Transactions of the American Entomological Society 126(3+4): 293-326, 2000

Exotic Ants in Florida

MARK DEYRUP

Archbold Biological Station, P.O. Box 2057, Lake Placid, FL 33862

LLOYD DAVIS

3920 NW 36th Place, Gainesville, FL 32606

STEFAN COVER

Dept. of Entomology, Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge, MA 02138

ABSTRACT

More than 50 species of exotic ants have established breeding populations in Florida. This is the largest exotic ant fauna of any U.S. state. An annotated list of species (including distribution, origin, and pest status) includes 4 new records for the U.S. Historical records suggest early modes of transport; air traffic provides new opportunities. A great majority of species arriving before 1940 are from the Old World tropics; since then a great majority are from the New World tropics. In the eastern U.S. there is a major increase in exotic ants from north to south. The proportion of exotics is higher among ants than among several other insect groups surveyed; several reasons might explain this. The ecological impact of exotic ants in Florida varies, from species usually confined to human habitations (low ecological impact) to species that are common in undisturbed as well as disturbed habitats (possibly high ecological impact). The latter 9 species are discussed briefly. Some exotic ants, such as *Linepithema humile* (Argentine ant) are less dominant in Florida than elsewhere. An annotated list is presented for another 11 species that are possible exotics. Two species reported as exotics are probably native.

In the future, more ants will probably become established in Florida. It would be useful to identify likely invaders and interdict them pro-actively. The future of Florida's natural communities is less bleak than it might seem, because there is already some ecological resistance to exotic ants, and this resistance is likely to increase.

INTRODUCTION

Species of ants have moved into Florida in such numbers that one might suspect they had read promotional literature provided by state agencies. With 52 species and counting, Florida has the dubious distinction of having more species of introduced ants than any other state. The purpose of this paper is to give a briefly annotated list of introduced ants of Florida, and make some comments on their diversity, composition, distribution, and possible overall impact of this fauna. For the purposes of this paper, we define an exotic species in Florida as one which brought

by humans, usually unwittingly. We include several species, such as *Pheidole obscurithorax* and *Brachymyrmex musculus* that were brought to adjacent states and seem to have spread into Florida by their own powers.

METHODS

This project is part of a larger, decade-long survey of Florida's ant diversity. The field work forming the basis for the great majority of records employed Tulgren funnels for litter extraction, Townes flight intercept traps for alates, various baits on the ground, on trees, and buried in perforated vials, and inspection of tree trunks, hollow twigs, dead wood, and the ground surface. For this survey we attempted to maximize species and locality records, rather than establish a protocol that would allow replicable sampling. Florida is a large and heterogeneous state, with a large ant fauna; a survey of the whole state using methods of quantitative ecology would have been impractical. Instead, we mounted small expeditions around the state, choosing collecting sites by our knowledge of Florida biogeography, earlier publications on ants, and access to habitats.

The goal at each site was as complete a list as possible within the time available, which varied from years (Archbold Biological Station and the University of Florida's Ordway Preserve) to minutes (for example, ants collected at a gas station while we were traveling to another site). Our collecting was guided by our knowledge of the behavior and habitats of species, and by our ability to identify many species in the field; these are additional factors that would make it difficult to replicate our study. Under these conditions, positive data (finding a species of ant) are immediately useful, while negative data (not finding a species of ant) are only useful after long effort, and are dependent on the apparency of the individual species. Our study is comparable to breeding bird surveys and Christmas bird counts, which are inconsistently gathered data that eventually accumulate scientific usefulness and validity. Some of our judgements will have to be either taken on faith or rejected by the reader; for example, when we suggest that the author of an earlier survey would have found a particular species of exotic ant if it had been as abundant as it is today.

Nomenclature follows Bolton (1995) except where noted. English names are either traditional names used in Florida, or original. Voucher specimens are in the arthropod collection of Archbold Biological Station, Lake Placid, Florida, or in the Florida State Collection of Arthropods in Gainesville.

ANNOTATED LIST OF EXOTIC ANTS IN FLORIDA

Prionopelta antillana Forel — Caribbean Thick-Waisted Ant

Common in rotten wood in parts of Marion and Sumter Counties. This is one of only two species of tropical exotic ants whose range in Florida does not include the tropical parts of the state. It will probably move to correct this omission. The biology of this species has not been studied, but the closely related species *P.*

amabilis Borgmeier is either monodomous or polydomous, and feeds on small soil arthropods, especially Campodeidae (Holldobler and Wilson 1986). Origin: Lesser Antilles or Central America. Pest status: none. First published Florida record: Smith 1967; earlier specimen: 1957.

Gnamptogenys aculeaticoxae (Santschi) — Spine-Thighed Grooved Ant

A rare species in Dade County; there is also a record from Escambia County. A colony from Homestead had many millipede fragments in the nest (Gary Umphrey 1987, pers. comm.).
Origin: Central or South America. Pest status: none. First published Florida record: Deyrup et al. 1989; earlier specimens: 1985.

Pachycondyla stigma (Fabricius) — Pantropical Nimrod Ant

Fairly common in south Florida, north to Volusia County. Nests in rotten wood or under bark of dead trees. We have found nests with small stockpiles of dead termites. Origin: uncertain; this seems to be a pantropical tramp species. Its wide distribution in the Old World tropics suggests that it is native there, since there are few New World ants that have become generally distributed in the Old World (see discussion below). Pest status: none. First published Florida record: Wheeler and Gaige 1920; earlier specimens: 1887.

Hypoponera punctatissima (Roger) — Pantropical Hypoponera

A common species in south and central Florida. Nests are usually in disturbed fields, lawns, edges of ditches, and marsh grass tussocks. Probably a predator of small soil organisms. Origin: Old World tropics. Pest status: queens often fly in large numbers, stinging when they land on human skin if they are touched, trapped under clothing, or stuck in sweat. We have had a number of complaints about this species, mostly from west-central Florida. First published Florida record: Smith 1933.

Odontomachus ruginodis Smith — Rough-Node Snapping Ant

A common species in disturbed areas, on beaches, and in open woods, including mangrove areas. This species is at home in both wet and dry areas. It occurs through south Florida, sporadically north into Orange County. It is probably primarily predaceous. Origin: West Indies. The reasons for considering this species introduced are discussed in Deyrup 1991. Pest status: none. First published Florida record: Wilson 1964; earlier specimen: 1931.

Anochetus mayri Emery — Mayr's Lesser Snapping Ant

A rare species in leaf litter and hollow twigs in Dade county. Probably predaceous on small soil organisms. Colonies are small, often with only a few individuals (Smith 1936). Origin: Neotropics. Pest status: none. First published Florida record: Deyrup et al. 1989; earlier specimens: 1987.

Pseudomyrmex gracilis (Fabricius) — Mexican Elongate Twig Ant

Common in hollow twigs on live trees and shrubs, as far north as St. Johns and Alachua Counties. Specimens were first collected in 1960 (Ward 1985), it was well established by 1972 (Whitcomb et al. 1972). Predaceous on a variety of arboreal insects (Whitcomb et al. 1972). Florida records were previously under the synonymized name *P. mexicanus* Roger (Ward 1993). Origin: Mexico or Central America. Pest status: we have had many complaints about this species stinging. It does not sting to defend its nest, but readily stings bare skin when touched or caught under clothing. Most victims are stung on the neck when they try to swat ants that have fallen out of trees and are traveling up the body, first reaching bare skin in the neck area. First published Florida record: Whitcomb et al. 1972; earlier specimens 1959.

Pheidole megacephala (Fabricius) — Pantropical Big-Headed Ant

Widespread in south and central Florida north to St. Augustine (St. Johns Co.), but sporadic, often occurring as a huge polydomous population, for example at the Selby Gardens in Sarasota County. This species is predaceous and scavenging, and may attend Homoptera for honeydew. In Hawaii this is the dominant ant in many habitats (Huddleston and Fluker 1968), with disastrous effects on the native arthropods, but in Florida it is a minor species. Origin: Old World tropics. Pest status: where concentrations of this species occur, large groups of scavenging workers may invade buildings. First published Florida record: Smith 1933.

Pheidole moerens Wheeler — Wandering Big-Headed Ant

Common throughout Florida, including the western part of the state. Occurs in both disturbed areas and mesic or moist woods. Nests are in rotten wood, hollow twigs and nuts, and in leaf litter; occasionally arboreal. The diet appears to be small arthropods and scavenged human food. This species rarely enters houses. The taxonomy of *moerens* and related species is unsettled, and this species could have its name changed eventually. Origin: Greater Antilles. Pest status: none. First published Florida record: Wojcik et al. 1975.

Pheidole flavens Roger — Yellow Big-Headed Ant

A relatively uncommon species in Dade, Monroe, Collier, and Palm Beach Counties. It is usually in dry or mesic woods, but can be in a variety of disturbed habitats. Often nests in dry rotten wood. Probably a predator of small arthropods and a scavenger. The taxonomy of *flavens* and related species is unsettled. Origin: Neotropics. Pest status: none. First published Florida record uncertain as there have been problems in identification; Smith 1951 may be the first reliable record.

Pheidole obscurithorax Naves — Argentine Big-Headed Ant

This species is established in Escambia, Santa Rosa, Okaloosa, Walton and Leon Counties. It nests in soil, producing conspicuous mounds in well-drained open areas. It is an aggressive predator and scavenger, even able to maintain colonies near large colonies of *Solenopsis invicta*. It is currently listed as a subspecies of *P. fallax* Mayr in Bolton's 1995 catalogue, but is due to be elevated to species (Edward O. Wilson 1995, pers. comm.). Origin: Argentina. Pest status: none. No previous published records from Florida; earlier specimens: 1992. Naves (1985) reported this species from Alabama, close to the Florida border.

Cardiocondyla emeryi Forel — Emery's Sneaking Ant

A common species as far north as Bradford County. Nests are in ground in open areas, and very inconspicuous. The natural diet is hard to determine from watching individuals returning to the nest, because even dead insects are "mined" and brought back to the nest in the form of macerated tissue or fluids; this species is probably a general scavenger (Creighton and Snelling 1974). Workers are avoided by larger predatory ants such as *Solenopsis geminata* (Fabricius) (Creighton and Snelling 1974). Origin: Old World tropics. Pest status: none. First published Florida record: Wheeler 1915.

Cardiocondyla nuda (Mayr) — Little Black Sneaking Ant

A common species as far north and west as Wakulla and Leon Counties. The inconspicuous nests are usually in extremely disturbed open areas such as dooryards and at the edges of sidewalks. This is probably another micro-scavenger. Origin: old World tropics. Pest status: none. First published Florida record: Wheeler 1932.

Cardiocondyla venustula Wheeler — Larger Black Sneaking Ant

A relatively uncommon species found throughout Florida. Nests in open areas such as fields and beaches. Origin: Old World tropics. Pest status: none. First published Florida record: Smith 1944; earlier specimens: 1932.

Cardiocondyla wroughtonii (Forel) — Yellow Sneaking Ant

A relatively uncommon species found as far north and west as Okaloosa County. Nests are usually in hollow stems of dead woody herbs or grass culms, often at the edge of wet areas or in marshes. Origin: Old World tropics. Pest status: none. First published Florida record: Wheeler 1932.

Cardiocondyla **species A** — Arboreal Sneaking Ant

A common species that is colored like *emeryi*, but has a less flattened head. It might be a species that already has an available name. It inhabits hollow twigs and beetle galleries in dead branches in trees, and bark fissures under lichens in the crown of trees. It occurs as far north as Bradford County. Origin: presumably the Old World tropics, like other *Cardiocondyla* that occur in Florida. Pest status: none. No previously published Florida records; earlier specimens: 1982.

Crematogaster agnita Wheeler — Lost Acrobat Ant

This species is known from the type series, collected by W. M. Wheeler in Guatemala, and from West Summerland Key, in Monroe County. The Florida nest was in the dead stub of a small tree just landward of the mangroves. Origin: Central America. Pest status: none. No previously published Florida records; earlier specimens: 1995.

Monomorium destructor (Jerdon) — Destructive Trailing Ant

A rare species in Florida, known from Key West and Tampa. This species lives in and around houses and is a general scavenger. Origin: Old World tropics. Pest status: in Key West abundant in the old part of town, and seems to cause the same problems as those caused by *M. pharaonis*. First published Florida record: Smith 1933.

