

Research article

## Nest raiding by the invasive Argentine ant on colonies of the harvester ant, *Pogonomyrmex subnitidus*

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**Abstract.** Invasive ants often displace native ants, and published studies that focus on these interactions usually emphasize interspecific competition for food resources as a key mechanism responsible for the demise of native ants. Although less well documented, nest raiding by invasive ants may also contribute to the extirpation of native ants. In coastal southern California, for example, invasive Argentine ants (*Linepithema humile*) commonly raid colonies of the harvester ant, *Pogonomyrmex subnitidus*. On a seasonal basis the frequency and intensity of raids vary, but raids occur only when abiotic conditions are suitable for both species. In the short term these organized attacks cause harvester ants to cease foraging and to plug their nest entrances. In unstaged, one-on-one interactions between *P. subnitidus* and *L. humile* workers, Argentine ants behaved aggressively in over two thirds of all pair-wise interactions, despite the much larger size of *P. subnitidus*. The short-term introduction of experimental Argentine ant colonies outside of *P. subnitidus* nest entrances stimulated behaviors similar to those observed in raids: *P. subnitidus* decreased its foraging activity and increased the number of nest entrance workers (many of which labored to plug their nest entrances). Raids are not likely to be the result of competition for food. As expected, *P. subnitidus* foraged primarily on plant material (85% of food items obtained from returning foragers), but also collected some dead insects (7% of food items). In buffet-style choice tests in which we offered Argentine ants food items obtained from *P. subnitidus*, *L. humile* only showed interest in dead insects. In other feeding trials *L. humile* consistently moved harvester ant brood into their nests (where they were presumably consumed) but showed little interest in freshly dead workers. The raiding behavior described here obscures the

distinction between interspecific competition and predation, and may well play an important role in the displacement of native ants, especially those that are ecologically dissimilar to *L. humile* with respect to diet.

**Keywords:** Argentine ants, harvester ants, invasion, nest raiding, *Pogonomyrmex*.

### Introduction

The displacement of native ants is a well-documented effect of ant invasions (Hölldobler and Wilson, 1990; Passera, 1994; Holway et al., 2002). Competition for food is often considered important in such interactions (Porter and Savignano, 1990; Tennant and Porter, 1991; Human and Gordon, 1996; Holway, 1999; Morrison, 2000), but this explanation is limited to cases where invasive ants and native ants overlap in their use of food resources. Although omnivorous invasive ants undoubtedly compete for food against native ants with similarly broad diets, this mechanism provides a less compelling explanation for the displacement of ant species that primarily consume seeds (Erickson, 1971; Case, 2000). Learning more about interactions between invasive ants and granivorous ants seems important because seed-eating ants often fill ecologically important roles (Hölldobler and Wilson, 1990; MacMahon et al., 2000; Johnson, 2001), and the loss of harvester ants can indirectly affect a diversity of organisms, including plants (Bond and Slingsby, 1984) and vertebrates (Suarez and Case, 2002).

Nest raiding is one mechanism that may be relevant to the displacement of granivorous ants. The effects of raids require careful and prolonged observation because individual events may occur infrequently and unpredictably. Hook and Porter

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(1990), for example, documented raids conducted by the red imported fire ant, *Solenopsis invicta*, on a colony of *Pogonomyrmex barbatus* in central Texas. This *P. barbatus* colony lost an estimated 1200 workers to *S. invicta* over a period of seven weeks and was believed to die as a result of the attacks. In California we have observed the invasive Argentine ant (*Linepithema humile*) raiding the nests of native harvester ants (e.g., *Messor andrei*, *P. californicus* and *P. rugosus*) as well as those of native ants with more omnivorous diets (e.g., *Liometopum occidentale*, *Solenopsis xyloni* and *Tapinoma sessile*). Anecdotal reports also describe *L. humile* raiding nests of *Solenopsis geminata* in Hawaii (Fluker and Beardesley, 1972) and *Anoplolepis custodiens* in South Africa (DeCock, 1990). Raiding behavior is not unique to introduced populations of *L. humile*. In northern Argentina, for example, we have observed Argentine ants conducting raids on the nests of *S. invicta*. This latter observation suggests that raiding may have evolved as a result of intense interspecific competition.

