The Little Fire Ant, *Wasmannia auropunctata*: Distribution, Impact and Control

by

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ABSTRACT

The little fire ant, *Wasmannia auropunctata*, has been increasing in importance as an exotic pest. Here we review published and unpublished information on its distribution, ecology, impact, and control. *Wasmannia auropunctata* occurs throughout most of the warmer parts of the New World, from subtropical Argentina to subtropical Mexico and through much of the Caribbean, though it is not clear whether this species in native to this entire region. During the past century, exotic populations of *W. auropunctata* have become established in numerous other places, including the Galapagos Islands, West Africa (Gabon, Cameroon, and possibly the Republic of Congo and the Democratic Republic of Congo), Melanesia (New Caledonia, Solomon Islands, Vanuatu, and possibly Tuvalu), Polynesia (Wallis and Futuna and Hawaii), the mainland US (Florida and possibly California), and on subtropical Atlantic islands (the Bahamas and Bermuda). The latitudinal range of known outdoors populations of *W. auropunctata* is from 32°40'S in Argentina to 32°20'N in Bermuda. *Wasmannia auropunctata* is also a greenhouse pest in more temperate regions, such as England and Canada. In many areas, *W. auropunctata* can be a significant agricultural pest, not only stinging agricultural workers, but also enhancing populations of Homoptera. Homoptera cause damage both through sapping plants of nutrients and by increasing the occurrence of diseases, including viral and fungal infections. In addition, *W. auropunctata* has negative impacts on many animals, both invertebrates and vertebrates, though most reports on such impact have been anecdotal. The impacts of *W. auropunctata* populations seem to be most severe on tropical islands where it is not native, such as the Galapagos, New Caledonia, and the Solomon Islands. Reports of widespread blindness in both domestic and native mammals caused by *W. auropunctata* stings deserve serious attention. Chemical control of *W. auropunctata* may be possible for small exotic populations spread over

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a few dozen hectares or less. For large exotic infestations, the only hope for long-term control appears to be classical biocontrol.

Key words: exotic pests, little fire ant, pest ants, pest control, tramp ants, *Wasmannia auropunctata*

INTRODUCTION

Several exotic ant species are known to have dramatic ecological impacts (Williams 1994). When these ants invade, they disrupt the indigenous invertebrate fauna and can transform the entire biological community. Among the most destructive tramp ants are the red imported fire ant (*Solenopsis invicta*; Lofgren 1986, Porter & Savignano 1990), the Argentine ant (*Linepithema humile*; Haskins & Haskins 1988, Human & Gordon 1997, Holway 1998, Suarez *et al.* 1998), the big-headed ant (*Pheidole megacephala*; Haskins & Haskins 1988, Heterick 1997, Hoffman *et al.* 1999), and the long-legged ant (*Anoplolepis gracilipes*, formerly *Anoplolepis longipes*; also called the crazy ant, Hardy 1979, Haines *et al.* 1994, Feare 1999). In recent years, the little fire ant, *Wasmannia auropunctata* (formerly *Ochetomyrmex auropunctata*), has emerged as a major exotic pest that "could easily be in the early phases of a pantropical explosion" (Deyrup 1991).

In Neotropical lowland forests where it is native, *W. auropunctata* is often very common, but usually does not dominate intact communities (Levings & Franks 1982, Tennant 1994, Alonso 1998). However, in disturbed areas, such as agricultural and forestry land, and in regions outside its native range, *W. auropunctata* commonly shows extreme population explosions and "is capable under some circumstances of wiping out entire ant faunas over large areas ... forming in many places a living blanket of ants that kill and eat nearly all other ants in their path" (p. 63, Hölldobler & Wilson 1994). Although the workers are relatively non-aggressive and generally sting people only when provoked, the sting is very painful, out of all proportion to the ant's small size (Creighton 1950). "So feared are they that it is difficult to get laborers to work in groves or fields where these ants are abundant" (Smith 1965).

In many areas, *W. auropunctata* can be a significant agricultural pest, not only stinging agricultural workers, but also enhancing populations of Homoptera (Spencer 1941, Delabie *et al.* 1994, de Souza *et al.* 1998). Homoptera cause damage both through sapping plants of nutrients and by increasing the occurrence of diseases, including viral and fungal infections. In addition, *W. auropunctata* has direct negative impacts on many animals, both invertebrates and vertebrates (see below).

Common names for *Wasmannia auropunctata*

The generally accepted common name for *W. auropunctata* is the "little fire ant," so named because of its small size and "fire-like" sting. This name, however, is somewhat misleading because *W. auropunctata* is not closely related to "true" fire ants of the genus *Solenopsis*.

Numerous other common names for *W. auropunctata* have been used in the literature. English names include "small fire ant" (Florida, Spencer 1941), "little red fire ant" (Galapagos, Lubin 1984), "little introduced fire ant" (Galapagos, Lubin 1983), "West Indian stinging ant" (California, Keifer 1937); "cocoa tree-ant" (Solomon Islands, Ikin 1984); and "electric ant" (New Caledonia, Jourdan 1997a,b). Spanish names include "pequena hormiga de fuego" (= little fire ant, Mexico, Flores-Maldonado *et al.* 2000), "satana" (= devil or she-devil, Cuba Wheeler 1932), "satanica" (= satanic or little she-devil, Cuba, Smith 1954), "santanica" (= little Saint Anna, probably a mis-spelling, Cuba, Wheeler 1913a), "hormiga roja" (= red ant, Galapagos, Ulloa-Chacón *et al.* 1991), "hormiga colorada" (= reddish ant, Galapagos, Ulloa-Chacón *et al.* 1991), "hormiguilla" (= little ant, Puerto Rico, Wheeler 1932), "albayalde" (= lead carbonate or white lead, a white pigment used in painting, Puerto Rico, Smith 1942, 1954), "abdelaya" (unknown meaning, Jourdan *et al.* 2002), "Castellaña" (= Spaniard, Costa Rica, R. Vargas, pers. com.), and "quiscala" (= nuisance?, Costa Rica, R. Vargas, pers. com.). French names include "petit fourmi de feu" (= little fire ant, Galapagos, Ulloa-Chacón *et al.* 1991), "fourmi électrique" (= electric ant, New Caledonia, Jourdan 1997a,b), and "fourmi rouge" (= red ant; Vanuatu, Anonymous 1999). Portuguese names include "pequena formiga de fogo" (= little fire ant, Brazil, Bueno & Campos-Farinha 1998) and "formiga pixixica" (= very small ant, Brazil; Delabie 1989a, a name also applied to *Solenopsis geminata*). African names include "tsangonawenda" or "sangunagenta" (unknown meaning, Gabon, Schweitzer 1931, 1951, Wetterer *et al.* 1999) and "tchabe" (= Cabe, a west central African tribe, Cameroon, Bruneau de Miré 1969).

Identification of *Wasmannia auropunctata*

Wasmannia auropunctata workers are slow-moving, monomorphic, ~1.5 mm in length, and light brown to golden brown in color, with the gaster often somewhat darker. The pedicel, between the thorax and gaster, has two segments, the petiole and postpetiole (Fig. 1). The petiole is distinctively "hatchet-shaped," with a node that is almost rectangular in profile and higher than the postpetiole. The antennae have 11 segments, with the last two segments enlarged into a club. The antennal scape (first antennal segment) is received into a groove (scrobe) that

extends almost to the posterior border of the head. The thorax has long and sharp epinotal spines. The body is heavily sculptured and sparsely covered with long, erect hairs.

Wasmannia auropunctata queens are much larger (~4.5 mm) and darker than the workers (Fig. 2). In dense colony aggregations, the multiple queens are quite conspicuous peppered among the lighter-colored workers.

Invasive traits of *Wasmannia auropunctata*

Wasmannia auropunctata has many traits, shared with other highly successful and destructive invasive ant species, that make these ants more likely invade new areas and more likely to succeed once they arrive

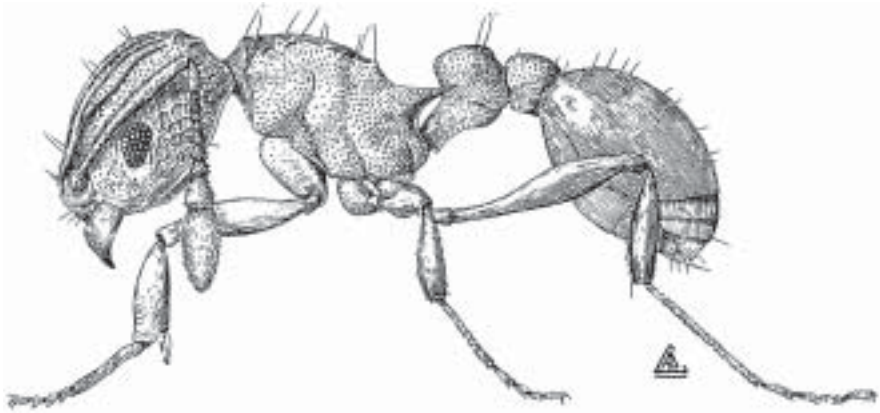

Fig. 1. *Wasmannia auropunctata* worker (from Smith 1947).