Monomorium floricola (Jerdon) — Bicolored Trailing Ant

A common species in Florida, occurring as far north as Putnam county. Nests are usually in hollow twigs and branches, or in the dry stems of herbs and grasses. Foraging trails occasionally appear in buildings; these trails usually, but not always, originate from outside. Origin: Old World tropics. Pest status: may cause minor annoyance when it appears indoors. First published Florida record: Emery 1895; earlier specimens: 1887.

Monomorium pharaonis (Linnaeus) — Pharaoh's Trailing Ant

A common species in Florida, occurring throughout the state. Nests are in and around buildings; it is an aggressive scavenger that makes conspicuous foraging trails. It is highly polydomous, and correspondingly difficult to eradicate. Origin: Old World tropics. Pest status: this is the most persistent of Florida ant pests that breed indoors. In recent years baits have been developed that effectively control this ant. Although it rarely stings, it is very annoying in other ways, appearing in huge numbers in kitchens in homes and institutions, and frequently infesting rooms in hospitals and nursing homes. It often gnaws through the packaging of candy bars or breakfast cereal to infest the contents. First published Florida record: Smith 1930; earlier specimens: 1908.

Monomorium ebeninum Forel — Caribbean Trailing Ant

This species has been found a few times in the Florida Keys. Nests may be in the ground or in dead branches or in bromeliads. It is an aggressive scavenger, but does not seem to invade houses in the Bahamas, where it is much commoner than in Florida. Origin: West Indies. Pest status: none. First published Florida record: Deyrup et al. 1988; earlier specimens: 1986.

Solenopsis invicta Buren — Red Imported Fire Ant

A common species throughout Florida, found in many habitats. Its occurrence is generally positively correlated with habitat openness, disturbance and high water tables. It is an aggressive scavenger and predator, and also tends honeydew-producing insects. The name *invicta* is a junior synonym of *wagneri* Santschi, but a formal appeal has been submitted to retain the name *invicta*. Origin: Brazil. Pest status: this species is obviously the worst ant pest in Florida. It thrives around human habitation and fiercely defends its nests with waves of painfully stinging workers. Its ecological effects are also pervasive, although not as well documented in Florida as in some other areas (Porter and Savignano 1990). It also has a long history of indirect ecological effects in Florida by provoking massive use of insecticides. There are hundreds of scientific references on this species, and some excellent review articles, such as those of Tschinkel (1993) and Vinson (1997). First published Florida record: Council for Agricultural Science and Technology 1950, cited in Wojcik 1983; earlier specimens: 1948 (the long interval between first specimens and publication was caused by failure to distinguish between *S. invicta* and an earlier import, *S. richteri* Forel).

Tetramorium bicarinatum (Nylander) — Guinea Groove-Headed Ant

A moderately common species occurring as far north and west as Walton county. Nests are usually in dead wood or hollow stems or under loose bark, usually at the edges of wet areas. This species is not particularly associated with disturbed habitats, and if it were not a notorious tropical tramp (Bolton 1979), one would never suspect from its ecology that this was an introduced species. Origin: Old World tropics. Pest status: minor; known to occasionally enter houses, and is capable of stinging. First published Florida record: Emery 1895.

Tetramorium caldarium (Roger) — Confused Groove-Headed Ant

A relatively uncommon species occurring as far north as Hernando County. Most specimens are from open disturbed areas, usually near buildings. Origin: Old World tropics. Pest status: none. First published Florida record: Bolton 1979.

Tetramorium lanuginosum Mayr — Wooly Groove-Headed Ant

We have never found this species in Florida; it is evidently rare or local. It is also known from several other southeastern states, so it is unlikely to have been eliminated by cold weather in the southern part of its range. Origin: Old World tropics. Pest status: none. First published Florida record: Smith 1933.

Tetramorium simillimum (Smith) — Similar Groove-Headed Ant

A common species found as far north as St. Johns County. Nests are usually in soil in open areas, often around buildings or parking lots. Origin: Old World tropics. Pest status: none. First published Florida record: Wheeler 1932.

Wasmannia auropunctata (Roger) — Little Fire Ant

A common species in south Florida, occurring sporadically as far north as Marion County. Nests are in leaf litter, in rotten wood or hollow twigs on the ground, at the bases of trees, and frequently in flower pots. Habitats that are wet

or dry, shaded or open, are all acceptable. On some sites the populations are huge, the massed workers forming golden patches on the underside of any object that has been left on the ground. This species is a general scavenger, and seems quite dependent on extra-floral nectaries. Origin: South America. Pest status: this species packs a sting out of all proportion to its size, and humans are frequently stung by ants that have fallen out of trees, or are foraging across lawn chairs, or floating on the surface of swimming pools. Foraging columns often move for many yards, and may invade homes, where stray ants sting the occupants. First published Florida record: Smith 1929; earlier specimens: 1924.

Strumigenys eggersi Emery — Egger's Pygmy Snapping Ant

A common species whose range extends as far north as Union County. Found in both moist and dry woods, as well as shaded yards and gardens. Nests are in leaf litter, or in hollow twigs or nuts in the litter. Members of this genus feed on small soil organisms, especially Collembola.
Origin: Central or South America. Pest status: none. First published Florida record: Brown 1960.

Strumigenys gundlachi (Roger) — Gundlach's Pygmy Snapping Ant

An uncommon species in mesic woods and gardens in Dade, Monroe, and Collier Counties. Nests are in leaf litter. Members of this genus feed on small soil organisms, especially Collembola. Origin: Central or South America. Pest status: none. First published Florida record: Brown 1960.

Strumigenys lanuginosa Wheeler — Wooly Pygmy Snapping Ant

A rare species in mesic woods in Dade and Monroe Counties. Members of this genus feed on small soil organisms, especially Collembola. Origin: Mexico or Central America. Pest status: none. First published Florida record: Deyrup et al.1989; earlier specimens: 1987.

Strumigenys rogeri Emery — Roger's Pygmy Snapping Ant

A common species in bayheads and swamp forest, found as far north as northern Orange County. Members of this genus feed on small soil organisms, especially Collembola. Origin: Africa. Pest status: none. First published Florida record: Deyrup and Trager 1984; earlier specimens: 1965.

Strumigenys silvestrii Emery — Sylvestri's Pygmy Snapping Ant

A rare but widely distributed species, known from a few sites from the keys north to Gadsden County. Found in leaf litter in woods. Members of this genus feed on small organisms, especially Collembola. Origin: South America. Pest status: none. First published Florida record: Johnson 1986; earlier specimens: 1984.

Smithistruma margaritae (Forel) — Opaque Moustache Ant

A rare species known from a few sites in north Florida: Marion, Leon, Okaloosa and Escambia Counties. Origin: Neotropics. Pest status: none. First published Florida record: Deyrup et al. 1989; earlier specimen: 1983.

Trichoscapa membranifera (Emery) — Bare Pygmy Snapping Ant

A moderately common species found throughout Florida. It often occurs in open areas such as pastures and lawns. The diet is small soil organisms, especially Collembola and Campodeidae (Wilson 1953). Origin: Old World tropics. Pest status: none. Although a form of this species was described from specimens apparently collected in the southeastern U.S. in the 1800's (Brown 1948), the first published Florida record seems to be that of Smith 1951; earlier specimens: 1943.

Quadristruma emmae (Emery) — Bow-Jawed Pygmy Snapping Ant

A common species found as far north as Volusia County. It occurs in both dry and mesic woods, and in disturbed areas such as gardens. The diet is entomobryid Collembola (Deyrup and Deyrup 1999). Origin: Old world tropics. Pest status: none. First published Florida record: Brown 1949; earlier specimens: 1945.

Epitritus hexamerus Brown — Japanese Pygmy Snapping Ant

A rare species known from two sites in central Florida. The sites were in mesic forest. This species is subterranean, rather than living in leaf litter, and preys on arthropods, especially centipedes and diplurans (Masuko 1984). This is our only known example of an ant apparently introduced into Florida from Japan. Origin: Japan. Pest status: none. First published Florida record: Deyrup 1988; earlier specimens: 1987.

Cyphomyrmex rimosus (Spinola) — Larger Little Fungus Ant

A common species found throughout Florida. It occurs in both undisturbed mesic or wet woods and various disturbed habitats. It depends on fungi that it grows on compost beds of vegetable matter mixed with scavenged bits of dead insects; it does not cut pieces of leaves from living plants. The reasons for considering this species introduced are listed in Deyrup 1991. Origin: southern South America. Pest status: none. First published Florida records: Deyrup and Trager 1986 (as *C. fuscus* Emery), Johnson 1986; earlier specimens: 1957.

Ochetellus glaber (Mayr) — Australian Shining Ant

An abundant but localized species found in Orange County, where it has been present for many years (first published record, as *Iridomyrmex glaber*, in Smith 1979). Colonies may be in dead wood or in tussocks of marsh grass. Origin: Australia. Pest status: none. First published Florida record: Smith 1979.

Linepithema humile (Mayr) — Argentine Ant

This species occurs sporadically throughout Florida, in places forming massive populations. It occurs in both moist and dry open habitats, usually in heavily disturbed sites. It is a general scavenger and predator, and tends honeydew-producing Homoptera. Origin: Argentina. Pest status: can become a nuisance by sheer numbers, trailing long distances to outdoor eating areas and into buildings. First published Florida record: Wheeler 1932; earlier specimens: 1914.

Tapinoma melanocephalum (Fabricius) — Ghost Ant

Common in south Florida, to Volusia county. Almost always in disturbed areas, in many sites seems confined to areas around buildings. Nests are in bark mulch, under objects on the ground, and under loose bark and the bases of palm fronds. It is a general scavenger and attracted to honeydew. Origin: Old World tropics. Pest status: can enter buildings through screens and small cracks, becoming a general annoyance. First published Florida record: Smith 1930.

Technomyrmex albipes (Smith) — White-Footed Ant

Common in places in coastal counties, and apparently spreading rapidly. So far, it is only known from urban areas. Nests are in rotten wood, under loose bark on trees, in piles of debris on the ground, in "Spanish style" roofs with curved tiles, and other dry sites off the ground outdoors. It is a general scavenger and attracted to honeydew. Origin: Old World tropics. Pest status: can achieve high densities locally, and become a pest at outdoor eating areas; it may enter buildings when there is easy access from outside. First published Florida record: Deyrup 1991b; earlier specimens: 1986.

Myrmelachista ramulorum Wheeler — Gray Tree Ant

This arboreal species was collected on an orange tree in Polk City, Polk County (Smith 1979). We have not found this species in Florida. It might have been eliminated by the 1989 freeze that killed large areas of citrus in Polk County. Origin: New World tropics. Pest status: none. First published Florida record: Smith 1979.

Brachymyrmex brevicornis Emery — Short-Feelered Rover Ant

Known in Florida from a single collection in Columbia county in a mesic forested area. The identity of this species and virtually all other *Brachymyrmex* is problematical. Origin: Argentina (assuming this species is *brevicornis*). Pest status: none. No previous published Florida records; earlier specimens: 1991.

Brachymyrmex musculus Forel — Little Mouse Rover Ant

This species occurs throughout Florida, achieving its highest densities in north Florida. It usually occurs in disturbed areas, but seems to thrive in some pine plantations. Nests are under loose bark, or at the bases of pine trees, occasionally arboreal, or under shingles. First reported in the U.S. (Louisiana) in 1978 (Wheeler and Wheeler 1978). The identity of this species and virtually all other *Brachymyrmex* is problematical. Origin: Central America (assuming this species is *musculus*). Pest status: occasionally enters open buildings in large numbers. No previous published Florida records; earlier specimens: 1988.

Brachymyrmex minutus Forel — Tropical Yellow Rover Ant

An uncommon species, known from tropical hammocks in Dade and Monroe counties. Nests are in leaf litter. The identity of this species and virtually all other *Brachymyrmex* is problematical. Origin: West Indies. Pest status: none. First published Florida record: Ferster and Prusak 1994; earlier specimens: 1984.

