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Distribution, spread, and ecological associations of the introduced ant *Pheidole obscurithorax* in the southeastern United States

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Abstract

A field survey of the southeastern United States showed that *Pheidole obscurithorax* Naves, an ant introduced from South America, inhabits a 80-km-wide band along the coast between Mobile, Alabama, and Tallahassee, Florida, and is continuing to increase its range. In Tallahassee *P. obscurithorax* is rapidly spreading, and its nest density increased by a factor of 6.4 over a two-year period. Evidence suggests that *P. obscurithorax* has spread gradually by natural means. It coexists with the fire ant *Solenopsis invicta* Buren, appears to be part of a largely exotic community of ants that are tolerant of highly disturbed habitats, and seems to have little negative effect on the ant communities that it invades.

Keywords: abundance, community, Formicidae, Myrmicinae, nest density, nonnative, pitfall trap, range, rarefaction

Introduction

Species introduced to new areas, whether naturally or by humans, can alter the receiving community. These invasive species are increasingly recognized for the economic and conservation problems they create through direct (competition, predation, herbivory, parasitism, hybridization, habitat alteration) and indirect effects on a community (Elton, 1958; Vitousek et al. 1987; Pimm 1991; Simberloff et al. 1997; Brown and Lomolino 1998; Manchester and Bullock 2000; Pimentel et al. 2001). Elton's (1958) early view that disturbed and less speciose habitats are most susceptible to invading species is now thought to be overly simplistic. The success of an invader in any habitat depends on the species present, their interactions within the community, their interactions with the invading species (Simberloff 1986), and the historical path by which the community arose (Vermeij 1991; Lodge 1993). This complexity is often compounded by the presence and effects of nonindigenous species already present in the community (Simberloff 1997), by the amount of disturbance to the habitat (Tschinkel 1988), and by the location and size of the area being invaded (Brown and Lomolino 1998; Holway et al. 2002). Of the many invading organisms, social insects are among the most destructive. They affect large geographic areas, damage agricultural systems, are expensive to control, and reduce biodiversity in the communities they invade (Vinson 1986; McKnight 1993; Williams 1994; Simberloff 1997). Among these, the fire ant *Solenopsis invicta* Buren and the Argentine ant, *Linepithema humile* Mayr, are well-known invaders of North America that disrupt ant and other arthropod communities (Porter and Savignano 1990; Holway 1998; Gotelli and Arnett 2000).

Given the publicity about destructive invasive organisms, introduced species that have little effect on the communities they invade are often overlooked, and ants are no exception. McGlynn (1999) reported that only 2% (147/9358) of all known ant species have become established outside their native ranges and that only 6% (9/147) of these are considered invasive in that they out compete native ants. Within Florida alone, a hot spot for introduced species, 25% (52/207) of the ant fauna is exotic and only 3% (7/207) are "potential ecological villains" (Deyrup et al. 2000). Many introduced species that do not have large obvious effects on communities often go unnoticed and are understudied, while a small number of invaders are studied in great detail (Vermeij 1996; McGlynn 1999). Regardless of the apparent effects of invaders, documenting their distributions, habitat characteristics, and species associations as well as investigating any effects they have on the communities they invade, be they small or large, is important for future comparisons.

Pheidole obscurithorax Naves is an ant native to northern Argentina and Paraguay (Wilson 2002). It occurs in mature flood plain and open pasture along the Parana River (A. V. Suarez, personal communication) and presumably along the Paraguay River, which are traveled by ocean-going vessels. Its occurrence in North America was first observed in the port city of Mobile, Alabama, in the early 1950s (Naves 1985; under the name, *P. fallax obscurithorax*). Several other ant species with ranges along the Paraguay River system (*Brachymyrmex patagonicus* Mayr, *Linepithema humile*, *Solenopsis invicta*, and *Solenopsis richteri* Forel) have been transported to the southeastern United States via the ports of New Orleans, Mobile, and Pensacola (Naves 1985). *Pheidole obscurithorax* coexists in disturbed habitats with the fire ant *Solenopsis invicta*, which was introduced at Mobile in the late 1930s (Buren et al. 1974), but has been much slower to expand its

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range, the extent of which is unknown. It was first observed in Tallahassee, Florida (400 km east of Mobile), in 1998 (W. R. Tschinkel, personal observation). To date no documented investigations of *P. obscurithorax* have been conducted, although its occurrence in the southeastern United States is well documented (Naves 1985; McGlynn 1999; Deyrup et al. 2000; Wilson 2002). The goals of the study reported here were to determine (1) its range and likely site of introduction in the southeastern United States, (2) whether any habitat characteristics are associated with its success, and (3) whether it is associated with differences in ant communities across its range and (4) to document its spread and population increase in Tallahassee, Florida, over a two-year period.

Materials and Methods

Southeast survey

A field survey was conducted during the summer of 2001 across five states (Florida, Georgia, Alabama, Mississippi, and Louisiana) in the southeastern United States. Approximate site locations were initially chosen such that they were located 80 to 96 km apart along five east-west transects centered on the longitude of Mobile (presumed site of entry) spanning and extending beyond the expected range of *P. obscurithorax*. The initial survey determined that *P. obscurithorax* occupied a much smaller range than expected. We therefore implemented a second, more intensive sampling regime, involving sites at 40-km intervals within the smaller potential geographic range of *P. obscurithorax*, which resulted in a larger sample of sites with *P. obscurithorax*. Fifty-five sites were surveyed; 41 of these were located within the second sampling area described above. The map shows all 55 sites (Fig. 1), but to avoid any bias due to uneven sampling or the inclusion of sites potentially not suitable for *P. obscurithorax*, we included only the data collected from the 41 sites within the second sampling area for all analyses.

