the control (0.36 ± 0.68 mg) (Tukey test, $p < 0.05$) (Fig. 1). Overall, colonies provided prey items had greater surviving worker mass ($F_{1,55} = 4.17$, $p = 0.046$) due to marginally higher worker mass (4.95 ± 1.09 mg) relative to prey deprived colonies (3.66 ± 1.62 mg) within the Low Aphid treatment ($F_{1,19} = 4.33$, $p = 0.052$). While both resource types yielded significant results, examination of per-capita worker survival indicates the much stronger effect of access to aphids. There were relatively minor differences in worker survival with 50.6 ± 35.0 % and
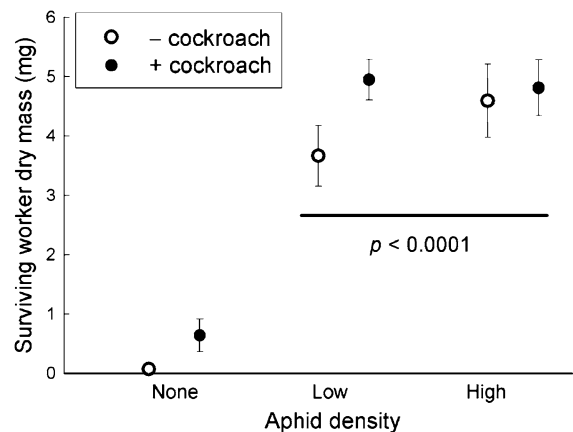

Fig. 1 Worker survivorship (the mass of initial workers alive by Day 40) was higher when colonies had access to aphids. Means plotted $\pm$1SE

without 43.4 ± 39.8 % access to cockroaches. In contrast, only 4.9 ± 9.0 % workers survived without access to aphids, compared to low (66.1 ± 24.4 %) and high (71.4 ± 27.5 %) high aphid densities. Viewed over time, the number of surviving workers was enhanced by access to aphid mutualists (two way repeated measures ANOVA day × aphid: $F_{12,336} = 43.98$; $p = 0.0001$) but not prey items (day × cockroach: $F_{6,336} = 2.42$; $p = 0.11$) (Fig. 2).

Third, resources from aphids significantly increased colony brood production ($F_{2,55} = 7.45$, $p = 0.001$) at both low (1.03 ± 1.21 mg) and high (1.24 ± 1.42 mg) aphid densities relative to control colonies that had no brood production (Tukey test: $p < 0.05$) (Fig. 3). Prey, in contrast, did not increase brood production ($F_{1,55} = 1.69$, $p = 0.20$).

After 1 week, colonies fueled by aphid honeydew, but lacking supplemental prey, had greater colony foraging (ANOVA Aphid × Roach × Pin type: $F_{2,47} = 4.66$; $p = 0.01$) and per capita foraging (ANOVA Aphid × Roach × Pin type: $F_{2,47} = 4.15$; $p = 0.02$) at pinned cockroaches (Fig. 4). However, by the last week, few workers foraged at platforms (Fig. 4), although they were observed patrolling leaves of cotton plants (see Supplementary Table S1).

