Particle Size Preference of Six Ant Species (Hymenoptera: Formicidae)[1]

Reid M. Ipser[2] and Wayne A. Gardner[3]

Department of Entomology, College of Agricultural and Environmental Sciences, University of Georgia, Griffin Campus, 1109 Experiment Street, Griffin, Georgia 30223, USA

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Abstract Bait particle size preferences of six ant species among four particle sizes (2.36, 2.0, 1.44, and 0.85 mm) were determined in laboratory assays. Based on weight of bait particles removed over a 3-h observation period, *Solenopsis invicta* Buren *Aphaenogaster fulva* Roger and *Aphaenogaster lamellidens* Mayr preferred the 2.36 mm bait particles. *Formica pallidefulva* Latreille workers equally preferred the 2.36 and the 2.0 mm particles. *Linepithema humile* (Mayr) equally preferred the 2.0 and 1.44 mm particles while *Pheidole dentata* Mayr preferred the 0.85 mm particles. Particle size preference in these assays was positively correlated with mean width of the head capsules of the worker ants. These results suggest that particle size of formulated baits might be matched with ant species to improve efficacy against targeted pest ant species while minimizing impact to nontarget native species. Competitive interactions of the invasive *S. invicta* with the four native ant species (*A. fulva*, *A. lamellidens*, *F. pallidefulva*, *P. dentata*) in this study showed that *S. invicta* workers rapidly dominated foraging areas and subsequently raided nests of the native ants.

Key Words ant bait, Formicidae

The red imported fire ant, *Solenopsis invicta* Buren, and the Argentine ant, *Linepithema humile* (Mayr), are native to South America, but both have expanded their ranges into North America where they compete with native ant species for ecological niches. This usually results in the competitive displacement of native species, with concomitant reductions in species richness and diversity (Camilo and Phillips 1990; Holway 1998; Human and Gordon 1996; Porter and Savignano 1990). Competitive displacement is not limited to native ant species but also includes other invertebrate fauna, as reported by Cole et al. (1992) following successful establishment of *L. humile* in Hawaii.

Competitive interactions between invasive and native ant species primarily involve competition for the same food resource. *Solenopsis invicta* effectively displaces other ant species from food baits (Camilo and Phillips 1990; Jusino-Atresino and Phillips 1994; Porter and Savignano 1990), even when the competing species discovers and dominates the resource first (Banks and Williams 1989). *Solenopsis invicta* domination of baits is achieved by mass recruitment and

[1]Received 5 April 2019: accepted for publication 23 April 2019.
[2]Present address: Nisus Corporation, 100 Nisus Drive, Rockford, TN 37853, USA
[3]Corresponding author (email: wgardner@uga.edu).

chemical aggression against competing ant species, behaviors that are also observed in their South American native ranges (Calcaterra et al. 2008). *Linepithema humile* workers often monopolize foraging areas and effectively discover food resources first and recruit to baits in higher numbers than do native ants (Holway 1999; Human and Gordon 1996).

Yet, there are reports of native ant species effectively competing with either *S. invicta* or *L. humile* for habitat resources and, thus, coexisting with either of these invasive species (Apperson and Powell 1984; Holway 1999). Drees and Gold (2003) suggested that conservation of native ant species, especially those that directly or indirectly compete with *S. invicta* or *L. humile*, should be a component of any biologically based management plan for these invasive pest species.

Management of these two invasive pests has relied primarily on chemical insecticides, with active ingredients being increasingly formulated as bait granules containing gustatory attractants (Drees and Gold 2003; Jordan et al. 2013; Williams et al. 2001). Baiting tactics, however, are not necessarily species specific; baits targeted at pest ant species may also be attractive to and foraged by nontarget ant species.

