Ecology of *Dorymyrmex flavus* (Hymenoptera: Formicidae) in Central Texas, Including Aspects of Competition With *Solenopsis invicta* Buren

by

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**ABSTRACT**

*Dorymyrmex* species, commonly known as “pyramid ants” are found throughout the United States, but are most common in the South. Considered as occasional pests of urban lawns, principally for their unsightly mound building activities, they are an under-represented group which appears to compete with Red Imported Fire Ant *Solenopsis invicta* (Buren). *Dorymyrmex flavus* McCook is one of six species in this genera found in Texas. While the basic biology of this group is somewhat similar to other species within the genus, there is vague or limited information about their occurrences in Texas. Evaluation of natural populations from central Texas demonstrate that *D. flavus* is an opportunistic omnivore, but will readily feed on honeydew and other arthropods, both by hunting and scavenging. The colony sizes in central Texas are reputed to be much smaller than those of the same species found in Florida, with numbers of less than 1000 workers in late summer and early fall. This species is monomorphic. The species was found to swarm in June, well into the fall season, and nests were observed in open areas and sandy substrates, such as Zulch Fine Sandy Loam. Colonies of *D. flavus* continue to thrive in *Solenopsis invicta* Buren infested areas. This is accomplished by being an effective defender of the nest, possessing an ability to seal off tunnels and escape during invasions, spatially occupying soils that are not well suited to *S. invicta*, occurring in clumps to increase numbers to defend a territory, and being extremely aggressive towards newly mated *S. invicta* queens, which diminishes future threats of competition.

Key Words: *Dorymyrmex flavus, Solenopsis invicta*, ecology, ant behavior, competition.

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INTRODUCTION

*Dorymyrmex flavus* McCook is a species of Dolichoderine (subfamily Dolichoderinae) ant native to the southern United States (Johnson 1989). *Dorymyrmex flavus* (Fig. 1A) is a species that has received little attention in research, compared to several other *Dorymyrmex* species. This species ranges from New Jersey south, down the Atlantic Coast, and westward through Texas, with unclear boundaries. It is reported from Mexico and some western states, but the complete distribution is undetermined (Johnson 1989). Along with the other species in the genus *Dorymyrmex*, it has received many taxonomic revisions and designations since being first described by McCook in 1879 as *Dolymyrmex insanus* var. *flavus* (Snelling 1995). Since its initial description, subsequent designations, in order, have been: *Dorymyrmex pyramicus*, *Dorymyrmex* (*Conomyrma*) *pyramicus*, *Conomyrma insane*, and most recently, *Dorymyrmex flavus* (Snelling 1995). Commonly known as “pyramid ants” because of a pyramid-shaped projection on top of the propodeum, *Dorymyrmex* [*=Conomyrma* (Snelling 1995)] species are found throughout the United States, being most prevalent in the South. Of the 12 species native to the United States, six are found in Texas. These include: *D. flavus*, *D. insanus* (Buckley), *D. smithi* Cole, *D. bureni* (Trager), *D. lipan* and *D. bicolor* (Wheeler) (Snelling 1995).

The worker of *D. flavus* has a yellow or light gray alitrunk, with a predominately yellow head and gaster (Fig. 1A). These colors can vary slightly between colonies or localities, with the most common deviation being a dark gray dorsum of the alitrunk. The lateral mesonotal profile can be convex or flat, with an angle on the posterior of the mesonotum. Like all species in the genus, there is a cone-shaped projection on the dorsum of the propodeum; however, unlike some other *Dorymyrmex* species, there is not a convex swelling on the propodeum anterior to the cone in *D. flavus*. The queen is monocolored yellow-brown to dark gray (Johnson 1989).

Workers are occasionally structural pests during foraging; however, nests have not been reported indoors (Hedges 1992, 1998). Typically, they are aggressive ants, quickly attacking other species encountered near their nests, especially during the warm season (Johnson 1989). This active and predaceous nature has earned these ants the occasional nickname “lion ants” (Hung 1974).
Fig. 1. A) Morphological comparisons of (a) *D. flavus* head capsule (b) *D. flavus* worker (c) *S. invicta* worker head capsule (d) *S. invicta* worker. Photos courtesy of Joe MacGowan, Mississippi Entomological Museum. B) A total of 50 *D. flavus* workers, from the same colony, had their head widths ($\chi = 0.72 \pm 0.004$ SEM) measured anteriorly across the compound eyes.
*D. flavus* is omnivorous, feeding on honeydew from various homopterans, scavenging on arthropod remains, and attacking small soft-bodied prey (Johnson 1989). *Conomyrma flava* (McCook) [=*D. flavus*] workers are known to forage year-round, with winter surface activity being confined to mild days (Johnson 1989). Often, two species within *Dorymyrmex* may live in close sympatry, and there has been at least one observance of a mixed nest consisting of *D. insanus* and *Conomyrma flavopecta* (M.R. Smith) [=*D. flavopectus* (Snelling 1995)] in Florida (Buren et al. 1975). In this case, *D. insanus* was described as a temporary, non-obligate social parasite of *D. flavopectus* (Buren et al. 1975). Mating flights of *D. flavus* occur during the summer in Texas, from late May into early September, with the winged alates emerging near dusk and flying before darkness (Johnson 1989).