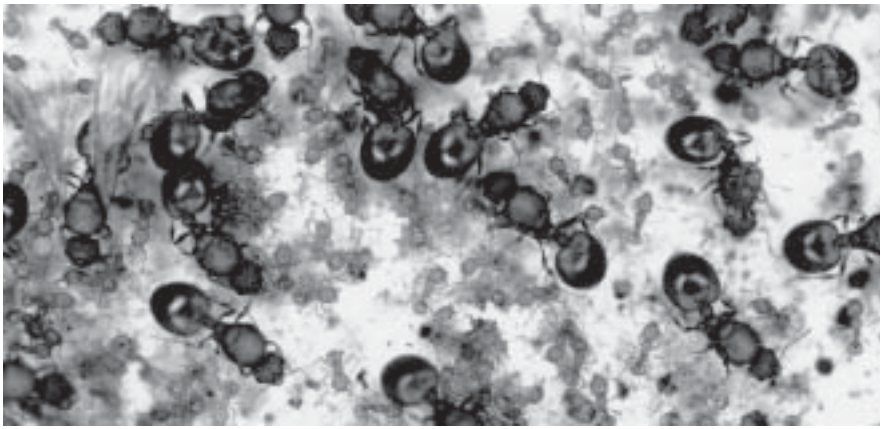

Fig. 2. *Wasmannia auropunctata* workers and queens (photo by SDP).

(Brandão & Paiva 1994, Passera 1994). These traits include generalist feeding and nesting habits, superficial nests, high colony mobility, polygyny (multiple queens in a colony), colony budding, low intraspecific aggression, high interspecific aggression, small size, and tending of extrafloral nectaries and Homoptera.

Many researchers have noted the generalist feeding and nesting habits of *W. auropunctata* (e.g., Smith 1942, Kusnezov 1951, Way & Bolton 1997), allowing them to thrive in a wide range of conditions. *Wasmannia auropunctata* colonies do not excavate nests deep underground, but instead exploit an extremely broad array of superficial cavities, both natural and manmade. They commonly nest under rocks, and under and within logs, branches, plant debris, coconuts, epiphytes, and ant-plants. Cavities within human products and structures prove equally attractive. "Habitats that are wet or dry, shaded or open, all are acceptable" to *W. auropunctata* (Deyrup *et al.* 2000). *Wasmannia auropunctata* colonies tend to be highly mobile, readily moving to more favorable sites when they become available. Colonies or colony fragments often move into new objects that arrive in their territories and accompany these objects when they are transported elsewhere. *Wasmannia auropunctata* is thought to "spread largely or entirely by budding off of groups of workers accompanied on foot by inseminated queens" (Hölldobler & Wilson 1977). Because *W. auropunctata* colonies have multiple queens, any transported colony fragment containing at least one queen can found a new population at its destination.

Associated with having multiple queens, *Wasmannia auropunctata* is a unicolonial species "in which no colony boundaries exist and local populations are comprised of networks of intercommunicating aggregations of workers, brood, and fertile queens" (Hölldobler & Wilson 1977). Lack of intercolony territoriality allows populations to reach much higher densities than territorial monogyne colonies. Numerous ant species have both monogyne and polygyne forms (Hölldobler & Wilson 1977). For example, in *S. invicta*, monogyne colonies are the common form in native areas, but the polygyne form can dominate in some exotic populations. Although having multiple queens appears to be the general rule for *W. auropunctata*, even in native populations (L. Alonso, pers. comm.), Wheeler (1901) collected a single-queen *W. auropunctata* (*rugosa*?) colony in Mexico (see below), suggesting the possibility of monogyny in some native populations.

Wasmannia auropunctata, like other highly successful invaders, shows a high level of aggression against other ant species, allowing them to exclude completely many other competitor ant species and

thereby dominate an area (Brandão & Paiva 1994, Way & Bolton 1997, Delsinne *et al.* 2001). McGlynn (1999b) found that exotic populations of invasive ant species, including *W. auropunctata*, generally have smaller workers than native populations of the same species. McGlynn (1999b) considered small size to be a trait that allowed the invasive ant populations to be more successful in interspecific combat. Alternatively, smaller size may be a response to lack of intraspecific combat, that perhaps allows greater foraging efficiency.

Wasmannia auropunctata workers commonly feed on nectar produced by plant extrafloral nectaries (Schemske 1980, Smilely 1986, Horvitz & Schemske 1990) and on sugary honeydew excreted by various Homoptera, including aphids, mealybugs, scales, and whiteflies (Spencer 1941, Smith 1942, Delabie *et al.* 1994, Naumann 1994). Deyrup *et al.* (2000) noted that *W. auropunctata* seems quite dependent on extrafloral nectaries. The ants' success in disturbed habitats may be due, in part, to higher densities of Homoptera that thrive on secondary growth plants. This abundant source of carbohydrates may allow *W. auropunctata* to maintain extremely dense populations.

DISTRIBUTION

Nine of the ten known species in the genus *Wasmannia* are found only in the Neotropics (Table 1). *Wasmannia auropunctata* is the sole member of the genus to extend its range outside the Neotropics (Fig. 3). Kempf (1972), in his catalog of known records for ants in the Neotropics, listed seven variants of *W. auropunctata* (Table 1), all currently recognized as subspecies (Table 1; Kempf 1972, Bolton 1995). Kempf (1972) considered only one subspecies, *W. auropunctata auropunctata*, to be an invasive form spread through human commerce. In most reported cases of *W. auropunctata* outside the Neotropics, the subspecies has not been specified, though it seems plausible that most or all are *W. auropunctata auropunctata*.

Although *W. auropunctata* is now known from virtually all Neotropical countries in South America, Central America, and the Caribbean (Table 1; Fig. 3), it is unclear how extensive the native Neotropical range of *W. auropunctata* was before being spread by humans. The only Neotropical populations that seem certain to be exotic are those of the Galapagos Islands. At some locales (e.g., Cocos Island), two subspecies of *W. auropunctata* co-occur. It is possible that these are co-occurring natives, co-occurring exotics, or a mix of native and exotic forms.

South America

Kempf (1972) listed records of *W. auropunctata* throughout much of

tropical South America (Table 1, Fig. 3), including Argentina, Bolivia, Brazil, Colombia, Ecuador, the Guyanas, Paraguay, and Peru. Brandão (1991) extended Kempf's catalog of known Neotropical sites of *W. auropunctata auropunctata*, adding the Galapagos and Uruguay (though Uruguay is subtropical/temperate). *Wasmannia auropunctata* has also been reported from Venezuela (e.g., Lubin 1984), including Margarita Island, off the Venezuelan coast (Kempf 1972). It has been found in Ecuador both east of the Andes (Jatun Sacha - L. Alonso, pers. comm.) and west of the Andes (Endesa Forest Reserve - L. Alonso, pers. comm.). It has also been recorded west of the Andes in Colombia (Choco State - Armbrecht *et al.* 2001, Beunaventura - L. Alonso, pers. comm.).

The only South American country for which we could find no records of *W. auropunctata* is Chile (Snelling & Hunt 1975). It possible that *W. auropunctata* is not native west of the Andes in southern South America; known Peruvian sites (Wilson 1987, Tobin 1997) are east of the Andes.

Table 1. Neotropical distribution of the ten species of *Wasmannia* and seven subspecies of *Wasmannia auropunctata* (Kempf 1972; Lubin 1984; Brandão 1991; Maes, & MacKay 1993; Heraty 1994; this paper), arranged roughly south to north within geographic area. South America (a = Argentina. p = Paraguay, b = Brazil, B = Bolivia, P = Peru, e= Ecuador, g = Guyanas, v = Venezuela, C = Columbia); Central America (p = Panama, c = Costa Rica, n = Nicaragua, h = Honduras, g = Guatemala, b = Belize, m = Mexico); Caribbean (d = Dutch Antilles, t = Trinidad, g = Grenada, s = St. Vincent, b = Barbados, S = St. Lucia, m = Martinique, D = Dominica, G = Guadeloupe, v = Virgin Islands, p = Puerto Rico, r = Dominican Republic, h = Haiti, j = Jamaica, and c = Cuba); Pacific islands (g = Galapagos, c = Cocos).

	S. America apbBPegvC	C. America pcnhgbm	Caribbean dtgsbSmDGvprhjc	Pacific gc
Wasmannia species				
affinis	—b———	p———	————————	—
auropunctata	apbBPegvC	pcnhgbm	dtgsbSmDGvprhjc	gc
iheringi	—b———	———	————————	—
lutzi	—b———	———	————————	—
rochai	—b—g—	p———	-t————————	—
scrobifera	————	———	d————————	—
sigmoidea	—b—g—	———	—gs———p——	—
sulcaticeps	a———	———	————————	—
villosa	—b———	———	————————	—
williamsi	a———	———	————————	—
auropunctata subspecies				
auropunctata	a?bBe?g??	pcnhgb?	dtgsbSmDGvprhjc	gc
australis	apb———	———	————————	—
laevifrons	—BP——	———	————————	—
nigricans	-pb———	———	————————	—
obscura	—b——C	———	————————	—
pulla	————	p———	————————	—
rugosa	apb———	-c—g-m	————————	-c