Despite the potential importance of nest raiding, little is known about how this phenomenon might contribute to the loss of native ants. In this study we investigate raiding by Argentine ants on a native harvester ant, *Pogonomyrmex subnitidus*, in southern California. Although rigorous dietary studies for these two species do not exist, the potential for a large degree of resource overlap appears small. *Pogonomyrmex subnitidus*, like its congeners (MacMahon et al., 2000), appears primarily granivorous. Argentine ants, in contrast, consume a broad variety of food resources, often in liquid form (e.g., honeydew produced by Hemiptera) (Newell and Barber, 1913). Because *L. humile* feeds extensively on liquids, documenting the sources of food in its diet requires techniques other than simple inspection (see Tennant and Porter, 1991). Because we expect that *P. subnitidus* and *L. humile* overlap little in their use of food resources, nest raiding by Argentine ants may be largely responsible for the demise of *P. subnitidus* in areas invaded by *L. humile*. To learn whether or not this is the case, we address the following questions. (1) How common are raids on harvester ant colonies? (2) Compared to the native ant *Dorymyrmex insanus*, do Argentine ants act more aggressively toward harvester ants? (3) What short-term effects do raids have on harvester ant activity? (4) What is the extent of food resource overlap between harvester ants and Argentine ants? Answers to these questions would represent a first step in addressing a general but largely unexplored mechanism for the loss of native ants as a result of invasion by Argentine ants.

## Methods

### Study site

We conducted this study in 2002 and 2003 at the Torrey Pines State Reserve (TPSR) and adjacent open areas in coastal San Diego Co., CA (32°56 N, 117°15 W). Interior portions of TPSR still support native ants, but Argentine ants have extensively invaded the reserve's edges (King, 1999). Areas of overlap between Argentine ants and the harvester ant, *Pogonomyrmex subnitidus*, thus occur mostly within 200 m of the edge of TPSR.

### Observational surveys of raiding behaviour

To document seasonal variation in Argentine ant raiding behavior, we monitored 25 colonies of *Pogonomyrmex subnitidus* over a five-month period from Jan to May 2002. All *P. subnitidus* colonies were in open chaparral and interacted with Argentine ants at some point during the sampling period. We visited each colony several times a month, to determine if raids were occurring, and, if so, to estimate raid intensity (see below). During each visit we also measured ground temperatures in the immediate vicinity of each *P. subnitidus* colony.

Based on observations, we devised a qualitative scale to describe raid intensity. The scale takes into account the behaviors of both ant species as well as the relative numbers of workers within 3 m of the *P. subnitidus* nest mound. (1) Mutual Tolerance. Fewer than 25 Argentine ants are present and little interspecific aggression is evident. (2) Harassment. The number of harvester ants exceeds the number of Argentine ants. Argentine ants attack harvester ants, but these conflicts do not appear to disrupt harvester *P. subnitidus* activity. (3) Raid. The number of *P. subnitidus* approximately equals the number of Argentine ants. Argentine ants attempt to enter the harvester ant nest entrance and attack *P. subnitidus* workers involved in nest entrance plugging. A few harvester ants may be immobilized, and their activity may decline slightly. Argentine ants form at least one recruitment trail to the site. (4) Heavy raid. Approximately twice as many Argentine ants are present compared to the number of *P. subnitidus*. Harvester ant foraging activity appears reduced, and nest entrances are either closed or are in the process of being plugged. Argentine ants attempt to enter harvester ant nest entrances. Argentine ants form at least one recruitment trail to the site and have immobilized 5 to 10% of harvester ant workers present. (5) Severe Raid. Argentine ants outnumber *P. subnitidus* by a few hundred. Harvester ant foraging stops, and the majority of *P. subnitidus* either attempt to plug the entrance to their nest or grapple with raiders. Numerous Argentine ants enter the *P. subnitidus* nest entrance; many harvester ants are immobilized and some are dead as a result of the fighting. Argentine ants form at least one recruitment trail to the site.