Camponotus sexguttatus Emery — Six-Spotted Carpenter Ant

Known from a few collections in Dade and Broward Counties. Nests were in saw grass stems at the edge of marshy areas. Origin: West Indies. Pest status: none. No previous published records; earlier specimens: 1993.

Camponotus planatus Roger — Short Carpenter Ant

A common species in parts of Dade and Monroe Counties, where it lives in tropical hardwood hammocks; also found sporadically in coastal counties north into Palm Beach on the East Coast and Hillsborough on the West Coast. It is a general predator and scavenger, and tends honeydew-producing Homoptera. Nests are in hollow branches and in abandoned termite galleries. The reasons for considering this an exotic species are discussed in Deyrup 1991. Origin: Central America. Pest status: none. First published Florida record: Wheeler 1910.

Paratrechina bourbonica (Forel) — Robust Crazy Ant

A common species in open disturbed sites in peninsular Florida, as far north as Alachua County. A general scavenger, usually found in urban areas. Nests are usually in soil. Origin: Old World tropics. Pest status: occasionally a minor nuisance in outdoor eating areas, rarely enters buildings in numbers. First published Florida record: Smith 1930; earlier specimens: 1924.

Paratrechina guatemalensis (Forel) — Guatemala Crazy Ant

A common species in Dade, Broward, and Monroe Counties, less common farther north to Hillsborough and Indian River Counties. Found in mesic disturbed areas, and can also invade relatively undisturbed hammocks. Nests are

usually in leaf litter. Origin: Central America. Pest status: occasionally a minor nuisance in outdoor eating areas, rarely enters buildings in numbers. First published Florida record: Trager 1984.

Paratrechina longicornis (Latreille) — Slender Crazy Ant
Found in Florida as far north and west as Leon County, but much commoner in south Florida. This species is usually in disturbed areas, but can invade mangrove swamps. It is a general scavenger, and also tends honeydew-producing Homoptera. Nests are in accumulations of dry litter or mulch, or under objects on the ground. Origin: Old World tropics. Pest status: a minor nuisance in outdoor eating areas, and frequently enters buildings where there is easy access to the outside. First published Florida record: Smith 1930.

Paratrechina pubens (Forel) — Hairy Crazy Ant
This species has had a foothold in Coral Gables, Dade County, for many years, but does not seem to be spreading rapidly. It is abundant on the campus of the University of Miami, where it resembles a pale *P. bourbonica*, foraging on sidewalks and running up and down tree trunks. Origin: New World tropics. Pest status: so far, this is a minor and localized pest. There are two reports of large infestations in buildings (Klotz et al. 1995). First published Florida record: Trager 1984; earlier specimens: 1953.

Paratrechina vividula (Nylander) — Shining Crazy Ant
Known from northern and western Florida, with isolated records from Highlands County. Nests are usually in open disturbed areas such as lawns and fields. Nests are usually in soil. Origin: probably Mexico or Texas (Trager 1984). Pest status: none. The first published record is Smith 1930, but specimens identified as *vividula* prior to 1984 are usually some other species (Trager 1984), so the first certain published record is Trager 1984; earlier specimens: 1982.

DATES AND RATES OF ARRIVAL OF ANTS IN FLORIDA

Ants are generally unobtrusive immigrants, and may not be discovered until many years after their arrival; we can infer this from the fact that species may are sometimes widely distributed by the time they are discovered (e.g. *Strumigenys rogeri*). We also know that a dozen or so species of ants had become distributed through much of the tropics and occurred in European greenhouses in by 1900 (Donisthorpe 1915); some of these apparently were not collected or reported from Florida until 1930 or later. Virtually all myrmecologists who have assiduously collected Florida ants have added exotic species to the list; this suggests that there is a reservoir of uncollected exotics. The rate of arrival of ant species in Florida is not accurately reflected in collection records, but it may still be useful to tabulate these records to see whether the rate of discovery of exotics is diminishing.

Dates	Number of Exotic Ant Species Discovered in Florida (First Specimens)
Before 1900	3
1901-1920	4
1921-1940	13
1941-1960	10
1961-1980	5
1981-2000	17

The pattern of discovery of new Florida exotics may change slightly as older specimens are found in collections, but it is unlikely that this will change the pattern enough to show a diminishing rate of discovery of exotics. The 1921-1940 increase in discovery and recording of new exotics represents the period of greatest activity of Marion Smith and William Wheeler in Florida. Since 1981 there has been an unusually large number of people collecting ants in Florida (see acknowledgments below), so we may expect that the rate of discovery of new exotics will begin to fall as the reservoir of uncollected exotics becomes exhausted.

We may be unable to say whether the establishment of exotic ants in Florida has increased or decreased in recent decades, but we can safely say that it has not stopped entirely. There is one species, *Technomyrmex albipes*, that was clearly spotted early (Deyrup 1991b) in its stage of invasion, which is proceeding rapidly. Two additional species, *Pheidole obscurithorax* and *Brachymyrmex musculus*, are conspicuous species that had been reported just west of Florida (Naves 1985, Wheeler and Wheeler 1978, respectively), then discovered in western Florida during the present study. The following consideration of how ants are transported to Florida may help explain why we have an intuitive feeling that new exotics will continue to arrive and become established.

Travel Accommodations for Ants Immigrating to Florida

The earliest ant colonists probably arrived on wooden sailing ships, which were often verminous, with plenty of dark, damp crannies. Ants such as *Paratrechina longicornis*, *Tapinoma melanocephalum*, *Monomorium pharaonis*, and *M. floricola* would have found many places to stow away. Other species might have traveled in cargo: we suspect that *Pachycondyla stigma*, *Hypoponera punctatissima*, and *Tetramorium bicarinatum* might have been moved about the tropics in piles of timber.

A large number of species, including species that would not at first seem suited to a long ocean voyage, must have been imported in plant stock. From at least the early 1700's through the 1800's, useful and ornamental plants were shipped around the World with missionary zeal, often at governmental behest. As immortalized in the book and movie "Mutiny on the Bounty," nursery plants, and any attendant ants, might receive better treatment and living conditions than the sailors. Peculiarly relevant to Florida was the 1838 Act of Congress to encourage the introduction and promote the cultivation of tropical plants in the United States. In this same year Dr. Henry Perrine established his Florida Tropical Plant Company, and made it his special goal to bring plants from

the Yucatan, for which he received congressional approval and support (Douglas 1978). The energetic and resourceful Perrine imported hundreds of species, including many specimens in containers of soil. There is a record of more than a hundred boxes of plants that Perrine shipped from the Yucatan to the lighthouse keeper on the south end of Key Biscayne (Douglas 1978), and this must have been only a small fraction of Perrine's enterprise. Perrine's efforts to import every possible exotic were cut short in 1840, but there were plenty of other importers who felt that, with the right combination of exotic plants, tropical Florida could become a paradise of yeoman farmers. "The prosperity and strength of any country can be measured by the number of small, self-supportive homesteads which it contains," wrote the Florida horticulturist John Gifford as late as 1934 (Gifford, 1972). Ants were probably among the most permanent beneficiaries of this Jeffersonian idealism.

The early effectiveness of the plant trade in transporting tropical ants can be judged by the list of 34 species found in the greenhouses at Kew Gardens in England; the "propagating pits" in particular seem to have been a convention center for tropical ants (Donisthorpe 1915). The nursery trade has not lost its traditional role as purveyor of ants: in the early stages of *Solenopsis invicta*'s takeover of the Southeast, its range "consisted of a contiguous zone around Mobile and numerous incipient populations centered on nurseries throughout the southeastern U.S." (Tschinkel 1993).

Customs and quarantine regulations now prevent the wholesale, Perrine-style importation of ants into Florida. Certain groups of ants, such as the Dacetini, may have reduced chances of importation. On the other hand, ever-increasing air traffic provides new opportunities for species to arrive in cargo, so we might expect an increased rate of importation of species that form large mating swarms and are attracted to the lights around the loading bays of airplanes. Moreover, the vigilance of agricultural inspection is to some extent offset by the burgeoning volume of international trade, of which some fraction always bypasses inspection. Once species have a foothold in the U.S., their dispersal and long-term chances of persistence are increased by the astonishing amount of vehicular transport in this country. Not only commercial trade is involved; it is commonplace for people who are changing jobs to move their dooryard potted plants long distances, and when companies are generous with moving expenses, we have even known people to relocate their woodpiles.

In conclusion, we would hesitate to say that the rate of introduction of ants from abroad is likely to decrease, but can confidently state that any species that is adapted to Florida and already occurs elsewhere in the United States has increasing chances of reaching Florida. Moreover, weedy species that require disturbed habitats will encounter ever more such habitat: the target of suitable habitat that such species must hit on arrival is constantly enlarging.

The Origins of Florida's Exotic Ants

The precise origins of exotic ants are seldom easy to determine because many ants became generally distributed centuries before the inception of myrmecological surveys. In most cases one can only assign a general homeland, such as the Neotropics, basing our judgement on relationships. There are, for example, numerous species of *Cardiocondyla* in the Old World, but in the New World there are only a small number of species, all of which are widespread through the tropics and subtropics and generally associated with humans. It is excessively unlikely, therefore, that the widespread species of *Cardiocondyla* originated in the New World. In Florida we are dealing almost exclusively with tropical and subtropical exotics, so we are unaffected by the confusing factor of naturally dispersing Holarctic lineages, such as the *Leptothorax acervorum* complex. The following is a tabulation of the origins of Florida exotic ants.

Region	Number of Species	Known from before 1940	Known from Florida only after 1940
New World Tropics•	28	4	24
Old World Tropics••	22	16	6
Australia	1		1
Temperate Asia	1		1

• Includes New World subtropics and Argentina
•• Includes southern Mediterranean

It seems surprising that only 28 out of 52 species come from the New World tropics and subtropics, while 24 are from the much more distant Old World. There are two factors involved. The first is the dubious native effect: a number of Neotropical species could have become established in Florida in the 400+ years of commerce before the first ant survey, and if these species are Cuban in origin or might have spread around the Gulf of Mexico during a warm climatic period, we would not know whether they had arrived on their own in pre-Columbian times. A list of such species appears below under the heading "dubious natives." The second, more interesting factor is that Old World tropical and subtropical synanthropic ants seem more aggressive and travel-hardy. This can be seen in the Hawaiian Islands, where the entire ant fauna is exotic, including some 15 species and subspecies that serve as object lessons to taxonomists and biogeographers, since they were first described as Hawaiian endemics (Wheeler 1934). Of the 42 species reported from Hawaii by Huddleston and Fluker (1968), only two species originate in the New World. More recently, one additional neotropical species has arrived in Hawaii (Reimer 1994). *Solenopsis geminata*, *Linepithema humile*, and *Wasmannia auropunctata* are the only New World ants that seem to be moving toward a pantropical distribution (Passera 1994). The genesis of tramp species of ants in the Old World was first discussed by Brown (1973), who proposed two compatible hypotheses. The first is that in the Old World human settlements have

been much larger and of much longer duration, accumulating an ant fauna that is adapted to the ecological disturbance that we cause, the resources that we offer, and the transport that we provide. His second hypothesis is that the Old World contributes more aggressive ants because there is a long-term evolutionary dynamism in old World ants. We might attribute this to the large size and diversity of the land masses involved. The evolution of world-dominating new taxa has been primarily in the Old World tropics since at least the mid-Tertiary, with the evolution of *Camponotus*, *Pheidole*, and *Crematogaster*; groups such as *Tetramorium* and tropical *Monomorium* are in an earlier phase of expansion, having made some evolutionary breakthrough relatively recently (Brown 1973). Humans have provided a conduit through which elements of this newest evolutionary wave can pour directly from one tropical region to another.

As can be seen in the tabulation above, the majority (16 out of 22) of exotics originating in the Old World were recorded in Florida before 1940, while most (24 out of 28) New World exotics were first recorded in Florida after 1940. This makes it appear that Florida has endured an early wave of exotics from the Old World, a later wave from the New World. This impression is backed up by the fact that most of the exotic ants that seem to have had recent population explosions in Florida are of New World origin. A possible explanation is that the tropical and subtropical areas of the New World are going through the same process that occurred long ago in the Old World. As huge expanses of South and Central America have been converted to man-modified habitat in this century, out of the thousands of species of native ants there are a few that were preadapted to this kind of disturbance. These are now dominating their native regions, and by their very abundance have greatly increased chances of being imported to Florida.