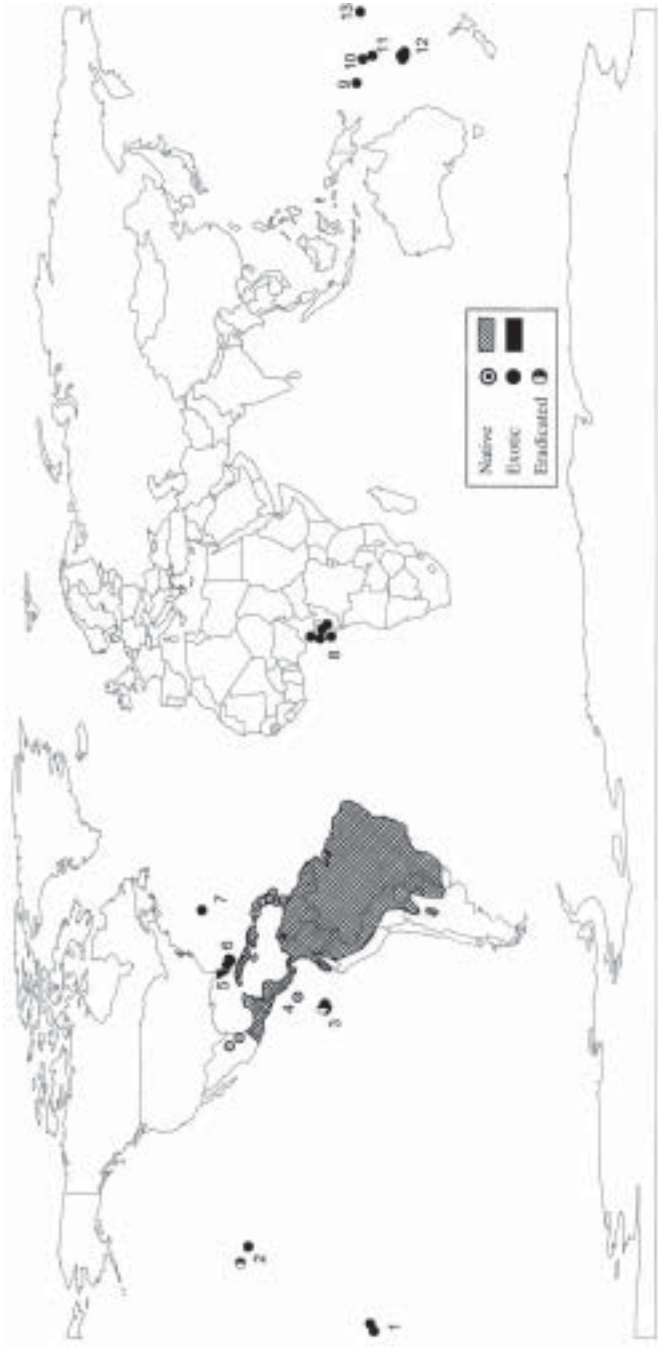

Fig. 3. World distribution of *Wasmannia auropunctata*. 1) Wallis and Futuna, 2) Hawaii, 3) Galapagos, 4) Cocos Island, 5) Florida, 6) Bahamas, 7) Bermuda, 8) Cameroon and Gabon, 9) Solomon Islands, 10) Santa Cruz Islands, 11) Vanuatu, 12) New Caledonia, 13) Tuvalu (not confirmed).

Some other native South American ants, such as the Tribe Attini that includes the infamous leaf-cutting ants (*Atta* spp. and *Acromyrmex* spp.), are not found west of the Andes in Peru and Chile (Weber 1972).

The six subspecies of *W. auropunctata* recorded in South America have widely disjunct and intermingled records. Kempf (1972) and Brandão (1991) listed records *W. auropunctata auropunctata* in ten Brazilian states scattered across the entire country: Amazônia (which included Roraima), Pará, Rondônia, Mato Grosso (which included Mato Grosso do Sul), Rio Grande do Norte, Paraíba, Guanabara (part of Rio de Janeiro), São Paulo, Santa Catarina, and Bahia. Kempf (1972) listed four other *W. auropunctata* subspecies in Brazil, each with widely disjunct populations: *australis* in Paraná and Rio Grande do Sul (in addition to Paraguay and Argentina, see below), *nigricans* in São Paulo (and Paraguay), *obscura* in Ceará and São Paulo (and Colombia); *rugosa* in Ceará and perhaps Rio Grande do Sul (as well as Central America, see below). Della Lucia *et al.* (1983) and others have reported *W. auropunctata* in Minas Gerais state. A re-evaluation of the validity of the different subspecies of *W. auropunctata* would be very useful.

At its southernmost limits, *W. auropunctata* occurs in and may be native to subtropical South America in southern Paraguay and Brazil and northern Argentina and Uruguay. Kusnezov (1951), in a map of the known range of *W. auropunctata* in southern South America, showed three separate populations in Argentina. One was continuous with a population in eastern Brazil reaching south into Argentina through the states of Formosa, Chaco, Santa Fé, Missiones, and Corrientes to a southernmost point in Entre Ríos state at 32°40'S, just west of Uruguay. A second population was continuous with a population in eastern Bolivia and western Paraguay, reaching south into Argentina through Jujuy and Salta states to a southernmost point in Tucumán state at 27°30'S. Finally, a small and isolated third population, south of the second population, in Córdoba state between 30° and 32°20'S. Kempf (1972) listed records from ten states in Argentina, the same ten shown on Kusnezov's (1951) map. The distribution of *W. auropunctata* in Argentina suggests that approximately 32°40'S may represent the latitudinal extreme for this species. Strikingly, the latitude of the northernmost established population of *W. auropunctata* in Bermuda is 32°20'N (see below).

Kusnezov's (1951) map showed *W. auropunctata* just to the west of northern Uruguay, but not in Uruguay itself, and Kempf (1972) listed no records of *W. auropunctata* in Uruguay. De Zolessi *et al.* (1985) included *W. auropunctata* as an ant species considered "important or new" in Uruguay, though they did not say in which of these two

categories they placed *W. auropunctata*. De Zolessi *et al.* (1989) listed *W. auropunctata* at two sites, both in northern third of Uruguay (Pintado Grande in Artigas Department: 30º06'S; and Punta Arroyo Laureles in Tacuarembó Department: 31º50'S). It seems likely that *W. auropunctata* is native to Uruguay. Uruguay is entirely south of 30ºS, but its northern parts are well within the same latitudinal range of *W. auropunctata* populations in Entre Ríos and Tucumán states of neighboring Argentina (Kusnezov 1951).

Central America and Mexico: Kempf (1972) listed Central American records (Table 1) of *W. auropunctata* from Panama, Costa Rica (including Cocos Island in the Pacific), Honduras, Guatemala, and Mexico. In addition, Maes & MacKay (1993) reported *W. auropunctata auropunctata* from Nicaragua. Maes & MacKay (1993) also proposed, based on the known distribution of *W. auropunctata rugosa*, that this second subspecies probably also occurs in Nicaragua. We could find no published records of *W. auropunctata* in Belize, but in the collection at the Museum of Comparative Zoology, we found several Belize specimens that S. & J. Peck collected from Berlese samples at "Hummingbird Gap, 45 km northwest of Stann Creek," Belize on 19 August 1972. The only Central American country still lacking records of *W. auropunctata* is El Salvador. This apparent gap in the Central American distribution of *W. auropunctata* seems likely to be an artifact of insufficient sampling.

Although *W. auropunctata* is considered an exotic species in the Galapagos off the Pacific coast of Ecuador (see below), Hogue & Miller (1981) considered both *W. auropunctata auropunctata* and *W. auropunctata rugosa* as native to Cocos Island, north of the Galapagos. Cocos Island was the only Pacific locality for *W. auropunctata* listed by Wheeler (1935).

There are records of *W. auropunctata* from many different states in tropical Mexico: Oaxaca (this study, see below), Morelos (Wheeler 1901, Kempf 1972), Tabasco (Kempf 1972), Chiapas (Goodnight & Goodnight 1956, Brown 1957, MacKay *et al.* 1991), Quintana Roo (Dejean *et al.* 1995), Vera Cruz (Jeanne 1979, Horvitz & Schemske 1990), and Tamaulipas (Atresino & Phillips 1992, Rojas-Fernández 1996, 2000). Despite extensive studies of the myrmecofauna in more northern areas of Mexico (e.g., Rojas-Fernández & Fragoso 1994 in Durango), the only record of *W auropunctata* in subtropical Mexico is a single record from Nuevo Leon (this study, see below).

In Cuernavaca (in the state of Morelos, south of Mexico City), Wheeler (1901) collected one colony of *W. auropunctata* identified by Forel (1901) as *W. auropunctata rugosa*: "a single large nest under a stone in a hilly pasture south of town. The nest contained hundreds of workers with a

single queen." Perhaps following Wheeler (1901), Kempf (1972) listed only the subspecies *W. auropunctata rugosa* in Mexico (in Morelos and Tabasco states). In other studies of *W. auropunctata* in Mexico, authors made no mention which subspecies they collected. It seems unlikely that all *W. auropunctata* in Mexico are subspecies *rugosa*, though this should be examined.

The northernmost published records of *W. auropunctata* in Mexico come from the Gómez Farías section of El Cielo Biosphere Reserve (23º00'-23º05'N) in Tamaulipas state (Atresino & Phillips 1992, Rojas-Fernández 2000), just south of the Tropic of Cancer (23º27'N). Curiously, Flores-Maldonado *et al.* (1999) did not find *W. auropunctata* at a nearby site, just north of the Tropic of Cancer.

In the Museum of Comparative Zoology collection, we found many unpublished records from Mexico, including the first records of *W. auropunctata* from the Mexican states of Oaxaca and Nuevo Leon. In August 1973, A. Newton collected *W. auropunctata* at two sites in Oaxaca state: 7.3 km south of Valle Nacional at 500m elevation and 14 km south of Valle Nacional at 1600m elevation. On 22 June 1969, S. & J. Peck collected *W. auropunctata* in Nuevo Leon state near Monterrey: Mesa de Chipinque, 1645 m elevation. At approximately 25º40'N, this last record is the northernmost known record of *W. auropunctata* in Mexico.

