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Changes in the native fauna of the Galápagos Islands following invasion by the little red fire ant, *Wasmannia auropunctata*

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CONTENTS

| | |
|----------------------------|-----|
| Introduction | 229 |
| Methods | 230 |
| Results | 232 |
| Discussion | 237 |
| Summary | 240 |
| Acknowledgements | 241 |
| References | 241 |

INTRODUCTION

Island biotas may undergo rapid and irreversible changes in species composition and diversity as a consequence of accidental colonizations by aggressive and rapidly-spreading species. Such accidental colonization incidents are by no means due solely to man's activities. Nonetheless, some of the most dramatic introductions known have been caused by man, either deliberately (rabbits to Australia; goats, pigs and cattle to Galápagos) or accidentally (rats to the Hawaiian Islands and Galápagos).

Ants are among the most ubiquitous and destructive of invading species. The invertebrate fauna of the lowland forests of the Hawaiian Islands have undergone a drastic reduction in species diversity, with concomitant extinction of many endemic species as a result of the introduction of an ant of African origin, *Pheidole megacephala* (Fabricius) (Myrmicinae) (Illingworth, 1917; Zimmerman, 1970). In Bermuda, there has been a succession of invasions of cosmopolitan 'tramp' ants (i.e., species which are readily transported by human commerce), most recently *P. megacephala* and the Argentine ant, *Iridomyrmex humilis* (Mayr) (Myrmicinae), with each new introduction changing the distributions and abundances of previous invaders and of native species (Haskins & Haskins, 1965; Crowell, 1968). Likewise, a number of widely distributed 'tramp' ants have made their way to the Galápagos Islands since the advent of permanent human settlements in the islands (and perhaps some even earlier, with the buccaneers and whalers). One of the most recent introductions

is that of *Wasmannia auropunctata* (Roger) (Myrmicinae), the 'little fire ant', which was brought to Santa Cruz Island (Indefatigable) sometime in the early part of this century (Silberglied, 1972; Clark *et al.*, 1982) and has since spread to other inhabited islands (see below). Thought to have originated on continental South America (Kusnezov, 1951), *Wasmannia* now occurs widely throughout the Neotropics and in parts of the Old World tropics and Pacific basin (see Clark *et al.*, 1982 and Fabr es & Brown, 1978 for reviews of the current distribution). *Wasmannia* is considered a pest species in many areas due to its painful sting (disproportionately so, considering that workers are a mere 1.2 mm long) and to its occurrence in high population densities, particularly in agricultural crops, to the exclusion of other ants (Spencer, 1941).

Clark *et al.* (1982) determined the distribution of *W. auropunctata* on Santa Cruz Island in 1975-76 and showed that in areas of high population densities, it has displaced many other species of ants. They suggested that these displacements may have come about primarily through interference competition (see also Meier, in press). I have expanded the scope of these previous studies by examining the distribution of *Wasmannia* on other islands in the archipelago, the distribution of other species of ants, and some of the faunal changes that can be attributed to the presence of *Wasmannia*.

METHODS

The Gal pagos Islands need no introduction. Descriptions of the topography, climate, and vegetation zones of these primarily desert equatorial islands may be found in Darwin (1860) and Wiggins & Porter (1971). Collections of ants were