North-South Patterns in Distribution of Exotic Ants

The overwhelming number of exotic ants in the eastern U.S. are southern. From northern Canada to Washington, D.C. there are only nine species of exotic ants. Six of these are listed by Smith (1979): *Brachyponera solitaria* (Smith), *Hypoponera gleadowi* (Forel), *H. punctatissima*, *Myrmica rubra* (Linnaeus), *Tetramorium caespitum* (Linnaeus), *Anergates atratulus* (Schenk), and *Formica lugubris* Zetterstedt. *Paratrechina flavipes* (F. Smith) was reported by Trager (1984) and *Vollenhovia emeryi* Wheeler by Holldobler and Wilson (1990).

The poor representation of exotic ant species in the Northeast must be primarily because ants as a group are most diverse in the tropics and subtropics, so the list of species that could be transferred to and from such areas is much longer than the list of species that could be introduced into a North Temperate area. In addition, many northeastern ants belong to Holarctic species complexes, so chances are reduced that an import from northern Eurasia would find a vacant ecological role. Although the extent of disturbed habitat enlarged enormously with European settlement, there would already have been many ants that had previously subsisted in chronically disturbed areas and barrens, ready to expand their ranges,

like the goldenrods, asters, hawkweeds, and other native plants of fields and meadows. One may also question whether northern exotics would easily be identified as such, given the aforementioned Holarctic species complexes. It may be some time before we have enough genetic information to be sure that northeastern populations of species such as *Lasius alienus* (Foerster), *L. niger* (Linnaeus) and *L. flavus* (Fabricius) have New World pedigrees extending back before the *Mayflower*.

Within Florida there is a similar north-south trend, as can be seen from the following list.

Region	Total Fauna	Exotics	Percent Exotics	Source
Florida Keys	84	32	38	Deyrup 1991a, & recent collections
Everglades	75	28	37	Ferster and Prusak 1994, and recent collections
S.-Central (Highlands Co.)	126	25	20	Deyrup 1991a
North (Alachua Co.)	118	18	15	Johnson 1986 and recent collections
North (Ordway Pres.)	100	8	8	Davis, unpublished list

The Ordway Preserve while logged about 50 years ago, is currently almost entirely native habitat, while the other four areas all have extensive areas of recent disturbance.

As mentioned above, warmer climates have a greater ant diversity, hence more ant species can potentially immigrate to the southern part of Florida. Moreover, the south end of the peninsula is a recently formed area of tropical and subtropical climate without a history of natural access to mainland tropical and subtropical areas, so its native ant fauna might have been depauperate and vulnerable to invasion by exotics, much like a depauperate island.

Disturbed site ants find in south Florida an area that is not only richly disturbed by humans, but also affected by natural disturbances in the form of fires, floods and hurricanes. These natural disturbances might also favor the establishment and spread of certain exotic tropical species. In Puerto Rico, Torres (1984) concluded that disturbance, especially opening up of the forest, increases ant diversity. Horvitz (1997) found evidence that there was an increase in the exotic ant *Wasmannia auropunctata* in natural habitats in some tropical Florida sites as a result of the 1992 Hurricane Andrew. She attributed this to abundant nest sites in hollow stems of pioneer plants, along with a period of high rainfall following the hurricane. She cautioned against applying this too widely, since some native organisms seemed more resilient than exotics, but it is easy to see how the coincidence of a natural disturbance, that disrupts the balance of

the native ant fauna, and the arrival of a new exotic could favor establishment of the exotic in its first few chancy generations in the new land.

Proportions of Exotic Species among Ants and Other Insect Groups

A notable proportion of ant species of Florida, about a quarter of the fauna, are exotic. This statistic would be even more alarming if it were true for many other groups of arthropods, but, fortunately, ants are unusual. Frank and McCoy (1995) have made a list of 27 groups of insects, showing the wide variation in the proportion of exotic species in Florida. The group with the largest proportion of exotics is, not surprisingly, the Coccidae, with 30 exotics out of a fauna of 44 species. Families of beetles of stored products pests also had large proportions of exotics. Among the 14 insect groups with 100 or more Florida species, the ants have by far the largest proportion of exotic species. The group that comes closest to the ants is the hemipteran family Lygaeidae, with 9%. Frank and McCoy's study is strongly supported by work on 7 groups of insects at the Archbold Biological Station, conveniently located in central Florida, where one might expect a median proportion of exotics that have a north-south distributional bias.

Group	FL	Exotics Species	% Exotics	ABS Species	Exotics	% Exotics
Formicidae	207	52	25%	117	25	22%
Butterflies	200a	1a	0.5%	65b	1b	1%
Orthoptera	242a	10a	4%	84c	3c	4%
Odonata	156a	12a	8%	51d	0d	0%
Scarabaeidae	292a	17a	6%	98c	6c	6%
Tabanidae	99a	0a	0%	43c	0c	0%
Scolytidae	142e	25e	18%	57f	12f	21%

Code for sources is as follows. a, Frank and McCoy 1995; b, Minno 1992; c, data from Archbold collection; d, unpublished Archbold Biological Station survey by Fritz Davis; e, unpublished lists by Thomas Atkinson; f, Deyrup and Atkinson 1987.

The general reason for the high proportion of exotics among the ants is that ants are poor dispersers, but good passengers and colonists. Since this would apply to many groups of insects, there must be some crucial details that are needed for an understanding of the phenomenon.

Groups of powerful long-range dispersers are likely to have reached Florida long ago, at least partially saturating its habitats with naturally immigrating species. The most obvious example is the butterflies: there is only one exotic (European) on Frank and McCoy's list (1995), but there is a large group of West Indian species in tropical Florida, all considered to be naturally occurring. Unlike butterflies, the aerial dispersal of ants is by gravid females with small, deciduous wings, not a happy combination for a long trip over open water. Flying ants are often attracted to lights in large numbers, and it seems significant that among the 177 species and thousands of individuals of insects collected in light traps on oil platforms

in the Gulf of Mexico there were no ants (Sparks et al. 1986). We assume that some percentage of ants did fly from neotropical sites to Florida; this is why we have not automatically classed as exotics species such as *Leptothorax torrei* (Aguayo) and *Platythyrea punctata* (F. Smith). Other species may have been transported in floating trees, especially in dislodged mangroves; this is why we have not automatically classed as exotics species such as *Zacryptocerus varians* (F. Smith) and *Solenopsis corticalis* Forel.

Once a fertile queen or a small colony has been imported into a suitable habitat, the chance of successful establishment may be better for ants than for most other insects. This is partly because the colonizing propagule, in the form of the queen ant, usually retreats into a secluded chamber, exposing herself as little as possible. The first workers immediately begin to feed and protect the queen. Once established, the colony has a good chance of reproduction because males and queens may be released repeatedly and en masse, so that there may be opportunities for sibling mating if there are no other colonies around. Inbreeding depression may not be as serious a problem in ants as in some other groups of insects. Since male ants are haploid, even ants that are normally outbreeding cannot build up the number and variety of deleterious recessives found in outbreeding populations of species that have diploid males. Ants are therefore preadapted for inbreeding, as suggested by known successful point-source invasions. All the *Solenopsis invicta* in the United States are believed to be derived from one or a few queens, and the early phases of infestation probably also consisted of dispersal by shipment of small numbers of breeding individuals. It would be difficult to claim that this species has been enfeebled by inbreeding depression in the United States.

A number of Florida's exotic ants show probable evidence of routine sibling mating, manifested by flightless males, as in *Hypoponera punctatissima*, occasionally in *Technomyrmex albipes*, and all species of *Cardiocondyla*. In other species one finds in nests a suspicious abundance of winged females and absence of males, suggesting that there may be some parthenogenesis. Examples of this include *Tetramorium simillimum* and *Strumigenys eggersi*. Species with flightless queens, such as *Monomorium floricola*, are likely to be primarily sibling mating. Some other species have winged queens, but the queens do not normally fly, and mating depends on siblings or on males from other colonies that come to the nest. Species with this behavior include *Monomorium pharaonis, Linepithema humile, Wasmannia auropunctata*, and *Paratrechina longicornis* (Passera 1994).

Scolytid beetles provide an outgroup when we are considering these ideas. The scolytid fauna of Florida includes almost as high a proportion of exotics as the ants, and would probably equal the ants if there was a good way to identify Neotropical exotics in the fauna. In a study of scolytid beetles of the Archbold Biological Station Deyrup and Atkinson (1987) were conservative in their assignment of exotic status, treating only the species from the Old World as certified exotics. Wood (1982), much more liberal in his designation of exotics, identifies as exotics an additional 5 species that occur at the ABS (for 17, or 30%) and an

additional 11 species in Florida (for 35, or 25%). There is some reason to believe that long range dispersal of scolytids is weak, as only one specimen was collected in the traps on oil platforms mentioned above, even though many species are attracted to light. The breeding systems of most of the exotic species involve sibling mating, as postulated as a preadaptation of many exotic ants. Of the 12 species of certain exotics at the ABS, 11 are habitual or obligate sibling mating (Deyrup and Atkinson 1987) and of the 25 species listed for the state, 22 are sibling mating species in the tribes Xyleborini and Cryphalini.

Parthenogenesis automatically speeds up the rate of population growth, as does the reduction in number and size of males found in sibling mating scolytids, but it may be that the insurance that the colonists will not fail for lack of sufficient mates at the appropriate moment is a more important factor for establishment of an exotic population. The initial stages of colonization by a species of ant are likely to be greatly hampered by any mechanisms that strongly favor outbreeding, the same mechanisms that allow accumulation of beneficial adaptations within lineages in the parent population. In the discussions of sex ratios and investment in males and females in ants, summarized by Holldobler and Wilson (1990), the value and consequences of habitual sibling mating are not intensively explored. We do not fault these authors: our own minds boggle at the thought of trying to separate the effects of "normal" kin selection by workers, kin selection associated with sibling mating, the adaptive pressures for rapid colonization in new or frequently perturbed habitats, and variable asymmetrical changes in functional fitness in individual males versus females under different levels of allocation of resources.

In summary, the well-documented high proportion of exotic ants relative to other insect groups in Florida appears to have multiple causes, and we should not expect some new, generally applicable rule governing exotics. The details of the explanation, which also apply to the Xyleborini and Cryphalini in the scolytids, are likely to be as follows. 1. Ants are small, with concealed nests, and can easily stow away hidden and insulated. 2. Many ants are generalist feeders. 3. Ants have relatively poor powers of independent long-distance dispersal. 4. Ants as a group are mostly tropical and subtropical, and find many ecological opportunities in the isolated tropical and subtropical areas of Florida. 5. Ants often have reproductive systems that permit or encourage sibling mating. 6. Ants have built-in immunity to some of the short-term deleterious effects of inbreeding.

IMPACTS OF EXOTIC ANTS ON THE NATIVE FAUNA OF FLORIDA

One of the many remarkable and unique features of our own species is that we actually care about the fate of other species. This sense of responsibility is no small burden, for we humans are not only a direct threat to much of the Earth's biological diversity, but we are also, in a negative sense, a "keystone species," a species whose presence is re-

quired by many other species if they are to thrive. Most exotic ants in Florida are not only beholden to humans for their original transport, but are also dependent on us for habitat preparation and maintenance. In one sense this is bad news, as it suggests that populations of a variety of exotic ants, like other weed species, will follow us wherever we settle in Florida. The park ranger's house, carefully set back in the woods, will be a nexus of exotic species. Moreover, the fight against weedy species is a battle that can never be fully successful, because we are struggling with an aspect of our own ecology. There is not, as it were, enough room in our ecological niche to swing an effective club without bashing our own toes.

In another sense, the weedy nature of most exotic ants is encouraging, because it means that they may be unable to disrupt our preserves of natural habitat, which will probably end up as our most important repositories of biological diversity. Species like *Monomorium pharaonis* have no impact on native species because they occur only in the entirely alien ecosystem in and around buildings. If we catagorize Florida's exotic ants by their degree of dependence on disturbed habitat, it is obvious that the occurrence of 52 species of exotics in the state is not quite the disaster that it seems at first. This analysis is subjective, even intuitive, based on years of general collecting and observation, rather than on transects taken through disturbed habitat into pristine habitat. This section should be taken as a series of hypotheses, bearing in mind that it may be a long time before anybody has the energy or resources to do detailed studies of the ecology of 52 species of ants. An understanding of the effects of exotic species must be based on knowledge of particular species, not on general theories of the ecology of invasive species (Simberloff 1997).

