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Consumption of introduced prey by native predators: Argentine ants and pit-building ant lions

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Abstract When populations of native predators are subsidized by numerically dominant introduced species, the structure of food webs can be greatly altered. Surprisingly little is known, however, about the general factors that influence whether or not native predators consume introduced species. To learn more about this issue, we examined how native pit-building ant lions (*Myrmeleon*) are affected by Argentine ant (*Linepithema humile*) invasions in coastal southern California. Compared to areas without *L. humile*, invaded areas contained few native ant species and were deficient in medium-sized and large bodied native ants. Based on these differences, we predicted that Argentine ants would negatively affect ant lion larvae. Contrary to this expectation, observational surveys and laboratory growth rate experiments revealed that *Myrmeleon* were heavier, had longer mandibles, and grew more quickly when their main ant prey were Argentine ants rather than native ants. Moreover, a field transplant experiment indicated that growth rates and pupal weights were not statistically different for larval ant lions reared in invaded areas compared to those reared in uninvaded areas. Argentine ants were also highly susceptible to capture by larval *Myrmeleon*. The species-level traits that presumably make Argentine ant workers susceptible to capture by larval ant lions—small size and high activity levels—appear to be the same characteristics that make them unsuitable prey for vertebrate predators, such as horned lizards. These results underscore the difficulties in predicting whether or not numerically dominant introduced species serve as prey for native predators.

Keywords California · *Linepithema humile* · Invasion · *Myrmeleon* · Predation

Introduction

Studies on biological invasions commonly address non-native species that either compete with native taxa or consume them. By comparison, much less is known about the importance of introduced species as prey for native consumers. When non-native species become common, however, they can serve as key sources of food (Maerz et al. 2005; King et al. 2006). Numerical responses of native consumers to subsidies of non-native prey can intensify levels of predation on native prey (Noonburg and Byers 2005) and even increase the prevalence of disease (Pearson and

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Callaway 2006). In other situations native species fail to consume introduced species. Novel defenses or inferior nutritional quality, for example, can reduce the suitability of non-native species as a resource (Suarez and Case 2002; Phillips and Shine 2006). Populations of native consumers can decline when unpalatable introduced species displace palatable native prey (Fisher et al. 2002).

Because consumers vary greatly in how they use resources, it may be difficult to predict whether or not native species will consume introduced species. In general the relative importance of native species versus introduced species as prey will depend on (1) specific qualities of the consumer, and (2) characteristics of the native and introduced prey species that affect the costs and benefits of capture and consumption. The success of efforts to place introduced species in a food web context hinges on a clearer understanding of these issues.

In this study we examine how native pit-building ant lions (*Myrmeleon exitialis* and *M. rusticus)* are affected by changes in their prey base caused by Argentine ant (*Linepithema humile*) invasions. Ants are important prey for pit-building ant lions (Wilson 1974; Topoff 1977; Griffiths 1980; Gotelli 1996; Morrison 2004), and the displacement of native ants by *L. humile* could negatively affect ant lions several ways. First, ants present in invaded areas consist mostly of small-bodied Argentine ants. The loss of large and medium-sized ants may reduce the growth and survival of larval ant lions because second and third instars commonly consume relatively large prey (Wilson 1974; Heinrich and Heinrich 1984). Although the ability of larval ant lions to capture prey decreases with increasing prey size (Wilson 1974; Griffiths 1980; Gotelli 1996), the energetic value of individual prey items often increases with increasing prey size (Griffiths 1980). Second, some areas invaded by *L. humile* have few ants of any kind in summer when larval ant lions (and many native ants) are most active. This pattern results from the Argentine ant's vulnerability to desiccation (Holway et al. 2002; Schilman et al. 2005) and from its nomadic behavior. Exposed areas adjacent to water sources, for example, may lose native ants as a result of Argentine ant presence during winter and spring. As conditions become drier in summer, *L. humile* often retreats to contiguous mesic areas, leaving formerly invaded areas with few, if any, ants (Markin 1970; Holway and Suarez 2006). In such circumstances larval ant lions would face periods of reduced food availability if they were unable to switch to alternative prey.