### Unstaged behavioral interactions

To quantify how Argentine ants and native ants interact with harvester ants and vice versa, we observed the outcome of naturally occurring one-on-one interactions between two pairs of species: *P. subnitidus* and *L. humile*, and *P. subnitidus* and *Dorymyrmex insanus*. This latter species was the only common diurnally foraging native ant active in the study area that encountered *P. subnitidus* often enough for us to collect behavioral data. Although slightly larger than *L. humile* workers (c. 0.44 mg dry mass), *D. insanus* workers (c. 0.59 mg dry mass) are much smaller than *P. subnitidus* workers (c. 7 mg dry mass).

In 2003 we located 12 sites where *P. subnitidus* and *L. humile* occurred together and 10 sites where *P. subnitidus* and *D. insanus* occurred together. At each of the 22 sites, we recorded the outcomes of at least 25 unstaged, one-on-one interspecific interactions. The three focal species did not all co-occur at any site. At all sites the two focal species nested within 10 m of one another, and interspecific encounters took place often.

We classified behaviors resulting from one-on-one encounters into three categories: aggressive, defensive and neutral (Table 1). Aggressive behaviors were initiated by an attacker and directed at a recipient, often resulting in either injury or retreat. Attacks elicited defensive behaviors from the recipient. Neutral behaviors appeared neither defensive nor aggressive. Given the number of ants foraging at each site, it is unlikely that individual workers were included in more than one interaction. We excluded interactions that involved more than two individuals.

For each of the 22 sites we calculated the proportion of neutral, defensive and aggressive behaviors exhibited by each species. Two sets of data were collated: (1) the behavioral responses of *L. humile* and *D. insanus* when encountering *P. subnitidus*, and (2) the behavioral responses of *P. subnitidus* to encounters with the two smaller species. For statistical analysis, we considered the proportions of neutral, defensive and aggressive behaviors at each site as separate data points. We used two-

sample t-tests to compare the means of each behavioral category between *D. insanus* and *L. humile*. We arcsin-square root transformed proportions prior to analysis.

*Short-term introduction experiment*

Although raids appeared to increase the nest maintenance activity of *P. subnitidus* and to reduce foraging activity, the unpredictable timing of raids impeded our ability to quantify their short-term effects on harvester ant colonies. To learn more about these effects, we simulated raids by introducing experimental colonies of Argentine ants near actively foraging *P. subnitidus* colonies. Colony introductions of this kind (Bhatkar et al., 1972; Roubik, 1978; Schaffer et al., 1983; Torres, 1984; Human and Gordon, 1996, 1999; Thomson, 2004) are commonly used to study interactions between native and introduced social insects.

We collected Argentine ants used in this experiment from sites adjacent to TPSR. From this material, we constructed 10 experimental colonies. Each consisted of about 1500 workers, approximately 100 pieces of brood, and one queen housed in a round plastic container (28 cm in diameter). Each nest container held three nesting chambers: aluminum foil-wrapped test tub with 5 cm<sup>3</sup> of water plugged with cotton. We provided colonies with water *ad libitum* and fed them sugar water and domestic crickets (*Acheta domestica*) three times a week. Before use in experimental trials, we starved colonies for 48 h. Twenty-four hours prior to use in the field, we moved each experimental colony into a Fluon<sup>TM</sup>-lined container with same dimensions as the nest container. This field container had a hole drilled into the side through which a 30-cm length of plastic tubing was inserted to serve as an exit tube. Both ends of the tube were plugged until experimental trials took place. Each experimental colony was used once.

We selected ten colonies of *P. subnitidus* at TPSR for this experiment. All colonies were in close proximity to areas invaded by Argentine ants (King, 1999), but were not experiencing raids at the time of the experiment. Each harvester ant colony was observed for 2 days: a control (day 1) and a treatment (day 2). On day 1, the foraging and nest maintenance activities of harvester ants were observed in the absence of Argentine ants for 60 min. Day 2 trials resembled day 1 trials except that we introduced Argentine ants near the harvester ant nest mound. Control and treatment trials could not be randomized across the two days of the experiment because colony introductions appeared to reduce harvester ant activity over multiple days. Because we wanted to compare the for-

aging and nest maintenance activity of harvester ants in the presence and absence of Argentine ants, we minimized temperature differences between days by conducting trials on consecutive days and over similar temperature intervals (35°C–43°C).