Caribbean

Cuba is the type locale for *Wasmannia auropunctata*. Wheeler's (1905) "list of the known West Indian species" had records of *W. auropunctata* only from Cuba (Roger 1863), St. Vincent (Forel 1893), and Grenada (Forel 1897). As additional ant collections from the Caribbean were studied, most island fauna included *W. auropunctata*: Puerto Rico (Wheeler 1908), Jamaica (Wheeler 1911), Dominica (Wheeler 1913b), Haiti (Wheeler 1914, Wheeler & Mann 1914), Trinidad (Wheeler 1916, 1922a), Barbados (Wheeler 1923), St. Croix (Beatty 1944), and St. John (Pressick & Herbst 1973). Kempf (1972) listed records of *W. auropunctata* from many parts of the Caribbean: La Sola, Margarita, Curaçao, Trinidad, Grenada, St. Vincent, Barbados, St. Lucia, Martinique, Dominica, Guadeloupe, St. Thomas, Puerto Rico, Mona, Culebra, Dominican Republic, Haiti, Jamaica, and Cuba. Jaffe & Lattke (1994) recorded *W. auropunctata* from Guadeloupe, Marie Galante, Les Saints, and Martinique.

Wasmannia auropunctata auropunctata, the invasive subspecies, is the only form known from the Caribbean, suggesting the possibility that some or all Caribbean populations may be non-native, introduced by human commerce. Wilson (1985) did not find ants of the genus

Wasmannia among the ant fauna of the Dominican amber (at least 20 million years old) from the island of Hispañola and concluded that *Wasmannia* was a relatively new arrival, "possibly introduced by commerce." Baroni Urbani (1995), however, listed an unpublished record of the genus *Wasmannia* in Dominican amber.

The hypothesis that *W. auropunctata* is long-time native to the Caribbean seems to be supported by presence of a eucharitid wasp, *Orasema minutissima*, that parasitizes *W. auropunctata* in Cuba, Puerto Rico, St. Vincent, and Trinidad (Mann 1918, Heraty 1994). However, this parasite may have come with *W. auropunctata* fairly recently. In addition, this parasite also attacks *Wasmannia sigmoidea* in Puerto Rico (Heraty 1994), an ant species known from both South America and the Caribbean (Table 1), allowing the possibility that the parasite could pre-date a much more recent arrival of *W. auropunctata* on the islands.

Exotic populations of *Wasmannia auropunctata*

During the past century, *W. auropunctata* has invaded tropical and subtropical areas in other parts of the world (Table 2). *Wasmannia auropunctata* has become established in west central Africa, "evidently from South America" (Wheeler 1922b), Gabon (Santschi 1914, Wheeler 1922b) and Cameroon (Bruneau de Miré 1969, Wetterer *et al.* 1999). A table in Fowler *et al.* (1994) indicated that *W. auropunctata* was also recorded from Congo, but the cited reference, Van der Meer Mohr (1927), contained no such report. *Wasmannia auropunctata* has also invaded several Pacific island groups, including New Caledonia (Fabres, & Brown 1978), Wallis and Futuna (Gutierrez 1981 in Jourdan 1997a), the Solomon Islands (Ikin 1984, Wetterer 1997), Tuvalu (Waterhouse 1997), Cook Islands (1997), Hawaii (Anonymous 1999; N. Reimer, pers. comm.), and Vanuatu (B. Phillips, pers. comm., Chazeau & de Larbogne 1999, Rapp 1999, Anonymous 2000).

Wasmannia auropunctata has been found in some northern subtropical parts of the New World: Florida (Wheeler 1929), California (Keifer 1937, Mallis 1969), Bermuda (Crowell 1968, this study), and the Bahamas (Smith 1954, Deyrup *et al.* 1998). All of these appear to be exotic populations.

Finally, *W. auropunctata* is also a greenhouse pest in temperate regions, such as England (Wheeler 1929) and Canada (Ayre 1977, Anonymous 1979, Naumann 1994).

Galapagos Islands

Silberglied (1972) made the first published report of *W. auropunctata* in the Galapagos Islands, although he thought it was likely that a report

Table 2. Earliest known records of *Wasmannia auropunctata* in exotic locales.

Locale	Year	References
Gabon	1914	Santschi 1914
Florida	1924	Wheeler 1929; Smith 1929
Bermuda	1925	Wetterer & Porter, this study
Galapagos	1935?	Silberglied 1972; Kastdalen 1982
Bahamas	1951	Smith 1954
Cameroon	1959	Bruneau de Miré 1969
New Caledonia	1972	Fabres & Brown 1978
Solomon Islands	1974	Ikin 1984
Wallis and Futuna	1981	Gutierrez 1981 (in Jourdan 1997a)
Vanuatu	1998	Rapp 1999; Anonymous 2000
Hawaii	1999	Anonymous 1999; Conant & Hirayama 2000
Santa Cruz Islands	1999	P. Ward (pers. comm.)
Greenhouse / indoor temperate populations		
England	1907	Donisthorpe 1927 (in Wheeler 1929)
California	1936	Keifer 1937; Mallis 1969
Manitoba	1977	Ayre 1977
Ontario	1978	Anonymous 1979
Br. Columbia	1994	Naumann 1994
Quebec	1999	S. Johnson (pers. comm.)

of a 1905 expedition noting that ants "made sleeping rather impossible" referred to *W. auropunctata*. As a result, some paper list 1905 as the earliest date for *W. auropunctata* in the Galapagos (e.g., Peck *et al.* 1998). Kastdalen (1982, but cited in unpublished form by Silberglied 1972) wrote that in 1935 the "fire ant" (assumed by Silberglied and others, e.g., Meier 1994, to be *W. auropunctata*), was found on Santa Cruz Island in the Galapagos "only in a small area about half way between the farms and the beach. Silberglied (1972) found that by 1972, *W. auropunctata* was found over wide areas of Santa Cruz, as well as on the islands of San Cristóbal, Santiago (San Salvador), and Isabela. *W. auropunctata* has also spread to the islands of Santa María (Floreana), Pinzón, Marchena, and Santa Fe (Abedrabbo 1994, Roque-Albelo & Causton 1999), as well as smaller islands, such as Albany and Eden (C. Causton, pers. comm.). The population on Santa Fe has been eradicated (see below).

West Central Africa

Santschi (1914) recorded *W. auropunctata* from Libreville, Gabon (confirmed by Wheeler 1922b). Subsequently, Bruneau de Miré (1969) reported *W. auropunctata* from the coastal region of Cameroon near

Kribi, "spread along the Kribi - Ebolowa road axis and in the interior in the plantations on both sides of the road, for a distance of 40 km around the outside of the village of Bidou II, near Kribi. It is also found along the old mine road that leaves through the south of the village of Bidou II."

More recently, biologists working in the Lopé Reserve, central Gabon noted the sting of a small red ant in 1984 when the station was first established (C. Tutin, pers. comm.). In December 1997, specimens collected in Lopé were identified as *W. auropunctata*. A local man in Lopé, who worked for the first logger to come to the region, claimed that *W. auropunctata* was unknown in the area prior to around 1965 when logging started. At that time, there were no roads into the area. He said that the ants arrived in the packaging of food flown in from Booue and Libreville to feed the forestry workers (Wetterer *et al.* 1999).

In March 1998, Wetterer *et al.* (1999) found *W. auropunctata* in Petit Loango Reserve on Gabon's southwest coast (about 350 km south of Libreville). In April 1999, E. J. Wickings found *W. auropunctata* in her house at the Centre International de Recherches Medicales, Franceville (CIRMF), in southeastern Gabon (01°40'S, 13°30'E; 500 km southeast of Libreville), near the border with the Republic of Congo. The region encompassing all currently known localities of *W. auropunctata* in Africa extends more than 600 km along the western coastline of Gabon and at least 400 km inland.

Jourdan *et al.* (2002) related unconfirmed, but highly plausible reports that *W. auropunctata* may be present in the Republic of Congo and the Democratic Republic of Congo (formerly Zaire), immediately to the south and west of Cameroon and Gabon.

Melanesia and Polynesia

The earliest records of *W. auropunctata* in the Western Pacific come from New Caledonia (Fabres & Brown 1978). Since its first introduction to New Caledonia around 1972 (Fabres & Brown 1978), *W. auropunctata* has spread from Grande Terre, the main island of New Caledonia, to the Loyalty Islands, the Isle of Pines, and Walpole Island (Jourdan 1997a).

The current distribution of *W. auropunctata* in the Solomon Islands is largely unknown. Ikin (1984) reported that *W. auropunctata* was thought to have arrived in the Solomons at least 10 years earlier and by 1984 was "widely distributed" in the islands. Wetterer (unpublished) found that *W. auropunctata* was extremely common on all three islands visited: Guadalcanal, Savo, and Vulelua. Recently, D. M. Olson collected this species on Utupua Island (10 October 1999 in secondary forest; P. Ward, pers. comm.). Utupua is part of the Santa Cruz Islands far east of the rest of the Solomon Islands, just north of Vanuatu.

Wasmannia auropunctata was first detected in Vanuatu in 1998. Brian Phillips (pers. comm.) reported the ants suspected to be *W. auropunctata* on the island of Vanua Lava in the Banks Group during survey work in early June 1998. Phillips sent JKW *W. auropunctata* specimens collected from Sola, Vanua Lava in December 1998. Phillips alerted local and international authorities and subsequent work identified populations occupying an area of about 10 km^2 on three islands: Vanua Lava, Mota, and Gaua (Rapp 1999, Anonymous 2000, Jourdan *et al.* 2002). Chazeau & de Larbogne (1999) only found *W. auropunctata* on Vanua Lava, but witnessed quarantine officials who "stopped a man bringing back infested taros from Vanua Lava which he intended to plant on Mota Lava."

Gutierrez (1981 in Jourdan 1997a) recorded *W. auropunctata* in Wallis and Futuna, on all three main islands (Wallis, Futuna and Alofi). In 1965, Hunt made an extensive ant survey of Wallis and Futuna (Wilson & Hunt 1967) and did not record *W. auropunctata*, so it probably arrive there after this date.