Rats and Mice of the Ant World

Some ants resemble black rats (*Rattus rattus*) and house mice (*Mus musculus*) in their close association with humans and human dwellings. As in the case of mice and rats, there is no very obvious reason for this dependence, and one can occasionally find strays or even groups of colonies some distance from buildings. We assume that it is a combination of biotic factors (e.g. competition, predation, types of food supplies) and microclimate (e.g. dependably dry nesting sites) that bind these species so closely to us. These species are not likely to have much impact on native species. The best examples of this category are *Monomorium pharaonis* and *M. destructor*. Other species that are usually restricted to areas around buildings are *Paratrechina longicornis*, *P. bourbonica*, *Tapinoma melanocephalum*, *Paratrechina pubens*, and *Technomyrmex albipes*. The first three of these species show a tendency to "go native" along the beaches and coastal hammocks in south Florida. Black rats and house mice show a similar tendency (Layne 1997). *Technomyrmex albipes* is in an early phase of expansion, and it is not certain that it will be excluded from natural habitats.

Widespread Dependent Weeds among the Ants

Some ants resemble weedy plants, such as spotted spurge, *Chamaesyce maculata* (L.) Small, hyssop spurge, *C. hyssopifolia* (L.) Small, or beggars'

lice, *Desmodium incana* DC. These plants and ants are at least locally abundant in highly disturbed areas (urban, suburban, roadsides, improved pasture) throughout their range. Such species include *Hypoponera punctatissima*, *Tetramorium simillimum*, *Cardiocondyla emeryi*, *C. nuda*, and *Wasmannia auropunctata*. *Hypoponera punctatissima* and *Wasmannia auropunctata* may occur in enormous numbers, and must have considerable impact on some native species that can live in disturbed areas. An example is provided by the zebra long-wing butterfly, *Heliconius charitonius* (Linnaeus), a native species that feeds on species of *Passiflora* that occur in disturbed areas. *Wasmannia auropunctata* is attracted to the extra-floral nectaries of the host, and can be seen attacking the butterfly eggs. When we placed egg-bearing cuttings in water and allowed access to the ants, many fewer eggs hatched than when we placed the cuttings on an ant-free table. This same species of ant has caused serious ecological problems elsewhere, as will be discussed below.

Widespread dependent weed ants usually occur together with native ants, such as *Dorymyrmex bureni* Trager, *Solenopsis abdita* Thompson, *Camponotus floridanus* (Buckley) and *Pheidole floridana* Emery; neither heavy disturbance nor the presence of many exotic species can exclude all native species in most Florida habitats. These native species are reminders that Florida has its own native weedy species that could become problems if exported to other tropical and subtropical regions.

Localized or Less Abundant Disturbed Site Species

These are species that resemble monk parakeets, *Myiopsitta monachus*, a species that is closely associated with disturbed sites, and seems to have the potential to occupy far more territory than it has secured in the more than 25 years since its first appearance (James 1997). Species that show this pattern are *Paratrechina pubens*, *Ochetellus glaber*, *Pheidole obscurithorax* (a recent arrival), *Cardiocondyla venustula*, *Tetramorium caldarium*, *Trichoscapa membranifera*, *Odontomachus ruginodis*, *Pheidole megacephala*, and *Linepithema humile*. The latter two species are discussed below as examples of species that have had far less impact in Florida than elsewhere.

Armadillo Ants

The exotic nine-banded armadillo, *Dasypus novemcinctus*, and some species of exotic ants are examples of species at home in both disturbed and undisturbed habitats, but not dominant organisms even within their trophic roles, as far as we can tell. These include the south Florida species *Brachymyrmex minutus* and *Pheidole flavens*; a group of species that range into central Florida, *Pachycondyla stigma*, *Monomorium floricola*, *Prionopelta antillana*, and *Cardiocondyla* species A; two widespread species, *Tetramorium bicarinatum* and *Cardiocondyla wroughtonii*. Although we view these ants with suspicion, there is no reason to assume that they are having any significant effects on native species. The effects of such species might vary by habitat: the armadillo, which has been studied in detail in Florida, seems to have little effect in most habitats, but may be a significant predator of small reptiles endemic to Florida scrub habitat (Layne 1997).

Rare Exotic Ants

About a quarter of the exotic ants in Florida have been found so rarely that we assume they have negligible ecological impacts. These species are *Anochetus mayri, Gnamptogenys aculeaticoxae, Tetramorium lanuginosum, Crematogaster agnita, Epitritus hexamerus, Smithistruma margaritae, Strumigenys gundlachi, S. lanuginosa, S. silvestrii, Myrmelachista ramulorum, Brachymyrmex brevicornis,* and *Camponotus sexguttatus.* The number of rare exotics is only surprising because our thinking is conditioned by an understandable emphasis on dominant and highly invasive exotics. Generalist species with high reproductive rates and the ability to spread quickly and decisively through a new area are rather uncommon; they constitute only a small portion of biological diversity. Many "normal" species, those with restricted ecological roles, and low reproductive rates must have been imported into Florida, and a few of these species may have found appropriate ecological niches open to them. *Epitritus hexamerus, Gnamptogenys aculeaticoxae,* and *Crematogaster agnita* may be examples of such species. Some exotic species may be scarce because of competition from other, more aggressive exotics; for example, the very common species *Strumigenys eggersi* and *S. rogeri* may be putting pressure on *S. gundlachi, S. lanuginosa,* and *S. silvestrii,* although we have no evidence of this. Some species may have become established during a temporary favorable climatic period, and are now experiencing a reversal. *Myrmelachista ramulorum* might have suffered the same fate as northern citrus groves, wiped out in a series of freezes. At the other extreme, some species may be rare because they are only now becoming established. *Camponotus sexguttatus* might be an example of a species whose population has not yet reached a critical mass needed for expansion. Some species may be difficult to find because we have no good collecting methods. *Epitritus hexamerus,* a subterranean predator (Masuko 1984), may be an example. The term "rare," applied to inconspicuous animals such as ants may not mean very much: if colonies of a species of exotic ant were as rare in Florida as the "common" exotic red fox, it might never have fallen into the hands of an entomologist. In any case, we are not at this point concerned with impact of rare exotic ants on native species, although we may be forced to revise this opinion when more is known about the ecology of these species.

Possible Ecological Villains

We include as a final category the exotic species that are abundant in both disturbed and undisturbed habitats, and appear to dominate their trophic roles, thus possibly displacing native competitors, affecting populations of native prey species, and having various indirect effects. Only two of these species, *Solenopsis invicta* and *Pseudomyrmex gracilis,* are familiar to most Floridians. The remaining five species are only known to a handful of specialists.

Solenopsis invicta

We include this species here with some hesitation, as it appears in Florida to be a weedy species that is dependent on humans for habitat maintenance (Tschinkel 1988, 1993), and its frequent occurrence in undisturbed habitats might be a large-scale overflow from the massive populations elsewhere. There is no doubt that this species can reduce the numbers and diversity of native species in natural habitats. The best overview of the ecological effects of *S. invicta* is that of Vinson (1994), which considers competition, predation on vertebrates and invertebrates, feeding on plants, and fostering sap-sucking insects. In the last 20 years much of the work on *S. invicta* has concentrated on the invasion front of the polygyne form in Texas, which lent itself to before-and-after studies. A study of the effects of polygyne fire ants in a Texas prairie preserve showed a 99% decrease in abundance and a 66% decrease in diversity of native ants (Morris and Steigman 1993). Polygyne *S. invicta* at another Texas site caused a 40% decline in arthropod species diversity (Porter and Savignano 1990).

Similar studies are difficult in Florida, which was fully occupied by *S. invicta* 20 years ago, with patchy distribution of the polygyne form. There are few studies of the effects of *S. invicta* on native species in Florida, and none that we know of in natural habitats. A long-term study (Wojcik 1994) of the correlation between abundance of red imported fire ants and various native and exotic species of ants on roadsides shows a steady increase in domination by fire ants, also correlated with the increased urbanization of the area. Naturalists who have lived in Florida for several decades have told us that they suspect that a decrease in the numbers of certain reptiles and birds may be due to predation on eggs and hatchlings, a claim supported by a study by Mount (1981) elsewhere in the Southeast. In this period of time however, there have been many other disruptions, including large-scale habitat conversion, major drainage projects and diversions of water flow, enormous numbers of new roads, pervasive use of agricultural chemicals, and many additional widespread exotic plants and animals. Although *S. invicta* is most abundant in the most disturbed habitats, it is difficult to find any extensive terrestrial sites in Florida that lack *S. invicta*. This ant has large colonies and superb foraging and recruiting ability, and could, in theory, have considerable impact even where colonies are sparse. Its greatest impact on native species must be in semi-disturbed areas, such a cattle ranches with some improved pasture or forest plantations with heavy site preparation, areas that may be important for certain native species even though the original ecosystem has been strongly modified.

Human reactions to *S. invicta* are probably the most serious indirect ecological effect of the species. We can put behind us the disastrous attempt at eradication by blanketing the South with Mirex. At the level of the individual homeowner, however, fire ants are still being attacked with any number of absurd or dangerous substances, from grits and tobacco juice to gasoline. On the positive side, we may have learned an ecological lesson that should persist as long as *S. invicta*: yes, we *can* send a man to the moon; no, we *can't* get rid of fire ants.

Pseudomyrmex gracilis

This species is much larger than any of the seven native species of *Pseudomyrmex*. It might compete with these native species for food, but seems to nest in larger diameter holes in twigs and stems. It is more likely to exclude various native carpenter ants: *Camponotus decipiens* Emery, *C. snellingi* Bolton, *C. impressus* (Roger), *C. nearcticus* Emery, *C. discolor* (Buckley). It is a very abundant species in south and central Florida, and does not seem to distinguish between disturbed and undisturbed habitats. Aside from competition with native arboreal ants, this species could affect native phytophagous species, especially butterflies and moths. The buildup of populations of *P. gracilis* in Florida make it highly probable that it

will be accidentally introduced into the West Indies, where it could have greater impact than in Florida.

Camponotus planatus

At present this species is most common in the Florida Keys, where it is a dominant ant of tropical hammocks, including the best examples of hammocks on Key Largo. There are populations in several mainland sites, but it has not yet made significant inroads into the Everglades. It is probably a significant competitor of native ants and other insects that live in wood, and its activities as a predator and a guard of sap-sucking insects should also have ecological importance.

Cyphomyrmex rimosus

This species appears to have entered the state from the north or northwest, where it is most common, but it now occurs throughout the state. It is found in a great variety of natural and modified habitats. This is a fungus-growing species that is unlikely to compete with other arthropods, with the exception of *Trachymyrmex septentrionalis* (McCook) in sandy uplands and the supposedly native *Cyphomyrmex minutus* Mayr in south Florida. It is possible that some scavenging arthropods will be affected by high populations of *C. rimosus*, but in general this species will probably have minimal impact on native species.

Pheidole moerens

Occurring throughout the state in a great variety of habitats, this species may have already partially replaced *Pheidole dentigula* M. Smith and *P. floridana* Emery. Nests are in rotten wood, in leaf litter, and in hollow twigs and nuts on the ground, so *P. moerens* may compete for nest sites with native species in the genera *Smithistruma, Paratrechina, Solenopsis, Hypoponera, Strumigenys* and *Brachymyrmex*. It seems likely that dense populations of this species have some effect on native insects that serve as prey, but the diet of *P. moerens* has not been investigated in Florida.

Strumigenys eggersi, Quadristruma emmae

These two species of ants are the only dacetine ants that are commonly found in dry and mesic habitats of south and central Florida. There is little evidence that native dacetines (*Smithistruma* spp., *Strumigenys louisianae*) were ever common in these areas, but if these two exotics continue their northward expansion we may be able to get some idea of their effect on native ants, since we have records of hundreds of litter samples from north Florida. These species are probably more or less specialized predators on entomobryiid Collembola. If they have not had an impact by reducing or replacing the populations of native predators of Collembola in south Florida, they must be a novel predator of the Collembola themselves in this area.

