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Authors: Lawson, Katy J., and Oi, David H.

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Minimal intraspecific aggression among tawny crazy ants (Hymenoptera: Formicidae) in Florida

Katy J. Lawson[1], *and David H. Oi*[1,*]

Abstract

Tawny crazy ants, *Nylanderia fulva* (Mayr) (Hymenoptera: Formicidae), are an invasive species found in states along the Gulf Coast of the USA. Their large populations are aggressive and can displace ant species already present in the area. Because tawny crazy ants are not territorial toward their own species within a locality, it was hypothesized that they may exhibit unicoloniality in their invasive range. To test this hypothesis, tawny crazy ants from separate locations in Florida were confined in small, enclosed arenas, and their interactions were observed and documented using a rating scale of aggression behaviors. Carbohydrate consumption also can affect aggression in ants, so starved and non-starved ants were tested separately. For non-starved ants, the level of aggression between worker ants increased if they were from different locations, but this interaction rarely escalated to fighting. When starved ants from different locations were given access to sucrose solution, the ants would exhibit trophallaxis rather than fighting over the food source. Queens from different colonies would quickly nest together. Thus, intraspecific aggression was not evident among tawny crazy ants collected from widely separated locations in Florida.

Key Words: invasive ants; territoriality; competition; unicolonial; *Nylanderia fulva*

Resumen

La hormiga loca rojiza, *Nylanderia fulva* (Mayr) (Hymenoptera: Formicidae), es una especie invasora que se encuentra en los estados a lo largo de la costa del Golfo de los Estados Unidos. Sus grandes poblaciones son agresivas y pueden desplazar especies de hormigas ya presentes en el área. Debido a que las hormigas locas rojizas no son territoriales hacia sus propias especies dentro de una localidad, se planteó la hipótesis de que pueden exhibir unicolonialidad en su rango invasivo. Para probar esta hipótesis, las hormigas rojizas locas de lugares separados en Florida fueron confinadas en pequeños espacios cerrados, y sus interacciones se observaron y documentaron utilizando una escala de calificación de los comportamientos de agresión. El consumo de carbohidratos también puede afectar la agresión en las hormigas, por lo que las hormigas con hambre y sin hambre se probaron por separado. Para las hormigas no hambrientas, el nivel de agresión entre las hormigas obreras aumentaba si eran de diferentes lugares, pero esta interacción rara vez escalo a un combate. Cuando las hormigas hambrientas de diferentes lugares tenían acceso a la solución de sacarosa, las hormigas exhibían trofalaxis en lugar de pelear por la fuente de alimento. Reinas de diferentes colonias anidarían juntas rápidamente. Por lo tanto, la agresión intraespecífica no era evidente entre las hormigas locas rojizas recolectadas de lugares extensamente separados de la Florida.

Palabras Claves: hormigas invasoras; territorialidad competencia; unicolonial; *Nylanderia fulva*

The tawny crazy ant, *Nylanderia fulva* (Mayr) (Hymenoptera: Formicidae), is an invasive ant native to South America. Initially, large populations of this ant in Florida most likely were misidentified in the 1990s and early 2000s as *Nylanderia* (=*Paratrechina*) *pubens* (Forel) (Hymenoptera: Formicidae) (Klotz et al. 1995; Warner & Scheffrahn 2010; Gotzek et al. 2012). Tawny crazy ants commonly displace other invasive and native ant species (LeBrun et al. 2013), and their extremely dense populations may damage electrical wiring and piping (Meyers 2008), serve as vectors for pathogens (McDonald 2012), and damage crops (Zenner-Polania 1990; Wetterer & Keularts 2008). It seems that colonies are unicolonial, at least over short distances (D. H. O. personal observation), and are characterized by multiple egg-laying queens within each nest with constant intermingling of workers and queens from different nests (Hölldobler & Wilson 1990).

Tawny crazy ants fight with other ant species. For example, Horn et al. (2013) demonstrated that tawny crazy ants and red imported fire ants, *Solenopsis invicta* Buren (Hymenoptera: Formicidae), often fight to the death when they interact. Tawny crazy ants can outcompete red imported fire ants in their invaded ranges when they overlap, in part by the detoxification of *S. invicta* venom (Chen et al. 2014; LeBrun et al. 2014). The reduction in species diversity and abundance of other ants in tawny crazy ant dominated habitats suggests that these ants also outcompete other ant species besides red imported fire ants (LeBrun et al. 2013).