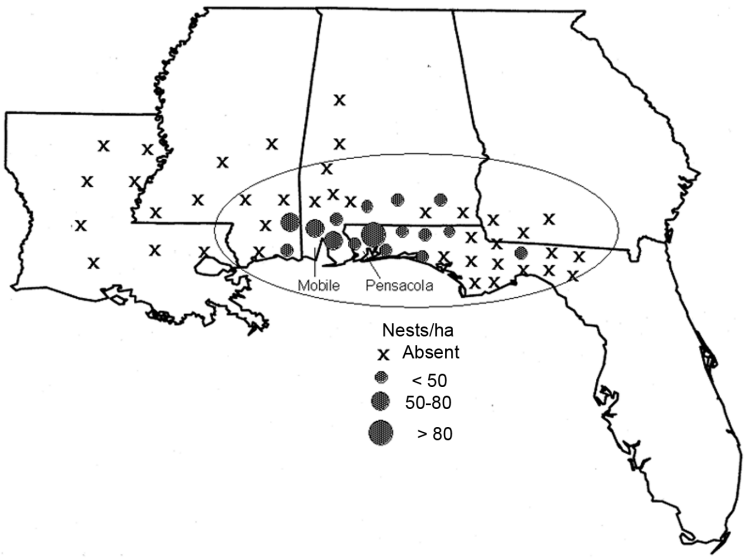

Figure 1. *Pheidole obscurithorax* nest densities at each site plotted on a map of the southeastern United States. Sites within the oval are those included in analyses. *P. obscurithorax* occurs within a narrow band along the coast, and its nest densities are highest near Pensacola, Florida.

All sites were located on rights of way along two-lane highways as in Porter et al. (1991). Characteristics were recorded at every site (latitude, longitude, elevation, surrounding vegetation type, type and percent of ground cover, grass height, and soil and air temperature), soil samples were collected, and standard survey methods (Porter et al. 1991) were used to estimate the nest densities of three conspicuous and easily identifiable ant species (*Dorymyrmex bureni* Trager, *P. obscurithorax*, and *S. invicta*). More specifically, ant nests were counted along four transects parallel to the road, two on each side of the highway (one along the pavement and the other along the tree/shrub line). Each transect was 54 m long by 2 m wide (108 m^2) for a total of 432 m^2 surveyed per site.

Bait traps were used at each site to collect ground-foraging ants. In order to attract and collect a wide array of ant species, we used two bait types placed inside individual glass test tubes—oil-rich carbohydrate (shortbread cookie crumbs) and protein (hot dog pieces)—and three collection times (15, 30, and 45 min). The use of cookie crumbs may allow less-dominant species to remain at baits with dominant species, and the use of time intervals may allow collection of both quick recruiters and those that are slower to recruit but may eventually dominate the bait (Bestelmeyer et al. 2000). At each site 60 baits were arranged linearly into groups of six (three carbohydrate and three protein) such that each group was placed 10 m from the next; baits within each group were arranged hexagonally with 1m spacing. Two previously designated baits from each group (one carbohydrate and one protein) were collected at each of the three collection times. Ants collected at baits were taken to the lab, counted, and identified to species (species identifications were aided by M. Deyrup; see Appendix I and II for site localities and species presence data).

Ant species abundance was estimated as the total number of bait tubes at each site that trapped a particular species rather than the number of individual ants trapped (counts of individual ants are estimates of both recruitment effort and abundance). Because the number of individuals collected is correlated with increasing number of species, and because of controversy over the use of diversity indices (Hurlbert 1971; Heck et al. 1975; James and Rathbun 1981; Gotelli and Colwell 2001), we used EstimateS software (Colwell 2000) to generate rarefaction curves to estimate expected number of species (species richness) at sites with and without *P. obscurithorax*.

We used the hydrometer method to conduct soil-texture analyses on the collected soil samples in order to determine the proportions of sand, clay, and silt at each site (Bouyoucos 1927, 1936, 1962).

Because of the unexpected distribution of *P. obscurithorax* (see results below), we tested the a posteriori hypothesis that wind direction after summer rains influences the flight paths of ants on mating flights or of newly mated queens. We collected precipitation and wind data for Mobile Regional Airport for four years (1998-2001) from the NOAA database online. For a randomly selected subset (n = 25) of the 76 days on which 0.25-1 inch of rain fell during June-July, wind speed and direction were collected. We used a Rayleigh test (Batschelet 1965) to determine whether a particular wind direction predominates.

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Pitfall-trap study

During the summer of 2002 a pitfall-trap study was conducted in Tallahassee, Florida. This study was designed to complement our investigation of *P. obscurithorax*'s associations with ant communities over a large geographic area (southeast survey) but on a smaller scale. Eight roadside sites were chosen in Tallahassee where *P. obscurithorax* occurred at varying nest densities (40-600 nests per ha) and had an average of 275 nests per ha. Roadside sites had similar habitat characteristics (ground cover, surrounding vegetation, % canopy, etc.). At each site 10 pitfall traps were spaced 10 m apart along linear transects. Pitfall traps consisted of 50-ml plastic centrifuge tubes partially filled with 15 ml of a soap/ propylene-glycol solution buried with their openings (32 mm diameter opening) flush with the ground surface. All 80 traps were set up on the same day and were left in place, undisturbed, for seven days (560 trap days). On the seventh day all traps were collected and the holes filled. Trap contents were sorted manually or by salt extraction (Lattke 2000) depending on the amount of debris collected in the trap. All ants were counted and identified to species. Pitfall traps are commonly used to estimate the abundances and species compositions of ground-foraging ants (Bestelmeyer et al. 2000). Although they have been shown to sample species compositions adequately, they tend to be biased toward fast-moving species (Andersen 1991).

For each ant species, abundance was calculated as the number of individuals captured per pitfall trap. To investigate the association between *P. obscurithorax* abundance and species richness, we constructed rarefaction curves based on the number of species captured in each trap for three categories of *P. obscurithorax* abundance: (1) low (0 to 8 *P. obscurithorax* captured), (2) moderate (9 to 17 *P. obscurithorax* captured), and (3) high (>17 *P. obscurithorax* captured).

Tallahassee survey

Twenty-one roadside sites were surveyed in Tallahassee, Florida, during June 2000 and again during June 2002. At each site we estimated *P. obscurithorax* nest densities by counting visible nests along linear transects from 54 to 108 m long and 1 m wide (at least 54 m^2 per site).

Results

General observations

Pheidole obscurithorax is a large, dark ant up to 6 mm in length, and its workers are dimorphic; the majors are larger than the minors and have enlarged heads. It nests in soil in open areas, where it produces conspicuous nests, each generally with a single large (1- to 5-cm-wide) opening often covered by a leaf or other collected material. During one successful excavation of a colony in Tallahassee, a single queen was located 3m below the surface. *Pheidole obscurithorax* is omnivorous and collects a variety of arthropod prey, including other ants, and less frequently plant material such as flower petals. Its midden piles are often littered with heterospecific ant body parts, especially those of *S. invicta*, an abundant ant often found nesting near *P. obscurithorax* nests. *Pheidole obscurithorax* uses a combination of foraging tactics; if a prey item is small enough, scouts carry it unaided back to the nest. If the prey item is too large, teams of workers carry the prey to the nest whole. The size of prey handled and the speed at which it is carried to the nest are remarkable. The workers defend their prey items from other ants, including *S. invicta*, and *P. obscurithorax* both wins battles and loses them. Although little is known about its reproductive biology, small mating flights before dawn after summer rains have been observed (S. R. Storz, personal observation).