Here we test how changes in the availability and size of ant prey caused by *L. humile* invasions affect *Myrmeleon exitialis* and *M. rusticus*. We conducted an observational survey, a lab experiment, and a field transplant experiment to test if differences in the types of ant prey available (i.e., Argentine ants versus native ants) reduce the growth rate and survival of larval *Myrmeleon*. In addition, we compare the ability of *Myrmeleon* larvae to capture *L. humile* and *Dorymyrmex insanus*, a common native ant species, to determine if these species differ in capture susceptibility. This study represents a unique attempt to understand how the behavioral and ecological characteristics of native predators and their introduced prey contribute to patterns of prey consumption in the context of a widespread biological invasion.

Materials and methods

Study site and system

We conducted fieldwork in 2003 and 2004 at Torrey Pines State Reserve (TPSR) in coastal San Diego Co., CA (32°56′N, 117°15′W). Vegetation at TPSR consists primarily of chaparral and coastal sage scrub with open stands of Torrey Pine (*Pinus torreyana*). Argentine ants displace nearly all above ground foraging native ants in San Diego (Suarez et al. 1998; Holway 2005) and have invaded portions of TPSR (Carney et al. 2003; Zee and Holway 2006).

We detected two species of *Myrmeleon* at TPSR: *M. exitialis* and *M. rusticus*. Vouchers of both are deposited at the Texas A&M University Insect Collection (TAMUIC). Differences in wing veination can be used to separate adults of the two species, but diagnostic larval characters are not known (J.D. Oswald, pers. comm.). By rearing larvae from known locations to maturity, we discovered that the two species occupy different parts of TPSR. While larvae of both species were common in open, sandy areas, *Myrmeleon exitialis* occurred primarily at disturbed sites (e.g., along roadsides) and was the only species collected at UC San Diego, 5 km south of TPSR.

We detected *M. rusticus* only in the interior of TPSR. Like other pit-building ant lions (Griffiths 1980; Arnett and Gotelli 1999), *M. exitialis* and *M. rusticus* larvae pass through three larval instars. First-instar larvae appear in mid-summer, pit-building activity is most conspicuous between June and October, and larvae over winter.

Observational survey

In October 2003 we measured body weights and mandible lengths of larval *Myrmeleon* in TPSR to determine if larvae from areas with native ants differed in size, on average, compared to larvae from areas with *L. humile*. We focused on body size for two reasons. First, in other pit-building ant lions, larval weight correlates positively to adult body size, adult fat content and egg size (Griffiths 1985). Second, larval body size is positively related to starvation resistance in other *Myrmeleon* (Arnett and Gotelli 2003). Because larvae of the two *Myrmeleon* species cannot at present be distinguished in the field, we restricted our sampling to areas in TPSR where we detected only *M. rusticus*. It is possible that a few *M. exitialis* were present in these samples.

We collected single larvae from each of 110 sites separated by at least 20 m. Larvae were weighed and measured in the lab and were returned to their original locations after we conducted pitfall trapping. We placed three pitfall traps in the configuration of a triangle (with sides 3 m in length) centered on the pit where we collected each larva. Traps consisted of 35 ml plastic vials containing 15 ml of non-toxic saline detergent solution and remained in the ground for 72 h.

Using ants captured in pitfall traps, we constructed frequency distributions of mean worker head lengths for species in invaded and uninvaded areas (Table 1). Specimens came from the 110 sites where we collected larval ant lions and from 54 additional sites at TPSR where the species identity of ant lion larvae was uncertain. We placed three traps per site and used the same total number of traps in invaded sites ($n = 246$) as in uninvaded sites ($n = 246$). For all ant species we measured head lengths for only one worker per site. For common species, we measured individual workers from at least 15 different sites; for less common species we measured workers from all (or nearly all) sites where that species was found. We considered head length to be the maximum distance from the apex of the head to the anterior-most margin of the clypeus (Kaspari and Weiser 1999). For *Pheidole*, which usually have a dimorphic worker caste, we measured only minors. Voucher specimens of all ants are deposited in the Bohart Museum of Entomology, University of California, Davis (UCDC).