Colonies starved of prey did not appear to switch from aphid honeydew to body tissue. Aphid populations grew the same in both + and −cockroach treatments ($F_{12,216} = 0.68$; $p = 0.69$), increasing significantly on all plants in the high Aphid treatment ($F_{12,216} = 13.29$; $p = 0.0001$). By Day 40, +cockroach
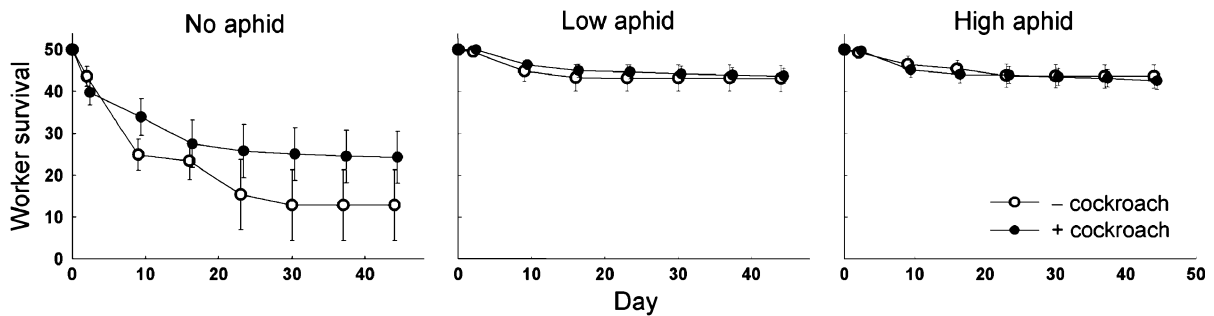
Fig. 2 Weekly measures of number of surviving workers were higher when colonies were provided aphids. Means plotted ±1SE
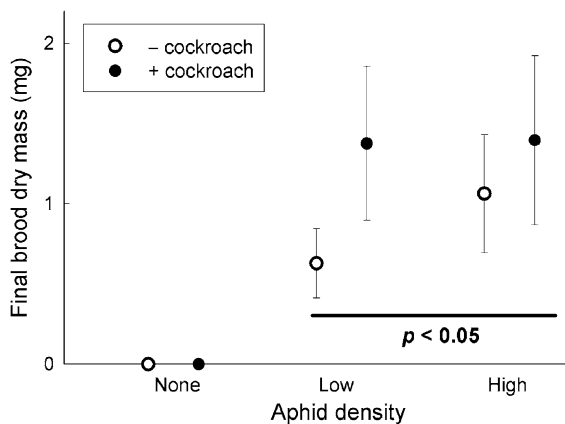

Fig. 3 After 40 days, colonies produced brood (larvae, pupae, callow workers) with access to aphids, but not prey. Means plotted ±1SE

plants had 811 ± 423 aphids, and −cockroach plants had 808 ± 522 aphids.

Discussion

Successful invasive establishment is governed not only by the supply of food resources, but also by their nutritional quality. This is especially true for newly arrived Argentine ants that must overcome a severe founding bottleneck, transitioning from protein-rich prey to carbohydrate-rich honeydew from hemipteran mutualists as they become established supercolonies. Our results support the RLH, suggesting this dietary shift is driven more by increased access to hemipterans after establishment, than by any specific benefits of prey early in colony development. Propagules had greater survival, maintenance, and growth with access to aphids relative to prey, even at low aphid densities, and even when propagules were otherwise starved.

Our results also suggest that aphid honeydew fueled higher worker foraging rates in the critical week following introduction. Thus, while invasive ant–hemipteran partnerships are typically studied long after establishment, the present study highlights the importance of studying the ability of small propagules to gain access to these mutualists shortly after arrival.

While protein is known to fuel brood production in ant colonies (Sorensen and Vinson 1981), colony growth in this study occurred with access to carbohydrate-rich aphid honeydew, but not protein-rich insect prey. A possible explanation is that colonies had limited ability to process harvested prey because they were introduced without brood, and larvae are both critical for processing solid food (Oster and Wilson 1978), and for helping colonies regulate subsequent nutrient intake and assimilation (Dussutour and Simpson 2009). However, adult workers provided only prey would still have access to cockroach hemolymph. In addition, higher queen survival when workers tended aphids outside the nest suggests that liquid resources could be transmitted throughout colonies soon after introduction, when few brood were present. This fuel from aphids also enabled workers to forage for prey at higher rates during this early establishment phase (Fig. 4). Further study will be needed to track the flow of aphid-derived resources among nestmates, within the social context of the nest.

The outcomes of mutualisms are dynamic and can vary depending on the life stage of the interacting partners, especially when long- and short-lived species interact (Bronstein 1994; Palmer et al. 2010). This is especially true for fast growing populations of soft-bodied aphids (Stadler and Dixon 2005; Mondor et al. 2008) and their partners, long-lived and well-defended ant colonies (Oliver et al. 2008). For the incipient colony propagules studied here, the benefits of