*Dorymyrmex* species generally nest in open areas, usually on disturbed terrain without a closed forest canopy, and often occur near human developments. The colonies usually consist of a few thousand individuals, and are often in the vicinity of nests of other ant species, particularly those of *Pogonomyrmex* species (Hedges 1992). Nests are usually in sandy soil with good drainage and poorly developed sod. The nest entrance is surrounded by a symmetrical crater of excavated soil (Fig. 2A), with the size of the entrance hole varying between species (Johnson 1989).

Worker numbers are generally believed higher in *D. flavus* than in *D. insanus*, with both presumably ranging into the thousands; however, there are variations of colony size within a given location (Johnson 1989). Therefore, the size of colonies in central Texas may be different than those observed elsewhere. Another colony characteristic to be documented is the caste structure, the first part being the number of reproductives within a colony. Nickerson et al. (1975a) notes that *D. flavopecta* (M.R. Smith) exhibits a monogyne, monodomous colony structure. Johnson (1989) states that *D. flavus* has a polydomous structure. There is no consensus about colony structure across broad geographic ranges where this species occurs, and that was the impetus to compare populational observations of *D. flavus* from central Texas and Florida. In addition, worker size is described, with particular attention given to the size of the workers relative to each other. Workers falling into distinct groups with significant differences in size indicates polymorphy, much like the *Dormyrmex pyramicus* (Roger) described by Smith (1965). If no such
grouping exists, the ants are considered monomorphic. Food preferences of *D. flavus* remain undefined. Hedges (1992) states that *Dorymyrmex* species generally prefer sweets, while Johnson (1989) goes further, noting that they are omnivorous.

Nesting preferences and physical characteristics are poorly understood for this species. As noted before, the preferred substrate is a sandy-type soil with good drainage (Johnson 1989); however, soil types are subject to local variation, and documenting the exact soil types utilized by *D. flavus* in central Texas may be an important part of describing the nesting sites. Another...
observable character is the structure of the nests and location of the nests, in terms of physical proximity to nearby vegetation and preferred light exposure. Any inquilines found within the excavated nests will be identified, as will any closely associated ant species. A likely close associate to *D. flavus* is another *Dorymyrmex* species, the only other local possibility being *D. insanus*. It has been noted that nests of these two species are often found near one another (Johnson 1989). Another possible candidate for association is a *Pogonomyrmex* species, which has been found near *Dorymyrmex* species nesting sites (Hedges 1992, 1998). This is probably due, in part, to the fact that they prefer open spaces with a good amount of sunlight (Cole 1968), much like *Dorymyrmex* species.

Another objective has been to document some of the interactions of *D. flavus* with *Solenopsis invicta* Buren (RIFA). *Solenopsis invicta* is an aggressive species, and has displaced much of the native ant fauna in central Texas by direct or indirect competition (Claborn *et al.* 1988). With both species being primarily nocturnal foragers utilizing the same foraging areas synchronously, it is unknown how the two apparently coexist (Claborn *et al.* 1988). Like all dolichoderine ant species, *D. flavus* has no sting for defense. This, coupled with the high fecundity and overwhelming numbers of *S. invicta* (Jones & Phillips 1987), makes *D. flavus*’ success against *S. invicta* subject to inquiry. Past studies have been conducted on the refuse piles often present near entrances of *Dormyrmex* nests. Hung (1974) found large numbers of dismembered and whole carcasses of various insects, mainly other ant species, in one such pile near a *D. insanus* nest. The highest proportion of the ant carcasses, both whole and dismembered, proved to be *S. invicta* remains. It is not known whether these ants were killed by the *D. insanus* or if their carcasses had been scavenged for food. However, aggression by *D. insanus* toward *S. invicta* was confirmed by Nickerson *et al.* (1975b), who observed *D. insanus* workers preying on founding queens of *S. invicta* following their nuptial flight. *Dorymyrmex insanus* is the other *Dorymyrmex* species in central Texas which competes successfully in *S. invicta* territory (Claborn *et al.* 1988), by employing many of the same tactics for colony survival as *D. flavus*.

The purpose of this study was to clarify the ecology of *D. flavus* from central Texas. With this intent in mind, observations on colony characteristics (e.g., colony size and caste proportions and structure), food preference, nesting
architecture and site selection, and interspecific competition with *Solenopsis invicta* were evaluated under field and controlled laboratory conditions.