From measurements made in the lab, we first categorized ant lion larvae by instars. Instar designations were made based on frequency distributions of mandible lengths. We then used 2-way analysis of variance (ANOVA) to compare larval weights by instar between invaded sites ($n_{\text{instar1}} = 6$, $n_{\text{instar2}} = 19$, $n_{\text{instar3}} = 9$) and uninvaded sites ($n_{\text{instar1}} = 8$, $n_{\text{instar2}} = 59$, $n_{\text{instar3}} = 9$). These sample sizes are uneven because we excluded invaded sites at which the species of ant lion was uncertain. We used analysis of covariance (ANCOVA) to test if ant lions from invaded and uninvaded sites differed with respect to mandible length; larval weight was treated as a covariate. In both analyses, we log transformed weight and mandible length data prior to analysis.

Lab growth rate experiment

In this experiment we tested if the growth rates of *Myrmeleon* larvae depend on the ant species available for consumption. We collected 20 *M. exitialis* larvae (all second instar) from a *Eucalyptus* grove at UC San Diego in spring 2004. We used *M. exitialis* in this lab experiment because we did not receive permission to remove larval *Myrmeleon* from TPSR, which was the only site where we found *M. rusticus*. We randomly assigned larvae to a diet of either *Dorymyrmex insanus* ($n = 10$) or *L. humile* ($n = 10$). Like *L. humile*, *D. insanus* is in the subfamily Dolichoderinae and both species have relatively small, comparably sized, monomorphic workers. Moreover, *D. insanus* is common at TPSR (Carney et al. 2003, Zee and Holway 2006) in sandy areas favored by *Myrmeleon*.

We reared each *Myrmeleon* larva and their ant prey in a 3-l plastic container filled with 1.5 l of sieved dirt obtained from the collection site. Containers were kept at 23°C and exposed to an ambient photoperiod. To prevent ants from desiccating, each container contained a small test tube (12 × 75 mm), half filled with water and plugged with cotton. The rims of all containers were lined with Fluon$^{\text{TM}}$ to

Table 1 Native ants from Torrey Pines State Reserve at sites with pit-building *Myrmeleon*

Species	Percent occurrence at sites without *L. humile* (n = 82)	Percent occurrence at sites with *L. humile* (n = 82)
Camponotus dumetorum	1.2	0
Camponotus festinatus	2.4	0
Crematogaster californica	23.2	0
Dorymyrmex insanus	20.7	2.4
Formica francoeuri	4.9	0
Formica moki	3.7	0
Monomorium ergatogyna	1.2	0
Myrmecocystus testaceus	8.6	0
Neivamyrmex nigrescens	1.2	0
Neivamyrmex opacithorax	1.2	0
Pheidole pilifera	3.7	0
Pheidole hyatti	6.1	0
Pheidole vistana	25.6	0
Pogonomyrmex subnitidus	6.1	0
Prenolepis imparis	15.9	2.4
Solenopsis amblychila	4.9	0
Solenopsis molesta	13.4	28.0
Solenopsis xyloni	58.5	0
Tapinoma sessile	3.7	0
Temnothorax andrei	14.6	17.1

prevent ants from escaping. To stimulate ant foraging, we placed a few drops of sugar water (20% sucrose) on a 1-cm^2 piece of foil in each container daily. We began the experiment by adding 0.03 g of living workers of one of the two ant species to each container. This mass of ants equated to approximately 75 *L. humile* or 50 *D. insanus*. At 14-day intervals, we removed any remaining ants, weighed and measured the mandibles of each ant lion, and added another 0.03 g of ants. After 6 weeks, we estimated the daily growth rate of each ant lion (after Griffiths 1980) as follows: [ln (end weight)−ln (initial weight)]/(42 days) and used separate two-sample t-tests to compare growth rates and mandible lengths across the two diet treatments. All larvae were reared to adulthood and then vouchered.