Strumigenys rogeri

This species is the common dacetine in bayheads, baygalls, and other swamp forest habitats in south and central Florida. Samples collected by Walter Suter between 1960 and 1970 suggest that several species of *Smithistruma*, as well as *Strumigenys louisianae*, were much more common in the absence of *S. rogeri* than they are today, although our survey methods may not replicate Suter's, and there have been many other changes in Florida since 1970. Since this species is apparently moving northward, it might be useful to do some intensive sampling ahead of its advance.

Brachymyrmex musculus

This species seems to adapt well to open pine forests (high pine and flatwoods habitats) in north Florida, as well as to the usual open disturbed areas favored by many exotics. Huge nests may be found in the loose bark at the bases of large pine trees, a nesting site also favored by native species of *Paratrechina, Pheidole, Solenopsis,* and *Brachymyrmex*. The diet of *B. musculus* is unknown, except that they eagerly feed on honeydew, and are therefore likely to promote the increase of sap-sucking insects.

Exotic ants that do not seem to fulfill their potential

If a malevolent agency had been introducing exotic ants into Florida, it would have found some of the most promising species disappointing in performance. The Argentine ant, *Linepithema humilis*, is an excellent example. This species was probably brought to New Orleans on coffee ships before 1891 (Smith 1965) and was found in Gainesville in 1914 (Wheeler 1932). It is widely dispersed in Florida, and can form dense populations that send streams of ants into buildings, and quickly develop the habit of investigating parked cars on the well-founded expectation that there will be a few old french fries under the front seat. Van Pelt (1958) discovered that a colony had moved into a station wagon parked for a few days in the town of Palatka, and suggested that this species is easily distributed in vehicles. In Florida it occurs in disturbed habitats, as it does in California (Ward 1987). The Argentine ant also seems to be dependent on the availability of permanent water or frequent rains (Ward 1987, Majer 1994). Florida has great expanses of disturbed habitat with access to water, and the Argentine ant has had about a century to occupy the state, but it remains an uncommon species, except in a relatively small number of heavily infested sites. It is possible that the Argentine ant is under constant siege by other ants, such as *Solenopsis invicta* and *Dorymyrmex bureni*. In Hawaii it is apparently excluded from lower elevations with more tropical habitat by *Pheidole megacephala* (Reimer 1994), and its failure to occupy more territory in Western Australia is attributed to the presence of a diverse native ant community in less disturbed habitats (Majer 1994).

Pheidole megacephala, like *Linepithema humile*, has been in Florida for a long time and is the dominant ant on a few sites. These two species appear to be mutually exclusive, and vie for supremacy in Bermuda (Haskins and Haskins 1965) and Hawaii (Reimer 1994). In Florida, *P. megacephala* occurs from Tampa through the Florida Keys, with one record from the coast of St. Johns Co. Its rarity in north Florida is probably due to cooler winter temperatures. We have no explanation why it is not a dominant species in tropical and subtropical parts of the state.

Wasmannia auropunctata is much more common than the two species discussed above. It occurs throughout south Florida, and is recorded from about 80 sites. It practically blankets the ground in a few places, but it is generally a minor species in the fauna. Where it is most abundant, it is easy to see how this ant could become a major pest (because of its powerful sting) and reduce populations of native species, as it has in the Galapagos (Clark et al. 1982, Lubin 1984). We have recently found sites on the island of New Providence, Bahamas, with huge concentrations of *W. auropunctata*. The factors that trigger or support these outbreaks are un-

known. At two outbreak sites in south Florida there are unusual concentrations of plants that produce large amounts of extra-floral nectar, and are visited day and night by hordes of *W. auropunctata.* It may be that this resource has tipped the balance in favor of *W. auropunctata* and caused these very local outbreaks.

Solenopsis invicta, although a major ecological and economic problem throughout Florida, does not seem to live up to its potential as a pest, especially compared to the situation in Texas. Heavy outbreaks of *S. invicta* in Florida seem to require constant maintenance by humans in the form of perennial habitat disturbance and, on upland sites, frequent irrigation. The sand soils characteristic of most of Florida may be suboptimal for *S. invicta* because sand drains quickly and is also permeable to a great variety of burrowing animals, some of which might be enemies of ants. Tschinkel has suggested (1988) that subterranean *Solenopsis* of the subgenus *Diplorhoptrum* might reduce populations of *S. invicta* in sandy uplands. Since *S. invicta* originates in habitats where the soil is periodically saturated, forcing the fire ants themselves to build elevated nests, it seems logical that this ant would better adapted to defend itself against enemies from above rather than enemies from below.

Florida's resistance to more severe outbreaks of these four species could use more study. It would be useful to know the conditions that lead to outbreaks or suppression of these species in Florida, as this might allow us to manage populations, not only in Florida, but elsewhere. Some of this resistance may be due to factors that cannot be transferred to other areas, such as climate and soil. Some biotic factors, such as competition from other ant species, are also not transferable, since it would be unwise to bring an aggressive ant species to a new area. It is possible, however, that there are habitat management practices, or host-specific natural enemies that might have wide applications.

Dubious Natives

A number of Florida ants are neotropical species that we would hesitate to label as exotics, even though we have some grounds for suspicion. These species are treated individually below.

Platythyrea punctata (Fr. Smith)

This species occurs through the islands of the Caribbean and from Central America north to southern Texas (Brown 1975). The Florida population is currently isolated, though this species might have moved around the Gulf of Mexico to Florida when the climate was warmer. Nests, which often are in dry dead wood, could easily have been shipped to Florida in timber. Unmated workers are able to produce female offspring parthenogenetically (Heinze and Holldobler 1995), so it would be easy to establish a breeding population. *Platythyrea punctata* is well adapted to disturbed areas, at least in Florida and the Bahamas. The chance that this species was brought by man to south Florida is extremely good; the question is whether such immigrants would have found an indigenous population already established. The first published record that we know of (Creighton 1950) seems rather late for such a large, distinctive species, but these ants are wary and often dart away in the leaf litter before they can be caught.

Pseudomyrmex cubaensis Forel, *P. elongatus* Mayr

The first of these species occurs in the Greater Antilles, Bahamas, and south Florida, the second from Costa Rica to Texas, Jamaica, and south Florida (Ward 1985). The Florida populations are isolated. These species are common in coastal

mangroves, and could have arrived in Florida in floating trees. Moreover, Simberloff and Wilson showed (1969) that one or both of these species (the two species were not clearly distinguished until Ward's 1985 revision) are regular and early colonists of isolated mangrove islets, and must therefore have the habit of flying over open water for hundreds, if not thousands of meters. *Pseudomyrmex elongatus* could have moved around the Gulf when the climate was warmer. On the other hand, colonies of both species can be found in small dead twigs on live trees and shrubs, and the chance of importation in nursery stock is good. The problem of deciding which species are exotic is shown by the two species *Pseudomyrmex gracilis* and *P. elongatus*, which currently have similar distributions. If *P. gracilis* had been introduced into Florida just a few decades earlier, before systematic ant surveys, we probably would have concluded that this species was native to the area.

Solenopsis geminata (Fabricius)

There is no reason why a species could not be imported to a place where it is already native. Normally, one would assume that the native population, having evolved adaptive adjustments to the area, would exclude the representatives of the exotic population, or absorb and dilute the small number of immigrants beyond recognition. If, however, the exotic population has undergone natural selection that makes it better able to coexist with humans and take advantage of the resources and habitat modification that humans offer, the exotic population might be favored. Populations of *S. geminata* have been transported around the World; we have seen specimens from, among other places, a mid-Pacific islet, Johnson Atoll. Some of the confusing variation found among Florida populations could be due to the occurrence of one or more exotic populations overlaid on native populations.

Solenopsis corticalis Forel

This species appears to be a complex, and the distribution records are therefore not reliable. *Solenopsis corticalis* was first reported from Florida in 1988 (Deyrup et al.), but there are specimens from the southeast coast dating back to 1945 (Thompson 1989). It should have been found in Wilson's survey of the Florida Keys (1964) if it had been as abundant then as it is now. If this species continues to show obvious changes in range and abundance we will be even more inclined to consider it an exotic.

Leptothorax torreyi (Aguayo)

This species occurs in Cuba, the Bahamas, and tropical Florida. It is a litter-inhabiting ant that one would not expect to be an effective long distance disperser, but readily relocated in containers of soil. The first Florida report is recent (Deyrup et al. 1988), but it is a species that is unlikely to be found except by litter extraction.

Leptothorax allardycei (Mann)

This species occurs in Cuba, the Bahamas and tropical Florida. It is a twig-nesting species that might have been imported in nursery stock. The first published record is Wheeler 1931.

Eurhopalothrix floridana Brown and Kempf

This species was not discovered until 1960, but there is a specimen from 1897 collected in Key West (Deyrup et al. 1997). *Eurhopalothrix floridana* probably occurs in Mexico, but the records need to be confirmed (Deyrup et al. 1997). If the distribution of this species turns out to be Florida and southern Mexico, without populations in northern Mexico, it would be difficult to claim that it is native to

Florida.

Cyphomyrmex minutus Mayr

This is a common species through the West Indies and around the Caribbean and Gulf of Mexico into Texas (Snelling and Longino 1992). It adapts well to disturbed sites and readily colonizes potted plants, so there is a high probability that it was brought to Florida at least once, but it might also be native to the state, having flown from the Bahamas or moved around the Gulf of Mexico. It was recorded from Florida in Smith 1930.

Trachymyrmex jamaicensis (Andre)

The first published record of this West Indian species in Florida is Smith 1951. His note says, "introduced?" On the one hand, this is a large conspicuous ant that one might expect to have been found earlier if it had been present. On the other hand, it is only common in a few places in tropical Florida, and it does not seem to occur in heavily disturbed or cultivated areas, either in the Keys or in the Bahamas, so it may have been displaced by the early attempts at agriculture. There is a hypothesis that it may have been affected by spraying for mosquitos (Deyrup et al. 1988). The nests are deep and it is unlikely that they would be in containers of plants.

Brachymyrmex obscurior Forel

This species occurs on beaches as well as in all kinds of open, artificially disturbed sites. Smith (1933) considered that it was probably introduced. One of the authors once saw queens land inside a small airplane with an open door in Fort Lauderdale, and head for the open door again when the plane landed in San Salvador in the eastern Bahamas. It often occurs in potted plants. There is a very good chance that this species was transported to Florida in commerce early and often, but it could also have been already naturally established, having moved around the Gulf of Mexico. The taxonomy and consequently the distribution of the brown *Brachymyrmex* is very uncertain. As in the cases of most other dubiously native neotropical species in Florida, the only chance to show that this species was imported would be a genetic study that showed that the Florida population is most closely related to populations that are unlikely to have reached Florida without assistance. Showing that the species was native would be just as problematic, requiring evidence of genetic distinctness of the Florida population, or pre-Columbian specimens.

Camponotus floridanus (Buckley)

This very abundant species lives in almost all disturbed and natural habitats in Florida. It readily colonizes containers left outside, and could easily be transported to new areas. Related species or forms of the subgenus *Myrmothrix* (a group in serious taxonomic disarray) are among the ants that Donisthorpe (1915) reported arriving in England, usually in bunches of bananas, but also in orchids. It occurs through the Florida panhandle, and as Creighton (1950) pointed out, it appears closely related to the Texas form that used to be called *Camponotus abdominalis transvectus* Wheeler. There is a good chance that this complex once occurred around the Gulf of Mexico, and was later separated into eastern and western populations. Further work on the taxonomy of this section of *Camponotus* is needed before we will be happy with either the nomenclature or provenance of the Florida species.