For the two days of each replicate, we monitored harvester ant activity over a 60-min period. We centered a 25 x 25 cm quadrat on each *P. subnitidus* nest mound to delineate a focal area; this quadrat was elevated slightly so as to not obstruct foraging activity. Every 10 min, we counted the number of returning foragers, departing foragers and nest entrance workers. A returning forager was defined as a worker that entered the quadrat from a foraging trail and went directly inside the nest, whereas a departing forager was a worker that emerged from the nest and directly left the quadrat. A nest entrance worker was defined as a worker that was engaged in maintenance on the nest mound. Our estimate of nest entrance workers was the maximum present at any one time. We recorded ground temperatures every 10 min throughout each trial.

On the second day of each replicate, we placed an experimental colony of Argentine ants within 50 cm of a harvester ant nest mound. After observing harvester ants for 30 min, we opened the exit tube of the experimental *L. humile* colony and let Argentine ants explore the vicinity of the *P. subnitidus* nest mound. We were cautious to prevent the exit of *L. humile* queens or brood from nest containers. In the presence of workers, queens have the potential to establish new colonies, and brood may be reared into reproductive castes even in the absence of queens (Vargo and Passera, 1991; Hee et al., 2000; Aron, 2001).

For data analysis, we first divided the 10 min counts of each replicate into four bins: day 1 (0–30 min), day 1 (31–60 min), day 2 pre-introduction (0–30 min), and day 2 post-introduction (31–60 min). Within each category and replicate, we then averaged 10 min counts. Again for each replicate, we calculated the difference between means as follows: [day 1 (31–60 min) – day 1 (0–30 min)], and [day 2 post-introduction (31–60 min) – day 2 pre-introduction (0–30 min)]. These differences thus provide time-averaged estimates of how harvester ant activity changed during each replicate trial. Using paired t-tests, we compared differences across the two days of the experiment for returning foragers, departing foragers and nest maintenance workers.

Diet choice experiment 1 – harvester ant selected food items

The purpose of this experiment was to determine if Argentine ants retrieve food collected by harvester ants. In May 2003 we selected five active *P. subnitidus* colonies in TPSR. For each colony, we collected individual food items from approximately 40 returning foragers. Items (n = 204)

<b>Aggressive</b>	<b>Behavior of attacker</b>
<i>Bite</i>	Attacker bites recipient. Attacker may cling to recipient.
<i>Lunge</i>	Attacker increases speed of movement toward recipient, making physical contact. Attacker may deviate from original direction to lunge at recipient.
<i>Re-lunge</i>	After contacting recipient, attacker at first moves away but then moves back quickly and lunges at recipient.
<i>Climb</i>	Attacker climbs on top recipient.
<i>Tussle</i>	Attacker and recipient wrestle briefly (<5 sec) and then separate.
<b>Defensive</b>	<b>Behavior of recipient</b>
<i>Avoid</i>	A worker deviates conspicuously from original route, avoiding the ant she would have otherwise intercepted. No physical contact.
<i>Circle</i>	Physical contact. Recipient runs around rapidly in tight circles.
<i>Bounce</i>	Physical contact. Recipient "bounces" off of attacker and runs away.
<i>Speed up</i>	Physical contact. Recipient accelerates but continues in original direction.
<i>Struggle</i>	When attacker clamps down on recipient's antennae or legs, recipient tries to free herself with frenzied movements.
<i>Chemical</i>	When attacked, recipient directs tip of abdomen toward attacker.
<b>Neutral</b>	
<i>Contact</i>	Two workers make antennal contact and then separate.
<i>Ignore</i>	Two workers pass within 0.5 cm of one another without interacting.
<i>Pause</i>	One worker pauses within 0.5 cm of another worker.

**Table 1.** Behaviors observed in unstaged, one-on-one interspecific interactions between *Pogonomyrmex subnitidus*, *Dorymyrmex insanus* and *Linepithema humile*.

were pooled across colonies and then sorted into five categories: flowers (whole and parts), stems and leaves, seeds and pods, dead insects (whole and parts), and non-plant organic matter.