**MATERIALS AND METHODS**

**Colony Size.**

Entire colonies from various locations in Brazos County, Texas were brought into the laboratory, and counted (Talbot 1943). Colonies were collected by shoveling them into 16 L plastic buckets and transporting them back to the laboratory. They were then placed into 55 x 40 cm plastic boxes dusted with baby powder to prevent escape. The ants were separated from the soil by providing a test tube filled with moistened cotton, which they used as a nesting site. After the colony moved into the test tube “nest”, it was removed and maintained in a 31 x 17 cm plastic box lined with Fluon® AD-1 (Northern Products, Inc.) to keep the ants from escaping. The colony was provided with frozen crickets, 5-10% honey water solution, and water. Special efforts were made to collect colonies after rains as the colony nears the surface of the soil during inundation events. For the actual count, the colony was immersed in EtOH, counted, and separated into castes: workers, brood, and reproductives. Four colonies, from various locations in Brazos County, were surveyed for this study. Three colonies used in this investigation were collected from mid-November to early December. The fourth was collected in late October.

**Colony Structure.**

Colonies used in this study were collected and maintained as described above. An investigation was conducted to determine if the colonies were polydomous and polygynous (having more than one egg laying queen). If more than one dealated queen was discovered in an excavated colony, all dealated queens present were dissected and their spermatheca inspected for evidence of fertilization. More than one fertilized queen would indicate polygyny. A second study was performed on worker size to determine if *D. flavus* is polymorphic or monomorphic. Using a Wild® M5 stereomicroscope (Heerbruug, Switzerland) at 25x, 50 workers’ head capsules were measured with an ocular micrometer calibrated with a stage micrometer, and the results, in millimeters, were plotted on a graph. The heads were measured at their widest point, across the compound eyes. From the graph, the average size of
the workers was determined, as well as any distinct groupings by size. More than one grouping would indicate polymorphism.

**Food Preference.**

Colonies were collected and maintained in the laboratory in the same manner as previously described. Before each trial, the ants were starved for 72 h, but were provided with water. The foods tested included two sources of sugars (5% honey-water solution and strawberry jelly), one source of insect protein (frozen crickets), and one source of animal protein and fat (vienna sausage). The foods were provided to the ants in the same box in which they were maintained, at equal distances from the nest, to ensure equal access. The test involved making counts of foragers at each food source three times per day (10 am, 2 pm, and 9 pm) for 4 d. Any factors that could have influenced food choice of a particular *D. flavus* colony, such as large amounts of brood or reproductives, were noted. The results were tested statistically using a one-way analysis of variance to determine if one or more types of food preference was significantly different than the others.

**Soil Type, Location, and Inquilines.**

To describe the nest in terms of soil type the Brazos County Soil Survey was used. Three locations where *D. flavus* nests were excavated were found on the survey map, and the soil type determined. Any common links between the different soil types were noted, such as drainage, content, and texture. In addition, these findings were compared to the soil types utilized by the other members of the genus *Dorymyrmex*. In the description of the physical proximity of the *D. flavus* to vegetation and light exposure, observations of these conditions were made and photographs were taken of the nest areas. Again, similarities between these areas and the preferred habitat of other *Dorymyrmex* species were noted. The investigation into any inquilines and ant associations of *D. flavus* was conducted throughout the entire study. Any arthropods found within the excavated nests were identified, as were any ant species observed living in close association with *D. flavus*.

**Nest Structure.**

The structure of the underground *D. flavus* nest was described using an apparatus that facilitates cross-sectional viewing of the tunnels and chambers of
the nest (Fig. 2B). It consists of a 61 x 61 cm square frame of 2.5 x 5 cm pine. Two pieces of single pane glass were attached to either side of the frame using silicon glue. The apparatus was then filled with the same substrate in which the ants were collected, with adequate moisture added. A healthy colony of *D. flavus* was added, including reproductives, workers, brood, and eggs. The soil column was thick enough to accommodate large chambers or tunnels, but thin enough to permit thorough observation of the nest. Two weeks were allowed for the ants to excavate the nest in the soil. The direction and depth of tunnels were noted, as was the location of any brood chambers.

**Field Studies.**

A total of 10 observation sessions were conducted in the field during a time period from summer to late winter, 1997. Each session was 30 min long. They involved observing foragers of *D. flavus* interact with foragers of *S. invicta* along a definite territorial border between the two species in Lick Creek Park, Brazos County, College Station, Texas. Attention was paid to any aggressive or evasive behavior between the foragers during the encounters. During late summer mating flights of *S. invicta*, the reaction of *D. flavus* workers toward the newly mated *S. invicta* queens was also observed, similar to the study conducted by Nickerson *et al.* (1975b) on *D. insanus*. The second part of the field study consisted of an analysis of *D. flavus* refuse piles. The piles were collected with a spade and placed into clean jars. Samples were then brought back to the laboratory and examined under a Wild® M5 stereomicroscope at 12x. Any identifiable arthropod remains were noted. Ant carcasses were identified using a key based on the head capsules.

