

Speak softly and carry a big stick: Submissive behavior contributes to the displacement of a unicolonial global invader

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Introduction

PROBLEM: Invasive organisms' behavioral adaptations contribute to their successful establishment in an environment, but are often overlooked.

- The behaviorally aggressive global invader Argentine ant (*Linepithema humile* Mayr) (**Ar**) forms large supercolonies, displacing native taxa and causing a cascade of negative impacts across trophic levels.
- We found small populations of the new invasive Asian needle ant (*Pachycondyla chinensis* Emery) (**As**) nesting near (<1m) and displacing **Ar** across an urban landscape.
- Although climate matching can account for **As**'s ability to establish nests before **Ar** are active, how the behaviorally and numerically subordinate **As** can persist in a landscape inundated with the aggressive **Ar** remains unknown.

WHY CARE: Understanding the factors driving the **Ar:As** dynamic may help explain how small populations of behaviorally submissive species establish, and also elucidate possible control tactics for future spread prevention.



The Argentine ant (*Linepithema humile*)



The Asian needle ant (*Pachycondyla chinensis*)

Objectives

Determine if:

- Workers from overlapping populations of **As** and **Ar** are less aggressive towards each other than towards "strangers" from non-overlapping populations
- Lower aggression is the result of interspecific habituation, the reduction in behavioral response through repeated exposure

Asian needle ants and Argentine ants have overlapping populations in invaded urban landscapes. Despite their comparatively low worker populations and subordinate behavior, Asian needle ants displace Argentine ants.



Methods & Results

I. 5 x 5 aggression assays to determine group effects of invasive interspecific aggressive behavior.

- We placed five **Ar** ants in an arena with 5 **As** ants.
- We recorded **Ar** survivorship after 24h.
- Interspecific assay treatments included neighbor **As** vs. neighbor **Ar** and neighbor **As** or **Ar** vs. strangers (**Ar** or **As**).



II. Dyad aggression assays to determine Argentine ant behaviors eliciting aggressive response.

- We introduced one **Ar** to one **As** in an arena.
- A blind observer recorded every **Ar** behavior upon interspecific contact for five minutes.
- Behaviors were ranked and scored for analysis as: submission/avoidance (0), posturing (1), low aggression (2), and high aggression (3).



III. Habituation assays to determine the role habituation plays in low interspecific aggression.

- To test **As** habituation, we exposed **As** individuals to stranger **Ar** individuals in an arena for 30s and then re-exposed the **As** to novel **Ar** individuals 1, 2, or 24h later. We recorded the number of **Ar** attacks required to elicit an **As** aggressive response.
- To test **Ar** habituation, we exposed **Ar** to stranger **As** for 30s and then re-exposed individuals to **As** 0.5, 1, 2, or 24h later and recorded the **Ar** incidence of high aggression in 30s assays.
- For both sets of assays, we executed unexposed controls concurrently.

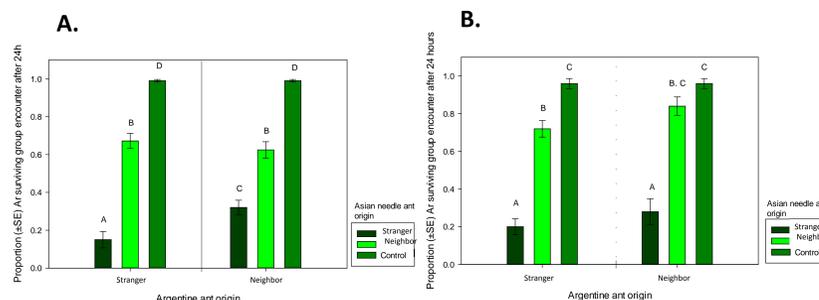
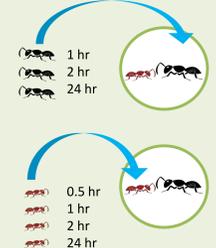


Fig. 1 Proportion Argentine ant strangers or neighbors surviving a 24h 5X5 encounter with Asian needle ant neighbors or strangers at the Morrisville, NC location (A) or Greenville, SC location (B)

- Argentine ants experience higher survivorship in assays against neighbors than strangers from two areas of species overlap (Fig. 1) (ANOVA: RTP location: $F_{193,197}=89.946$, $p<0.001$; Greenville, SC location: $F_{45,49}=33.587$, $p<0.003$)

Table 1 Probability neighbor **Ar** will display aggression levels 0-3 towards neighbor **As** or stranger **As**

Aggression	0	1	2	3
Towards Neighbors	0.42	0.51	0.05	0.03
Towards Strangers	0.07	0.51	0.23	0.19



Argentine ant and Asian needle ant strangers fight (top); neighbors do not fight (bottom)

- Argentine ants are more likely to display high aggressive behaviors towards Asian needle ant strangers and low aggressive behaviors towards Asian needle ant neighbors. (PROC GLIMMIX $F_{1,18}=12.33$ $p=0.0025$, Table 1)

Asian Needle Ant Habituation

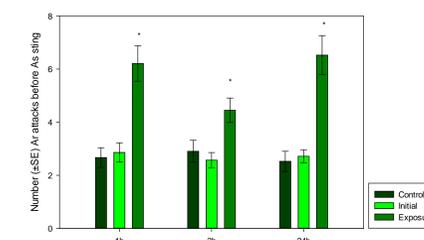


Fig. 3 The number of Ar attacks before As aggressive response after repeated exposure to Ar

Argentine Ant Habituation

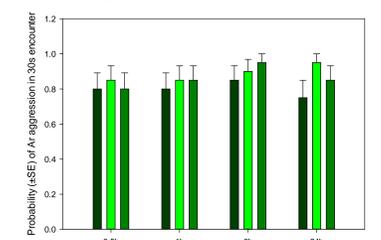


Fig. 4 The incidence of Ar high aggression after repeated exposure to As

- Surprisingly, while **As** are less aggressive towards **Ar** strangers upon re-exposure (linear contrast: 1h [$F_{2,12}=19.12$, $p<0.0001$]; 3h [$F_{2,53}=4.86$, $p=0.0115$]; 24h [$F_{2,53}=27.60$, $p<0.0001$], Fig. 3)
- Ar** remain highly aggressive towards **As** strangers, regardless of prior exposure (linear contrast: 0.5h ($F_{2,57}=0.11$, $p=0.9$), 1h ($F_{2,57}=0.12$, $p=0.888$), 3h ($F_{2,57}=0.52$, $p=0.599$) and 24 h ($F_{2,57}=1.35$, $p=0.268$), Fig. 4).

Summary and Discussion

- The typically aggressive Argentine ant is less aggressive toward its behaviorally and numerically subordinate Asian needle ant neighbors but remains aggressive towards strangers.
- Asian needle ants are also less aggressive towards neighbors. Asian needle ants appear to habituate but Argentine ants do not.
- Argentine ants may not recognize neighboring Asian needle ants as intruders. Argentine ant invasion success depends, in part on its intraspecific colonial inclusiveness (a flexible recognition template leading to the formation of supercolonies) and its interspecific exclusiveness (high interspecific aggression). Asian needle ants may be disguising themselves with Argentine ant recognition cues to avoid detection.



Asian needle ants move freely throughout the normally aggressive Argentine ant nests at the bases of oak trees, most likely because of Argentine ant recognition errors.

Acknowledgements

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