For presentation to Argentine ants, we placed food items in petri dishes (8.75 cm in diameter) with six holes (1 x 0.5 cm) cut into the sides. In each dish we drew a ring of five evenly spaced circles (1.5 cm in diameter) such that each circle was equidistant to the edge of the dish. Each of the five categories of food items was arranged inside one of the circles so that items in each food group occupied an approximately equivalent area on the floor of the petri dish. The spatial sequence of food groups in each dish was randomized in each trial.

We assessed the Argentine ant's preference for harvester ant selected food items at 8 sites. At each site we placed stocked petri dishes within 2 cm of a *L. humile* recruitment trail that led to a harvester ant mound where a raid of level 2, 3 or 4 was taking place. We conducted trials during raids to provide a relevant context for these choice tests. Argentine ants were allowed to enter each dish and to examine food items. We recorded all food items removed from petri dishes; items were not replaced or reused. Trials ended when no food was removed for 10 min.

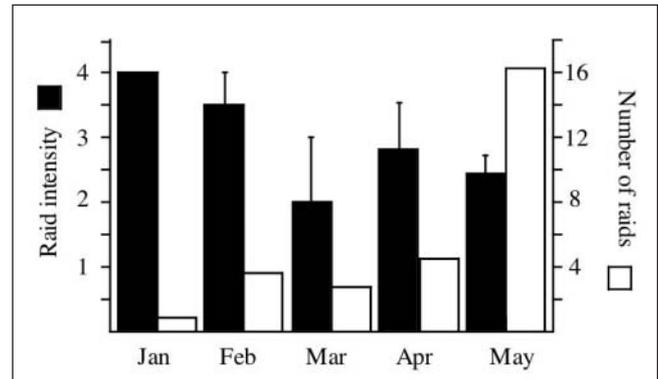
#### Diet choice experiment 2 – harvester ants

Here we assessed the Argentine ant's attraction to different developmental stages of *P. subnitidus*. We collected harvester ant larvae and pupae by excavating the surface layer of a *P. subnitidus* colony from Del Mar, San Diego Co., CA. Workers from this nest were also collected, both to care for the brood and for use in feeding trials. We again examined the Argentine ant's preference for harvester ant larvae, pupae and adults at sites where raids of level 2, 3 or 4 were taking place. We presented Argentine ants with freeze-killed harvester ants placed on a small plastic disc (3 cm in diameter). On each disc we placed one larva and two pupae and positioned the disc next to an *L. humile* recruitment trail and within 10 cm of their nest entrance. In a separate set of trials, we presented Argentine ants with two freeze-killed adult harvester ant workers in the same manner used to present brood. For all food items, we measured the time from discovery to the point at which food items entered the *L. humile* nest. Trials ended when all items were taken into an Argentine ant nest, or when items remained unmoved for 10 min. We conducted five trials for each food type (brood or adults) at ten separate sites.

## Results

### Observational surveys of Argentine ant raiding behaviour

Argentine ant raids on *P. subnitidus* colonies occurred often, but their frequency varied from month-to-month, reaching a maximum during the survey period in May (Fig. 1). All 25 of the monitored *P. subnitidus* colonies interacted with Argentine ants during the survey period with nearly half (12/25) experiencing heavy or severe raids at some point. One *P. subnitidus* colony succumbed to Argentine ants during the monitoring. At this site we observed consecutive severe raids accompanied by considerable harvester ant mortality, and then a sudden absence of all ant activity by either species anywhere in the vicinity of the former *P. subnitidus* colony. Many raids occurred in late afternoon or early evening when ground temperatures for both species were conducive to foraging (26°C–40°C). Typically, afternoon raids began with a group of Argentine ant workers congregating in the shade of vegetation near a *P. subnitidus* nest. As afternoon temperatures dropped, Argentine ants would push forward a loose, column-like trail onto the harvester ant nest mound. Raids



**Figure 1.** Seasonal variation in the frequency (open bars) and intensity (closed bars) of Argentine ant raids on colonies of the harvester ant, *Pogonomyrmex subnitidus*. Raid intensities estimated on a five-point scale: 1 = mutual tolerance, 2 = harassment, 3 = raid, 4 = heavy raid, 5 = severe raid. Each month the mean ( $\pm$  SE) raid intensity was estimated from the maximum observed raid level at each *P. subnitidus* colony averaged across all colonies raided. The number of raids equals the number of *P. subnitidus* colonies attacked in that month (out of 25 colonies).