Diet has been known to influence nestmate recognition and aggression behaviors of ants (Obin & Vander Meer 1988; Hölldobler & Wilson 1990; Silverman & Liang 2001; Suarez et al. 2002; Buczkowski & Silverman 2006). High carbohydrate consumption also may increase competitiveness and enhance invasive ant domination of resources and territory (Holway et al. 2002). Interestingly, tawny crazy ants fed a low-carbohydrate diet were more aggressive toward red imported fire ants (Horn et al. 2013). It is not known if a carbohydrate deficit also would cause more intraspecific aggression in tawny crazy ants.

Though tawny crazy ants are combative when faced with other ant species, it has not been determined if they will act aggressively toward other conspecific ants from widely separated locations. However, taw-

[1]USDA-ARS, Center for Medical, Agricultural, and Veterinary Entomology, 1600 SW 23rd Drive, Gainesville, Florida 32608, USA; E-mail: katyjlawson@gmail.com (K. J. L.), david.oi@usda.gov (D. H. O.)
*Corresponding author; E-mail: david.oi@usda.gov

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ny crazy ants from different nests collected from a single site did not display antagonistic behaviors toward each other (Horn et al. 2013). We hypothesized that tawny crazy ants from geographically separated locations also would react in a non-aggressive manner when placed together providing further support for the unicoloniality hypothesis. In this study we evaluated intraspecific interactions between tawny crazy ant workers and colony fragments obtained from nests collected in different counties in Florida. In addition, interactions among starved tawny crazy ants were evaluated.

Materials and Methods

Tawny crazy ant colonies were collected from leaf litter, dead branches, and nested nursery pots from various sites throughout Florida. These sites were located in Gainesville (Alachua County; 29.623238°N, 82.473108°W), near Winter Garden (Lake County; 28.490978°N, 81.668617°W), Southport (Bay County; 30.290666°N, 85.643474°W), Morriston (Levy County; 29.287087°N, 82.478179°W), Callahan (Nassau County; 30.574470°N, 81.827450°W), and Lithia (Hillsborough County; 27.876511°N, 82.181960°W). Within each site, 1 to 8 queen-right colonies were collected from areas that were at least 3.7 m apart. A total of 27 colonies collected from the 6 sites were used in aggression testing (Fig. 1).

Colonies were maintained in the laboratory from 1 d to 7 mo and were fed a diet of 10% (w/v) sucrose solution, frozen crickets (*Acheta domesticus* [L.]; Orthoptera: Gryllidae), and live house fly (*Musca domestica* L.; Diptera: Muscidae) larvae. Colonies nested within glass tubes (150 × 16 mm) adapted from test tube nests described by Banks et al. (1981). Nest tubes were covered with a black, polypropylene plastic food container (17 cm L × 12 cm W × 6 cm H; Sterling King Products, Lyons, Illinois, USA) to provide a darkened harborage.

Fig. 1. Florida map displaying county boundaries and the cities where tawny crazy ants were collected. The number of colonies used from each location are: 1 from Southport, 2 from Lithia, 3 from Callahan, 5 from Morriston, 8 from Gainesville, and 8 from Winter Garden. The Gainesville and Morriston collection sites are the closest together, located 38 km (23 miles) apart. The most separated sites, located 434 km (270 miles) apart, are Winter Garden and Southport.

AGGRESSION TEST AMONG NON-STARVED ANTS

Five tawny crazy ant workers were arbitrarily removed from 2 of the 18 available test colonies; these 10 ants were placed together in a polystyrene Petri dish (9.5 cm diam). The sides of the dish were coated with fluon (PTFE D-210, Daikin America, Inc., Orangeburg, New York, USA) to prevent escape. At 1 min intervals for 10 min (Horn et al. 2013), ants were observed for 5 to 10 s, and the behavior of each ant was given a rating using the aggression scale of Suarez et al. (1999). The ratings were as follows: 0 = ignore (ants had no interaction), 1 = touch (ants performed antennation or touched mandibles), 2 = avoid (ants would get very close or touch, and then 1 or both ants would retreat in the opposite direction), 3 = aggressive (biting, leg pulling, or charging; usually aggression is exhibited when 1 ant is performing these behaviors and the other is not fighting back), and 4 = fighting (2 ants grappling, locking mandibles onto a body part for more than a couple of s, or carrying another ant in its mandibles). There were 10 total observation periods, 1 for each of the first 10 min per period. To determine if ants would settle in a harborage together 1 h after they were initially placed in the container, a small nest tube and a cover were added to the container. After 2 h, the number of paired ant groups (where a majority of ants from both groups settled together within the nest tube, i.e., ≥ 8 ants) was then tabulated. There were 21 total colony-colony combinations used in the study, each pair having 2 to 13 replications, based on colony availability (Table 1). A total of 77 aggression tests were conducted with non-starved ants.