Field transplant experiment

In spring 2004 we developed a field protocol for measuring the growth of individual ant lion larvae. At each of 10 sites at TPSR (five invaded sites and five uninvaded sites), we placed five ant lion enclosures 1–2 m apart in a circle. Enclosures consisted of sections of PVC pipe (15.2 cm in diameter and 5.1 cm long) buried such that soil levels inside enclosures were 2.5 cm lower than those outside. Ants freely entered and left enclosures, but ant lions could not climb out. After installation, we left enclosures for several days to eliminate any "digging in" effect.

In May 2004 we stocked each enclosure with one 3rd instar *M. rusticus* from TPSR. Every 14 days we removed each ant lion from its enclosure and weighed it on a field scale (Ohaus Navigator$^{\text{TM}}$). Larvae were then returned to their enclosures. We excluded larvae that disappeared from enclosures (n = 6) or that turned out to be *M. exitialis* (n = 1) from all analyses. We continued the experiment until all larvae pupated; this took approximately 84 days. All pupae were reared to adulthood and then vouchered.

Third instar larvae developed rapidly. After 28 days, over 50% of larvae at 7 out of the 10 sites had pupated. For this reason we made the following comparisons. We used a two-sample t-test to compare larval growth rates at invaded and uninvaded sites after 28 days. We estimated daily growth as follows:

[ln (end weight)−ln (initial weight)]/(28 days). Data points in this analysis were mean growth rates at each site. After 42 days, we used a two-sample *t*-test to compare the proportion of larvae that had pupated at invaded versus uninvaded sites. These proportions were arcsin square-root transformed prior to analysis. We also used a two-sample *t*-test to compare pupal weights between invaded and uninvaded sites.

Susceptibility to capture experiment

Growth and survival for sit-and-wait predators, such as *Myrmeleon*, may be strongly influenced by the relative ability of different prey species to elude capture. In November 2004 we tested whether or not Argentine ants differ from *Dorymyrmex insanus* in their susceptibility to capture. We placed individual workers into field enclosures containing a single larval ant lion. Enclosures consisted of sections of PVC pipe (15.2 cm in diameter and 5.1 cm long) partially inserted into sandy ground. We coated the inner rim of each pipe with Fluon^{TM} to prevent ants from escaping. Prior to introducing ants into enclosures, we gave ant lions 24 h to construct pits.

Ants used as prey came from colony fragments collected from the field. We kept each fragment in a plastic nest container (as in Thomas et al. (2005)) in the lab until needed. For each colony fragment we tested 6–7 individual workers against larval ant lions; we used larvae only once. All ant lion larvae ($n = 84$) were collected from TPSR and were in their second instar. We randomly assigned larvae to treatment group. Most larvae used were probably *M. rusticus*, but a few may have been *M. exitialis*. No obvious differences in larval size or pit diameter were noted. For these reasons, it seems unlikely that our uncertainty about species identity represents a bias.

We assessed capture vulnerability as follows. To reduce the extent to which ants became disturbed, we let each worker walk onto an index card (6 × 8 cm) placed inside the nest container and then walk off the card onto the floor of the enclosure. After each ant was introduced, we recorded whether or not it had been captured after 30 min. We calculated the proportion of ants eaten out of those tested from each colony fragment and then arcsin square-root transformed these proportions. We used a two-sample *t*-test to make an interspecific comparison.