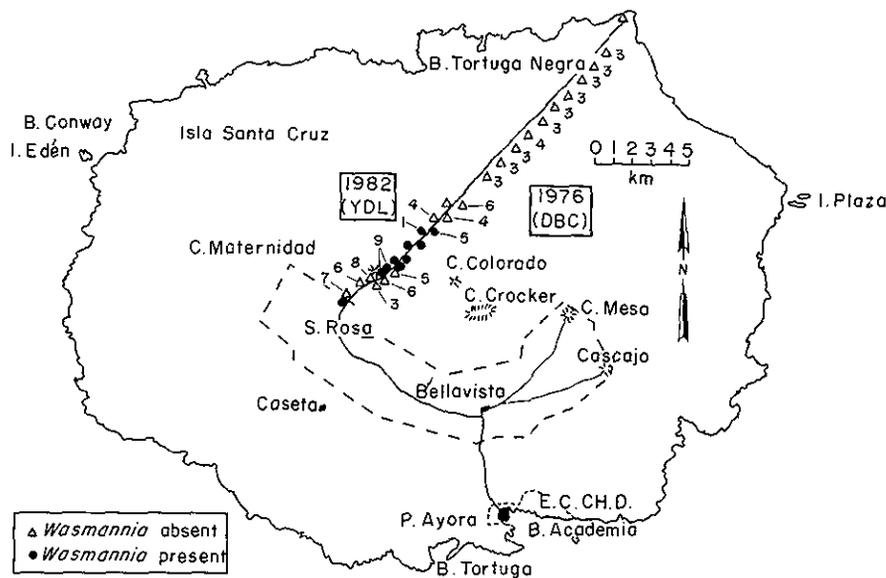


Figure 1. The numbers of species of ants found on two censuses of transects along the Puerto Ayora-Baltra Road, Santa Cruz Island, one in 1976 (Clark *et al.*, 1982) (symbols and numbers on the E side of the road), and another in 1982 (present study) (symbols and numbers on the W side of the road). Numbers beside the symbols are the numbers of other species of ants (excluding *Wasmannia*) observed at a site.

made in as many different habitats as possible, ranging from mangroves, beaches and lava on the coast, low-elevation arid zone vegetation (cacti and scrub forest), to transition and humid zone forests, agricultural areas and high elevation grasslands. Studies of the impact of *Wasmannia* on other invertebrates were carried out on two islands: Santa Cruz Island, in transition zone scrub forest and lower humid zone *Scalesia* forest (from 375–600 m elevation) along the Puerto Ayora-Baltra Road (Fig. 1), and San Salvador Island, in lower transition zone scrub forest (*Psidium-Bursera*) at Guayabillos (230 m) and denser *Psidium-Psychotria* forest at Trágica (330 m) (Fig. 2).

During 1981–82 ants were collected on the following islands (for a list of synonymies of island names, see Linsley & Usinger 1966): Pinta, Marchena, Isabela (Volcán Sierra Negra), San Salvador, San Cristóbal, Santa Cruz, Plaza Sur, Eden, Pinzón, Rábida and Chámpion. D. J. Anderson collected ants on Fernandina Island and M. Alvarez and M. Coulter on Floreana Island; these collections were kindly made available. Preliminary identifications have been made by R. R. Snelling and specimens are deposited at the Los Angeles County Museum of Natural History. A more detailed study of the Galápagos ant fauna is currently in progress.

During March–April 1982, I searched for and collected ants along nine transects at 0.5 to 1 km intervals along the Puerto Ayora–Baltra Road on the northern side of Santa Cruz Island, repeating part of a similar census conducted in 1976 (Clark *et al.*, 1982). Each transect was 100 m long by 2 m wide and divided into ten 10 m sections, and was oriented perpendicular to the north–south axis of the road. Soil samples taken from the transects sometimes yielded species of ants that were not found in the visual search.