Wasmannia auropunctata has been repeatedly intercepted by quarantine inspectors, on products entering Hawaii (Wheeler 1934a, Swezey 1945), and has recently become established there. *Wasmannia auropunctata* has been reported from two of the Hawaiian islands. An October 1999 press release by the Hawaii Department of Agriculture (Anonymous 1999) wrote: "To date the Department has identified five sites of infestation - four on the island of Hawaii and one on Kauai. Most of these sites are nurseries and the dispersal of this ant to uninfested areas could be very likely." "On the Big Island, the ant has been discovered at four locations, including a nursery in the Hawaiian Paradise Park in Puna, a nursery in Kapoho, a nursery in Panaewa, and a fruit tree orchard in Papaikou. Although the first detection of the little fire ant was reported to the Department in March [1999], the ant may have been on the Big Island for at least six years." "The most recent detection occurred on October 6 [1999] when the ant was found on a 20-acre estate in Kalihiwai, Kauai. **Brackets vs. parenthesis - does this have a different meaning?**Entomologists believe the ant was transported to Kauai [in September 1999] on some palms from a Big Island nursery." Conant & Hirayama (2000) reported 13 separate infestation on the Big Island, and as of September 2002, P. Conant (pers. comm.) reported 21 separate infestations, six of which, each covering less than 2 acres, he may have eradicated. All rooted plants leaving the Big Island must be tested for *W. auropunctata* using chopsticks coated with peanut butter that are put in the pots for 45 min then checked by an inspector. The Kauai population has apparently been eradicated, through use of

Amdro.(Conant & Hirayama 2000).

Waterhouse (1997) listed *W. auropunctata* in Tuvalu and the Cook Islands. Waterhouse died in 2000, so in 2002, we contacted the agricultural offices in both countries for confirmation. Itaia Lausaveve, Acting Director of Agriculture in Tuvalu, did not have any records of this species, but wrote of an ant that seems likely to be *W. auropunctata*: "There is however one red ant species that was reported (1999) from Niulakita island in the Southern group that this particular species was causing eye infection to young poultry (chickens) leading to blindness and even to death in extreme cases." Dr. Maja Poeschko, an entomologist in the Cook Islands, replied "To my knowledge the little fire ant *Wasmannia auropunctata* is not present in the Cook Islands. Most probably the record is based on a misidentification of the tropical fire ant *Solenopsis geminata* which is quite common."

Florida

The earliest record of *W. auropunctata* in Florida were specimens from 1924 collected in Coconut Grove, near Miami (Wheeler 1929). Smith (1929) also received specimens collected near Miami. Wheeler (1932) added a third record from Fort Lauderdale and wrote that *W. auropunctata* "is now very abundant under stones in the vicinity of Miami. Spencer (1941) listed records of *W. auropunctata* from citrus groves or nurseries in 10 counties in peninsular Florida (Brevard, Broward, Collier, Dade, DeSoto, Orange, Osceola, Polk, St. Lucie and Volusia), and stated "it is probable that the ant is present in many other places in the lower two-thirds of Florida." In 1947, Fernald reported that *W. auropunctata* "is now present in nearly all of the peninsular portion of the state," though this may have been an exaggeration. Deyrup *et al.* (1989) listed *W. auropunctata* known from 15 counties in peninsular Florida (Alachua, Broward, Collier, Dade, Glades, Highlands, Hillsborough, Indian River, Lake, Martin, Monroe, Okeechobee, Palm Beach, Polk and Sarasota), while Ferster *et al.* (2000) listed records from 22 counties (Broward, Collier, Dade, Glades, Hardee, Hendry, Hernando, Highlands, Indian River, Lake, Manatee, Marion, Martin, Monroe, Okeechobee, Orange, Osceola, Palm Beach, Polk, St. Lucie, Sarasota and Seminole). In addition, in the Archbold Field Station ant collection there were *W. auropunctata* specimens collected on Sanibel Island in Lee County by Z. Prusak (30 Aug 1996) and M. Deyrup (17 Jan 2002). Combining these records with those from Spencer (1941), Deyrup *et al.* (1989), and Ferster *et al.* (2000) yields 28 counties that constitute most of the southern three-fourths of peninsular Florida (all except Charlotte, Pinellas, Pasco, Sumter and Citrus counties). The northernmost record

in Florida is from Alachua County, situated at about 29°30'N (Johnson 1986), although *W. auropunctata* is apparently very rare in this county (SDP, pers. obs.) and may not maintain year-round outdoors populations (M. Deyrup, pers. comm.). It is unclear whether *W. auropunctata* is still spreading north in Florida, or even whether it has spread at all in Florida in the past 50 years.

Atlantic islands

In addition to southern Florida, *W. auropunctata* is established in two other northern subtropical areas: the Bahamas and Bermuda. Very little has been published about *W. auropunctata* in either of these locations.

Only four of the larger Bahamian island groups that have been moderatly well surveyed for ants (Bimini, Andros, New Providence, and San Salvador), and *W. auropunctata* has been found on three of them (Deyrup *et al.* 1998, Morrison 1998). Smith (1954) published the first record of *W. auropunctata* in the Bahamas, in the Bimini Islands. Deyrup *et al.* (1998) recorded *W. auropunctata* on New Providence and North Andros in the Bahamas. *Wasmannia auropunctata* was not found on San Salvador (Deyrup 1994), nor on many smaller islands (Morrison 1998), suggesting that this species is patchily distributed in the Bahamas. Smith (1954) did not consider it an introduced species, even though Wheeler (1905, 1934b) and Mann (1920) previously had not found this species in the Bahamas. Deyrup *et al.* (1998), however, listed it as "introduced, probably from South America," and Morrison (1998) listed it as exotic in the Bahamas.

The earliest known specimens of *Wasmannia auropunctata* from Bermuda we found in Harvard University's Museum of Comparative Zoology, collected by L. Ogilvie on 18 October 1925 (JKW, pers. obs.). Crowell (1968), in his study of the exotic ants *Linepithema humile* and *Pheidole megacephala*, included the first published Bermuda record of *W. auropunctata*, though he noted that "the presence of *Wasmannia auropunctata* has been recognized by the Bermuda Department of Agriculture and Fisheries since 1950." Lieberburg *et al.* (1975), in their further study *L. humile* and *P. megacephala*, also found *W. auropunctata* in Bermuda, but reported only their presence. At 32°20'N, the Bermuda population of *W. auropunctata* is the northernmost established outdoors population of this species.

California

We found only two records of *W. auropunctata* from California. Keifer (1937) reported that "the West Indian stinging ant, *Wasmannia auropunctata*, occasionally intercepted for the past few years, is re-

ported established in Los Angeles County." In addition, Mallis (1969) "examined specimens collected in a San Francisco warehouse in 1936." Although Los Angeles (34°N) is well north of the apparent latitudinal limits of *W. auropunctata*, the warming effects of the city may allow the ant to persist this far north. It seems likely that in San Francisco (37°45'N), *W. auropunctata* cannot survive the winters outside of buildings. The lack of any more recent California records suggests that *W. auropunctata* has not spread widely there and may, in fact, no longer persist in California. Only southernmost California may be within the potential range of *W. auropunctata*: San Diego, on the Mexican border, sits just below 32°40'N.

Temperate greenhouses

The earliest records of *W. auropunctata* in temperate areas were from greenhouses in England. Donisthorpe (1927 in Wheeler 1929) "first discovered this very small species in Kew Gardens in 1907; it is one of the commonest ants at Kew." In addition, in 1922 it was found "in a banana store in Manchester" (Donisthorpe 1927 in Wheeler 1929).

Ayre (1977) reported nine tropical or subtropical ants, including *W. auropunctata*, living in the Tropic House of Winnipeg's Assiniboine Park in Manitoba, Canada. Ayre (1977) concluded that none of the exotic ant species were likely to survive in Winnipeg, except under greenhouse conditions. In addition, *W. auropunctata* has been found in the Toronto Zoo in Ontario, Canada (Anonymous 1979). Finally, Naumann (1994) reported on *W. auropunctata* living in a greenhouse exhibit at the Vancouver Aquarium in British Columbia, Canada. Susan Johnson, an entomologist at the Biodôme in Montreal, Canada wrote to the Entomology Discussion List (13 Oct 1999): "We have an infestation of *Wasmannia auropunctata*, the little fire ant, in our indoor tropical forest. Some of the animal keepers react to the bites for several days. Does anyone know of a remedy for reducing this effect?"

Future spread of *Wasmannia auropunctata*

Outdoors populations of *Wasmannia auropunctata* reach as far south as 32°40'S in Argentina and as far north as 32°40'N in Bermuda (Fig. 3). Outside of the Neotropics, *Wasmannia auropunctata* currently occupies very little of this range (Fig. 3). There are vast areas of the world between these limits where *W. auropunctata* may be able to invade. In Africa, it is probable that this species has already invaded Equatorial Guinea, located between its known distributions in Cameroon and Gabon. There seems to be little in the way of geographic barriers to prevent its expansion over much of tropical Africa (except deserts), only reaching its latitudinal limit in southernmost South Africa. In the

Pacific, it seems likely that *W. auropunctata* may also soon be found in tropical areas that receive exports from infested areas. For example, lumber is exported from the Solomon Islands, and processed in other countries, such as Malaysia. Jourdan *et al.* (2002) reported that *W. auropunctata* may be present in Sumatra, Indonesia. In addition, this ant may soon invade the tropical lowlands of Asia and Australia. In Asia, much of China and almost all of India falls within the potential range of this ant. A spread northward from Florida to 32°40'N in the southeastern US would include southernmost South Carolina, the southern halves of Georgia, Alabama, and Mississippi, and almost all of Louisiana. Yet after more than 75 years in Florida, *W. auropunctata* has not spread into the northernmost part of the state or into any adjacent states, suggesting that other factors in addition to latitude limit its range. The future spread of *W. auropunctata* could be computer modeled using climate data, as has been done with the red imported fire ant, *Solenopsis invicta* (Korzukhin *et al.* 2001).