Specificity and efficacy of active ingredients might be increased by matching particle size of the bait with a target ant species. Hooper-Bui et al. (2002) found a correlation of worker ant head width with preferred particle size. They reported that the three species with larger head capsule widths (*Pogonomyrmex californicus* [Buckley], *Formica* spp., and *S. invicta*) preferred larger bait particle sizes of $>$2,000 μm. *Monomorium pharaonis* (L.), with the smallest head width of the six species tested, preferred particles ranging from 240 to 590 μm in size. Two other species—*Solenopsis xyloni* McCook and *L. humile*—with intermediate head widths preferred particles 840–1,000 μm in size. Neff et al. (2011) also reported that the smaller *S. invicta* workers selected smaller bait particles while larger workers selected large particles. Reed et al. (2015) corroborated the observations of Hooper-Bui et al. (2002) and Neff et al. (2011) with *S. invicta* but also found that a shift from larger to smaller workers, caused by the presence of *Pseudacteon* phorid flies, resulted in a shift to a smaller particle size preferred by the foraging ants.

Our objectives in the study reported herein were to: (a) determine particle size preference of *S. invicta*, *L. humile*, and four ant species native to North America; (b) correlate particle size preference with head capsule width of foraging workers of each ant species; and (c) examine competitive interactions between species for bait particles. The four native species included in the study were *Aphaenogaster fulva* Roger, *Aphaenogaster lamellidens* Mayr, *Formica pallidefulva* Latrielle, and *Pheidole dentata* Mayr. They were selected because of their distribution and frequency of occurrence in a survey of ground-dwelling ants in Georgia (Ipser et al. 2004) and their amenability for maintaining and handling in the laboratory.

Materials and Methods

Ant colonies. Colonies of the six ant species included in the study were originally collected and established from field populations of each in Spalding County, GA. *Solenopsis invicta* were collected by digging and placing colonies and associated soil in 20-L plastic buckets for transport to the laboratory where they were separated from the soil using procedures of Jouvenaz et al. (1977). Extracted ants were placed in plastic arenas (55 long × 44 wide × 13 high cm) with the upper 10 cm of inner walls coated with Fluon (Northern Products, Woonsocket, RI, USA) to prevent ant escape. At least one artificial nest consisted of a Petri dish (12 diam × 3.5 high mm) with its top blackened with paint and its bottom filled one third of its depth with hardened dental plaster, which was wetted to provide a source of moisture. Colonies were fed three times each week on an alternating of diet of canned tuna and crickets. Colonies of *L. humile* and the four native species were established by placing field-collected ants with some associated soil and ground litter directly into the plastic arenas, with the upper inner walls coated with Fluon to prevent escape. Test tubes containing sugar water and water alone were plugged with cotton and placed in each arena to provide food and moisture. Colonies of all species were maintained at 26–27°C at 70–75% relative humidity (RH) on a 12:12-h photoperiod.

Bait particles. Four sizes of bait particles were created for the study by grinding freeze-dried crickets in a Braun grinder (Braun Intertec, Minneapolis, MN, USA) and sieving to corresponding sizes of 8 (2.36 mm), 10 (2.00 mm), 14 (1.44 mm), and 20 (0.85 mm) using Fisherbrand U.S. Standard Brass Sieves (Fisher Scientific, Waltham, MA, USA). Crickets were purchased from Luke Farms (Port Allen, LA, USA), stored in a freezer, and thawed to 25°C prior to grinding. The numbers of particles associated with a range of 15–16 weights of particles for each particle size were counted, recorded, and subjected to correlation analysis (PROC CORR; SAS Institute, Inc. 2015).

Particle size preference. Preference testing was conducted by connecting the previously described colony arena with a foraging arena of the same size and also coated with Fluon on the upper 10 cm of the inner walls to prevent ant escape. The colony arena containing an active colony of ants was connected to the empty foraging arena with Tygon tubing (1 cm diameter; Sigma-Aldrich, St. Louis, MO, USA) or a bridge constructed of wooden garden stakes (2.8 wide × 30.5 long cm; Forestry Suppliers, Jackson, MS, USA), thus allowing foraging worker ants access to both arenas. Tubing was used for *S. invicta* and *L. humile* foraging, but foraging workers of *A. fulva*, *A. lamellidens*, *F. pallidefulva*, and *P. dentata* would not consistently use the tubing to access baits in the foraging arena. For those species, wooden stakes were attached end-to-end with tape to create a bridge 95 cm in length to extend between the colony and foraging arenas.