Camponotus tortuganus Emery

This species is worrisome because there are no other ants that are restricted to

south Florida. It also seems susceptible to importation because it eagerly moves into man-made containers and structures of many kinds. Structurally, *C. tortuganus* is almost identical to *C. conspicuus inaequalis* Roger from Cuba and the Bahamas, but the typical red and black coloration of *C. tortuganus* does not match the coloration of *C. conspicuus inaequalis* that we have seen from the Bahamas. Our guess is that *C. tortuganus* is either a native Florida geographic isolate of *C. conspicuus inaequalis*, or it represents an form of *conspicuus* imported from outside the range of *inaequalis*. We have seen a series from the Florida Keys that is colored exactly like Bahamian *inaequalis* (Deyrup et al. 1988), but we are not quite ready to add this to our list of Florida exotics until the taxonomic status of this complex is a little clearer. Nature may outpace taxonomists: the experiment to test whether *C. tortuganus* and *C. conspicuus inaequalis* are reproductively isolated may already be under way in the Florida Keys.

Unlikely Exotics

Ponera exotica Smith

The name of this species reflects Marion Smith's belief that it was imported from Asia, where there are related species. The distribution and habitat preferences of this species, however, suggest that it is native (Johnson 1987, MacKay and Anderson 1991). Its resemblance to Asian species might mean that this is an Arctotertiary relict lineage rather than a recent import. We provisionally consider this species to be native.

Camponotus socius Roger

This species was described long ago from specimens that supposedly came from Brazil (Roger 1863). As Creighton (1950) remarks, it is most unlikely that this species is native to Brazil, where the types were collected, and also native to the southeastern U.S., without any occurrences in between. Even Creighton, whose greatest strength was not in field ecology, noted that in the Southeast *C. socius* shows all the characteristics of a native species. It appears to us as a classic coastal plain ant, adapted to the sand soils of frequently burned, open pine woodlands. It is hard to imagine that it is equally at home in the province of Amazonas in Brazil, from which it is reported (Kempf 1972). Moreover, of all Florida *Camponotus* species, *socius* is the least likely to have been transported to or from Brazil, as the nests are deep in sandy soil in undisturbed habitats. Before admitting that this species had been introduced either in Florida or Brazil, we would want to be sure that there are not two species lumped under that name (if this turns out to be the case, there is already a name available for the Florida species). It is also possible that the specimens that Roger used for his 1863 description of the species were mislabeled, and came from southern North America rather than northern South America.

THE FUTURE OF EXOTIC ANTS IN FLORIDA

We can make several predictions about the future of exotic ants in Florida, based on the history of these ants here and elsewhere. We can then suggest some actions based on these predictions.

All but one of the "tropical tramp" species listed by Passera (1994) already occur in Florida. The missing species is *Anoplolepis longipes* (Jerdon), whose behavior and impact as described by Haines et al. (1994) seem to resemble those of a particularly large and aggressive *Paratrechina*. Every effort should be exerted to exclude this pest, which is most likely

to arrive from Pacific islands. It is already in the identification key for Nearctic ants (Holldobler and Wilson 1990), in the expectation that it will arrive soon. It would be sensible to produce a "wanted" poster of this ant, in the hope that it could be eradicated as soon as it first appears.

We can make a list of ants that appear to have spread explosively through all or part of Florida in the last 50 years. These are: *Solenopsis invicta, Pseudomyrmex gracilis, Strumigenys eggersi, S. rogeri, Quadristruma emmae, Cyphomyrmex rimosus, Pheidole moerens,* and *Brachymyrmex musculus.* There are a few species that appear to be in the early phase of such a spread: *Odontomachus ruginodis, Paratrechina guatemalensis,* and *Technomyrmex albipes.* We doubt that anybody would have predicted the phenomenal success of most of these species, the exceptions being the well known pests *Solenopsis invicta* and *Technomyrmex albipes.* There is every reason to believe that more species of ants will invade Florida, but we don't know which to expect. It would make sense to begin a world survey of the tropical and subtropical ants that occur in the most disturbed sites, and make a list of the most abundant species, irrespective of their significance as obvious pests. Forewarned would not be forearmed in all cases, but we might be able to exclude some species from Florida if we knew which were the most probable invaders. Such a list of ants would be useful throughout the tropics and subtropics.

Many biologists will be distressed to hear that there are at least 52 species of exotic ants in Florida, and that there are virtually no places in the state completely free of exotic ants. This may seem to fit depressingly into the global pattern of species introductions and resultant large scale loss of biological diversity (Lovel 1997). In Florida, however, there may be no reason to panic or despair just yet. Florida biota coevolved with a rich ant fauna of at least 155 species, and there are no organisms that have a Hawaiian naivete with respect to ants. As mentioned above, many exotic ant species are rare or local in Florida, and many of the common species are tied to artificial communities. Protection of our native species from exotic ants is primarily a function of reducing our own direct impacts on natural habitats and setting aside tracts of natural habitat. Restraining exotic ants is, to a large extent, a case of restraining our traditional inclination to transform and improve every habitat. Beyond this, the most important task is to evaluate our management of habitats such as native range and timberland to minimize the kind of disturbances that foster exotic species at the expense of native species. Exotic ants would be a good indicator group because there are so many of them and because they are easily attracted to bait or extracted from litter.

Finally, when an aggressive invasive species enters an area of high biological diversity such as Florida, that species is likely to have a limited period of dominance. This is because the dominant exotic species is selecting for species that resist its influence, and because the dominant species itself constitutes a huge resource base that other species can adapt to exploit. One would expect exotic ants to be particularly vulnerable in this respect because they are likely to have brought and maintained a narrow genetic base, through limited original stock and inbreeding. The success of polygyne *Solenopsis invicta,* for example, is probably only long-

term relative to human patience. The real problem is whether native species will be extirpated before a balance reasserts itself. Even exotic organisms that we purposely support by maintaining their preferred depauperate communities, such as crop plants, eventually begin to accumulate enemies from the surrounding fauna or accidentally imported enemies.

Unfortunately, these changes in species balance normally occur on a time scale of decades, or even hundreds of years, while long-term ecological monitoring is an infant enterprise. We have a few indications of declines in exotic ants, but nothing that could be dignified as data. For example, long-term residents of Miami mention that there used to be a rain of small, stinging ants (presumably *Wasmannia auropunctata*) falling out of trees and disrupting outdoor activities. Today this ant does not seem to be abundant enough to have such an effect. In a survey of ants of the Florida Keys (Deyrup et al. 1988), *Tetramorium bicarinatum* was found only twice, while it was common in the Keys 20 years previously (D. S. Simberloff, pers. comm.). *Solenopsis geminata* was spread through the Caribbean beginning in the 1500's through the 1700's (Cowan 1865). Early, hair-raising accounts of the depredations of this ant are completely at odds with its present status as a ubiquitous but unimpressive member of the fauna (Deyrup 1994). We have, of course, no idea of what island species disappeared during the dominance of *S. geminata.* In North America there is a network of long-term monitoring sites where it would be useful to periodically sample exotic species. Meanwhile, areas where aggressive exotics seem to have declined, or never materialized as a major problem, may provide clues of how we can speed the decline of these species elsewhere.

ACKNOWLEDGMENTS

We are much indebted the following naturalists for their skillful collecting of ants and their generous donation of specimens: Walter Suter, Zachary Prusak, Clifford Johnson, James Trager, Betty Ferster, Vincent Golia, John Mangold and Paul Skelley.

LITERATURE CITED

Bolton, B. 1979. The ant tribe Tetramoriini. The genus *Tetramorium* Mayr in the Malagasy region and in the New World. Bull. Brit. Mus. (Nat. Hist.) (Entomol.) 38: 129-181.

Bolton, B. 1995. A new general catalogue of the ants of the World. Harvard University Press, Cambridge, MA. 504 pp.

Brown, W. L., Jr. 1948. A preliminary generic revision of the higher Dacetini. Trans. Amer. Entomol. Soc. 74: 101-129.

Brown, W. L., Jr. 1949. Revision of the ant tribe Dacetini: 3. *Epitritus* Emery and *Quadristruma* new genus. (Hymenoptera: Formicidae). Trans. Amer. Entomol. Soc. 75: 43-51.

Brown, W. L., Jr. 1960. The Neotropical species of the ant genus *Strumigenys* Fr. Smith: group of *gundlachi* (Roger). Psyche 66: 37-52.

Brown, W. L., Jr. 1973. A comparison of the Hylean and Congo-West African Rain Forest ant faunas. P;. 161-185 *in* Meggers, B. J., E. S. Ayensu and W. D. Duckworth, eds. Tropical forest ecosystems in Africa and South America:

a comparative review. Smithsonian Institution Press, Washington, D.C. 350pp.
Brown, W. L., Jr. 1975. Contributions toward a reclassification of the Formicidae. V. Ponerinae, tribes Platythyreini, Cerapachyini, Cylindromyrmecini, Acanthostichini, and Aenictogitini. Search: Agriculture. Ithaca, N.Y. :Cornell Univ. Agr. Exp. Sta. No. 15: 115 pp.
Creighton, W. S. 1950. The ants of North America. Bull, Mus. Compar. Zool. Harv. Univ. 104: 1-585.
Clark, D. B., C. Guayasamin, O. Pizamino, C. Donoso, and Y. Paez de Villacis. 1982. The tramp ant *Wasmannia auropunctata*: autecology and effects on ant diversity and distribution on Santa Cruz Island, Galapagos. Biotropica 14: 196-207.
Cowan, F. 1865. Curious facts in the history of insects; including spiders and scorpions. J. B. Lippincott and Co., Philadelphia. 396 pp.
Creighton, W. S., and R. R. Snelling. 1974. Notes on the behavior of three species of *Cardiocondyla* in the United States. (Hymenoptera: Formicidae). J. N.Y. Entomol. Soc. 82: 82-92.
Deyrup, M. 1991a. Exotic ants of the Florida Keys. (Hymenoptera: Formicidae). Proc. 4th Sym. Nat. Hist. Bahamas: 15-22.
Deyrup, M. 1991b. *Technomyrmex albipes*, a new exotic ant in Florida (Hymenoptera: Formicidae). Fla. Entomol. 74: 147-148.
Deyrup, M. 1994. Biogeographical survey of the ants of the island of San Salvador, Bahamas. Proc. Fifth Sym.. Nat. Hist. Bahamas: 21-28.
Deyrup, M., C. Johnson, and L. Davis. 1997. Notes on the ant *Eurhopalothrix floridana*, with a description of the male (Hymenoptera: Formicidae). Entomol. News 108: 183-189.
Deyrup, M., and T. H. Atkinson. 1987. Comparative biology of temperate and subtropical bark and ambrosia beetles (Coleoptera: Scolytidae) in Indiana and Florida. Great Lakes Entomol. 20: 59-66.
Deyrup, M., C. Johnson, G. C. Wheeler, and J. Wheeler. 1989. A preliminary list of the ants of Florida. Fla. Entomol. 72: 91-101.
Deyrup, M., N. Carlin, J. Trager, and G. Umphrey. 1988. A review of the ants of the Florida Keys. Fla. Entomol. 71: 163-176.
Deyrup, M., and S. Deyrup. 1999. Notes on the introduced ant *Quadristruma emmae*, (Hymenoptera: Formicidae) in Florida. Entomol. News 110: 13-21.
Deyrup, M, and J. Trager. 1984. *Strumigenys rogeri*, an African dacetine ant new to the U.S. (Hymenoptera: Formicidae). Fla. Entomol. 67: 512-516.
Deyrup, M., and J. Trager. 1986. Ants of the Archbold Biological Station, Highlands County, Florida. (Hymenoptera: Formicidae). Fla. Entomol. 69: 206-228.
Donisthorpe, H. 1915. British ants, their life history and classification. William Brendon and Son, Plymouth. 373 pp.
Douglas, M. S. 1978. The Everglades: river of grass. (Revised edition). Banyan Books Inc., Miami. 447 pp.
Emery, C. 1895. Beitrage zur Kenntniss der nordamerikanischen Ameisenfauna. (Schluss). Zoll. Jahr. Abtheil. System. Geogr. Biol. Tiere 8: 257-360.
Ferster, B., and Z. Prusak. 1994. A preliminary checklist of the ants (Hymenoptera: Formicidae) of Everglades National Park. Fla. Entomol. 77: 508-512.
Frank, J. H., and E. D. McCoy. 1995. Precinctive insect species in Florida. Fla. Entomol. 78: 21-35.
Gifford, J. C. 1972. On preserving tropical Florida. Compiled and with a biographical sketch by Elizabeth Ogren Rothra. University of Miami Press, Coral Gables. 222 pp.
Haines, I. H., J. B. Haines, and J. M. Cherrett. 1994. The impact and control of the crazy ant, *Anoplolepis longipes* (Jerd.) In the Seychelles. Pp. 206-218 *in* Williams, D. F., ed. Exotic ants: biology, impact, and control of introduced species. Westview Press, San Francisco. 332 pp.
Heinze, J., and B. Holldobler. 1995. Thelytokous parthenogenesis and dominance hierarchies in the ponerine ant, *Platythyrea punctata*.