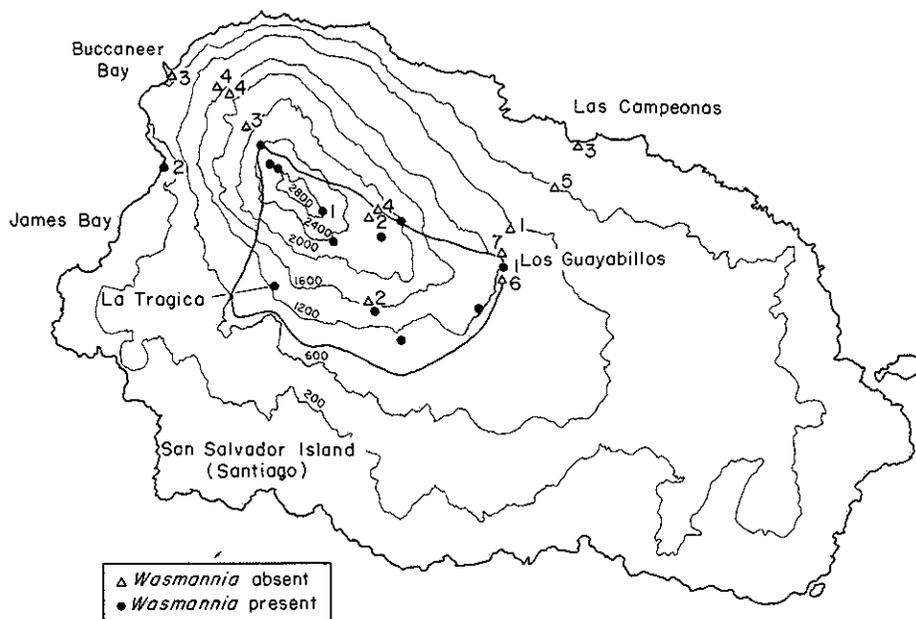


Figure 2. Map of San Salvador Island showing the approximate distribution of *W. auropunctata* (heavy line) and collection sites. Numbers beside the symbols indicate the number of other ant species collected at each site.

Five similar transects were searched along the north-western boundary of *Wasmannia* at Guayabillos on San Salvador Island, (see Fig. 2). In addition, 43 plots each 10 m × 2 m, were searched (under rocks, logs and debris) for scorpions, *Hadruroides maculata galapagoensis* Maury (Scorpionida, Iuridae), and for nests or groups (clusters of workers with brood) of *Wasmannia*. At the same site, a random sample of 50 guayabillo (*Psidium galapageium*) trees was examined for webs of two species of spiders, *Tidarren sisypthoides* (Walckenaer) and *Theridion calcynatum* Holmberg (Araneae, Theridiidae).

Two types of sticky traps were used to sample insects at two localities (Guayabillos and Trágica, see Fig. 2) on San Salvador Island: tree traps were sheets of plastic 19 cm × 10 cm tacked to tree trunks 1–2 m above ground; aerial traps were metal frames 25 cm × 25 cm, each strung with 25 threads (3 lb weight nylon fishing line), and hung from branches about 2 m above ground. The plastic sheets and nylon threads were coated with 'Tack-Trap' (Osticon Co.) and left out for 48 h. Insects were removed from the traps, immersed in kerosene to dissolve the adhesive and transferred to alcohol for counting and identification.

RESULTS

The distribution of Wasmannia and of other ant species

Twenty-nine ant taxa are currently known from the Galápagos Islands (Table 1, Fig. 3), four of which may be endemic species (Wheeler, 1919, 1924, 1933). Of the remaining, nearly half are common 'tramp' species, distributed by commerce throughout the tropics. While one can roughly date the entry of *Wasmannia* into the islands, it is more difficult to do so with the other less