AGGRESSION TEST AMONG STARVED ANTS

Ants selected for aggression tests with starved ants were obtained from the same colonies used in the non-starvation tests described earlier. Ant colonies were starved by removing the diet of sucrose solution, crickets, and house fly larvae 5 to 7 d before testing. This severely limited their carbohydrate intake based on previous studies which demonstrated that colonies quickly and consistently consumed sucrose solution after 4 d of deprivation (D. H. O. unpublished data). For each test, a total of 10 ants from 2 different colonies were arbitrarily selected from starved colonies. Once the 10 ants were placed in the Petri dish, interactions among ants were rated for the first 10 min using the Suarez et al. (1999) aggression scale. After 30 min, a 0.5 µL drop of 25% sucrose water was added to the center of the container holding the 10 ants. Another 10-min observation was performed with readings performed every min. Similar to the non-starved testing, the presence or absence of a majority of ants taking harborage in the same nest tube was recorded 110 min after the initial aggression observation ended (1 h after harborage placement). Fifty-one trials were conducted using starved ants.

QUEEN-RIGHT COLONY INTERACTIONS

To determine if freshly collected tawny crazy ant colony fragments would nest together, queen-right colonies were collected from the Winter Garden and Gainesville field sites. Colonies collected within each site were at least 30 m apart. A group of 100 workers, 1 queen, and 0.1 to 0.3 mL of brood were separated from each of the colonies and paired as follows: 5 Winter Garden-Gainesville pairs, 2 Gainesville-Gainesville pairs, and 2 Winter Garden-Winter Garden pairs. The Winter Garden and Gainesville colonies had been in the laboratory for 22 to 42 h and 1 to 20 h, respectively, when the study was initiated.

One group of ants was placed in a fluon-treated container (24 × 38 cm or 32 × 19.5 cm) with a single nest tube covered by a black plastic container. Ants were allowed 15 to 30 min to settle, resulting in the queen and most of the workers and brood going into the nest tube. After the settling period, a wooded placard (150 cm^2) was positioned in the container on the side opposite the nest tube, such that there was

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Table 1. Distances between tawny crazy ant colony sites and number of replications used in the study[a].

Location	Southport	Lithia	Callahan	Morriston	Gainesville	Winter Garden
Southport	0 km; 3; 0[a]	430 km; 2; 2	368 km; 2; 2	325 km; 2; 0	N/A	434 km; 6; 0
Lithia	–	0 km; 3; 0	302 km; 3; 3	160 km; 3; 1	196 km; 5; 2	85 km; 3; 1
Callahan	–	–	0 km; 3; 0	156 km; 4; 3	123 km; 3; 4	232 km; 13; 2
Morriston	–	–	–	0 km; 4; 0	38 km; 3; 1	118 km; 4; 3
Gainesville	–	–	–	–	0 km; 3; 3	148 km; 3; 9
Winter Garden	–	–	–	–	–	0 km; 4; 4

[a]The first number represents the distance between locations (in kilometers), the second number is the amount of non-starved replications of the test, and the third number is the number of starved replications.

1 cm of space under the placard for harborage. A similar sized group of ants from another source colony was then introduced into the container with the original ants. After 1 h, positions of queens, workers, and brood were recorded relative to the nest tube. In addition to the 1 h reading, colony fragment positions were recorded at 2 to 3 d intervals after the initial pairings for 2 wk.

