



Submissive behaviour and habituation facilitate entry into habitat occupied by an invasive ant



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An essential challenge in invasion ecology is discerning the role that behavioural adaptations play in competition among species. When evaluating the impacts of invasive species, the mechanisms underlying coexistence among organisms and the displacement of organisms within a community mosaic are often ignored, yet these interactions are necessary for fully understanding these impacts. Here, we examine behavioural mechanisms underlying the coexistence and subsequent displacement of an established global invader, the Argentine ant, *Linepithema humile* Mayr, by the newly invasive Asian needle ant, *Pachycondyla chinensis* Emery. In individual and group assays, we show that the numerically and behaviourally dominant Argentine ant is less aggressive towards *P. chinensis* workers from adjacent versus distant nests. Moreover, we show that *P. chinensis* displays submissive behaviour through recurrent contact with *L. humile*, which may contribute to the reported displacement of *L. humile* in the field. Understanding the factors that drive the coexistence of these two ants may help explain how small populations of a behaviourally submissive exotic species become established.

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Invasive species often rely on behavioural and numerical dominance to displace native species, causing negative effects across multiple trophic levels (Short & Petren 2008; Stokes et al. 2009; Dietzsch et al. 2011; Polo-Cavia et al. 2011; Young et al. 2011). Therefore, an essential challenge in invasion ecology is to understand the role that behavioural adaptations play in interspecific competition. When evaluating the impacts of invasive species introductions, the mechanisms underlying the species overlap among and displacement of organisms within a community mosaic are often ignored, yet are necessary for understanding these impacts (Chase & Leibold 2003; Wittman & Gotelli 2011). Exotic ants are an excellent model for examining the mechanisms and impacts of invasion because they share a range of adaptations, including behavioural traits, with other invasive species (Holway et al. 2002; Lessard et al. 2009; Lessard et al. 2009; Parr & Gibb 2012).

Although various studies point to an invasive ant's numerical and behavioural dominance as key to initial establishment and spread in a new environment, few studies have examined the role

these traits play in the persistence of invasive species over time (Holway 1999; Human & Gordon 1999; Hee et al. 2000; Morrison 2000; Sanders et al. 2001). In fact, understanding the behavioural adaptations that facilitate the persistence of native organisms under siege by invasive ants can provide a predictive framework for long-term impacts of invasion and faunal resurgence patterns (Wetterer et al. 2001; Oliveras et al. 2005). Furthermore, awareness of behavioural traits shared by members of invasive ant complexes can help to predict successions of invaders.

Linepithema humile (Mayr) relies largely on behavioural and numerical dominance to displace native taxa across its introduced range (Holway 1998; Human & Gordon 1999; Carpintero & Reyes-Lopez 2008). With enormous colonies defined by a lack of intra-specific aggression (Holway 1998; Holway et al. 1998), *L. humile* mass-recruit 24 h per day to secure and defend resources (Human & Gordon 1999; Mondor & Addicott 2007; Rowles & O'Dowd 2007). However, some native ants persist in environments dominated by *L. humile* by using an array of behaviours (Wetterer et al. 2001; Oliveras et al. 2005; Blight et al. 2010) or occupying microhabitats not used by *L. humile* (Sarty et al. 2006). By persisting, these native ants may in some way lessen the ecological impact of *L. humile* (Blight et al. 2010).

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The newly invasive Asian needle ant, *Pachycondyla chinensis*, is becoming increasingly prevalent across the eastern United States, and it is unique because it can successfully establish in both human-disturbed and undisturbed natural habitats (Nelder et al. 2006; Guenard & Dunn 2010). With small colonies typical of many ponerine species, *P. chinensis* makes an unlikely invader, possessing neither mass recruitment behaviour (Guenard & Silverman 2011) nor a propensity to dominate resources (Spicer Rice & Silverman 2013), which is typical of many successful invasive ants (Thomas & Holway 2005; Le Breton et al. 2007; Drescher et al. 2011).

Although the interactions among invasive ants and native ants are well documented (Holway 1999; Morrison 2000; Alder & Silverman 2005; Grangier et al. 2007; Le Breton et al. 2007; Buczkowski & Bennett 2008; Rowles & O'Dowd 2009; Blight et al. 2010; Drescher et al. 2011), examples of interactions between invasive ant species are rare (Kirschenbaum & Grace 2007; Lach 2008; Zheng et al. 2008; Kenis et al. 2009). We have previously documented that *L. humile* are being displaced by *P. chinensis* across an urban landscape, and that while *L. humile* are more abundant and dominate baits, *P. chinensis* establish nests earlier in the year. Furthermore, these ant species occupy nests in close proximity (<1 m) (Spicer Rice & Silverman 2013).

Here, we investigated possible behavioural mechanisms underlying the displacement of *L. humile* by *P. chinensis* using a combination of colony-level, group-level and dyadic behavioural assays. We also examined whether reported field colonies of overlapping *L. humile* and *P. chinensis* might be a consequence of repeated exposure and habituation. Understanding factors underlying *L. humile* and *P. chinensis* overlap may help explain how introductions of exotic propagules become established.