For each preference testing unit (i.e., colony arena + foraging unit), ants were allowed to acclimate to the foraging arena for 1 h before placement of bait particles in the foraging arena. At that time, individual weighing dishes (44 × 44 mm; VWR Scientific, West Chester, PA, USA), each containing 10 mg of a specific particle size, were placed equidistant from the opening of the tubing or the end of the bridge in the foraging arena. Location and order of the dishes with the respective particle sizes were randomly determined for each of 10 replications. Worker ants were then allowed to forage until all bait particles for at least one bait particle size were removed from the dishes and the foraging arena. Weights of particles remaining in each weighing dish were recorded, thus allowing for calculation of weight of each size of bait particles removed from the arena by each ant species. The number of particles transported by foragers of each species could then be estimated based on numbers of particles in a range of weights of the baits. Differences observed among the particle size treatments were then used to establish a particle size preference profile for each ant species.

In all, 10 replications of the treatments were conducted over time. For most species, colonies were used only once for the preference testing, but when colonies were used more than once, a minimum of 5 d was allocated between consecutive replications.

Head capsule width. Fifty worker ants for each of the six ant species were randomly selected in the particle size preference test (five workers per replicate) to measure head capsule widths. Measurements were made with a Wild microscope ocular (Wild, Heerbrugg, Switzerland) calibrated with an Olympus microscopic objective micrometer (Olympus Corp., Shinjuku, Tokyo, Japan). Individual ants were positioned with the frons facing the ocular, allowing the measurement to be taken above the compound eyes as described by Umphrey (1996). Mean head capsule width for each species was then regressed with preferred particle size (Sokal and Rholf 1995).

Interspecific competition for bait particles. *Solenopsis invicta* competition with each of the four native ant species for bait particles was examined using the colony and foraging arenas. In these assays, one foraging arena was placed between a colony arena containing an *S. invicta* and a colony arena containing either an *A. fulva*, *A. lamellidens*, *F. pallidefulva*, or *P. dentata* colony. Bridges constructed of wooden garden stakes (2.8 wide $\times$ 30.5 long cm) taped end-to-end linked each colony arena to the central foraging arena, allowing ants access from their respective colonies to the foraging arena. The ends of the respective bridges were placed in the foraging arena so that each was 15 cm from a linear arrangement of the four sizes of bait particles in individual weighing dishes (44 $\times$ 44 mm) as previously described. Ants were allowed to acclimate to the foraging arena for 24 h before placement of the bait particles in the foraging arena. Each pair of competing ant species was replicated 10 times over time at 25 $\pm$ 2°C and 70–75% RH on a 12:12-h photoperiod. Ant behaviors (e.g., foraging activity, recruitment), were observed and recorded periodically. Colonies were usually used only once in these assays, but when colonies were used more than once we allowed a minimum of 5 d between consecutive replications.

Statistical analyses. Data were subjected to analysis using a general linear model (Statistical Package for Social Sciences, SPSS) unless otherwise specified. A one-way analysis of variance was used to determine differences in weight of bait particles removed and differences in numbers of worker ants on the bait particles. Where statistically significant differences occurred, Tukey's honestly significant differences (HSD) test was used to separate means (Sokal and Rholf 1995).

Results and Discussion

Workers of each of the six ant species included in this study accepted and foraged the bait particles created from freeze-dried crickets. Within each respective particle size, the particles were uniformly sized and the numbers of particles were positively correlated with weight of bait particles ($F = 1{,}651.39$, df $= 14$, $P < 0.0001$, $R^2 = 0.9922$ for 2.36 mm particles; $F = 20{,}568.1$, df $= 14$; $P < 0.0001$, $R^2 = 0.9994$ for 2.0 mm particles; $F = 1{,}118.98$, df $= 14$, $P < 0.0001$, $R^2 = 0.9885$ for 1.44 mm

Table 1. Mean (±SD) head capsule width and mean (±SD) weight of bait particle sizes removed by *Solenopsis invicta*, *Linepithema humile*, *Aphaenogaster fulva*, *Aphaenogaster lamellidens*, *Formica pallidefulva*, *Pheidole dentata* workers in laboratory arenas.