**Spatial Interactions Between Colonies of *D. flavus* and *S. invicta*.**

This experiment was conducted in a controlled environment. A 6.5 x 1 m arena was constructed inside a greenhouse, and populated with a healthy *S. invicta* colony. The colony was housed in a box of appropriately moist soil, with access to the foraging area inside the arena. The foraging area of the arena was covered with 2 cm of sand, and surrounded by a strip of aluminum covered with fluon, to prevent the escape of ants. The colony was maintained on a 5% honey-water solution, mealworms, and water. The *S. invicta* colony was allowed to fully establish in the arena for 4 wks. The *D. flavus* colonies used...
in this experiment were brought directly from the field, put in the 31 x 17 cm box that housed them for the experiment, and maintained for 3 d before being introduced to the arena. The colonies were in the exact same soil in which they were collected, to ensure the most natural conditions possible. At both ends of the arena, a single healthy *D. flavus* colony was placed and allowed to assimilate to its new environment behind a barrier. After three days, the barriers were lifted and the interactions were observed between the foragers. Significance was placed on time to colony death, or time for *D. flavus* to establish a defined territory.

In the second tests, which measured the interactions of *D. flavus* with *S. invicta*, aggression levels between workers followed a protocol by Retana & Cerda (1994). The workers used in the study were collected directly from the field with an aspirator and placed into the testing container. Each trial consisted of 10 workers of *D. flavus* and 10 workers of *S. invicta* placed into a 9 cm circular petri dish or a 31 x 17 cm plastic box. Of the 10 *S. invicta* workers used in each trial, one was a major worker, and the other nine were medium workers. A total of 10 trials were conducted, five in the small petri dishes and five in the larger plastic boxes. The different sized containers were used to show a correlation of aggression levels with the varying size of the confrontation area. Twenty individuals of the same colony of each species were kept in a separate container to serve as non-treatment controls. The workers were left undisturbed for 3 h, after which time the numbers of live and dead ants were recorded. To be counted as alive, a worker could not be crippled, dismembered, or otherwise moribund. Only alert, mobile ants were counted as alive. To measure aggression levels and to determine the level of dominance, the numbers of live ants of each species following each trial were totaled, and an aggression index (AI) calculated. To calculate the index, the number of *S. invicta* alive was divided by the number of surviving *D. flavus*. According to the values of this index, total dominance is an AI of greater than 1.5, relative dominance is 1.1 to 1.5, and counter balance is an AI between 0.9 and 1.1. In the case of an AI of 1, with no deaths occurring in either species, a designation of no aggression was given (Retana & Cerda 1994).
RESULTS

Colony Size.

The results of the four counts are shown in Table 1. The mean colony size was one fertilized queen, 325 workers, 9.5 pupae, and 33.5 larvae, with a standard deviation for worker number of 319. The largest colony observed was 752 workers, and the smallest was 80. This shows a notable variance in colony size, and a marked drop in worker numbers with the onset of winter. The colony collected in October contained 18 winged males, and the colony collected in November contained only four winged males.

Table 1. Size of D. flavus colonies in Brazos County, Texas, collected from late October to early December. Each colony was divided into numbers of queens, workers, pupae, and larvae.

<table>
<thead>
<tr>
<th>Date Collected</th>
<th>Area Collected</th>
<th>Number of Queens</th>
<th>Number of Workers</th>
<th>Number of Pupae</th>
<th>Number of Larvae</th>
</tr>
</thead>
<tbody>
<tr>
<td>23 X 1997</td>
<td>Lick Creek</td>
<td>1</td>
<td>752</td>
<td>14</td>
<td>94</td>
</tr>
<tr>
<td>14 XI 1997</td>
<td>FM2818</td>
<td>1</td>
<td>387</td>
<td>10</td>
<td>26</td>
</tr>
<tr>
<td>5 XII 1997</td>
<td>FM 2818</td>
<td>1</td>
<td>80</td>
<td>8</td>
<td>14</td>
</tr>
<tr>
<td>3 XII 1997</td>
<td>Lick Creek</td>
<td>1</td>
<td>82</td>
<td>6</td>
<td>19</td>
</tr>
</tbody>
</table>

Colony Structure.

In this study, 50 worker head widths were measured (mm) to determine if D. flavus exhibits either polymorphy or monomorphy (Fig. 1B). The mean head size for D. flavus workers measured was 0.72 ± 0.03 mm. All values measured were within 0.13 mm and ranged between 0.65 mm and 0.78 mm. Approximately 67% of the distribution of the sample fell within 0.72 mm ± 0.023 mm, and 95% were inside 0.72 mm ± 0.06 mm.

Food Preference.

All of the colonies tested were similar in number of brood, workers, and reproductives. Two trials of this experiment were conducted with the same four colonies, one immediately following the other. In the first trial, no significant difference existed between the number of foragers observed at each food source when tested with a one-way ANOVA (F= 1.07, d.f.= 3,172, P=0.362); however, there were preferences for carbohydrate substrates. The results of the second trial were much like the first trial: when tested with a one-way ANOVA, no significant difference was observed in forager numbers at the different food sources (F= 2.07. d.f.= 3.220. P=0.105) over time.
Soil Type, Location, and Inquilines.