STATISTICS

For non-starved and starved trials, the aggression score per test was calculated as follows: (a) individual ant interaction scores for each of the 10 ants observed within a 1-min period were averaged; (b) because the duration of a test was 10 min, the mean score for each of the 1-min periods was averaged together to obtain an overall aggression score. Analysis of variance and Tukey's honest significant difference test (HSD) (Proc GLM, SAS vers. 9.4, SAS Institute, Cary, North Carolina, USA) was used to determine differences among overall aggression scores for the non-starved ants obtained from colonies collected at the same site, 38 to 232 km apart, and 302 to 434 km apart. For the starvation trials, Kruskal-Wallis tests (Proc RANK, Proc GLM, SAS vers. 9.4, SAS Institute, Cary, North Carolina, USA) were used to compare overall aggression scores of ants before and after they were given access to the sucrose solution due to the non-normal data distribution and heterogeneous variances. The number of paired ant groups that were within a nest tube were compared among the aforementioned pooled distances between colony collection sites with a 3 × 2 contingency table and chi-square test (non-starved ants) or Fisher's exact test (starved ants) (Proc FREQ, SAS vers. 9.4, SAS Institute, Cary, North Carolina, USA). Pearson's correlation (Proc CORR, SAS vers. 9.4, SAS Institute, Cary, North Carolina, USA) was used to determine the associations between distances among the sites from which the tawny crazy ants were collected and average aggression scores. Correlations were conducted separately for the non-starved, starved, and subsequently fed ants. For the queen-right colony interactions, the number of colony fragment pairs that occupied the same nest tube was tabulated for each observation period and numerically compared between colony pairs from the same and separate collection sites.

Results

AGGRESSION TEST AMONG NON-STARVED ANTS

There were few instances of fighting between tawny crazy ants, and if fighting did occur it ended quickly. Though all levels of aggressive behavior were observed, the only values to occur frequently (> 90% of all interactions) were 0 and 1, resulting in a low average overall aggression score of 0.57 ± 0.15 SD (n = 77) across all colony pairs (Table 2). Ants collected from the same site had a significantly ($P \leq 0.05$) lower overall aggression score than ants from different sites. However, the average scores were still low, 0.45 and 0.62, respectively (Table 3). Overall aggression scores were positively correlated with the distances between locations ($r = 0.43$; $P < 0.001$; n = 77), but scores did not reach the level of aggressive behavior because the maximum score was 0.93. Ants from the same site displayed ignoring and touching behaviors in 98.3% (n = 2,000) of the individual ant interactions. Ants from separated sites exhibited ignoring and touching in 97.2% (n = 5,600) of the interactions.

The number of pairs of tawny crazy ant groups that nested together were independent ($\chi^2 = 1.36$; df = 2; $P = 0.506$) of the distances between the locations from which the groups originated. Sixty percent (n = 20), 57% (n = 28), and 45% (n = 29) of the paired groups congregated inside nest tubes when their source colonies were collected at the same location, 38 to 232 km apart and 302 to 434 km apart, respectively. There was no mortality after the 10 min observation period in any of the trials, and there were only 2 ant deaths across all trials after 2 h; it is unknown if these deaths were due to fighting, because the ants were not being observed during this time.

AGGRESSION TEST AMONG STARVED ANTS

Before and after access to sucrose solution, starved ants from the same location had a mean overall aggression score of 0.55 ± 0.19 SD (n = 34), while starved ants from different locations had a mean score of 0.59 ± 0.13 SD (n = 68) (Table 2). These means were within the range

Table 2. The average overall aggression scores for each tawny crazy ant colony pair of non-starved, starved, and subsequently fed sucrose solution[a].

Location	Southport	Lithia	Callahan	Morriston	Gainesville	Winter Garden
Southport	0.32[a]; *; *	0.81; 0.58; 0.74	0.60; 0.75; 0.75	0.57; *; *	N/A	0.70; *; *
Lithia	–	0.48; *; *	0.59; 0.49; 0.74	0.72; 0.34; 0.69	0.64; 0.61; 0.66	0.54; 0.7; 0.6
Callahan	–	–	0.35; *; *	0.63; 0.50; 0.58	0.53; 0.48; 0.64	0.56; 0.48; 0.82
Morriston	–	–	–	0.54; *; *	0.66; 0.48; 0.59	0.67; 0.44; 0.69
Gainesville	–	–	–	–	0.55; 0.31; 0.57	0.54; 0.50; 0.59
Winter Garden	–	–	–	–	–	0.42; 0.43; 0.64

[a]The first number is the non-starved average aggression score. The second number is the starved aggression score before sugar water was added. The third number is the starved aggression score after sugar water was added.

*An asterisk represents no data for that combination. The number of replications used to calculate average scores is provided in Table 1.

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designated by ignoring and touching behaviors. Overall aggression scores were not significantly different among the pooled distances between collection locations for the paired ant groups before and after access to a sucrose solution (Table 3). Aggression scores were weakly positively correlated with the distances between locations for starved individuals (r = 0.34; P = 0.014; n = 51) and ants subsequently provided sugar water (r = 0.27; P = 0.0549; n = 51). Scores did not reflect aggression with maximum overall aggression scores of 0.88 and 1.04 for the starved and subsequently fed ants, respectively.