Species	Head Capsule Width (mm)	Bait Particle Sizes* 8 (2.36 mm)	10 (2.0 mm)	14 (1.44 mm)	20 (0.85 mm)
S. invicta	1.11 ± 0.17	10.0 ± 0.0 a	6.8 ± 2.0 b	5.5 ± 1.3 b	5.1 ± 2.2 b
L. humile	0.38 ± 0.02	6.5 ± 2.5 b	9.0 ± 1.9 a	8.1 ± 2.0 ab	5.7 ± 1.4 b
A. fulva	0.91 ± 0.03	10.0 ± 0.0 a	7.5 ± 7.0 b	5.0 ± 1.8 c	0.6 ± 0.7 d
A. lamellidens	1.01 ± 0.06	10.0 ± 0.0 a	6.3 ± 1.9 b	3.9 ± 1.5 c	0.9 ± 0.9 d
F. pallidefulva	1.22 ± 0.23	8.8 ± 2.5 a	7.3 ± 1.5 a	3.2 ± 7.8 b	0.3 ± 0.7 c
P. dentata	0.60 ± 0.03	0.8 ± 1.0 c	0.7 ± 0.9 c	4.0 ± 3.2 b	9.0 ± 1.0 a

* Bait particles from ground freeze-dried crickets and sizes determined with U.S. Standard Brass Sieves; means within rows and followed by the same lowercase letters are not significantly different (Tukey's HSD, $P = 0.05$).

particles; $F = 214.12$, df $= 15$, $P < 0.0001$, $R^2 = 0.9386$ for 0.85 mm particles). Workers of the six species also removed at least a small portion of each size of bait particle in these assays. Each species, however, exhibited preferences for bait particle sizes within the 3-h foraging period (Table 1).

Three of the four native ant species in the study preferred the largest (2.36 mm) bait particles (Table 1). *Aphaenogaster fulva* and *A. lamellidens* workers removed 100% of the 2.36-mm particles and showed a bait size preference profile, from greatest to least preferred, of 2.36 mm > 2 mm > 1.44 mm > 0.85 mm. Very little foraging of the smallest size (0.85 mm) of bait particles occurred with either of these two species; *A. fulva* removed only 6% of the 0.85-mm particles and *A. lamellidens* removed only 9%. *Formica pallidefulva* removed only 3% of the 0.85-mm particles, preferred the 2.36-mm and 2.0-mm particles, and showed a bait size preference profile, from greatest to least preferred, of 2.36 mm = 2.0 mm > 1.44 mm > 0.85 mm. *Pheidole dentata* was the only native species that did not prefer the largest bait particles. These workers removed 90% of the smallest (0.85 mm) particles while removing only 7% of the 2-mm particles and 8% of the 2.36-mm particles. Their bait size preference profile, from greatest to least preferred, was 0.85 mm > 1.44 mm > 2 mm = 2.36 mm.

Workers of the two invasive species—*S. invicta* and *L. humile*—demonstrated greater latitude than the native species in foraging all sizes of the bait particles. *Solenopsis invicta* workers removed 100% of the 2.36-mm particles within 3 h, but they also removed 51–68% of the smaller particles over the same period of time. Their bait size preference profile, from greatest to least preferred, was 2.36 mm > 2 mm = 1.44 mm = 0.85 mm. For *L. humile*, we observed an overlap of statistical differences among the four sizes of bait particles ranging from 57% removal of the 0.85-mm particles to 90% removal of the 2.0-mm particles. These results indicated that these two invasive species could effectively forage the range of bait particle sizes included in this study, an attribute that likely contributes to the success of these species in competitively displacing other species from food resources.