Results

Observational survey: ants

Ant communities in areas invaded by Argentine ants at TPSR were species poor compared to areas that lacked *L. humile*. We detected 20 native ant species in uninvaded areas, but found only four in invaded areas (Table 1). The only common native ants in invaded areas were two small hypogeic taxa: *Solenopsis molesta* and *Temnothorax andrei*. Invaded and uninvaded sites also differed dramatically in the sizes of the ant species present. Invaded sites were deficient in species larger than the relatively small *L. humile* (Fig. 1). The two native ant species detected in invaded sites that were larger than *L. humile* were both rare at these sites (Table 1).

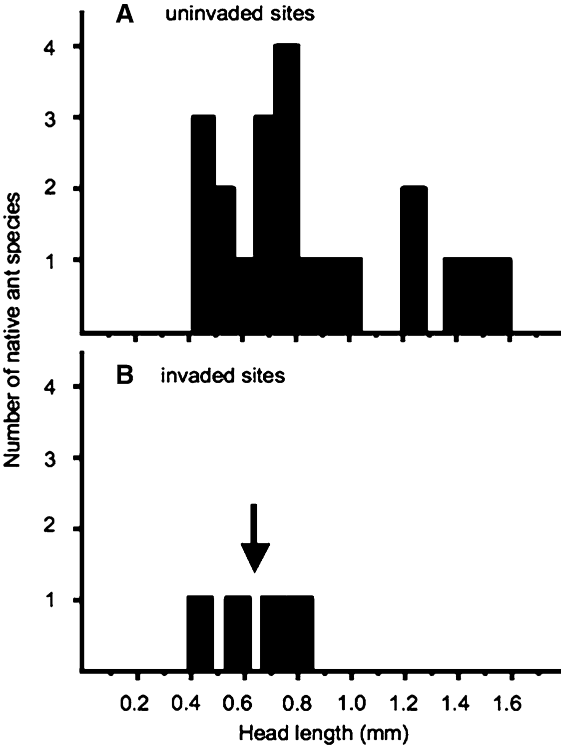

Fig. 1 Frequency distributions of worker head lengths for native ant species from Torrey Pines State Reserve at sites where larval *Myrmeleon* were present. **(A)** Sites without Argentine ants; **(B)** sites with Argentine ants. The arrow in the lower graph indicates the mean head length of Argentine ant workers (0.67 (±0.01) mm ($n = 25$))

Observational survey: ant lions

Ant lion larvae in all three instars were present in October. Most of the variation in larval weight was a function of developmental stage (Fig. 2; two-way ANOVA: $F_{2,104} = 176.88$, $P < 0.0001$), but larval weight also depended on invasion status (Fig. 2; two-way ANOVA: $F_{1,104} = 4.03$, $P = 0.047$). Larvae from invaded sites were larger compared to larvae from sites without Argentine ants; this disparity was most evident by the third instar (Fig. 2). No significant interaction existed between larval instar and invasion status (two-way ANOVA: $F_{2,104} = 1.98$, $P = 0.143$). Most of the variation in mandible length was a function of larval weight (ANCOVA: $F_{1,106} = 343.40$, $P < 0.0001$), but mandible length also depended on invasion status (ANCOVA: $F_{1,107} = 6.28$, $P = 0.010$). This difference was most evident late in larval development; mandibles were 6% longer, on average, in third instar larvae from invaded sites than in those from uninvaded sites.

Lab growth rate experiment

Second instar *M. exitialis* fed either Argentine ants or the native ant, *D. insanus*, maintained positive rates of growth and in all cases underwent pupation. Growth rates differed between the two experimental groups: antlion larvae fed *L. humile* had growth rates that were about 70% higher than those fed *D. insanus* (Fig 3A; two-sample *t*-test: $t_{17} = 4.77$ $P < 0.001$). After molting into their third instar, larvae fed Argentine ants had mandibles that were, on average, 11.0% longer than those of larvae fed *D. insanus* (two-sample *t*-test: $t_{18} = 2.42$, $P = 0.027$).