Southeast survey

P. obscurithorax inhabits a 80-km-wide band along the coast between Mobile, Alabama, and Tallahassee, Florida. Its highest nest density occurred north of Pensacola, Florida (Fig. 1). *P. obscurithorax* nest density declined with increasing distance from Mobile and Pensacola (Pearson $r = -0.55$ and $r = -0.69$ respectively, $P < 0.05$). *P. obscurithorax* abundance (number of bait tubes) also declined with increasing distance from Mobile (Pearson $r = -0.50$, $P < 0.05$) but not from Pensacola (Pearson $r = 0.03$, $P > 0.20$). *P. obscurithorax* presence was associated with shorter grass. Average grass height was greater at sites where *P. obscurithorax* was absent than that at sites where they were present (15.77 ± 0.87 cm vs. 12.08 ± 1.14 cm, average ± standard error; $t = -2.63$, d.f. = 39, P

Table 1. Site characteristics at sites with *P. obscurithorax* present and absent.

	Present			Absent					
Variable	Mean	Std.dev.	N	Mean	Std.dev.	N	t-value	d.f.	p-value
Latitude	30.6	0.3	17	30.5	0.4	24	0.59	39	0.55
Longitude	80.8	6.1	17	81.3	13.5	24	0.16	39	0.87
Elevation	171.6	112.2	17	169.7	99.4	24	0.06	39	0.95
Soil									
Avg. % sand	80.7	6.1	17	81.5	13.5	24	-0.21	39	0.83
Avg. % clay	4.2	1.9	17	4.8	4.8	24	-0.48	39	0.63
Avg. % silt	15	5.4	17	13.7	9.5	24	0.52	39	0.61
Ground cover									
% plant	72.5	16.8	17	75.7	13	24	-0.67	39	0.5
% bare	16.9	12	17	12.2	7	24	1.5	39	0.81
% litter	10.7	12.2	17	11.6	11.6	24	-0.23	39	0.81

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< 0.02). Within these roadside habitats, *P. obscurithorax* was not associated with any other habitat characteristics measured (Table 1). Grass height was not correlated with distance from Mobile or Pensacola.

If *P. obscurithorax* was introduced in Mobile, it appeared to have spread more extensively to the east (Fig. 1). We therefore hypothesized that, if winds blow predominately to the east after summer rains, the wind forces alates to fly eastward during mating flights which may explain the eastward spread of *P. obscurithorax*. For the 25 days of weather data collected, wind speed ranged from 0.7 to 9.2 mph. No predominant wind direction was detected (Rayleigh test, z = 1.8, P > 0.05) (Batschelet 1965).

Over 86,600 ants were collected at 1733 baits. Nineteen species of ants were collected, and the frequencies with which they occurred at the 41 sites were highly skewed. *S. invicta* occurred at 100% of the sites, whereas all other species occurred at less than 40% (Fig. 2). The collections followed a typical pattern of a few common species and many rare species. The proportions of bait tubes occupied by each ant species and the respective proportions of total ants collected showed a similar pattern. Eighty-five percent of the bait tubes were occupied by *S. invicta*, whereas the second and third most abundant species were *D. bureni* and *P. obscurithorax*, which occurred in 5 and 2% of the tubes respectively. *S. invicta* represented 92% of the individual ants collected. No other ant species represented more than 2% of the total, but their relative rankings differed somewhat from those of the frequencies collected at bait tubes (Fig. 2).

The abundances of the six most common ant species were not associated with either *P. obscurithorax* presence (Table 2) or its nest density (Table 3). Expected species richness estimated from the rarefaction curves was higher where *P. obscurithorax* was absent than where they were present (t = 29.3, df = 98, P < 0.0005) (Fig. 3). When approximately 800 ants are sampled, eight species are expected at sites with *P. obscurithorax*, but 16 species are expected at sites without *P. obscurithorax*. In fact, eight species of ants collected within the smaller sampling area (*Camponotus floridanus* Buckley, *Forelius analis* Andre, *Formica schaufussi* Mayr, *Linepithema humile*, *Monomorium viride* Brown, *Odontomachus brunneus* Patton, *Pheidole dentata* Mayr, and *Pheidole morrisi* Forel) were absent from sites occupied by *P. obscurithorax*, but many of these are common woodland species.

Table 2. Mann-Whitney U tests of the abundances of the six most common ant species at sites with P. obscurithorax present and absent.

	Present		Absent			
Species	Rank sum	N	Rank sum	N	U	p-value
Solenopsis invicta	443.5	17	417.5	24	143.5	0.11
Dorymyrmex bureni	516.0	17	345.0	24	192.0	0.75
Pheidole metallescens	533.5	17	327.5	24	174.5	0.43
Pheidole floridana	525.5	17	335.5	24	182.5	0.57
Brachymyrmex musculus	475.0	17	386.0	24	175.0	0.44
Pheidole moerens	477.0	17	384.0	24	177.0	0.47

Table 3. Spearman rank order correlations of the abundances of the six most common ant species and P. obscurithorax nest density. P-values are not corrected for multiple comparisons.