The prevalent soil type in which *D. flavus* colonies were found in Brazos County, Texas, was Zulch Fine Sandy Loam. All colonies used for this study were taken from this soil type in different locations around the county. This soil is moderately well-drained and very slowly permeable. The top layers where the nests occur were very hard, moderately acidic, and contained many fine roots. However, not all colonies observed occurred in this exact type of soil. There were several cases of the nests not occurring fully in soil at all, but in the cracks of parking lot asphalt. The usual location of *D. flavus* nests was observed to be in open areas, generally devoid of a canopy and with a high degree of sunlight exposure (Fig. 2A). Throughout this investigation, no inquilines were found living within *D. flavus* nests; however, there were some ant associations noted. On two occasions, *Monomorium minimum* (Buckley) workers were isolated from an excavated colony of *D. flavus*, and in one case, *S. molesta* workers were collected.

*D. flavus* exhibited a polydomous structure with a maximum depth for a nest at 61 cm, which likely would have been deeper in an unconfined situation. The nest contained three entrances and several brood chambers (Figs. 2A, 2B), at different depths, connected by a network of tunnels (Fig. 2B). The chambers varied from 2 to 3 cm wide, and generally were elliptical in shape (Fig. 2A). In a separate field observation, a *D. flavus* colony with an above-ground brood chamber was noted. The chamber was under a small section of leaf litter, in close proximity to the nest entrance. When the colony was disturbed, workers trailed to the chamber, and brood were quickly brought into the underground section of the nest.

Field Study.

The results of the interactions between *S. invicta* and *D. flavus* observed in the field are described in Table 2. The interactions were conducted between 1200 and 1500 hrs. Although both species are primarily nocturnal foragers (Claborn et al. 1988), an adequate amount of diurnal foraging was observed to record the varying nature of forager encounters in the field. *D. flavus* occurred in clustered colonies, with observable territories that were defended from intrusion by *S. invicta* workers. The common foraging area between the two species appeared to be on the sandy substrate where *D. flavus* nests
occurred (Fig. 2A). Few *D. flavus* workers were seen and no confrontations were observed outside this area. The large battles that were observed appeared to be stalemates after 30 min of observation, with neither side gaining a distinct advantage over the other. There was no aggression observed between members of different *D. flavus* colonies. A decrease in surface activity of both species with the onset of winter led to a drop in the number of encounters, as well as a drop in aggressive behavior in the encounters that did occur.

In the second part of the field study, an analysis of the contents of *D. flavus* refuse piles was conducted on four piles collected in July, August, and September, 1997. Similar to the study done by Hung (1974), the ant heads were keyed out, separated into species, and counted. Each species present was then divided into queens and workers. *S. invicta* accounted for all of the ant remains present in two piles, and over 98% of the remaining two. The *S. invicta* queen remains present in the piles increased in the late summer as *S. invicta* mating swarms became more frequent.

**Spatial Interactions Between Colonies of *D. flavus* and *S. invicta***

The barriers between the colonies were removed following the assimilation period on October 20, 1997 at 2:00 pm (Fig. 2D). The temperature in the greenhouse was 28° ± 2°C. When the barriers were lifted, the *S. invicta* workers immediately began scouting the previously barricaded *D. flavus* territory. A small number of *D. flavus* workers were foraging; however, the majority of the colony was inside the nest (Fig. 2A, 2B). The *D. flavus* foragers were much faster than *S. invicta*, and rapidly, fled when confronted individually. After 5 min, three *D. flavus* workers were observed on the opposite end of the 6.5 m table from where they originated. The scouting by both species continued for 30 more min, until the larger of the two *D. flavus* colonies was discovered. A raiding party of 100 - 200 *S. invicta* workers then mounted an offensive on the colony. This initial attack was successfully repelled by the *D. flavus* workers when all *S. invicta* raiders, including major workers, were killed during a 2 min battle. The combat technique for *D. flavus* seemed to be a grab and hold strategy using the mandibles. Often, limbs and antennae were severed, and at least two *S. invicta* workers were bitten in half at the petiole (Fig. 2C). The carcasses were disposed of in a pile outside the nest, about 5 cm away from the entrance. The surface activity of *D. flavus* then
ceased, with no workers being observed outside the colony. Approximately 50 min following the initial attack, a second offensive was mounted on the larger *D. flavus* colony. Another battle ensued, involving 100 - 200 workers of each species; however, unlike the first attack, one *S. invicta* major worker was able to escape, and was observed laying a pheromone trail away from the *D. flavus* nest. Within five min, hundreds of *S. invicta* workers followed the trail to the nest, and the *D. flavus* were greatly outnumbered. About 90 min after the barriers were initially lifted, both *D. flavus* nests were overrun by *S. invicta*, with no resistance observed at the smaller colony. The *S. invicta* workers were observed going in and out of the *D. flavus* nest, and several workers carried away brood. No further resistance was observed on the surface of the nest. After the conquering of the nest, several *S. invicta* workers leaving the *D. flavus* nest were seen attacking members of their own colony. This only occurred in the *S. invicta* workers that had gone into and come out of the *D. flavus* nest. There was no observable reason or stimulus for the attacks, but they were seen by three observers (J. Martin, S.B. Vinson, and R.A. Warriner) over a 30 min period following the overrun of the *D. flavus* nest. At 10:00 am on October 21, 1997, the nests were still busy with *S. invicta* workers, and there was no sign of *D. flavus*. The boxes that contained the two nests were then dumped, exposing a pocket of 100 - 150 *D. flavus* workers at the bottom of the box. They were alive 19 h after the final takeover of their nest. Many of the workers scattered onto the table, and were observed for as long as five days afterward on the table among the *S. invicta* workers. Those observed exhibited an avoidance strategy as they utilized their superior speed to keep away from the *S. invicta* workers. Furthermore, they were also able to attain food in the hostile environment; at least one was observed feeding on honey water solution provided for *S. invicta*.