These data also showed that, with these six ant species, size of bait particle foraged was positively correlated ($F = 304.08$; df $= 299$; $P < 0.001$; $R^2 = 0.505$) with width of worker head capsules. Similar relationships between head capsule width and preferred food particle size have been reported for *S. invicta*, *L. humile*, and other ant species (Hooper-Bui et al. 2002; Neff et al. 2011; Roulston and Silverman 2002). Our results with *S. invicta* corroborate those of Hooper-Bui et al. (2002); however, our results with *L. humile* differ slightly. Hooper-Bui et al. (2002) reported that populations of *L. humile* from California and Alabama preferred bait particle sizes of 0.85–1.00 mm. Our results show that the *L. humile* population from Georgia preferred larger particles of 2.0 mm. We also measured a larger mean width of the head capsule than Hooper-Bui et al. (2002) reported, which could account at least in part for the observed preference for larger particles. Regardless, both studies as well as those of Neff et al. (2011) and Roulston and Silverman (2002) demonstrate that bait particle size preference is related to head capsule width. And, for optimal foraging efficiency, worker ants should select and carry the largest food particles they can in order to maximize net energy intake relative to unit of effort exerted (Jordan et al. 2013).

Linepithema humile workers removed an estimated 382 bait particles from the forage arena over the 3-h observation period with 48% of those being 1.44-mm particles and 40% being 0.85-mm particles. *Solenopsis invicta* workers removed an estimated 298 total particles while *A. fulva* removed 174, *A. lamellidens* removed 145, *F. pallidefulva* removed 118, and *P. dentata* removed 338. Of the 338 particles removed by *P. dentata* workers, 27% were particle size 1.44 mm and 72% were particle size 0.85 mm.

Solenopsis invicta exhibited aggressive territorial and foraging behavior when competing against either *A. fulva*, *A. lamellidens*, *F. pallidefulva*, or *P. dentata* in the laboratory foraging arenas. In competing with each of the native ant species, *S. invicta* dominated the foraging arena by arriving in the arena before the competing native species and recruiting greater numbers of foragers to the arena than did their competitor. *Solenopsis invicta* would subsequently raid the opposing species nest in the housing arena to force native species workers to the periphery of the housing arena. Eventually, all brood were transported to the *S. invicta* nest, and remaining workers and queen(s) were killed. No bait particles were foraged until the competing native ant colony was totally eliminated. Due to the absence of the competing species during the period of foraging the bait particles, we did not record any bait size preferences by *S. invicta*.

A goal in defining bait size particle preference of these ant species was to determine if bait particle size could be matched to a specific target ant species and, thereby, increase efficacy of the bait while decreasing impact on nontarget ant species. The particle size preference for five of the six ant species in this study were very similar, with preference for larger bait particles. The preference profile for *P. dentata*, however, differed substantially from the preference profiles of the other five species. And, the profiles of *S. invicta* and *L. humile* indicated that these two invasive species can effectively forage the range of bait particle sizes included in this study. Based on these results, a bait particle measuring 2.0–2.36 mm would not be highly foraged by *P. dentata* but would be preferred by *S. invicta*, *L. humile*, *A. fulva*, *A. lamellidens*, and *F. pallidefulva*. Bait particles of 0.85 mm would be highly foraged by *P. dentata*, would not be preferred by *A. fulva*, *A. lamellidens*, or *F. pallidefulva*, and would be moderately preferred by *S. invicta* and *L. humile*. Therefore, if *P. dentata* resides in a habitat targeted for ant management while *A. fulva*, *A. lamellidens*, and *F. pallidefulva* do not, a mixture of 2.0–2.36-mm bait particles could be applied targeting *S. invicta* or *L. humile* to minimize impact on the native *P. dentata* population. On the other hand, a 0.85-mm bait particle could be used to target *S. invicta* and *L. humile* if *P. dentata* does not occur and *A. fulva*, *A. lamellidens*, or *F. pallidefulva* do occur in the habitat to be treated.

These results further indicate that in order to improve efficacy of granular baits, particle size should be tailored to include those sizes preferred by the targeted pest ant species. Baits containing particles measuring 2.36 mm would best target *S. invicta* while those measuring 1.44–2.0 mm would best target *L. humile*. Maximum recruitment and foraging by the two invasive species could also be facilitated by applying baits at optimal foraging temperatures ranging between 20–30°C (Markin 1970; Porter and Tschinkel 1987).

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