Fig. 4 The effect of aphid density, long-term cockroach prey availability, and pinned prey item on colony and per capita foraging rates during the first and final weeks of the experiment. To distinguish between aggressive response to pin placement and foraging for a prey item, colonies were either provided an empty pin (*P*) or a pinned cockroach (*C*). *Bars* show means ± 1 SE. During the first week, colonies with access to aphids, but starved of prey exhibited greater foraging responses at pinned cockroaches
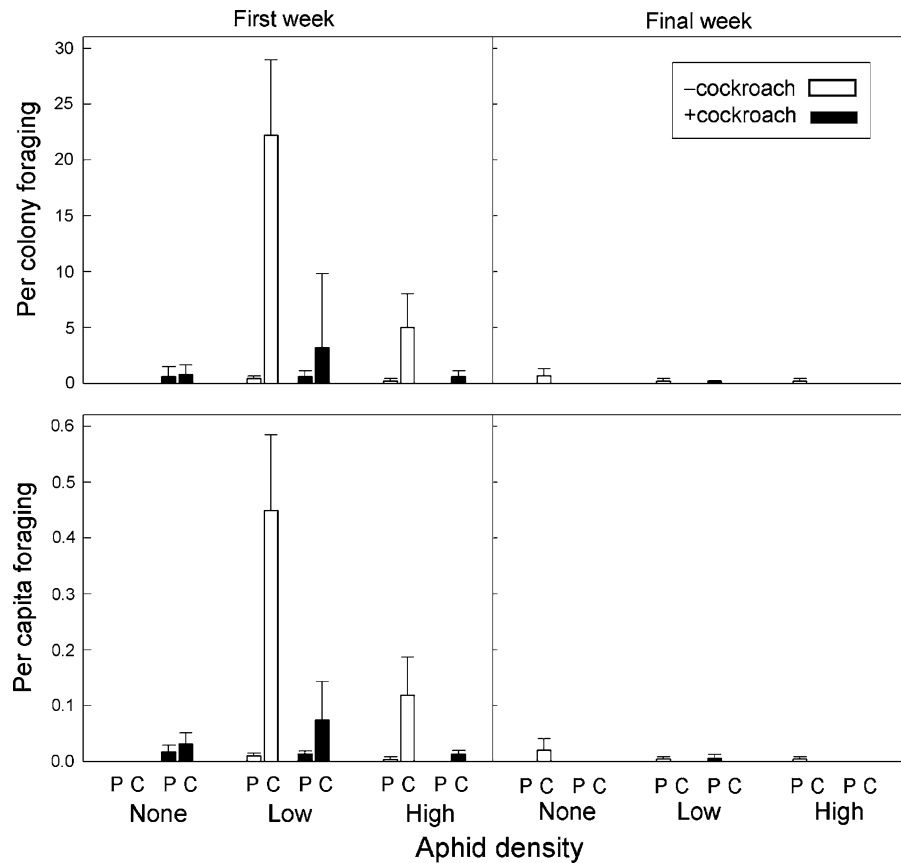
consuming aphid honeydew appeared to outweigh the benefits of consuming aphid body tissue. However, as colonies grow, their behavior towards aphids may increasingly depend on factors like the quality of aphid-derived resources (Cushman and Whitham 1991; Stadler and Dixon 2005) and the nutritional demands of reproductive allocation (Aron et al. 2001). In addition, the nutritional costs and benefits of consuming aphid body tissue or honeydew are also dynamic, as the chemistry of both can change in response to environmental conditions (Toft 1995; Yao and Akimoto 2002; Kay et al. 2004).

Support for the RLH is interesting, given that Argentine ants arriving in a new area tend to rely on prey items (Tillberg et al. 2007). Results from this study provide a framework for field studies examining how hemipteran access is shaped by propagule traits (e.g. worker number, brood availability, and connectivity to established supercolonies), as well as hemipteran density, and competition from resident ant

colonies. Towards developing a nutritional ecology of invasive establishment, it will also be important to overlay these interactions on a gradient of prey quantity and nutritional quality. It will be especially helpful to extend these observations further along the early invasion trajectory to test how the nature of conditional partnerships changes with colony size and demography.

The repeated formation of ant–hemipteran partnerships in invaded habitats across the planet (O'Dowd et al. 2003; Le Breton et al. 2005; Gaigher et al. 2011) places great importance on resolving how these associations with no co-evolutionary history initially form. Furthermore, once formed, how frequently do these partnerships shift from positive to antagonistic? Our results should spur such studies by helping to place these dynamic interactions in the context of early colony establishment, an especially vulnerable period in a colony's life history, and an especially important bottleneck determining subsequent invasive success.

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