ECOLOGY AND IMPACT

Ecology of *Wasmannia auropunctata* in Neotropical populations

Numerous papers have examined the ecology of *W. auropunctata* in Brazil. De Medeiros *et al.* (1995) found that *W. auropunctata* was one of three dominant species in ant mosaics in cacao plantations of Brazil (along with *Ectatomma tuberculatum* and *Azteca chartifex spiriti*). De Souza *et al.* (1998) found that Homoptera were higher in areas of cacao plantations dominated by *W. auropunctata*. Vasconcelos *et al.* (2000) found *W. auropunctata* in both intact forest and logged areas of the Brazilian Amazon.

Bueno & Fowler (1994) found that *W. auropunctata* was "the most consistently found native species" of ants found in Brazilian hospitals and "in inner portions of the hospitals, only the exotic species, and *W. auropunctata*, are consistently present." *W. auropunctata* was the only native ant species not easily controlled with conventional insecticides. In southern Bahia, Delabie *et al.* (1995) found *W. auropunctata* in 12 of 100 houses inspected.

In Salta state, Argentina, Bestelmeyer & Wiens (1996) found *W. auropunctata* was one of the most common ants at their sites, occurring in all habitat types studied: highly degraded, moderately degraded, moderately restored, and highly restored, though it was "best represented in the highly restored site."

Levings (1983) found that *W. auropunctata* was one of the most common and widespread ants on Barro Colorado Island, a forest reserve area in Panama, occurring in 28% Berlese samples and at 78% baits.

In the same site, Schemske (1980) found that *W. auropunctata* was one of the two dominant visitors at *Costus* extrafloral nectaries. Longino & Hanson (1995) reported that *W. auropunctata* "is very common in disturbed lowland habitats (<500 m) in Costa Rica and workers can be very abundant in second growth, where they are dominant predators and scavengers, and are often common at extrafloral nectaries." They noted that "Their large polydomous colonies have no discrete colony center and nests may be found almost anywhere: under stones, in dead wood, in leaf litter, in stems or under bark." At La Selva Biological Station in Costa Rica, Roth *et al.* (1994) found *W. auropunctata* common, but not dominant, at baits in old growth forest (0.4-3.9% of baits), on abandoned cacao plantations (0.7-2.1% of baits), and productive cacao plantations (0.5-2.4% of baits), but did not find *W. auropunctata* on banana plantations. In the same Costa Rican old growth forest, McGlynn & Kirksey (2000) found *W. auropunctata* at 21 of 132 baits (15.9%), and dominated 10 of the baits (7.6%).

In a rainforest in Chiapas, Mexico, Goodnight & Goodnight (1956) found that most of the ants they collected using Berlese funnels were *W. auropunctata*. They added "according to a personal communication from W.M.L. Brown, Jr., it has been found to form an equally great preponderance in Berlese samples taken in several other localities of Tabasco and Veracruz. He believes it may be the commonest ant of this region." Brown (1957), himself, mentioned that he possessed "a small number of Chiapas ants collected by C. J. Goodnight and L. J. Stannard during the last five years, mostly from soil and leaf-litter," and that *W. auropunctata* occurred in "nearly every Berlese sample taken." Also in Chiapas, MacKay *et al.* (1991) found *W. auropunctata* both in a primary growth forest and in an adjacent area that had been slashed and burned one month earlier, though they wrote that *W. auropunctata* "apparently foraged into the burned area from nests in the forest." In inundated forest in Quintana Roo, Dejean *et al.* (1995) found that *W. auropunctata* was a common inhabitant of epiphytes, and was the most common ant inhabitant of the epiphytic bromeliad *Tillandsia balbisiana*. They also twice recorded an unknown *Wasmannia* in epiphytes. Among described *Wasmannia*, the only likely candidate for this unknown *Wasmannia* is *W. auropunctata rugosa*. At Los Tuxlas Biological Station in southern Vera Cruz state (18°35'N), Jeanne (1979) recorded *W. auropunctata* on the ground and on leaves in both a forest plot and in an open field plot. Also at Los Tuxlas, Horvitz & Schemske (1990) found *W. auropunctata* was one of the most common visitors at *Calathea* extrafloral nectaries. In northern Mexico, Atresino & Phillips (1992) found *W. auropunctata* in both disturbed and undisturbed sites at elevations between 350 and

900 m. Flores-Maldonado (2000) found *W. auropunctata* in two Mango orchards in the same area.

Pressick & Herbst (1973) wrote that, in the moist forest of St. John, Virgin Islands, "the most dominant species were *Wasmannia auropunctata* and *Solenopsis azteca* which usually co-occur in the same log or twig. Way & Bolton (1997) found that "in Trinidad, the dominant *W. auropunctata* was always found in association with tree or bush vegetation, for example in monoculture cocoa where it nested predominantly in the ground. Yet in coconut palm plantations it was nesting abundantly in the trees sometimes with no evidence of contact with, or dependence on, ground conditions." Way & Bolton (1997) found that *W. auropunctata* nesting in coconut palms excluded other ant species; the higher the number of *W. auropunctata* in a tree, the fewer the other ant species able to coexist. In Puerto Rico, Smith (1942) noted that probably no ant surpassed *W. auropunctata* as an attendant of honeydew-excreting insects. Michaud & Browning (1999) also found *W. auropunctata* tending aphids in Puerto Rico (though *S. invicta* was the dominant tender). Culver (1974) found that *W. auropunctata* had a "spotty distribution" in Puerto Rico but was common where it was found. In the Virgin Islands, Miskimen & Bond (1970) described *W. auropunctata* as "fairly common" and "an aggressive field ant that attends scale insects and aphids."

Impact of *Wasmannia auropunctata* in exotic populations

The impact of exotic populations of *W. auropunctata* varies. *Wasmannia auropunctata* is well documented as a major pest in the Galapagos and New Caledonia. There is also some evidence suggesting serious impact in the Solomon Islands, Vanuatu, and Gabon. It appears to be a much less serious pest in more temperate areas, such as Florida, Bahamas, and Bermuda. For most other invaded sites, very little is known of impact.

Galapagos

Wasmannia auropunctata is considered a very important pest in the Galapagos. Kastdalen (1982) reported that where the "fire ant" "spreads all native ants disappear, and it becomes far more abundant than were all the others put together." Silberglied (1972) concluded that *W. auropunctata*'s "impact upon the Galapagos terrestrial invertebrate fauna appears to be the most serious of any introduced animal." Subsequent studies in the Galapagos have confirmed this conclusion. For example, in parts of the Galapagos where it has invaded, *W. auropunctata* has been implicated in the disappearance of native arthropod fauna (Clark *et al.* 1982, Lubin 1983, 1984, Meier 1985,

1994, for more references see Ulloa-Chacón *et al.* 1991). Clark *et al.* (1982) found that *W. auropunctata* "either exterminates or reduces to very low density all sympatric species" of ants. Lubin (1984) found that areas with *W. auropunctata* present had not only lower diversity and density of other ants, but also lower densities of other insects, as well as scorpions and spiders. Honeydew-producing Homoptera, however, increased in areas of *W. auropunctata* infestation. *Wasmannia auropunctata* is often associated with another serious pest: the cottony cushion scale- *Icerya purchasi,* and has been observed transporting immature stages and tending colonies. Meier (1985) noted that *W. auropunctata* tends extrafloral nectaries on cacti in the Galapagos both day and night. There is also growing evidence of *W. auropunctata* having a negative impact on young tortoises and birds (Roque-Albelo & Causton, 1999). Roque-Albelo & Causton (1999) noted that populations of *W. auropunctata* were higher during years with higher rainfall.

West Central Africa

The arrival and impact of *W. auropunctata* in Gabon appears to have been noted by Albert Schweitzer in 1914, shortly after he arrived in Lambaréné, Gabon (150 km southeast of Libreville) to establish his hospital. Schweitzer (1931) wrote (in a chapter dated January to June, 1914): "One of the worst species of ants which we have here, the sangunagenta, is also an importation, having come over in cases of goods brought from South America." Further, Schweitzer (1951) added that this ant "is now domesticated." Although it is not certain to which ant species Schweitzer referred, *W. auropunctata* is the only likely candidate. At present, people in Gabon commonly refer to *W. auropunctata* as "tsangonawenda" (Wetterer *et al.* 1999), which is very close to "sangunagenta" It would be very interesting to determine whether Schweitzer wrote anything more on this ant, particularly whether he documented why this species was considered "one of the worst," and in what sense it was "domesticated."

Subsequently, Bruneau de Miré (1969) reported *W. auropunctata* from the coastal region of Cameroon near Kribi, where cacao (*Theobroma cacao*) growers purposely transported *W. auropunctata* colonies from plantation to plantation as a biological control agent of certain insect pests, particularly Miridae (Hemiptera) (Bruneau de Miré 1969). Bruneau de Miré (1969) found that in areas with *W. auropunctata,* populations of most insects, including beetles, flies, and other ants, were reduced. In contrast, populations of plant-feeding bugs (Homoptera) that the ants tends, such coccids and psyllids, increased.

Villagers in this region reported that they intentionally transport *W.*

auropunctata between plantations for pest control, though the crop being protected was maize (*Zea mays*), not cacao as in Cameroon. The success of *W. auropunctata* of controlling other insects was well appreciated.