METHODS

Insect Collections

We collected *L. humile* Mayr from office parks in Morrisville, NC, U.S.A. (35°51'11.37"N 78°49'36.74"W) and Greenville, SC, U.S.A. (34°51'02.18"N, 82°23'44.07"W). We collected *P. chinensis* Emery from these same office parks and from locations without *L. humile*: Lake Johnson Park, NC, U.S.A. (35°45'33.44"N 78°43'01.33"W), Schenck Forest, NC (35.8171156°N, 78.7263642°W) and Falls Lake, NC (36.027528°N, 78.7192776°W). We conducted preliminary intraspecific internet aggression assays (E. Spicer Rice, unpublished data) and determined that *L. humile* from Morrisville and Greenville were distinct colonies and that *P. chinensis* from Morrisville, Greenville, Lake Johnson, Schenck Forest and Falls Lake were all from separate colonies.

Our laboratory has monitored the *L. humile* invasion at the Morrisville location for over a decade (Meissner & Silverman 2001). At this location, two distinct *L. humile* supercolonies occur across the landscape, nesting in mulch around buildings, trees and shrubs (Buczkowski et al. 2004; Spicer Rice & Silverman 2013). In a concurrent study, *L. humile* nests were initially found at the bases of 99% of the willow oak trees (*Quercus phellos*) across the office park, foraging across the ground and heavily along tree trunks for hemipteran honeydew (Brightwell & Silverman 2010; Brightwell & Silverman 2011; Spicer Rice & Silverman 2013). Preliminary pitfall data revealed that those ants persisting with *L. humile* had little spatial or temporal resource overlap, such as hypogaecic species (*Amblyopone* sp., *Strumigenis* sp. and *Pyramica* sp.) and winter-active *Prenolepis imparis*. The parasitic thief ant, *Solenopsis molesta*, occurred in isolated areas. A few species, like *Monomorium minimum* and *Formica* sp. also persisted in isolated areas of the park, particularly near wooded margins, where *L. humile* was not

evident or around magnolia trees (*Magnolia grandiflora*), which do not host aphids and scale and had no landscaping mulch for nesting around their bases.

A few small (<50 workers) *P. chinensis* nests were first recorded in 2008 at this site around willow oak bases shared with *L. humile*. While populations of both ants decreased during the colder winter months, a 4-year study revealed that *P. chinensis* resumed activity 2 months prior to *L. humile* (Spicer Rice & Silverman 2013). Both *L. humile* (Human & Gordon 1996; Alder & Silverman 2005) and *P. chinensis* (E. Spicer Rice, personal observation) forage at the same time, 24 h per day.

We collected ants from field debris and placed them in Fluon-coated plastic tubs furnished with artificial nests (95 × 15 mm petri dish lined with moistened plaster and covered with a tile) and a diet of 20% sucrose solution dispensed in a centrifuge tube with a floating cap and freshly killed German cockroaches, *Blattella germanica*, and held at 26 ± 1 °C and 50 ± 5% RH on a 12:12 h light:dark cycle.

Ethical Note

We understand aggressive interactions may result in pain and suffering for the organisms involved. While we did allow the insects in this study to interact aggressively with each other, resulting in the suffering and sometimes death of individuals, we made every effort to maximize the use of each individual in the study. In the assay design, we used the minimum number of animals possible. We performed only enough replicates to provide a robust data set for analysis. We did not overreplicate, nor did we overharvest these ants from the field, and we did alleviate pain and suffering of each ant whenever possible.

Staged encounters like those presented in this study are vital to a clear understanding of behavioural processes. In designing this study, we did not want to diminish ant populations at our field site, nor did we wish to contaminate the area by introducing more invasive species to contrive 'natural field' treatments. Furthermore, to eliminate all possible confounding factors like climate, nest space and innumerable worker ratios, and to observe the fundamental behaviours evident between these two species, conducting assays in the laboratory environment was vital to ensuring accurate measurements.

Furthermore, many of our laboratory colonies were later used as teaching colonies, sharing ant colony structure with wide audiences like the tens of thousands of citizens gathered at the North Carolina Museum of Natural Science's 'Bugfest' event and the hundreds present at our annual North Carolina Pest Management Association meeting. Rather than killing more ant workers, we preserved (in ethanol) the uneaten carcasses from our extended (24 h) assays to provide teaching specimens of invasive ants, which are shipped to various institutions and pest management programmes across the United States.

In many assays ants are allowed to fight and kill each other. Future research on *P. chinensis* and other Ponerine ants can build upon these experiments to determine nonlethal 'breaking points' for aggression. However, presenting the actual behaviour of these ants, without disrupting their natural reactions by prematurely halting their behavioural processes, is the only way for this research to move forward.

For example, while some ant species, like *Forelius pruinosus*, primarily rely on ritualized displays in aggressive interactions, *P. chinensis*, when heavily aggressed upon, responds with a fatal sting. We know this only because of the assays presented in this study. For this reason, we allowed ants to fight to the death.

It is important to consider that each species presented here was evaluated in a portion of its invaded range, where each species

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