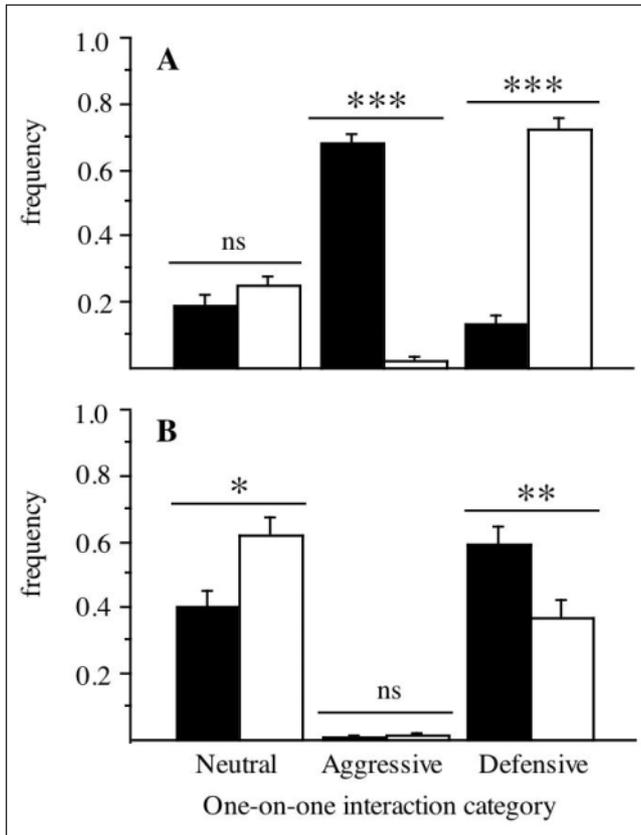
commonly involved multiple recruitment trails leading to the same mound. Upon reaching the nest mound, Argentine ants would disperse and move about erratically. The behaviors of the workers of both species during raids were predictable. Argentine ant workers commonly lunged at harvester ants, attempting to bite antennae, legs or petioles. Once an Argentine ant clamped down, the attacked harvester ant was likely to move slowly, or to pause to remove its adversary. This increased the chance that additional Argentine ants would attack that individual. Harvester ant workers impaired in this way could be overwhelmed and sometimes killed by groups of *L. humile*. Even during intense raids, harvester ants rarely initiated attacks against Argentine ants.

*Pogonomyrmex subnitidus* commonly plugged their nests in response to being raided. Plugging prevented other ants from entering the nest. Any *P. subnitidus* workers remaining on the surface after nest entrances were plugged were left to fend for themselves until the nest re-opened. Foragers that returned home to find nests closed often wandered about the mound still holding their food item. In some cases harvester ants trapped outside their nest would gather in a tight group near the nest entrance and try to wait out the raid.

In spite of witnessing numerous heavy and severe raids, we never observed Argentine ants removing any items from the nests of *P. subnitidus*. We often observed Argentine ants disappearing into the nest entrances of *P. subnitidus*, but these intruders were presumably unable to penetrate far enough into the nests to reach chambers containing brood.

### Unstaged behavioral interactions between species

One-on-one interactions between *P. subnitidus* and *L. humile* differed from those observed between *P. subnitidus* and *D. insanus*. Compared to *D. insanus*, *L. humile* acted aggressively



**Figure 2.** Mean (+1SE) frequencies of behavioral responses in unstaged, one-on-one interactions between workers. (A) Behaviors exhibited by *Dorymyrmex insanus* (open bars) and *Linepithema humile* (closed bars) in response to contact with *Pogonomyrmex subnitidus*. (B) Behaviors exhibited by *P. subnitidus* in response to contact with *D. insanus* (open bars) and *L. humile* (closed bars). Table 1 lists behaviors considered neutral, aggressive and defensive. Levels of significance are from two-sample t-tests: \* =  $p < 0.01$ , \*\* =  $p < 0.001$ , \*\*\* =  $p < 0.0001$ .