Paired tawny crazy ant groups that nested together were independent (Fisher's Exact Test, df = 2; P = 1.0) of the distance between locations from which groups were collected. Percentages of paired groups that were together within nest tubes were 29.4% (n = 17) when their source colonies were collected at the same location; 25.0% (n = 24) when collected 38 to 232 km apart; and 23.1% (n = 13) when collected 302 to 434 km apart. Across all trials, 2 ants died during the 2 h test period.

QUEEN-RIGHT COLONY INTERACTIONS

Among the paired tawny crazy ant colony fragments, most colonies nested together during all testing periods (Table 4). During the initial observations at 1 h, 8 of 10 replications of the combined colony fragments had queens, the majority of workers, and all brood in the nest tube. For the remaining 2 replicates (a Winter Garden-Winter Garden pair, and a Winter Garden-Gainesville pair), each had 1 queen in the nest tube with about half of the workers and most of the brood. The second queen with about 70 workers and very little brood were located under the wooden placard. On the final d of the test, across every replication, 2 queens, most of the workers, and all the brood were in 1 nest tube. Over the total 6 observation periods, 1 of the Winter Garden-Winter Garden pairs had queens apart for 1 reading, whereas 1 of the Gainesville-Gainesville pairs were apart for 2 observations. One of the Winter Garden-Gainesville pairs had 2 instances where the queens were apart, and 2 other Winter Garden-Gainesville pairs had 1 observation each where the queens were not together (Table 4).

Discussion

We found that non-starved tawny crazy ants from the same location exhibited an average overall aggression score closer to 0, while ants from different locations were scored closer to 1. This indicated that ants from different colonies were more likely to touch non-aggressively than ants from the same locality, which generally ignored each other. Increased scores were positively correlated with the distance between locations, and the aggression scores of paired groups from the different locations were significantly greater than pairs from the same location (Table 3). However, ants from separate locations exhibited behavior common with unicolonial ants by lacking territoriality and rarely exhibiting aggressive behavior. The maximum average aggression score during a 1-min observation period was 2.2 among 10 ants, where a score of 2 represented avoidance (i.e., ants approached each other then retreated). In general, with increasing distance between colony collection sites, tawny crazy ants ignored each other less and exhibited more non-aggressive investigative activity. Further evidence of unicoloniality was provided by the congregation of paired worker groups within single nest tubes that were at similar proportions regardless of whether they originated from the same or distant locations. The fusion of all paired colony fragments collected 148 km apart, as well as within the same location, further demonstrated the unicoloniality of the Florida tawny crazy ants.

Similar types of non-aggressive behavior for paired worker interactions and the fusion of colony fragments have been reported for Argentine ants collected over widely separated geographic locations within their introduced range (Holway et al 1998; Suarez et al. 1999; Chen & Nonacs 2000). However, unlike our study, with Argentine ants fighting and death also occurred between paired workers and colony fragments, thus providing evidence for the existence of different supercolonies (Suarez et al. 1999). In the polygynous social form of red imported fire ants, Morel et al. (1990) found that intraspecific interactions of polygyne workers were not aggressive (exhibiting investigative behavior such as antennation) toward intruding polygyne and monogyne workers that originated from nearby and distant colonies obtained from 3 counties in north-central Florida.

Starving crazy ant colonies did not influence their aggressive behavior. Aggression scores increased slightly with increasing distances between paired ant groups for the starved (r = 0.34; P = 0.014; n = 51) and subsequently fed ants (r = 0.27; P = 0.0549; n = 51). The low and nonsignificant correlation most likely reflected frequent trophallaxis that occurred once the starved ants were provided sucrose solution regardless of where the paired groups were collected. Ants in the starved colonies often were observed performing trophallaxis once the sucrose solution was provided. Sometimes all 10 ants would be engaged in feeding each other, thus at least 1 pair included ants from different locations. Paired groups also settled together within a single nest tube at similar frequencies among the pooled location distances.

The lack of aggression in the starved ants in our study agrees with the findings of Horn et al. (2013) for tawny crazy ants collected from a single locality, where they provided low and high concentrations of sugar water. In diet manipulations with Argentine ants, Grover et al. (2007) reported that depriving colonies of sucrose resulted in diminished aggression between ants from different supercolonies that typically fight. They speculated that less fighting was associated with poorer colony fitness and, thus, less competitiveness at monopolizing resources.