Species	r	p-value
Solenopsis invicta	0.27	>0.08
Dorymyrmex bureni	-0.08	>0.1
Pheidole metallescens	-0.13	>0.1
Pheidole floridana	-0.17	>0.1
Brachymyrmex musculus	0.23	>0.1
Pheidole moerens	0.29	>0.07

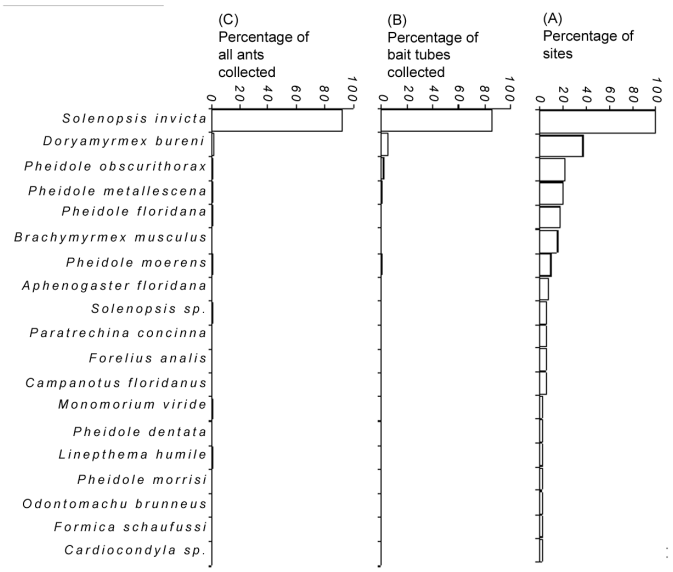

Figure 2. Collection frequencies of 19 bait-collected ant species. (a) Percentage of sites (n = 41) at which each species was collected. (b) Percentage of all bait tubes (n = 1733) that captured each species. (c) Percentage of all ants collected (n = 86,681). Each representation of collections shows a typical pattern of one or a few common and many rare species.

Pitfall-trap study

In the 80 pitfall traps, 2493 ants were captured, and 26 species were represented. Similar to those in the bait study, the distributions of percent of pitfall traps capturing each species and their relative abundances in the traps were highly skewed, but *P. obscurithorax* occurred in nearly as many pitfall traps as *S. invicta* and was ranked a close second in abundance behind *S. invicta* (Fig. 4). Interestingly, six of the seven most common ant species are introduced (*Solenopsis invicta, Pheidole obscurithorax, Brachymyrmex musculus, Cyphomyrmex rimosus, Pheidole moerens, Cardiocondyla nuda*).

P. obscurithorax abundance is not negatively associated with any of the six most common species' abundances. Rather, *P. obscurithorax* is positively, but weakly, associated with two of the commonest species (*Brachymyrmex musculus* Forel and *Cyphomyrmex rimosus* Spinola) (Spearman rank correlation, r = 0.30 and 0.29 respectively, P < 0.05). *P. obscurithorax* abundance is also positively, but weakly, associated with total ant abundance (Spearman rank correlation, r = 0.24, P < 0.05).

Expected species richness estimated from the rarefaction

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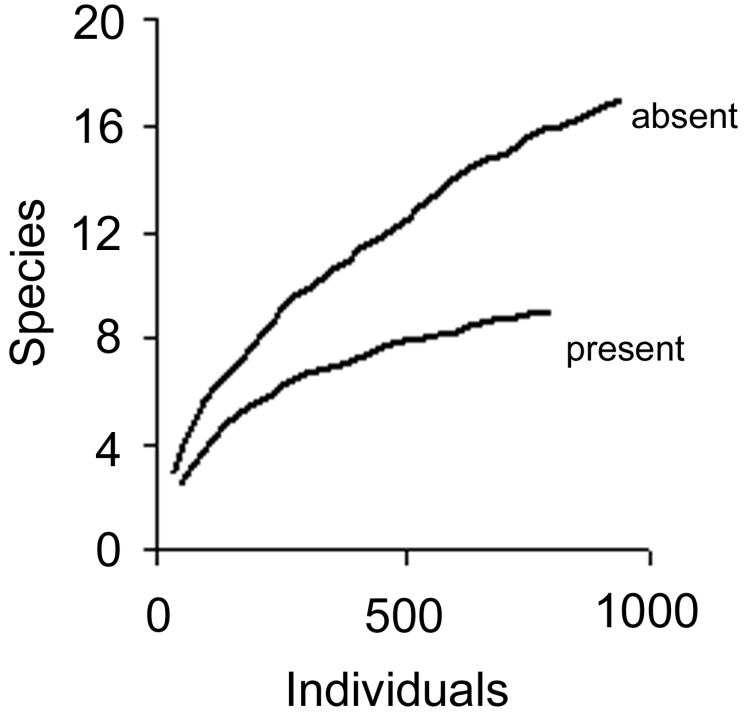

Figure 3. Rarefaction curve for southeast survey. Curves represent the expected number of species at sites with and without *Pheidole obscurithorax* determined by resampling of each data set 50 times without replacement for each category. "Individuals" are the numbers of baits that collected each species as a surrogate for abundance. Fewer species are expected at sites with *P. obscurithorax* than at sites without it.

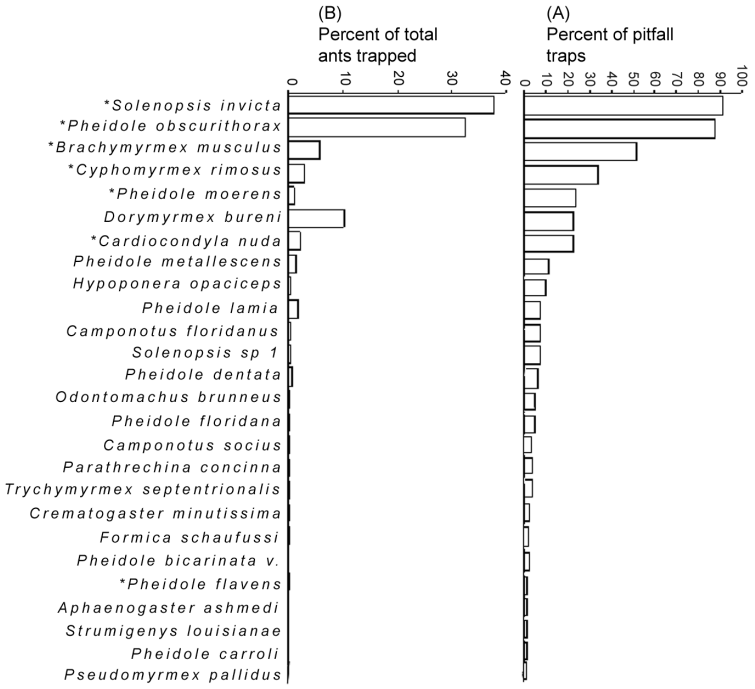

Figure 4. Frequency of 26 ant species collected in pitfall traps in Tallahassee. (a) Percentage of pitfall traps (n = 80) in which each species was trapped. (b) Percentage of all ants trapped (n = 2,493). Species marked with diamonds are nonnative. *Solenopsis invicta* and *Pheidole obscurithorax* were the most common ants trapped, and six of the most common ants are introduced.