Wetterer *et al.* (1999) found anecdotal evidence of an impact on vertebrates in Gabon. House cats (*Felis catus*) at Lopé often have *W. auropunctata* in their fur, and several cats developed corneal clouding and blindness. William Karesh, field veterinarian for Wildlife Conservation Society, found the cats' symptoms consistent with trauma, not communicable disease. The same symptoms developed in several cats in Franceville shortly after *W. auropunctata* were first noted. More disturbingly, elephants (*Loxodonta africana*) with cloudy corneas are common in Lopé and Petit Loango, as well as Wonga Wongué Reserve on the central coast of Gabon (100 km south of Libreville). The possible connection between *W. auropunctata* and eye maladies deserves further study.

Melanesia and Polynesia

In New Caledonia, the ant was initially confined to disturbed environments, but it has since spread to relatively undisturbed habitats, including sclerphyllous (dry, small-leafed) forests, rainforests, and ultramafic (magnesium- and iron-rich) shrublands (Guilbert *et al.* 1994, Jourdan 1997a, b). In two New Caledonian sclerphyllous forests invaded by *W. auropunctata*, this single ant species made up 15-65% of all arthropods collected using canopy fogging (Guilbert *et al.* 1994). The ants have a negative impact not only on endemic ants, but also native arachnids, beetles, and reptiles (Jourdan 1997a, Jourdan & Chazeau 1999, Jourdan *et al.* 2000, 2001, Delsinne *et al.* 2001). The spread of *W. auropunctata*, however, is positively correlated with population explosions of coccid Homoptera (Jourdan 1997a). Jourdan (1997a) called *W. auropunctata* "possibly the most dangerous pest ever introduced to this archipelago."

MacFalane (1985 in Way & Bolton 1997) considered *W. auropunctata* useful as a natural enemy of crop pests in Solomon Islands. In August 1997, while studying the distribution of ants in the Solomon Islands, Wetterer (unpublished) found that in areas of Guadalcanal Island with high densities of *W. auropunctata*, all epiphytic myrmecophytes (Hydnophytinae) were occupied solely by this species. Wetterer (unpublished) collected ants on Savo Island in and around a nesting area of the Melanesian Scrubfowl, *Megapodius eremita*, maintained by local egg harvesters near Mbalola and found high densities of *W. auropunctata* under virtually every piece of organic debris. A local egg harvester

reported that ants often attacked the eyes of emerging scrubfowl chicks. The locals, who all knew *W. auropunctata* from its painful stings, asserted that *W. auropunctata* arrived on Savo on young coconut trees imported to a plantation from the neighboring island of Guadalcanal. On Vulelua Island, the proprietor of a resort first noted *W. auropunctata* on log washed up on the shore from a nearby lumbering operation on Guadalcanal. Many locals on Guadalcanal reported that their dogs (*Canis domesticus*) were all gradually blinded by the ants' venom and rarely lived more than five years (Wetterer 1997).

In Vanuatu, Chazeau, & de Larbogne (1999) found that on Vanua Lava, around the towns of Sola and Mosina, *W. auropunctata* infested houses, gardens, and taro fields. "Dense lines of foragers can be observed along the walls in many houses, if not all, and everybody in Sola is familiar with the ant. *Wasmannia* coexists with *Anoplolepis gracilipes* but is dominant on baits and kills any *Anoplolepis* worker which persists in the foraged area." John Tennant (pers. comm. to JKW) wrote that on a visit to Vanuatu in August 2000 and during four months of field work in 2002, he noted a striking lack of butterflies around Sola. "Compared with, for example, Mota Lava, butterfly numbers are very low, despite the profusion of nectar sources ... at the time of my last visit, butterflies were abundant on Ureparapara, Mota Lava and Gaua, but almost absent even on bright sunny days along the waterfront at Sola. The presence of fire ants on Vanua Lava is one difference between these islands." Currently, officials in Vanuatu are very concerned about the prospect of this ant spreading throughout the archipelago, and are seeking international assistance in learning ant identification (L. Nimoho, pers. comm. to JKW, 2001). Exportation of agricultural products from infested islands in Vanuatu has been temporarily forbidden (Rapp 1999, Anonymous 2000).

Florida

In Florida, Spencer (1941) reported that "during 1935 and 1936 reports began to come in of annoyance to citrus fruit pickers by small stinging ants. These complaints have increased in number since then."

Ferster & Prusak (1994) found *W. auropunctata* occurred in many diverse habitats of the Florida Everglades: hardwood hammock, rocky pineland, coastal prairie, and slough areas, but not in wetland prairie or mangrove areas. On Long Pine Key in Everglades National Park, Clouse (1999) found *W. auropunctata* in 18% of litter samples from hammock areas, 2% of litter samples from Brazilian Pepper (*Schinus terebinthefolius*) stands, and in none of the samples from pinelands. In addition, Clouse (1999) found that *W. auropunctata* (along with *S.*

invicta) were the most noticeable ants in and around houses and gardens. In Palm Beach County, Wetterer & Wood (2002) found *W. auropunctata* on just 12 of 912 marked sea turtle nests (= 1%; compared with *Solenopsis invicta* on 328 nests or 36%); similarly, Wetterer and Moore (in prep.) found *W. auropunctata* on just 4 of 154 marked gopher tortoise burrows (= 3%; compared with *Solenopsis invicta* on 51 burrows or 33%).

Although Wilson (1964) did not record *W. auropunctata* in the Florida Keys, Wilson (in Fabres, & Brown 1978) found "a population on tiny Pigeon Key, in the Florida Keys, where *Wasmannia* occupied territory on one side of the islet, while the convergently similar ant *Tetramorium simillimum* (F. Smith) held the rest against it in what appeared at the time to be a standoff." In 1998, J. Owens resurveyed Pigeon Key and found no *W. auropunctata*, but did find *Solenopsis invicta* (T. McGlynn, personal communication).

Deyrup *et al.* (1988) recorded *W. auropunctata* from eight other islands in the Keys (Largo, Plantation, Upper Matecumbe, Bahia Honda, Big Pine, Sugarloaf, Middle Torch, and Key West). Williams (in Deyrup 1991) found that "trees of *Lignum vitae* on Lignum Vitae Key (a botanical reserve) have been severely attacked by a scale that is tended and defended by the exotic ant *Wasmannia auropunctata*." Fleming *et al.* (unpublished; in Horvitz 1997) found that *W. auropunctata* in the Florida Keys was much more common in more highly disturbed areas, accounting for 97.6% of all ants coming to tuna bait in Castellow Hammock State Park.

In general, it does not appear that *W. auropunctata* is a great pest in much of Florida, except on *Citrus* plantations (Spencer 1941) and areas where it has only recently invaded, such as the Florida Keys (see below). Deyrup *et al.* (1988) noted that, compared with its great impact in the Galapagos, *W. auropunctata* "has not had a similar effect during its long history in southern Florida." Deyrup *et al.* (2000) noted that *W. auropunctata* do not "seem to fulfill their potential" in Florida," and that "it practically blankets the ground in a few places, but it is generally a minor species in the fauna." Klotz *et al.* (1995) considered *W. auropunctata* only an occasional pest in Florida. They noted that the low incidence of reports of *W. auropunctata* as a pest was surprising given its common and widespread occurrence around structures in south Florida. "At two outbreak sites in south Florida there are unusual concentrations of plants that produce large amounts of extrafloral 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" (Deyrup *et al.* 2000). There is some indication that

densities of *W. auropunctata* have declined in some parts of Florida. Longtime Miami residents report "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 abundant enough to have this effect" (Deyrup *et al.* 2000). Competition with a wide diversity of native and exotic ants may help keep *W. auropunctata* in check on mainland Florida and possibly other continental areas.

Atlantic islands

Little is published concerning of the spread and impact of *W. auropunctata* in the Bahamas. Deyrup *et al.* (1998) commented that the "great abundance" of exotic ants, including *Wasmannia auropunctata*, in the Bahamas, was disturbing. Deyrup *et al.* (2000) wrote that they "have recently found sites on the island of New Providence Bahamas with huge concentrations of *W. auropunctata*."

Hilburn *et al.* (1990) noted that *W. auropunctata* was "now fairly common" in Bermuda. However, Wetterer *et al.* (in prep.) found that *W. auropunctata* actually appears to be quite rare in Bermuda.

Temperate greenhouses

Ayre (1977) considered *W. auropunctata* the most serious greenhouse pest ant due to its sting. Nonetheless, Ayre (1977) felt that, except for people who have a severe allergic reaction to the sting, *W. auropunctata* was "merely an annoyance." Finally, Naumann (1994) reported on *W. auropunctata* living in a greenhouse exhibit at the Vancouver Aquarium in British Columbia, Canada. He noted that the ants found tending scale insects and were most apparent on plants that hosted scales. "Although little fire ants do occasionally sting Aquarium staff, they are not a problem for visitors, and probably go unnoticed because of their small size."

Chemical control efforts

A wide variety of chemical poisons have been used to control *W. auropunctata*, including DDT, malathion and mirex (e.g., Fernald 1947, Osburn 1948, 1949, Nickerson 1983, Delabie 1989b). Williams & Whelan (1992) tested the attractiveness of different baits to *W. auropunctata*. A laboratory test, the order of preference for 13 food products from most to least was: peanut butter, honey, honey: water, pineapple juice, tuna oil, dark karo syrup, mint jelly, light karo syrup, soybean oil, orange juice, molasses, apple juice, and Coca Cola syrup. In a laboratory test of six oils, the preference order was soybean, tuna (vegetable oil from a tuna can), sunflower, peanut, safflower, and codliver. In a field test in the Galapagos, the preference order for food

and commercial ant control baits were: Amdro (hydramethylnon with soybean oil), peanut butter, lard, Raid Max (N-ethyl Perfluorooctanesulfonamide with peanut butter), Max Force (hydramethylnon with insects), honey-water, peanut butter oil, honey, and finally Logic (fenoxycarb with soybean oil), and water, both of which attracted no *W. auropunctata* workers.