Maintaining ant colonies in the laboratory for extended periods of time have influenced aggression behavior (Obin 1986). Chen and

Table 3. Comparisons of average (± SD) overall aggression scores of tawny crazy ant workers obtained from colonies collected at the same location (0 km), 38 to 232 km, and 302 to 434 km apart. Workers were either non-starved or starved then subsequently provided sucrose solution (SW).

	Average (± SD) overall aggression scores		
	0 km	38–232 km	302–434 km
Non-starved	0.45 ± 0.14a[a] (n = 20)	0.62 ± 0.13b (n = 28)	0.62 ± 0.14b (n = 29)
Starved	0.49 ± 0.17a[b] (n = 17)	0.50 ± 0.09a (n = 24)	0.58 ± 0.16a (n = 10)
Starved then SW	0.62 ± 0.20a[b] (n = 17)	0.62 ± 0.08a (n = 24)	0.74 ± 0.14a (n = 10)

[a]Averages (± SD) followed by the same letter within a row are not significantly different (P > 0.05; ANOVA and Tukey's HSD).
[b]Averages (± SD) followed by the same letter within a row are not significantly different (P > 0.05; Kruskal-Wallis test).

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Table 4. The number of tawny crazy ant colony fragment pairings where both queens and most of the workers and brood were in a single nest tube of the total number of specified colony pairings at the specified time intervals.

	Time after colony fragments were combined					
Pairings[a]	1 H[b]	D[b] 2 & 3	D 5 & 7	D 8 & 10	D 12	D 14
WG-G	4 of 5	5 of 5	5 of 5	3 of 5	4 of 5	5 of 5
G-G	2 of 2	1 of 2	1 of 2	2 of 2	2 of 2	2 of 2
WG-WG	2 of 3	3 of 3	3 of 3	3 of 3	3 of 3	3 of 3

[a]Locations of the source of the colony fragment pairings. WG-G: Winter Garden-Gainesville; G-G: Gainesville-Gainesville; WG-WG: Winter Garden-Winter Garden.
[b]H = hour; D = day

Nonacs (2000) reported fighting among 64% of Argentine ants paired from various cities in California that were tested within 3 wk of collection. However, retesting ants from aggressive colonies about 2 mo after collection resulted in a significant decrease in fighting. Also feeding different prey to laboratory reared colonies for ≥ 28 d, Silverman and Liang (2001) induced distinct cuticular hydrocarbon profiles, aggression, and colony dissociation among formerly tolerant Argentine ant colonies. In addition, isolation of *Camponotus fellah* Dalla Torre (Hymenoptera: Formicidae) workers from their parent colony was associated with changes in their cuticular hydrocarbon profiles and increases in aggressive interactions (Boulay et al. 2000). In our aggression tests, tawny crazy ants came from colonies held up to 7 mo in the laboratory. However, in the colony interaction test, aggression was not observed between any of the paired colony fragments despite being collected within 2 d of initiating testing. In addition, we observed queens from each paired group nesting together, including queens that were collected from sites 148 km apart. Thus, in our study, lack of aggression among the tawny crazy ants remained consistent regardless of the length of time they were maintained in the laboratory. Hence, we conclude that territoriality did not occur among tawny crazy ants collected from geographically distant sites in Florida based on our aggression testing.

The territoriality of invasive ants within and across geographically separate locations has been examined for several species. For example, lack of aggression among all Argentine ant nests sampled across the North Island (900 km area) of New Zealand suggested the existence of an extensive unicolonial population (Corin et al. 2007). In contrast, aggression scores of an invasive population of *Myrmica rubra* L. (Hymenoptera: Formicidae) in Maine increased with inter-nest distances within a locality and escalated to higher aggression levels (grasping/carrying) with pairings of colonies from spatially separate populations. This provided evidence of a multicolonial population structure in a geographically widespread invasion (Garnas et al. 2007). In addition to advancing the understanding of invasion biology, such studies have applications to controlling invasive ant proliferation and spread. Indeed, determining the social structure and the associated territorial behavior of red imported fire ants have influenced baiting strategies (Drees et al. 1992, 1993; Flanders & Drees 2004) and the use of pathogens for their biological control (Oi & Valles 2009; Valles et al. 2010). The apparent unicoloniality of the tawny crazy ant may facilitate the use of relatively recent discoveries of pathogens in this invasive ant (Plowes et al. 2015; Valles et al. 2016).

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