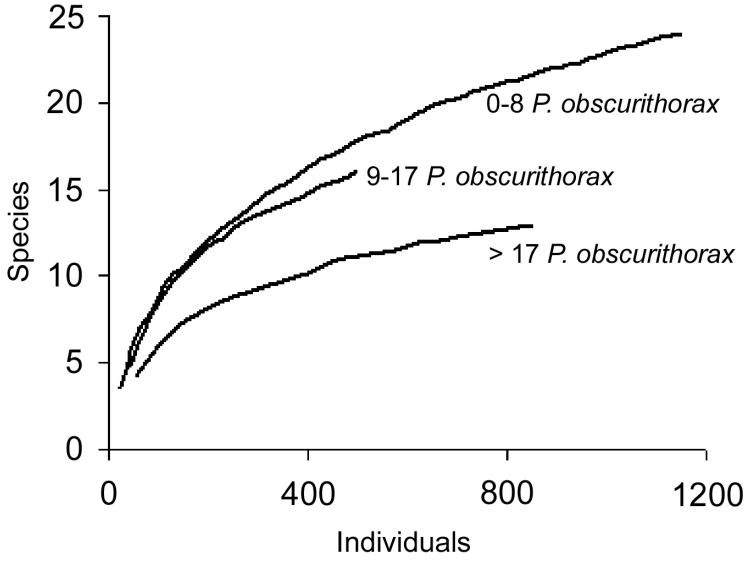

Figure 5. Rarefaction curves for pitfall-trap study. Curves represent the expected number of species per pitfall trap for three categories of *Pheidole obscurithorax* abundance and were determined by resampling of each data set 50 times without replacement for each category. Pitfall traps that capture the greatest number of *P. obscurithorax* are expected to capture the smallest number of species.

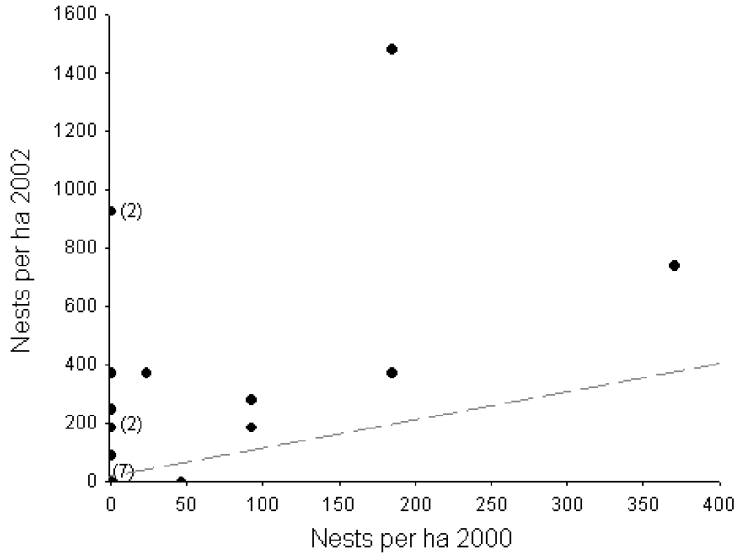

Figure 6. Relationship between *Pheidole obscurithorax* nest densities measured at 21 sites in Tallahassee in two years (Spearman rank correlation, $r = 0.5$, $P < 0.05$). Each number in parentheses is the number of sites represented by the point to its left. Dashed line signifies no change in density (isometric population growth); sites on the line did not change in density (n = 7), sites above the line increased in density (n = 13), and site below the line decreased in density (n = 1).

curves is highest in the low *P. obscurithorax* category and lowest in the high *P. obscurithorax* category, and the expected species richness of the moderate category falls in between (Fig. 5). The species-richness curve representing the high *P. obscurithorax* category is also shallower than the other two curves, suggesting a less even

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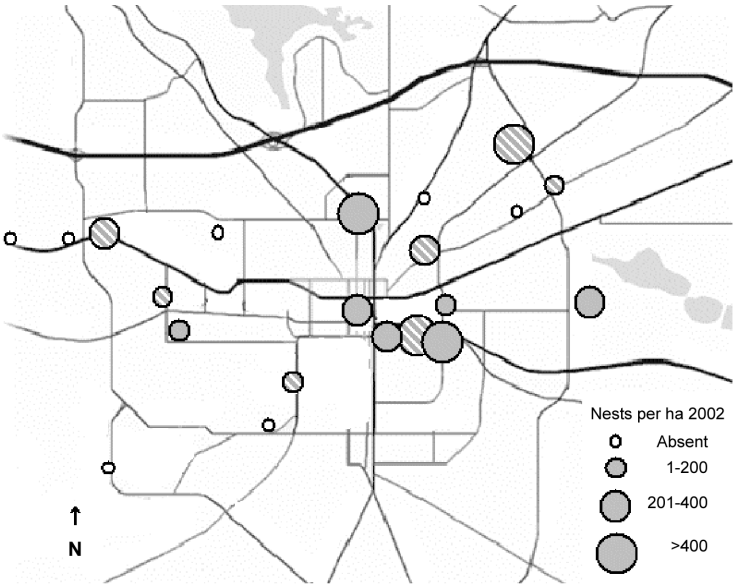

Figure 7. *Pheidole obscurithorax* nest densities at 21 sites in Tallahassee, Florida, in June 2002. Seven sites coded with hash marks were new infestations since June 2000. Densities are greatest near the center of town, and new infestations followed no apparent geographic pattern.

species distribution.

Tallahassee survey

P. obscurithorax nest density at the 21 roadside sites was greater in 2002 than that in 2000 (302.8 ± 87.2 nests per ha vs. 47.4 ± 20.6 nests per ha, average ± standard error; Wilcoxon matched pairs test, $P < 0.001$). On average, *P. obscurithorax* nest density in Tallahassee increased by a factor of 6.4 in two years. Nest density in June 2000 and nest density in June 2002 were positively related (Spearman rank test, $P < 0.05$; Fig. 6). With one exception, all sites occupied by *P. obscurithorax* in 2000 increased in nest density over the two-year period. Of the 14 sites not occupied by *P. obscurithorax* in 2000, seven were invaded by *P. obscurithorax* during the two-year period, and seven remained uninvaded (Fig. 7). Additionally, Figure 7 shows the distribution of nest densities in June 2002; populations located in the urbanized core have greater nest densities than those located in the periphery of the city ($t = 2.3$, $df = 19$, $P < 0.03$).