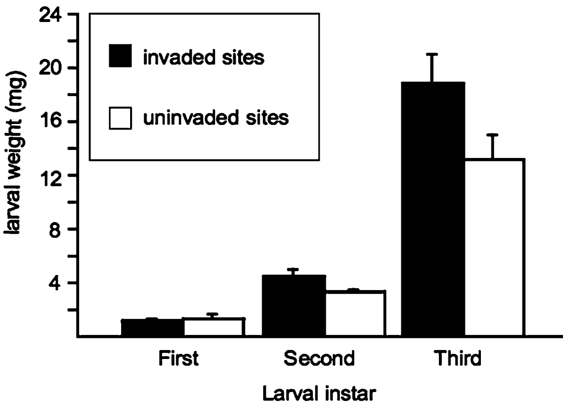

Fig. 2 Results of the observational survey. Mean (±SE) body weights of larval *Myrmeleon* from sites with and without Argentine ants at Torrey Pines State Reserve

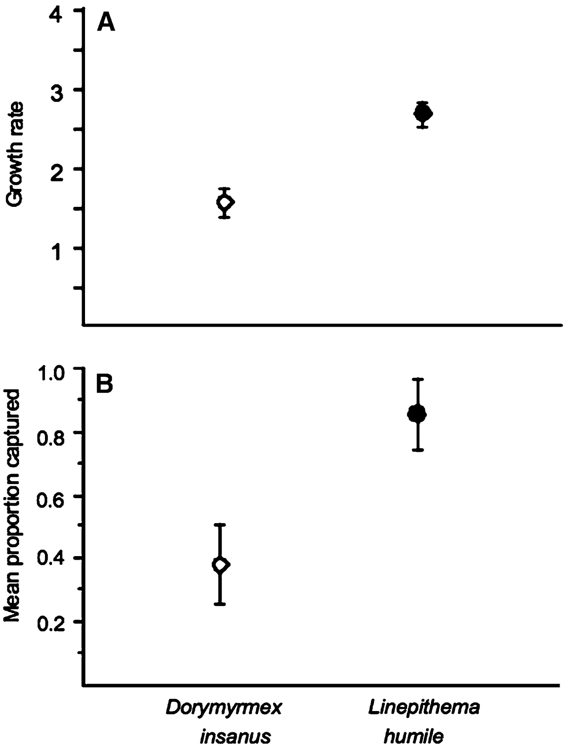

Fig. 3 **(A)** Results of the laboratory growth rate experiment. Mean (±SE) daily growth rate of *Myrmeleon exitialis* larvae fed either *L. humile* (Argentine ants) or *D. insanus* (a common native ant species). Daily growth estimated as follows: [ln (end weight)−ln (initial weight)]/(42 days). **(B)** Results of capture susceptibility trials. Mean (±SE) proportion of individual captures (out of at least 6 trials) for *L. humile* and *D. insanus* workers over a 30-min period

Field transplant experiment

Third instar *M. rusticus* larvae reared in field enclosures exhibited positive rates of growth and survived well. Survival to pupation was high in all replicates; only 6 larvae (out of 50) disappeared from enclosures. The fate of these larvae is unclear; some may have been preyed upon, while others may have burrowed out from underneath the enclosures.

The results of the transplant experiment indicate that larval growth rates and pupal masses were not statistically different for ant lions reared in invaded areas compared to those reared in uninvaded areas. Growth rates after 28 days did not differ between invaded and uninvaded sites (4.63 ± 0.30 (invaded) vs. 4.28 ± 0.44 (uninvaded) (mean (±SE)); two-sample *t*-test: $t_8 = 0.66$, $P = 0.529$) nor did pupal masses (0.019 ± 0.01 g (invaded) versus 0.018 ± 0.01 g (uninvaded); two-sample *t*-test: $t_8 = 0.34$, $P = 0.742$). At invaded sites, a slightly higher proportion of larvae reached pupation after 42 days compared to at uninvaded sites (0.58 ± 0.17 (invaded) vs. 0.15 ± 0.10 (uninvaded); two-sample *t*-test: $t_8 = 2.44$, $P = 0.040$).