**Group Tests Between Workers of *D. flavus* and *S. invicta*.**

The pooled results of the group trials, along with the calculated aggression indexes, on *S. invicta* workers and *D. flavus* workers are seen in Table 2. Casualties occurred in all 10 trials, but none in the control ants. The AI calculated for the trials in the boxes was 1.31, and the AI calculated for the trials in the petri dishes was 1.44. Both indicate relative dominance of *S. invicta* over *D. flavus* in this controlled environment, as does the overall AI
of 1.37. *Dorymyrmex flavus'* mode of attack was the previously mentioned strategy of grabbing and holding *S. invicta* with their mandibles. Major *S. invicta* workers were attacked most often at the antennae and legs, while media and minor workers were most often attacked at the petiole. *D. flavus* attacked very tenaciously, and often continued their hold long after they had been killed. Only one of the *S. invicta* workers killed, in all ten trials, was a major worker. Aggressive behavior was observed 5 - 10 min. faster in the smaller containers than in the larger containers. It is notable that the AI was lower in the larger containers, which may show that *D. flavus* workers are better suited to fighting in a more open space.

Table 2. Pooled results from 10 group trials between workers of *D. flavus* and *S. invicta*, and the calculated overall aggression index (AI). The separate AI's calculated for trials conducted in both types of containers are also included.

<table>
<thead>
<tr>
<th>Type of Container Used in Trial</th>
<th>No. of <em>S. invicta</em> Alive Following Trial</th>
<th>No. of <em>D. flavus</em> Alive Following Trial</th>
<th>Aggression Index <em>(S. invicta alive/ D. flavus alive)</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>31 cm x 17 cm Boxes (5 Containers)</td>
<td>38</td>
<td>29</td>
<td>1.31</td>
</tr>
<tr>
<td>9 cm Petri Dishes (5 Containers)</td>
<td>36</td>
<td>25</td>
<td>1.44</td>
</tr>
<tr>
<td>All trials (10 Containers)</td>
<td>74</td>
<td>54</td>
<td>1.37</td>
</tr>
</tbody>
</table>

**DISCUSSION**

**Colony Size.**

The results of this investigation indicate a markedly smaller colony size than mentioned by Johnson (1989). This is possibly due to a more temperate climate in central Texas than in central Florida, different levels of territory competition, and different types and amounts of food resources available. The average population of workers observed in this experiment was 325 ± 319 SD. The high degree of variation among the colonies resulted from a large drop-off in population during the winter months. This is in direct contrast to *S. invicta*, which experiences its greatest worker numbers in midwinter (Tschinkel 1993). Larval and pupal numbers also declined as the year progressed; however, their proportion of the total colony population did not, remaining at 8- 13% of the total colony population. The presence of winged males in the
colonies collected in October and early November indicates that *D. flavus* may continue to swarm through the middle of the fall season.

**Colony Structure.**

All observations of *D. flavus* from both the laboratory and field demonstrate monogyny. The colonies studied failed to produce a colony with more than one fertilized, egg-laying queen. However, this does not rule out the polygyne structure suggested by Johnson (1989). It is possible that *D. flavus* exists in both polygyne and monogyne colonies, much like *S. invicta* (Glancey 1987).

The possibility exists for different sized castes of workers, similar to the castes found in *D. pyramicus* (Smith 1965). The results showed a head width range of 0.13 mm, between 0.65 mm and 0.78 mm. The head width range for the worker castes found in *S. invicta* exhibits a range of 0.72 mm, going from 0.63 mm to 1.35 mm (Hölldobler & Wilson 1990). The head width of the largest workers was more than double that of the smallest workers. The *S. invicta* workers fell into several distinct size classes when plotted on a graph, each differing by at least 0.10 mm from the next caste (Hölldobler & Wilson 1990). This is nearly the entire range of similar sized *D. flavus* workers. In addition, the body parts among the workers are isometric, unlike *S. invicta*, which exhibits allometry, as antennae are proportionally shorter with the larger castes of workers (Hölldobler & Wilson 1990). These observations can lead to the conclusion that *D. flavus* is indeed monomorphic, and workers do not exist in distinct, size-differentiated castes.