Discussion

The distribution of *P. obscurithorax* and its density within its range (Fig. 1) suggest that it was introduced near Mobile, Alabama, or Pensacola, Florida. Both cities have ports that have presumably allowed the introduction of numerous exotics. If no geographic or weather-driven barriers exist directly to the west of Mobile, then the data suggest that Pensacola was the more likely site of arrival because *P. obscurithorax* has spread more or less equally to the east and west of Pensacola. Lending credibility to this hypothesis is that no significant pattern of east-blowing wind was found, at least during the three years for which data were collected, that would explain an eastward spread. Alternatively, if such barriers do exist, then *P. obscurithorax* could have been introduced in Mobile, and it has spread mostly eastward. If ant abundance indicates colony size/age in *P. obscurithorax*, then the negative association between distance from Mobile and *P. obscurithorax* abundance suggests that the populations near Mobile are older than populations further away. Lack of a similar relationship with distance from Pensacola lends support to Mobile as the likely site of entry. If rates of spread to the east and west were available, a more precise location of entry could be determined.

The gradual change in *P. obscurithora*x nest densities outward from Mobile and Pensacola and its continuous occurrence throughout its range suggest that *P. obscurithorax*'s range expansion is by queen flight rather than human transport. The apparent gap in distribution west of Tallahassee (Fig. 1) is likely due to sampling error in low-density areas rather than an actual gap in the range. *P. obscurithorax* has been observed in Jackson County, Florida, (J. R. King, pers. comm.) as well as at a rest area 80 km west of Tallahassee (S. R. Storz, personal observation); both of these localities fall within the apparent gap.

Although *P. obscurithorax* and *S. invicta* were introduced at approximately the same time, *P. obscurithorax* is clearly increasing its range more slowly, and, at least on the eastern front, its expansion still continues. It has not yet spread into peninsular Florida, but we presume, given enough time, it will. *P. obscurithorax*'s low rate of spread compared to that of *S. invicta* is probably due to differences in reproductive biology such as less frequent mating flights, fewer alates, or lack of high altitude, long distance mating flights. Additionally, *P. obscurithorax* probably does not choose nest sites in nursery material that is transported by humans, and small nests are probably deep (attempted and successfully excavated nests were up to 3 m deep) and not easily scooped up and moved. Why *P. obscurithora*x has spread little to the north is unknown. Habitat and/or climate are likely important factors, but roadside habitat characteristics measured in the current study (with the exception of grass height) failed to elucidate any strong patterns of association with the occurrence of *P. obscurithorax.*

P. obscurithorax was associated with highly disturbed habitat (roadsides with shorter grass) and, so far as we know, is not found in less disturbed habitat. We have not found it in woods adjacent to roadside localities or native longleaf pine forest south of Tallahassee. In Tallahassee *P. obscurithorax* is clearly thriving. The marked increase of existing populations during the study and the colonization of several new sites lend support to the idea that this species thrives where disturbance is greatest. Its abundance on the Florida State University campus and the frequent affinity of exotic species for disturbed habitats (Elton 1958) reinforce this finding. McGlynn (1999) characterized *P. obscurithorax* as belonging to the "generalized myrmicine" functional group, members of which are generalists in food and nest-site choice and defend food resources near their nests, but *P. obscurithorax*'s dependence on human activity (habitat disturbance) for successful invasion of and persistence in new habitats suggests it also shares characteristics with "opportunists" and "tramp" species.

To the extent that baits and pitfall traps adequately sample ant communities, *P. obscurithorax* does not appear to be causing

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decreases in species abundances, but, rather, it was positively associated with total ant abundance and with the abundance of two species of ants in pitfall traps. Although *P. obscurithorax* was associated with lower species richness at baits and in pitfall traps, we do not believe that *P. obscurithorax* is causing a decrease in species richness. The eight ant species collected within the range of *P. obscurithorax* that were not found to coexist with it were rare species collected at only one or two study sites, and at least six of these are common woodland species (D. Lubertazzi, M.S. Thesis, Florida State University, 1999) probably collected at the edge of their habitat. Highway roadsides are not species-rich habitats and may therefore provide little opportunity for nonnative ants to cause ecological effects. In addition, the large numbers of rare species may make detecting any effects difficult. Only an experimental study will be able to determine the cause of the smaller values of species richness associated with *P. obscurithorax*.

Interestingly, nearly all of the commonest and most abundant ants captured in pitfall traps are introduced. Either these exotic species have out-competed native species, or, more likely, native ants are not adapted to open, disturbed habitats and are, therefore, not likely to be found in abundance in these habitats. A similar pattern is found for birds where introduced species are commonly found in disturbed, open habitat and native species tend to occur in native habitats (Case 1996). Large expanses of open, disturbed habitat, mostly caused by human activities, may simply be native-species-poor habitats to begin with but are favored by introduced species already adapted to similar habitats. It is likely that *P. obscurithorax* belongs to a smaller subset of ants that are tolerant of even more highly disturbed habitat within the generally disturbed areas we surveyed. A comparison of urban sites (Tallahassee) with non-urban sites throughout the Southeast shows that the most disturbance-tolerant species (*S. invicta*, *P. obscurithorax*, *B. musculus*, *C. rimosus*, *P. moerens*, *D. bureni*, and *C. nuda*), all exotics except for *D. bureni*, rank higher, and cluster, in the more highly disturbed urban sites than the more rural ones. Two of these species do not occur in the rural samples, and those that do move down in rank. Altogether, the case for a community of ants that covaries with degree of habitat disturbance seems strong.

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Appendix I. Southeast survey site locality information. The first two letters of site ID represent the state. The date is the date of sampling. In range describes which sites were included in the analyses (Y = yes, N = no) as described in methods.