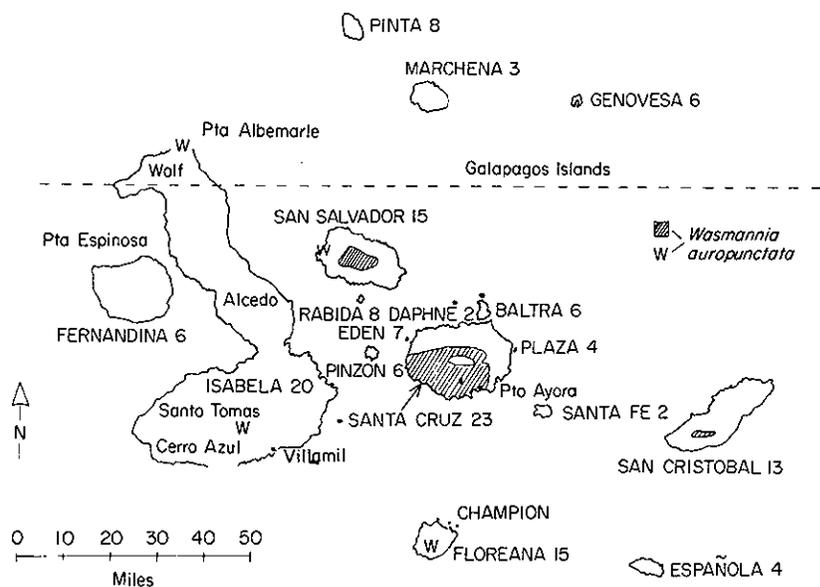


Figure 3. The distribution of *Wasmannia auropunctata* in the Galápagos Islands and the total number of species of ants known from each island based on the combined data from early and recent collections (Wheeler, 1919, 1924, 1933; Clark *et al.*, 1982; present study).

Table 1. A list of species of ants known from the Galápagos Islands, based on Wheeler (1919, 1924, 1933) and on recent collections (Clark *et al.*, 1982, present study). A, Endemic species¹; B, native species²; C, possible recent introductions³; D, species of unknown origin. Species which have spread recently (in the last 60 years) among the islands are marked (X). * = species that are affected or eliminated altogether by the presence of *Wasmannia*

| Subfamily | A | B | C | D |
|----------------|--|--|---|---|
| Ponerinae | <i>Hypoponera beebai</i> | <i>Hypoponera opaciceps</i> <i>Odontomachus bauri</i> * <i>Cylindromyrmex striatus</i> | | <i>Hypoponera</i> sp. <i>Leptogenys</i> sp.* |
| Myrmicinae | <i>Pheidole williamsi</i> * | <i>Solenopsis pacifica</i> ** <i>S. geminata</i> <i>Crematogaster chathamensis</i> * <i>Tetramorium simillimum</i> * <i>T. bicarinatum</i> (X)* <i>Monomorium floricola</i> (X)* <i>M. pharaonis</i> | <i>Wasmannia auropunctata</i> <i>Cardiocondyla nuda</i> * <i>C. emeryi</i> * <i>Strumigenys louisianae</i> | <i>Solenopsis</i> sp. A <i>Solenopsis</i> sp. B <i>Pheidole</i> sp. A* <i>Pheidole</i> sp. B* <i>Cyphomyrmex</i> sp.* |
| Formicinae | <i>Camponotus planus</i> * <i>C. macilentus</i> | <i>Paratrechina nesiotis</i> ** <i>P. longicornis</i> (X) | | |
| Dolichoderinae | | <i>Conomyrma albemarlensis</i> ** <i>Tapinoma melanocephalum</i> (X)* | | |
| Totals (%) | 4 (13.8) | 14 (48.3) | 4 (13.8) | 7 (24.1) |

¹Endemics are those species that have not been found outside the Galápagos, and may, therefore, be derived from now-extinct mainland populations.

²Native species include those found on early expeditions and may, therefore, have arrived on the islands by natural means of dispersal.

³Possible recent introductions include those species which were not collected on early expeditions.

*These species may be synonymous with mainland forms (*Solenopsis globularia*, *Crematogaster brevispinosa*, *Paratrechina fulva* and *Conomyrma pyramica*) of which they have been considered subspecies.

conspicuous species. Early expeditions of 1905, 1923, 1925, and 1932 encountered neither species of *Cardiocondyla* (Wheeler, 1919, 1924, 1933; Stitz, 1932), both currently conspicuous elements of transition and arid-zone faunas. Common, diurnal ants such as *Monomorium floricola* (Jerdon) and *Tapinoma melanocephalum* (Fabricius) have apparently increased their distribution in the islands since these early expeditions: the former was collected only on Floreana and Genovesa Islands and is now known from 11 islands; the latter was found on Santa Cruz, Española and Genovesa, and now occurs on six other islands as well.