**Food Preference.**

*D. flavus* possessed similar attraction to foods previously described by Johnson (1989). This species is omnivorous, feeding on honeydew from various homopterans, scavenging invertebrate remains, and attacking soft-bodied prey. Hedges (1992) states that the general preference of the genus *Dorymyrmex* is sweets, most likely honeydew. The results of the first experiment show no significant difference among the number of foragers observed at the different food sources (\( F = 1.07, \text{d.f.} = 3, 177, P=0.362 \)). Similar to the first trial, the results of the second trial (\( F = 2.07, \text{d.f.} = 3, 220, P= 0.105 \)) also do not show a significant difference; however, the 5% honey-water solution was used more than the other food sources. This solution was the food
source offered that was the most similar to the honeydew secreted by aphids and other homopterans. With Johnson’s (1989) observation of *D. flavus* consuming honeydew in Florida, this indicated that honeydew constitutes a large part of the diet of this species in Texas as well. A search through the refuse piles of *D. flavus* revealed a diverse collection of arthropod remains. Coleopterans, hemipterans, and other ants, most notably *S. invicta*, were the majority of the remains found in the piles. It was not determined which of these were scavenged, and which were actually preyed upon by *D. flavus*; however, *D. flavus* workers were observed preying on *S. invicta* workers in the field. In addition to the omnivorous diet of *D. flavus*, the small total number of foragers, relative to colony size, seen at the food sources over the 4 d of the experiment may indicate a relatively low food requirement. These experiments and observations into the food preference of *D. flavus* in central Texas suggest that the species is omnivorous, and seems to be equally adept at tending homopterans, scavenging arthropod remains, and preying on a variety of other insects, including *S. invicta*.

**Soil Type, Location, and Inquilines.**

Results described herein reveal the preferred soil type of *D. flavus* in central Texas to be similar to the type described by Johnson (1989) in Florida. Zulch Fine Sandy Loam is sandy, well-drained, and is associated with poorly developed sod. This soil is also moderately acidic and contains many fine roots, neither of which were addressed in Johnson’s (1989) described soil. Another similarity found to Johnson’s study (1989) is the open-area type location of the nests. In all cases observed, the nests had very little overhead vegetation, if any, and most were totally devoid of cover. These findings seem to indicate consistency in *D. flavus*’ nesting habits. However, the presence of the nests in the cracks of an asphalt parking lot may show a degree of adaptability to an urban environment. The cracks are well-drained and devoid of cover, a situation similar to the natural nesting sites observed.

There were no inquilines observed living within the *D. flavus* nests. With no references found that present any evidence to the contrary, it is not likely that inquilines inhabit the nests with any frequency. There are any number of reasons for this apparent lack of associated inquilines. These may include *D. flavus* not easily accepting inquilines, the *D. flavus* nest presenting an unsuit-
able environment for inquilines, or insufficient resources in the small colonies to sustain an inquiline population. However, ant associations were observed, including those with *S. molesta* and *M. minimum*. *Solenopsis molesta* is often found in close association with the nests of larger ants (Thompson 1989), and may act as both parasite and occasional predator on *D. flavus* colonies, as they do on *S. invicta* (Thompson 1989). No evidence has been presented that *M. miminum* acts as a predator on any associated ant colonies, so these associations may be due to a common interest in nearby resources and a lack of aggression between the two species.

**Nest Structure.**

The observed nest structure of *D. flavus* indicates a polydomous structure, with brood located in at least two chambers at all times. This experiment did not permit the daily and seasonal cycles in activity to be observed because it was conducted in a controlled laboratory environment. However, the construction of numerous chambers and the network of tunnels at varying depths reveal that there likely does exist a pattern of activity associated with changing moisture and temperature conditions. Much like *Pogonomyrmex occidentalis* (Cresson), brood, queen location and depth probably vary with the time of day and season (Lavigne 1969). However, unlike the monodomous *P. occidentalis*, *D. flavus* has numerous entrances into the nest which connect 10 - 12 cm. beneath the surface. The depth of the *D. flavus* nests was not determined; however, they were observed to tunnel to the maximum 61 cm allowed by the container. An above-ground brood chamber observed may allude to *D. flavus*’ resourcefulness in dealing with adverse conditions. Although the cause for this cannot be determined, a possibility is poor moisture or temperature conditions in the soil. If the soil was too dry and proved too hard to excavate any deeper, the colony may have used available leaf litter to cover and retain moisture over a portion of the brood until conditions were better for further tunneling.