Site ID	County	Locality	Date	In range?
FL 1	Okaloosa	Hwy 90, 3.9 mi W of Hwy 85	4/14/2001	Y
FL 2	Walton	Hwy 90, 4.1 mi E of Hwy 131	6/9/2001	Y
FL 3	Holmes	Hwy 90, 26.3 mi E of Hwy 131	6/9/2001	Y
FL 4	Bay	Hwy 79, 13.4 mi N of Hwy 98	6/9/2001	Y
FL 5	Jefferson	Hwy 90, 7.8 mi W of Hwy 19	8/1/2001	Y
FL 6	Madison	Hwy 90, 5.2 mi E of Hwy 145	8/1/2001	Y
FL 7	Gadsden	Hwy 90, 9.9 mi W of Hwy 12	8/16/2001	Y
FL 8	Jackson	Hwy 90, 17.5 mi E of Hwy 231	8/16/2001	Y
FL 9	Jefferson	Hwy 98, 11.6 mi E of Hwy 363	8/20/2001	Y
FL 10	Taylor	Hwy 121, 9.5 mi N of Hwy 19/27/221	8/20/2001	Y
FL 11	Leon	Hwy 20, 1.6 mi W of Capital Circle	8/21/2001	Y
FL 12	Wakulla	Hwy 319, 12.2 mi S of Hwy 276	8/21/2001	Y
FL 13	Calhoun	Hwy 20, 4 mi W of Hwy 71	8/25/2001	Y
FL 14	Gulf	Hwy 71, 23 mi S of Hwy 20	8/25/2001	Y
FL 15	Liberty	Hwy 20, 0.3 mi W of Hwy 65	10/5/2001	Y
FL 16	Liberty	Hwy 65, 21 mi S of Hwy 20	10/5/2001	Y
FL 17	Walton	Hwy 331, 0.2 mi N of Hwy 98	10/21/2001	Y
FL 18	Santa Rosa	Hwy 87, 6.8 mi N of Hwy 98	10/21/2001	Y
FL 19	Santa Rosa	Hwy 87, 11.3 mi N of Int 10	10/21/2001	Y
GA 1	Thomas	Hwy 319, 4 mi N of Hwy 319/19	8/17/2001	Y
GA 2	Decatur	Hwy 12, 1 mi W of Hwy 27	8/18/2001	Y
GA 3	Seminole	Hwy 91, 1.3 mi S of Hwy 84	8/18/2001	Y
AL 1	Baldwin	Hwy 184/112, 6.5 mi W of Hwy 29	4/14/2001	Y
AL 2	Mobile	Hwy 98, 12.5 mi NW of Int 65	4/15/2001	Y
AL 3	Greene	Hwy 14, 1.5 mi S of Int 20	5/5/2001	N
AL 4	Marengo	Hwy 43, 22.1 mi S of Hwy 80	5/5/2001	N
AL 5	Clarke	Hwy 43, 56 mi N of Int 65	5/5/2001	Y
AL 6	Baldwin	Hwy 59, 2 mi S of Int 65	5/5/2001	Y
AL 7	Escambia	Hwy 21, 1.1 mi N of Int 65	5/6/2001	Y
AL 8	Geneva	Hwy 79/167, 22.3 mi N of Hwy 90	8/16/2001	Y
AL 9	Geneva	Hwy 59, 0.8 mi E of Hwy 54/52	9/15/2001	Y
AL 10	Covington	Hwy 55, 12.1 mi N of Hwy 331/54/85	9/15/2001	Y
AL 11	Escambia	Hwy 29, 20 mi SW of Hwy 55/84/29	9/15/2001	Y
AL 12	Escambia	Hwy 31, 2.8 mi W of Hwy 29	9/15/2001	Y
AL 13	Baldwin	Hwy 59, 17.6 mi N of Hwy 65	9/15/2001	Y
AL 14	Mobile	Hwy 45, 23.8 mi N of Hwy 65	9/16/2001	Y
AL 15	Baldwin	Hwy 59/90, ? mi S of Int 10 (near Loxl	9/16/2001	Y
MS 1	Greene	Hwy 57, 13 mi SE of Hwy 49	4/15/2001	Y
MS 2	Harrison	Hwy 53, 6.2 mi W of Hwy 49	4/15/2001	Y
MS 3	Wilkinson	Hwy 61, 49 mi N of Hwy 190	5/3/2001	N
MS 4	Pike	Hwy 51, 8.4 mi N of Hwy 98	5/4/2001	N
MS 5	Simpson	Hwy 13, 2.1 mi S of Hwy 49	5/4/2001	N
MS 6	Forrest	Hwy 42, 0.3 mi W of Hwy 49	5/4/2001	Y
MS 7	Clarke	Hwy 18, at Int 59 intersection	4/5/2001	N
MS 8	George	Hwy 63, 2 mi S of Lucedale	9/16/2001	Y
MS 9	Stone	Hwy 26, 17.5 mi W of Hwy 57	9/16/2001	Y
MS 10	Jackson	Hwy 57, 2 mi N of Int 10	9/16/2001	Y
LA 1	Baton Rouge	Hwy 1, 1.4 mi N of Hwy 90	5/1/2001	N
LA 2	Pointe Coupee	Hwy 167, at Int 49 intersection	5/2/2001	N
LA 3	Rapides	Hwy 1, 1.7 mi SE of Int 49	5/2/2001	N
LA 4	Lasalle	Hwy 165, 0.2 mi S of Hwy 84	5/2/2001	N
LA 5	Ouachita	Hwy 15, 1.1 mi E of Hwy 165	5/2/2001	N
LA 6	Madison	Hwy 65, 1.4 mi S of Int 20	5/3/2001	N
LA 7	Tensas	Hwy 65, 47 mi S of Int 20	5/3/2001	N
LA 8	Livingston	Hwy 190, ? mi W of Int 55 (near Hamn	5/3/2001	N

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Appendix II. Species presence/absence data at southeast survey sites. An "X" signifies the species presence at each site, and a dash signifies its absence. Names of introduced species are blue.