Two species/area (S/A) curves can be drawn for Galápagos ants, one based on early collections up until 1932 ($\log S = 0.204 + 0.166 \log A$, $N = 15$ islands; $r = 0.232$, ns) and another for recent collections from 1981/82 ($\log S = 0.709 + 0.114 \log A$, $N = 12$ islands; $r = 0.722$, $P < 0.01$). There has been a 41% increase in the number of species collected since 1933.

Wasmannia auropunctata is currently found on the inhabited islands of Santa Cruz, Floreana, San Cristóbal and Volcán Sierra Negra on Isabela, as well as on San Salvador Island (previously inhabited) and at two isolated sites, one at Point Albermarle on the northern tip of Isabela and another at James Bay on San Salvador Island (Fig. 3).

The impact of Wasmannia on other species of ants

The boundaries of *Wasmannia* on Santa Cruz Island have not yet stabilized. When the 1976 census of ant species along the Puerto Ayora–Baltra Road (Clark *et al.* 1982) was repeated six years later, we found that although *Wasmannia* had not advanced northward (into the arid zone), it had spread south along the road into humid *Scalesia* forest at a rate of about 170 m per year (Fig. 1).

As was found to be the case in the 1976 census, *Wasmannia* overlapped with few or no other species of ants, except on those transects near the southern edge of its distribution, in areas that had been invaded since 1976 (Figs 1, 4). *Wasmannia* occurred on 36 of the 90 transect sections (9 transects, each containing ten 10 m sections) and on 81% of these sections it occurred alone, not overlapping with any other species of ant. Only three other species occurred on more than one-third of the sections: *Pheidole* sp. A on 37 sections, *Solenopsis* sp. A on 43 and *Paratrechina nesiotis* (Wheeler) on 52 sections, each co-occurring with 1–5 other species of ants (with a median of 2.0–2.8 species). *Paratrechina nesiotis* occurred alone on only one transect section, while the other two species were never found alone.

Only four other ant taxa were found in those areas where *Wasmannia* occurred in high densities: *Solenopsis* spp. A and B, *Hypoponera* sp. and *Strumigenys* sp., all hypogeic ants which were collected in soil samples. In six soil samples taken in the Giant Tortoise Reserve (Caseta, Fig. 1) on Santa Cruz, at 150 m elevation in lower transition zone vegetation, the average relative abundances of the different species were (*Wasmannia*/*Solenopsis*/*Hypoponera*) 1/0.008/0.0006. Average relative abundances in five soil samples from the agricultural and lower *Miconia*-guava zone (180–430 m elevation) were (*Wasmannia*/*Solenopsis*/*Hypoponera*/*Strumigenys*) 1/0.08/0.01/0.001.

The distribution of *Wasmannia* on San Salvador was patchier than on Santa Cruz. Areas of highest densities occurred in the SW portion of its distribution,

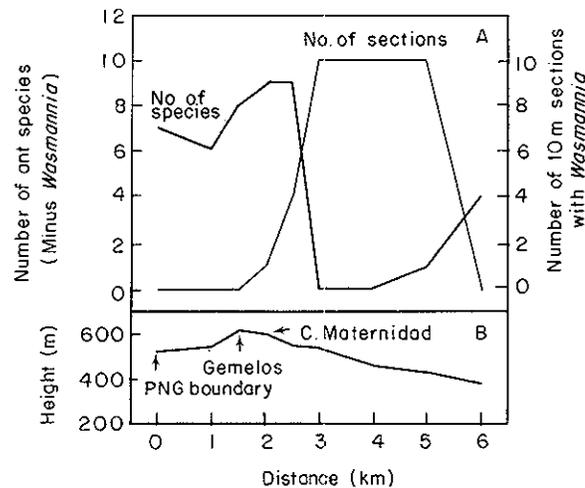


Figure 4. A, The numbers of species of ants (excluding *Wasmannia*) and the numbers of 10 m sections per transect on which *Wasmannia* was found on 9 transects along the Puerto Ayora–Baltra Road. B, Elevations of the transects and distance, in km, from the boundary of the Galápagos National Park on the northern side of Santa Cruz I. (see Fig. 1).