Susceptibility to capture

Compared to *D. insanus* workers, *L. humile* workers were more than twice as likely to be captured by *Myrmeleon* after 30 min inside enclosures (Fig. 3B; two-sample *t*-test: $t_8 = 2.88$, $P = 0.021$). This difference may have resulted from the Argentine ant's greater tendency to fall into pits. In contrast, *D. insanus* workers would usually pause at the lip of pits and then walk away.

Discussion

Despite strong interactions between ant lion larvae and their ant prey and despite major changes to this prey base (Table 1, Fig. 1), we found no evidence that larvae were smaller or grew more slowly in areas where *L. humile* had displaced native ants. In the observational survey and lab growth rate experiment, *Myrmeleon* were heavier (Fig. 2), had longer mandibles, and grew more quickly (Fig. 3A) when their main ant prey were Argentine ants rather than native ants. The results of the transplant experiment were not significant for larval growth rate or pupal mass, but larval ant lions from invaded areas pupated sooner compared to those in uninvaded areas. Because larval *Myrmeleon* occupy conspicuous pits, a shorter period of development might decrease the risk of predation.

Taken together, these results suggest that the Argentine ant is a suitable prey species for *Myrmeleon* and might even be superior to native ants despite its relatively small size. Griffiths (1980) argued that, depending on the size of ant lion larvae, relatively small ants might have a lower net energetic value compared to ants that are intermediate in size because ant lion larvae pay costs associated with handling time and pit reconstruction every time they capture a prey item. In the case of *L. humile*, these costs may be offset somewhat. First, as Dolichoderines, Argentine ants may be easier to feed on compared to many Myrmecines because of their thin, unarmored cuticles. Griffiths (1980), for example, noted that larvae of pit-building ant lions in the genus *Morter* were able to puncture the cuticles of Dolichoderines not only on the gaster but also elsewhere on the body, whereas *Morter* punctured Myrmecine species primarily on the gaster. This suggests that unarmored Dolichoderines, such as *L. humile*, may be easier to handle and to feed on compared to the Myrmecines common at our study sites, such as *Solenopsis xyloni* and *Crematogaster californica*. Second, our results on capture susceptibility suggest that Argentine ants rapidly fall prey, at least compared to the native ant, *D. insanus*, one of the more common native ants at our study sites (Table 1). If Argentine ants exhibit a high susceptibility to capture compared to native ants generally (i.e., in addition to *D. insanus*), they may be preyed on by larval ant lions more often than one would predict based on their abundance.

Our study illustrates potential difficulties in predicting how numerically dominant introduced species affect native predators. Species-level idiosyncrasies in the behavior, size or morphology of native predators as well as those of introduced prey appear key in determining the extent to which such prey are consumed and what, if any, additional ecological effects result. With respect to Argentine ant invasions, it is of interest that pit-building ant lions and coastal horned lizards (*Phrynosoma coronatum*), despite having outwardly similar diets, appear to be affected quite differently by changes in their ant prey base. Coastal horned lizards prefer native ants over *L. humile* in choice tests, require a range of worker sizes during their development, and lose weight (at least when young) when reared on a diet of *L. humile* (Suarez et al. 2000, Suarez and Case 2002). It is presumably for these reasons that horned lizard abundance at the landscape scale is inversely related to Argentine ant abundance (Fisher et al. 2002). Our results, in contrast, suggest that *L. humile* is more than adequate as a replacement food source for *Myrmeleon*. It could even be the case that invaded sites, compared to uninvaded sites, consistently export more antlions or larger antlions, on average. If so, the well-known negative effects of *L. humile* on native ants might also include indirect effects that result from the Argentine ant's positive influence on a predator it shares with other ant species.

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