more often and defensively less often when contacting *P. subnitidus* (Fig. 2A;  $t^{20} = 16.235$ ,  $p < 0.0001$  (aggressive),  $t^{20} = 10.984$ ,  $p < 0.0001$  (defensive)). The frequency of neutral behaviors exhibited in encounters with *P. subnitidus* did not differ between *L. humile* and *D. insanus* (Fig. 2A;  $t^{20} = 1.565$ ,  $p = 0.1333$ ). Responses of *P. subnitidus* to *L. humile* and *D. insanus*, reflected the behaviors exhibited by the two smaller ant species. Compared to how it behaved when it met *D. insanus*, *P. subnitidus* acted defensively more often and neutrally less often when interacting with *L. humile* (Fig. 2B;  $t^{20} = 2.968$ ,  $p = 0.0076$  (defensive),  $t^{20} = 2.844$ ,  $p = 0.01$  (neutral)). *Pogonomyrmex subnitidus* rarely acted aggressively towards either *L. humile* or *D. insanus* (Fig. 2B;  $t^{20} = 0.257$ ,  $p = 0.7998$ ).

#### Short-term introduction experiment

Argentine ants exited nesting containers once released and investigated *P. subnitidus* nest mounds. Aggressive interactions may have occurred less often than would occur in a

naturally occurring raid, but Argentine ants nonetheless attacked harvester ant workers. Consistent with our observations of naturally occurring raids, Argentine ant introductions caused an increase in nest entrance activity and a decrease in foraging activity (Fig. 3). Compared to day 1 trials (controls), day 2 trials (introductions) had more nest entrance workers (paired t-test:  $t^9 = 5.431$ ,  $p < 0.001$ ), but fewer returning foragers (paired t-test:  $t^9 = 3.309$ ,  $p = 0.010$ ). In the presence of Argentine ants, nest entrance workers primarily engaged in nest entrance plugging.

#### Diet choice experiment 1 – harvester ant selected food items

Plant material represented 85% of food items, on average, retrieved by *P. subnitidus* at TPSR in May (Table 2). Not surprisingly, the most common items retrieved by harvester foragers were seeds and pods. *Pogonomyrmex subnitidus* workers also commonly brought flowers back to their nests. Non-plant material represented an average of 15% of food items selected. These items included non-plant organic matter (e.g., bird droppings) and insects (e.g., body parts of adult Diptera, Hymenoptera, Coleoptera and Lepidoptera).

When Argentine ants were presented with harvester ant selected food items, they quickly discovered and recruited to dishes. The length of trials averaged 33 min (range: 18–51 min). Of the five food types available, Argentine ants were primarily attracted to dead insects; on average, they removed 69% of all food items of this type presented to them, and dead insects represented 81% of all items removed (Table 2). Some dead insects that elicited obvious interest from Argentine ants were not removed due to their large size. By comparison, other food items appeared much less attractive to Argentine ants (Table 2). Overall, Argentine ants removed approximately 7% of the harvester ant selected food items made available to them.

#### Diet choice experiment 2 – harvester ants as food

Argentine ants recruited quickly and consistently to *P. subnitidus* brood. They moved 93% (14/15) of brood pieces into their nests within 36 min, on average. In the one case in which a brood piece (a pupa) was not completely moved, it became entangled in plant material. Compared to pupae, larvae were more difficult for Argentine ants to carry, and transport of either required at least 4 ants working cooperatively. In some cases pupae were dismembered for easier transport. Argentine ants showed less interest in adult *P. subnitidus* workers. Argentine ants moved 25% (2/8) of adults into their nests. All other adults were abandoned within 40 min.

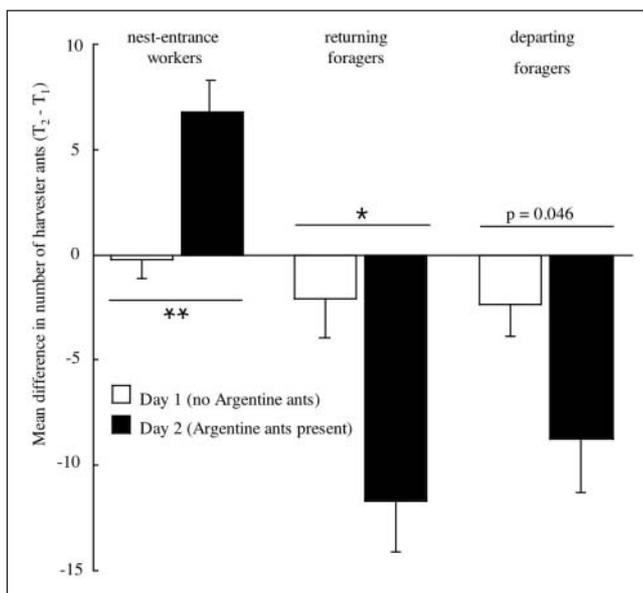
#### Discussion

Our observational findings document that Argentine ants commonly raid colonies of the harvester ant, *P. subnitidus*.