**Field Study.**

There was observed aggression between the two species, and a definite territory established by *D. flavus* within the common foraging area utilized by both species. Encounters between the two species are quite common, especially in the warmer months, despite their different habitats. This is
probably due to the fact that their preferred habitats often occur in close proximity to each other, resulting in a common foraging area. The clustering of many *D. flavus* colonies may help with establishing and defending this territory against the much larger colonies of *S. invicta*. Similar to *D. insanus* (Nickerson et al. 1975b), *D. flavus* workers were also observed preying upon founding queens of *S. invicta* following their nuptial flight. In addition to providing food, this behavior may be a method used to keep new colonies of *S. invicta* from forming nearby and competing with *D. flavus*. Furthermore, *D. flavus* appeared to be a capable opponent for *S. invicta* in the large-scale battles that were observed, which also likely aids in their continued success in infested areas.

In the analysis of the refuse piles found outside the entrances to the *D. flavus* nests, more evidence was uncovered about the interaction between *D. flavus* and *S. invicta*. Unlike Hung’s study (1974), which found seven different ant species in one pile, the piles examined in this investigation contained a much less diverse collection of ant remains. This is probably because of a more homogenous ant fauna in the area where the piles were collected. However, similar to Hung’s study (1974), *S. invicta* constituted the vast majority of remains found, and were the entire ant remains found in two piles. Hung (1974) did not attempt to distinguish whether the *S. invicta* remains found in the pile were scavenged or killed by *D. flavus*. From the previously mentioned observations of the aggressive nature of *D. flavus* toward *S. invicta*, it seems likely that at least some of the remains in the piles were not scavenged, but were killed by *D. flavus*.

**Spatial Interactions Between Colonies of *D. flavus* and *S. invicta***

Results obtained in this investigation provide some insight into the nature of *D. flavus* colony defense strategies. *D. flavus* was a worthy adversary when defending its nest, as evidenced by the quick victory in the initial raid by *S. invicta*. Lacking a sting, the prevailing *D. flavus* technique for combat is a grab-and-hold strategy, often severing limbs and antennae. In the laboratory setting, *S. invicta*’s superior numbers ultimately overcame the *D. flavus* resistance when a lone *S. invicta* worker was able to lay a pheromone trail leading to the nest. This trail was followed by hundreds of *S. invicta* workers during the final raid on the *D. flavus* nest. However, after no evidence of *D. flavus*
being alive in the nest, and a full 19 h following the takeover of both nests by *S. invicta*, a pocket of *D. flavus* workers was alive in the substrate in the nesting box. This pocket could not have been more than a few centimeters from *S. invicta* activity in the nest, and would surely have been detected and destroyed under normal circumstances. A possibility for the survival of these ants is an ability to seal off tunnels, and make themselves inaccessible to the *S. invicta* invaders. This would almost certainly be easier to accomplish in a field setting, without the space constraints that a controlled environment applies. Quite possibly, a much larger portion of the colony could survive in this manner if *D. flavus* was able to put more distance between itself and the invading *S. invicta*.

Another observation worth addressing is the attacks of *S. invicta* emerging from the *D. flavus* nest on members of their own colony. Since only workers emerging from the *D. flavus* nest exhibited this behavior, the stimulus for these attacks may be a pheromone put out by *D. flavus*, or the behavior may be *S. invicta* workers’ intense reaction to their own alarm pheromone. The tenacious ability to defend the nest and the ability to seal off tunnels during an invasion, coupled with the observed superior speed of *D. flavus* workers, may all be factors in *D. flavus*’ continued thriving in *S. invicta* infested areas.

**Group Tests Between Workers of *D. flavus* and *S. invicta***.

*Dorymyrmex flavus* and *S. invicta* demonstrate a high degree of aggression towards each other. This is shown by casualties seen in all 10 trials. The overall calculated aggression index (AI) was 1.37, giving a designation of relative dominance (Retana & Cerda 1994) of *S. invicta* over *D. flavus* in these trials. The trials were then evaluated using two separate groups, based on the container size used. When combined in this manner, the AI was 1.44 in the 9 cm petri dishes, and 1.31 in the 31 x 17 cm plastic boxes. This difference may indicate that *D. flavus* fares better in confrontations in a more open area, where it is able to take advantage of its greater speed. It is to be expected that aggression was seen sooner in the smaller containers; the incidence of face-to-face contact was naturally higher as the ants moved around. It is to be noted that only one of the 10 *S. invicta* major workers used in this experiment was killed by *D. flavus*, reaffirming the claim by Retana & Cerda (1994) that mortality increases in smaller ants as the size difference
between opponents increases. The large major workers proved much more difficult for *D. flavus* to kill than the smaller medium and minor workers. The results of these tests give *S. invicta* a certain degree of dominance over *D. flavus* in confrontations between groups of workers. However, the apparent ability of *D. flavus* workers to kill at least a portion of *S. invicta* workers in a confrontation should not be overlooked. Along with their speed and ability to avoid conflict when given adequate space, this may be another element in the survival of *D. flavus*.

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REFERENCES