Eradication of *W. auropunctata* using chemical means has been attempted in many areas, such as Hawaii (see above), with varying success. Perhaps the most extensive and best-documented eradication attempts are those in the Galapagos Islands.

Ulloa-Chacón, & Cherix (1994) summarized their efforts in using an insect juvenile hormone analog, methoprene, in controlling *W. auropunctata* on Santa Cruz Island in the Galapagos. They found that it had an important effect on brood development and queen fecundity. Treatment has no significant effect on worker population 6 weeks after treatment, and after three months with no further treatment, populations reductions only reached 50 to 75%.

Abedrabbo (1994) summarized efforts on Santa Fe Island in the Galapagos to control *W. auropunctata* using chemical poisons. In May 1975, *W. auropunctata* was first discovered on the island. Beginning in October 1975 and continuing into March 1976, an intensive attempt was made to eradicate the ants, by removing rocks and herbaceous vegetation from the affected area, burning the area and then applying a mixture of pyrethrin, resmethrin, and DDT. Later in 1976 and 1977, *W. auropunctata* was not detected in the area. In 1983, however, *W. auropunctata* was detected again. In 1985, a second intensive eradication attempt was conducted, cutting and burning the 2 hectares affected area, then applying the insecticides Aldrin, Ostation, and Basudin. In 1986, the ants were still present, and beginning in 1987 the chemical Amdro was used to control the ants. Between July 1988 and April 1990, *W. auropunctata* was found in only 2 of 7 surveys of the area, and was not found in any of the 6 surveys conducted between May 1990 and September 1991. In 2001, A.E Mieles still found no *W. auropunctata* on Santa Fe, and researchers now feel confident that *W. auropunctata* has been completely eliminated (C. Causton, pers. comm.).

On Marchena Island in the Galapagos, *W. auropunctata* was first detected in 1988 (Roque-Albelo *et al.* 2000). In 1993, control using Amdro was initiated. In 1993, the measured area of infestation was 5.2 ha, dropping in 1994 to 3.5 ha, and in 1996 to 1-1.5 ha. In 1998, however, 17 ha was found to be "occupied by dense mats of *W. auropunctata*" (Roque-Albelo *et al.* 2000), and in 2000, the infested area had increased to 22 ha (C. Causton, pers. comm.) In March 2001, a four-

year eradication program using Amdro was initiated on Marchena as a joint effort between the Galapagos National Park Service and Charles Darwin Research Station funded by the United Nations Foundation. Between March 2001 and April 2002, Amdro was applied four times to the infested area. In April 2002 researchers found only a small patch of 65 m^2 still infested with fire ants (C. Causton, pers. comm.). In 2003, a program will begin on the islets surrounding Santiago Island to eradicate *W. auropunctata* following the same methodology that was used on Marchena (C. Causton, pers. comm.).

RECOMMENDATIONS

In order to delay, reduce, or eliminate the ecological and economic impacts of *W. auropunctata*, we recommend that: 1) quarantine efforts should be expanded and targeted toward this ant, 2) efforts should be made to detect and eradicate incipient infestations on tropical and subtropical islands, and 3) a biological control program should be established to find, evaluate, and release promising natural enemies.

Improved Quarantine

Improved and targeted quarantine efforts are the first line of defense for areas not yet infested by *W. auropunctata*. Quarantine efforts can be especially effective for oceanic islands where vigilant efforts might delay infestations for decades or longer. Many island groups, however, lack all but the most rudimentary quarantine procedures for identifying and intercepting pest organisms. Nevertheless, much could be accomplished by educating inspectors, shippers, agricultural extension agents, and the general public so that they could recognize this ant, and understand the serious problems that will occur if it becomes established.

An effective education program could be developed relatively inexpensively. For shippers and the general public, this might consist of brochures, posters, and perhaps video information that could be distributed via television. For inspectors or extension agents, it might also include preserved voucher samples of the ants and an illustrated key to help identify the pest. The first step probably would be to survey the needs of threatened island groups. Island groups with known infestations should consider establishing compliance agreements with shippers of nursery stock, certain agricultural products, and other materials likely to carry the ants. An effective compliance agreement would likely involve periodic inspections and pest control efforts to limit the likelihood of accidental transport. The quarantine system used for the red imported fire ant, *Solenopsis invicta*, in the United States might

be a good model for such a program, although it would be useful to develop control and inspection methods specific to *W. auropunctata*.

Early Eradication

Incipient infestations of *W. auropunctata* should be eradicated whenever possible. Generally, an eradication attempt will require at least 4-5 treatments with an appropriate poison bait over a two year period plus extensive monitoring for several additional years. Fortunately, *W. auropunctata* is more susceptible to eradication efforts than most pest arthropods because they do not disperse by air and on the ground they usually only expand several dozen to several hundred meters per year unless they are accidentally transported in human commerce or floods. It is very important that eradication be attempted early. Based on experience in the Galapagos (Abedrabbo 1994), infestations of several hectares may be fairly easy to eradicate with persistence and several hundred to several thousand dollars. Eradication of infestations of a few dozen hectares is probably possible, but with at least ten times the effort and ten times the funds. Based on experience with *S. invicta* in the US (Lofgren 1986), infestations of several hundred hectares will be extremely difficult to eradicate even with massive inputs of labor and hundreds of thousands of dollars. Eradication of *W. auropunctata* in larger areas is likely impossible except for the most sophisticated and well-funded eradication programs with access to millions of dollars of resources. Early detection of new infestation is probably best accomplished by educating extension agents, farmers, nurserymen, and others to recognize the ants. Equally important in many cases is to have an eradication plan in effect and pre-approved by government officials so that precious months or even years are not lost before action is taken.

Biological control

Wasmannia auropunctata does not seem to have the destructive impact in its native range (Tennant 1994) as it does in many exotic infestations, suggesting that natural enemies may be keeping native populations in check. Classical biocontrol agents may be the only hope for controlling exotic populations of *W. auropunctata* in areas where it is firmly established. A classical biocontrol agent is one that expands naturally and becomes permanently established without the need for further releases. The advantage of using classical biocontrol agents is that their benefits are widespread, permanent, and without cost after the agent becomes established. The use of biological agents to control tramp ants is currently being studied for *Solenopsis invicta* (Porter 1998) and *Linepithema humile* (Orr & Seike 1998). For *S. invicta*, two parasitic phorid fly species have recently been released in the United

States (Porter *et al.* 1999) and several microsporidian pathogens are actively being evaluated (Williams *et al.* 1999; D. H. Oi, pers. comm.).

One parasite of *W. auropunctata* has been identified, the eucharitid wasp *Orasema minutissima* (Mann 1918). Johnson (1988) and Heraty (1994) recommended further evaluation of *Orasema* wasps as potential biocontrol agents of pest ants. Several pselaphid beetles (Mann 1921, Park 1942) and a staphilinid beetle (Silvestri 1946) have been identified as symbionts in *Wasmannia* colonies.

A preliminary search for possible biocontrol agents

In an attempt to discover additional natural enemies of *Wasmannia*, we recruited colleagues to inspect *W. auropunctata* colonies in Trinidad, Costa Rica, and Brazil (Porter & Wetterer, unpublished). From a total of 95 *W. auropunctata* colonies, a wide variety of organisms were extracted. Although no known parasites of *W. auropunctata*, such as eucharitid wasps, were identified, some associated organisms deserve additional attention, including gamasid mites and several unidentified fly larvae and microhymenoptera. Among the fungi, most were probably saprophytic, though *Verticillium* is possibly pathogenic. Determining the exact relationships of the organisms found in the nests will require much further study.

Recommendations for biological control program

The problem with biocontrol of *W. auropunctata* is that there are no proven agents and funding a comprehensive program would likely require several hundred thousand dollars per year for 5-10 years. This estimate is based on experience with finding, screening, and releasing phorid flies as biocontrol agents for *Solenopsis* fire ants. Smaller grants, however, could help in getting the process started.

A comprehensive biocontrol program would be very expensive because it would require most if not all of the following tasks: 1) Native populations of *W. auropunctata* should be carefully compared to exotic populations to determine if native populations are really less dense than exotic populations and what are the likely causes of any differences. 2) In order to find biotypes of natural enemies that are best adapted to attack exotic populations of *W. auropunctata*, researchers need to identify the original range of *W. auropunctata auropunctata*. Exotic populations of *W. auropunctata auropunctata* may be originally derived from only one population or from multiple populations. Ideally, DNA analysis of exotic and native populations should be used to identify specific source populations. 3) A thorough search for natural enemies would probably require several weeks to several months of efforts in each of several different areas. Furthermore, this search would likely

require scientists with expertise in parasites and others with expertise in pathogens. 4) Several months to a year or more are often necessary to obtain permits to export and then more permits are needed to import the presumptive control agent for study in quarantine. 5) Once candidate agents are found, researchers would need to find ways to rear enough agents. 6) Conduct host specificity tests to determine whether the organisms were environmentally safe for field release. 7) Then, if results justified it, more permits and reviews are needed for field release. 8) Finally, researchers would need to release prospective biocontrol agents and monitor their survival, expansion, and impacts on *W. auropunctata* populations. In short, a comprehensive biocontrol effort for *W. auropunctata* would probably require significant cooperative agreements between governments, conservation groups and scientific organizations concerned with the problem. Though difficult and expensive, classical biocontrol is the only likely long-term solution to the ecological ravages of exotic populations of *W. auropunctata* on tropical and subtropical islands.

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