Food categories	Mean ( $\pm$ SE) proportion of food items obtained from harvester ants <sup>1</sup>	Mean ( $\pm$ SE) proportion of food items retrieved by Argentine ants ...	
		... in each food category <sup>2</sup>	... of total removed <sup>2</sup>
seeds + pods	0.47 $\pm$ 0.09	0.04 $\pm$ 0.02	0.13 $\pm$ 0.06
flowers	0.27 $\pm$ 0.05	0.02 $\pm$ 0.01	0.04 $\pm$ 0.09
leaves + stems	0.11 $\pm$ 0.03	–	–
non-plant	0.08 $\pm$ 0.01	0.03 $\pm$ 0.03	0.02 $\pm$ 0.02
insects	0.07 $\pm$ 0.03	0.69 $\pm$ 0.09	0.81 $\pm$ 0.08

**Table 2.** Results of diet-choice experiment involving food items obtained from *Pogonomyrmex subnitidus* workers and then presented to Argentine ants.

1. Proportions averaged across five *Pogonomyrmex subnitidus* colonies.
2. Proportions averaged across ten separate sites.



**Figure 3.** Mean ( $\pm$  1 SE) differences between the second 30-min period ( $T_2$ ) and the first 30-min period ( $T_1$ ) for each trial in the short-term introduction experiments. Differences are time-averaged estimates of the extent to which harvester ant activity changed during each 60-min trial. Levels of significance are from two-sample t-tests: \* =  $p < 0.01$ , \*\* =  $p < 0.001$ .

In the short term, raids reduce foraging activity and cause worker mortality. The cumulative effect of successive raids can lead to the demise of colonies; one such mortality event occurred during the course of our monitoring. Although mature colonies of *P. subnitidus* may sustain losses due to raiding, recruitment of new colonies may be limited in areas with Argentine ants. Human and Gordon (1996), for example, found that tethered *Messor andrei* gynes were quickly dispatched by Argentine ants. Their observation illustrates the difficulties faced by harvester ants attempting to found new colonies in areas occupied by Argentine ants.

Our results provide insight into the disappearance of harvester ants from areas invaded by Argentine ants (Erickson, 1971; Human and Gordon, 1996; Suarez et al., 1998). As noted by other authors (Erickson, 1971; Case, 2000),

competition for food resources seems like an unlikely explanation for the displacement of these largely granivorous ants. Although we found some evidence for resource overlap between *L. humile* and *P. subnitidus*, 81% of the items removed by *L. humile* were dead insects, which made up only 7% of harvester ant selected food items. Competition for nest sites also appears to be of minor importance. The open, sandy areas that *P. subnitidus* favors as nesting sites at TPSR are not used by Argentine ants for this purpose. Argentine ants were highly attracted to the larvae and pupae of *P. subnitidus*, suggesting that *L. humile* may raid harvester ant nests to prey on brood in the event that a harvester ant colony should become weak enough. Obtaining direct evidence for such an occurrence remains difficult owing to the sporadic occurrence of intense raids and the short amount of time presumably needed for Argentine ants to plunder a defeated colony.

The Argentine ant's raiding behavior provides an example of an interaction that appears to lie somewhere between interspecific competition and predation. Such interactions are not without precedent in ants (Hölldobler and Wilson, 1990). Raiding behavior probably acts in concert with the Argentine ant's strong competitive ability (Human and Gordon, 1996, 1999; Holway, 1999) to allow this invasive species to displace native ants. The function and importance of nest raiding deserves further study, perhaps especially in cases involving native ants that are ecologically dissimilar to *L. humile* with respect to diet.

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