Site ID	*Aphaenogaster floridana*	*Brachymyrmex musculus*	*Camponotus floridanus*	*Cardiocondyla sp.*	*Dorymyrmex bureni*	*Forelius analis*	*Formica schaufussi*	*Linepithema humile*	*Monomorium viride*	*Odontomachus brunneus*
FL 1	-	-	-	-	-	-	-	-	-	-
FL 2	-	-	-	-	-	-	-	-	-	-
FL 3	-	-	-	-	-	-	-	-	-	-
FL 4	-	-	-	-	X	-	-	-	-	-
FL 5	-	-	-	-	-	-	-	-	-	-
FL 6	X	-	-	-	-	-	-	-	-	-
FL 7	X	-	-	-	X	-	-	-	-	X
FL 8	-	-	-	-	-	-	-	-	-	-
FL 9	-	-	-	-	X	-	-	-	-	-
FL 10	-	-	-	-	-	-	-	-	-	-
FL 11	-	-	-	X	X	-	-	-	-	-
FL 12	-	-	-	-	X	-	-	-	-	-
FL 13	-	-	-	-	-	-	-	-	-	-
FL 14	-	-	-	-	X	-	X	-	-	-
FL 15	X	X	X	-	X	-	-	-	-	-
FL 16	-	-	-	-	-	-	-	-	-	-
FL 17	-	-	-	-	-	-	-	-	-	-
FL 18	-	-	-	-	X	-	-	-	-	-
FL 19	-	X	-	-	X	-	-	-	-	-
GA 1	-	X	X	-	X	-	-	-	-	-
GA 2	-	-	-	-	-	-	-	-	-	-
GA 3	-	-	-	-	X	-	-	-	-	-
AL 1	-	-	-	-	-	-	-	-	-	-
AL 2	-	-	-	-	X	-	-	-	-	-
AL 3	-	-	-	-	-	X	-	-	X	-
AL 4	-	-	-	-	-	-	-	-	-	-
AL 5	-	-	-	-	-	X	-	X	-	-
AL 6	-	-	-	-	-	-	-	-	-	-
AL 7	-	-	-	-	-	-	-	-	-	-
AL 8	-	-	-	-	-	-	-	-	-	-
AL 9	-	-	-	-	X	-	-	-	-	-
AL 10	-	-	-	-	X	X	-	-	-	-
AL 11	-	X	-	-	X	-	-	-	-	-
AL 12	-	-	-	-	-	-	-	-	-	-
AL 13	-	X	-	-	-	-	-	-	-	-
AL 14	-	-	-	-	-	-	-	-	-	-
AL 15	-	-	-	-	-	-	-	-	-	-
MS 1	-	-	-	-	-	-	-	-	-	-
MS 2	-	-	-	-	-	-	-	-	-	-
MS 3	-	-	-	-	-	-	-	-	-	-
MS 4	-	X	-	-	-	-	-	-	X	-
MS 5	-	-	-	-	-	-	-	-	X	-
MS 6	-	-	-	-	-	-	-	-	X	-
MS 7	-	-	-	-	-	-	-	-	-	-
MS 8	-	X	-	-	-	-	-	-	-	-
MS 9	-	-	-	-	-	-	-	-	-	-
MS 10	-	-	-	-	-	-	-	-	-	-
LA 1	-	-	-	-	-	-	-	-	-	-
LA 2	-	-	-	-	-	-	-	-	-	-
LA 3	-	-	-	-	-	-	-	X	-	-
LA 4	-	-	-	-	-	-	-	-	X	-
LA 5	-	-	-	-	-	-	-	-	X	-
LA 6	-	-	-	-	-	-	-	-	X	-
LA 7	-	-	-	-	-	-	-	-	-	-
LA 8	-	-	-	-	-	-	-	-	-	-

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Site ID	*Paratrechina concinna*	*Paratrechina longicornis*	*Pheidole dentata*	*Pheidole floridana*	*Pheidole metallescens*	*Pheidole moerens*	*Pheidole morrisi*	*Pheidole obscurithorax*	*Solenopsis diplorhopteran*	*Solenopsis invicta*
FL 1	-	-	-	-	-	-	-	X	-	X
FL 2	-	-	-	-	-	-	-	X	-	X
FL 3	-	-	-	-	-	-	-	X	-	X
FL 4	-	-	-	X	X	-	-	-	-	X
FL 5	-	-	-	-	-	-	-	-	-	X
FL 6	-	-	-	X	X	-	-	-	X	X
FL 7	X	-	X	-	X	-	-	-	X	X
FL 8	-	-	-	-	-	-	-	-	-	X
FL 9	-	-	-	-	-	-	-	-	-	X
FL 10	-	-	-	-	-	-	-	-	-	X
FL 11	-	-	-	X	-	-	-	X	-	X
FL 12	-	-	-	X	X	-	-	-	-	X
FL 13	-	-	-	-	X	X	-	-	-	X
FL 14	-	-	-	-	-	-	-	-	-	X
FL 15	-	-	-	X	X	-	X	-	-	X
FL 16	-	-	-	-	-	-	-	-	-	X
FL 17	-	-	-	-	-	-	-	-	-	X
FL 18	-	-	-	-	-	-	-	X	-	X
FL 19	-	-	-	-	X	X	-	X	-	X
GA 1	-	-	-	-	-	-	-	-	-	X
GA 2	-	-	-	-	-	-	-	-	-	X
GA 3	-	-	-	-	-	-	-	-	-	X
AL 1	-	-	-	-	-	-	-	X	-	X
AL 2	-	-	-	-	-	-	-	X	-	X
AL 3	X	-	-	-	-	-	-	-	X	X
AL 4	-	-	-	-	-	-	-	-	-	X
AL 5	-	-	-	-	-	-	-	-	-	X
AL 6	-	-	-	-	-	-	-	X	-	X
AL 7	-	-	-	-	-	-	-	-	-	X
AL 8	-	-	-	-	-	-	-	-	-	X
AL 9	-	-	-	-	-	-	-	X	-	X
AL 10	-	-	-	-	-	-	-	-	-	X
AL 11	-	-	-	-	-	-	-	X	-	X
AL 12	-	-	-	-	-	-	-	X	-	X
AL 13	-	-	-	X	-	-	-	X	-	X
AL 14	-	-	-	-	-	-	-	X	-	X
AL 15	X	-	-	-	-	X	-	X	-	X
MS 1	-	-	-	-	-	-	-	-	-	X
MS 2	-	-	-	X	-	-	-	-	-	X
MS 3	-	-	-	-	-	-	-	-	-	X
MS 4	-	X	-	-	-	-	-	-	-	X
MS 5	-	-	X	-	-	-	-	-	X	X
MS 6	-	-	-	-	-	-	-	-	-	X
MS 7	-	-	-	-	-	-	-	-	X	X
MS 8	-	-	-	-	-	-	-	X	-	X
MS 9	-	-	-	-	-	-	-	-	-	X
MS 10	-	-	-	-	X	X	-	X	-	X
LA 1	-	-	-	-	-	-	-	-	-	X
LA 2	-	-	-	-	-	-	-	-	-	X
LA 3	-	-	-	-	-	-	-	-	-	X
LA 4	-	-	-	-	-	-	-	-	-	X
LA 5	X	-	-	-	-	-	-	-	-	X
LA 6	X	-	-	-	-	-	-	-	-	X
LA 7	-	-	-	-	-	-	-	-	-	X
LA 8	-	-	-	-	-	-	-	-	-	X

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