Naturwissenschaften 82: 40-41.
Holldobler, B., and E. O. Wilson. 1986. Ecology and behavior of the primitive cryptobiotic ant *Prionopelta amabilis* (Hymenoptera: Formicidae). Ins. Soc. 33: 45-58.
Holldobler, B., and E. O. Wilson. 1990. The ants. Belknap Press of Harvard University Press, Cambridge, Mass. 732 pp.
Horvitz, C. C. 1997. The impact of natural disturbances. Pp. 63-74 *in* Simberloff, D., D. Schmitz, and T. C. Brown, eds. Strangers in paradise: impact and management of nonindigenous species in Florida. Island Press, Washington, D.C. 467 pp.
Huddleston, E. W., and S. S. Fluker. 1968. Distribution of ant species of Hawaii. Proc. Hawaiian Entomol. Soc. 20: 45-69.
James, F. C. 1997. Nonindigenous birds. Pp. 139-156 Pp. 157-186 *in* Simberloff, D., D. C. Schmitz, and T. C. Brown, eds. Strangers in paradise: impact and management of nonindigenous species in Florida. Island Press, Washington, D.C. 467pp.
Johnson, C. 1986. A north Florida ant fauna (Hymenoptera: Formicidae). Insecta Mundi 1: 243-246.
Johnson, C. 1987. Biogeography and habitats of *Ponera exotica* (Hymenoptera: Formicidae). J. Entomol. Sci. 22: 358-361.
Kempf, W. W. 1972. Catalago abreviado das formigas da regias neotropical (Hymenoptera: Formicidae) Studia Entomol. 15: 1-344.
Klotz, J. H., J. R. Mangold, K. M. Vail, L. R. Davis, Jr., and R. S. Patterson. 1995. A survey of urban pest ants (Hymenoptera: Formicidae) of peninsular Florida. Fla. Entomol. 78: 109-118.
Layne, J. N. 1997. Nonindigenous mammals. Pp. 157-186 *in* Simberloff, D., D. C. Schmitz, and T. C. Brown, eds. Strangers in paradise: impact and management of nonindigenous species in Florida. Island Press, Washington, D.C. 467pp.
Lovel, G. L. 1997. Global change through invasion. Nature 388: 627-628.
Lubin, Y. D. 1984. Changes in the native fauna of the Galapagos Islands following invasion by the little red fire ant, *Wasmannia auropunctata*. Bio. J. Linn. Soc. 21: 229-242.
MacKay, W. P., and R. S. Anderson. 1991. New distributional records of the ant genus *Ponera* (Hymenoptera: Formicidae) in North America. J. N.Y. Entomol. Soc. 99: 696-699.
Majer, J. D. 1994. Spread of Argentine ants (*Linepithema humile)* with special reference to Western Australia. Pp. 163-173 *in* Williams, D. F., ed. Exotic ants: biology, impact, and control of introduced species. Westview Press, San Francisco. 332 pp.
Masuko, K. 1984. Studies on the predatory behavior of Oriental dacetine ants (Hymenoptera: Formicidae). I. Some Japanese species of *Strumigenys*, *Pentastruma*, and *Epitritus*, and a Malaysian *Labidogenys*, with special reference to hunting tactics in short-mandibulate forms. Insect. Soc. 31: 429-451.
Minno, M. C. 1992. Butterflies of the Archbold Biological Station, Highlands County, Florida. J. Lepidop. Soc. 46: 138-158.
Morris, J. R., and K. L. Steigman. 1993. Effects of polygyne fire ant invasion on native ants of a blackland prairie in Texas. Southwest. Natur. 38: 136-140.
Mount, R. H. 1981. The red imported fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae), as possible serious predator on some native southeastern vertebrates: direct observations and subjective impressions. J. Ala. Acad. Sci. 52: 71-78.
Naves, M. A. 1985. A monograph of the genus *Pheidole* in Florida (Hymenoptera: Formicidae). Insecta Mundi 1: 53-90.
Passera, L. 1994. Characteristics of tramp species. Pp. 23-43 *in* Williams, D. F., ed. Exotic ants, biology, impact, and control of introduced species. Westview Press, San Francisco. 332 pp.
Porter, S. D., and D. A. Savignano. 1990. Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. Ecology 71: 2095-2106.

Reimer, N. J. 1994. Distribution and impact of alien ants in vulnerable Hawaiian ecosystems. Pp. 11-22 *in* Williams, D. F., ed. Exotic ants: biology, impact, and control of introduced species. Westview Press, San Francisco. 332 pp.

Roger, J. 1863. Die neu aufgefuhrten Gattumgen und Arten meines Formiciden-Verzeichnisses, nebst Erganzung einiger fruher gegeben Beschreibungen. Berlin. Entomol. Zeit. 7: 131-214

Simberloff, D. 1997. The biology of invasions. Pp. 3-17 *in* Simberloff, D., D. C. Schmitz, and T. C. Brown, eds. Strangers in paradise: impact and management of nonindigenous species in Florida. Island Press, Washington, D.C. 467pp.

Simberloff, D., and E. O. Wilson. 1969. Experimental zoogeography of islands: the colonization of empty islands. Ecology 50: 278-296.

Smith, D. R. 1979. Formicoidea. Pp. 1323-1467 *in* Krombein, K. V., P. D. Hurd, Jr., D. R. Smith, and B. D. Burks, eds. Catalog of Hymenoptera in America north of Mexico. Smithsonian Institution Press, Washington, D.C.: 2735 pp.

Smith, M. R. 1929. Two introduced ants not previously known to occur in the United States. J. Econ. Entomol. 22: 241-243.

Smith, M. R. 1930. A list of Florida Ants. Fla. Entomol. 14: 1-6

Smith, M. R. 1933. Additional species of Florida ants, with remarks. Fla. Entomol. 17: 21-26.

Smith, M. R. 1936. The ants of Puerto Rico. J. Agr. Univ. Puerto Rico 20: 819-875.

Smith, M. R. 1944. Additional ants recorded from Florida, with descriptions of two new subspecies. Fla. Entomol. 27: 14-17.

Smith, M. R. 1951. Family Formicidae. Pp. 778-875 *in* C. F. W. Muesebeck, K. V. Krombein, and H. K. Townes, eds. Hymenoptera of North America north of Mexico. Synoptic Catalog. U.S. Dept. Agr. Monogr. 2: 1420 pp.

Smith, M. R. 1965. House-infesting ants of the eastern United States: their recognition, biology, and economic importance. USDA Tech. Bull 1326: 1-105

Smith, M. R. 1967. Family Formicidae. Pp. 343-374 *in* Krombein, K. V., and B. D. Burks, eds. Hymenoptera of America north of Mexico.. Synoptic catalog, second supplement. U.S. Dept. Agr. Monogr. 2: 584 pp.

Snelling, R. R., and J. T. Longino. 1992. Revisionary notes on the fungus-growing ants of the genus *Cyphomyrmex, rimosus* group. (Hymenoptera: Formicidae: Attini). Pp. 479-494 *in* Quintero, D., and A. Aeillo, eds. Insects of Panama and Mesoamerica: selected studies. Oxford University Press, Oxford. 692 pp.

Sparks, A. N., R. D. Jackson, J. E. Carpenter, and R.A. Miller. 1986. Insects captured in light traps in the Gulf of Mexico. Ann. Entomol. Soc. Amer. 79: 132-139.

Thompson, C. R. 1989. The theif ants, *Solenopsis molesta* group of Florida. (Hymenoptera: Formicidae). Fla. Entomol. 72: 268-283.

Torres, J. A. 1984. Diversity and distribution of ant communities in Puerto Rico. Biotropica 16: 296-303.

Trager, J. C. 1984. A revision of the genus *Paratrechina* (Hymenoptera: Formicidae) of the Continental United States. Sociobiology 9: 49-162.

Tschinkel, W. R. 1988. Distribution of fire ants *Solenopsis invicta* and *S. geminata* in north Florida in relation to habitat and disturbance. Ann. Entomol. Soc. Amer. 81: 76-81.

Tschinkel, W. R. 1993. The fire ant (*Solenopsis invicta*): still unvanquished. Pp. 121-136 *in* B. N. McKnight, ed. Biological pollution: the control and impact of invasive exotic species. Indiana Academy of Sciences, Indianapolis. 261pp.

Van Pelt, A. F., Jr. 1958. The ecology of the ants of the Welaka Reserve, Florida. (Hymenoptera: Formicidae). II. Annotated list. Amer. Midl. Nat. 59: 1-57

Vinson, S. B. 1994. Impact of the invasion of *Solenopsis invicta* (Buren) on native food webs. Pp. 240-258 *in* Willims, D. F., ed. Exotic ants: biology, impact, and control of introduced species. Westview Press, San Francisco. 332 pp.

Vinson, S. B. 1997. Invasion of the red imported fire ant (Hymenoptera:

Formicidae). Spread, biology, and impact. Amer. Entomol. 43: 23-39.
Ward, P. S. 1985. The Nearctic species of the genus *Pseudomyrmex* (Hymenoptera: Formicidae). Quaest. Entomol. 21: 209-246.
Ward, P. S. 1987. Distribution of the introduced Argentime ant (*Iridomyrmex humilis*) in natural habitats of the Lower Sacramento Valley and its effects on the indigenous ant fauna. Hilgardia 55: 1-16.
Ward, P. S. 1993. Systematic studies on *Pseudomyrmex* acacia-ants. J. Hymenop. Res. 2: 117-168.
Wheeler, G. C., and J. Wheeler. 1978. *Brachymyrmex musculus*, a new ant in the United States. Entomol. News 89: 189-190.
Wheeler, W. M. 1910. The North American ants of the genus *Camponotus* Mayr. Ann. N.Y. Acad. Sci. 20: 295-354.
Wheeler, W. M.. 1915. Some additions to the North American ant fauna. Bull. Amer. Mus. Nat. Hist. 34: 389-421.
Wheeler, W. M. 1929. Two Neotropical ants established in the United States. Psyche 22: 89-90.
Wheeler, W. M. 1931. New and little known ant of the genera *Macromischa, Croesomyrmex,* and *Antillaemyrmex*. Bull. Mus. Comp. Zool. Harvard Univ. 72: 1-34
Wheeler, W. M. 1932. A list of the ants of Florida with descriptions of new forms. J. N.Y. Entomol. Soc. 40: 1-17.
Wheeler, W. M. 1934. Revised list of Hawaiian ants. Occ. Pap. Bernice P. Bishop Mus. 10: 3-21.
Wheeler, W. M., and F. M. Gaige. 1920. *Euponera gilva* (Roger), a rare North American ant. Psyche 27: 69-72.
Whitcomb, W. H., H. A. Denmark, W. F. Buren, and J. F. Carroll. 1972. Habits and present distribution in Florida of the exotic ant, *Pseudomyrmex mexicanus*. Fla. Entomol. 55: 31- 33.
Wilson, E. O. 1964. The ants of the Florida Keys. Breviora 210: 1-14.
Wojcik, D. P. 1983. Comparison of the ecology of red imported fire ants in North and South America. Fla. Entomol. 66: 101-111.
Wojcik, D. P. 1994. Impact of the native red imported fire ant on native ant species in Florida. Pp. 269-281 *in* Williams, D. T., ed. Exotic ants: biology, impact, and control of introduced species. Westview Press, San Francisco. 332 pp.
Wojcik, D. P., W. A. Banks, and W. F. Buren. 1975. First report of *Pheidole moerens* in Florida (Hymenoptera: Formicidae). U.S. Dept. Agr. Coop. Econ. Ins. Rpt. 25: 906.
Wood, S. L. 1982. The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae): a taxonomic monograph. Mem. Great Basin Natur. 6: 1-1359.