near its original site of introduction at La Trágica around 1967 (J. Villa, pers. comm.) and the ants appeared to be expanding their range to the NNE (Fig. 2). Within this area, there were pockets of primarily denser vegetation from which *Wasmannia* was absent and where other species of ants could be found.

In a census of ants along the NW boundary of *Wasmannia* at Guayabillos, *Wasmannia* occurred on six of the eight transects and on all ten sections of each of these six transects. On 80% of these sections (out of 60), *Wasmannia* occurred alone, not overlapping with any other species of ants. By comparison, of three other relatively common species, two species (*Cardiocondyla emeryi* Forel and *Solenopsis pacifica* Wheeler) never occurred alone, and another (*Conomyrma albemarlensis* (Wheeler)) occurred alone on only one section.

Wasmannia overlapped with as many as six other species of ants along the boundary at Guayabillos: with *Cardiocondyla emeryi* on 10 transect sections, *Tetramorium simillimum* (F. Smith) and *Conomyrma albemarlensis* on two sections each, and with *Solenopsis pacifica*, *Pheidole williamsi* Wheeler and *Paratrechina nesiotis* on one section each. These and other ant species had significantly wider distributions on the transects in the absence of *Wasmannia*, where they were found on 4.9 ± 3.2 (mean \pm standard deviation) of the sections (all species combined, $N = 11$ species-occurrences), than in the presence of *Wasmannia*, where they occurred on only 1.7 ± 0.7 sections ($N = 10$ species occurrences; $t = 3.124$, $P < 0.01$).

A different distribution pattern was found in the agricultural zone of Santo Tomás and the nearby slopes of Volcán Sierra Negra and Cerro Grande on Isabela Island (Fig. 5). *Wasmannia* was restricted to a small area encompassing three farms at about 180–250 m elevation, where it had been introduced between 1966 and 1967 in a shipment of clumps of elephant grass (*Pennisetum purpureum*). *Wasmannia* did not overlap in distribution with one of the 'true' fire ants, *Solenopsis geminata* (Fabricius), and in fact, there appeared to be a 'no-man's-land' of several meters between adjacent areas of these two species along their common boundary. Although widespread in the islands, *Solenopsis geminata* may have also been introduced to Volcán Sierra Negra by settlers, as it was not recorded from Isabela by earlier expeditions.

Unlike *Wasmannia*, *S. geminata* overlapped with many other species of ants (up to nine other species in Santo Tomás), including many of the same species that were displaced by *Wasmannia* (e.g. *Pheidole* spp., *Paratrechina nesiotis* and *Tetramorium bicarinatum* (Nylander)). It remains unclear if the boundary between the two species is stable or if one is spreading at the expense of the other.

The impact of Wasmannia on other arthropods

Wasmannia influences the distribution not only of other species of ants, but of numerous other arthropods as well. A native iurid scorpion, *Hadruroides maculata galapagoensis*, and two web-building threidiid spiders, *Theridion calcynatum* and *Tidarren sisyphoides*, were displaced by *Wasmannia* (Table 2). At Guayabillos, on San Salvador I., the population density of scorpions was significantly lower in *Wasmannia*-infested areas, with 0.06 ± 0.14 scorpions per m^2 (mean \pm standard deviation; $N = 25$ plots, each $20 m^2$), than in adjacent non-infested areas, with 0.41 ± 0.23 scorpions/ m^2 ($N = 18$; $t = 6.324$, $P < 0.001$). On a single 50 m long transect across the boundary of *Wasmannia* at the same site, there was a

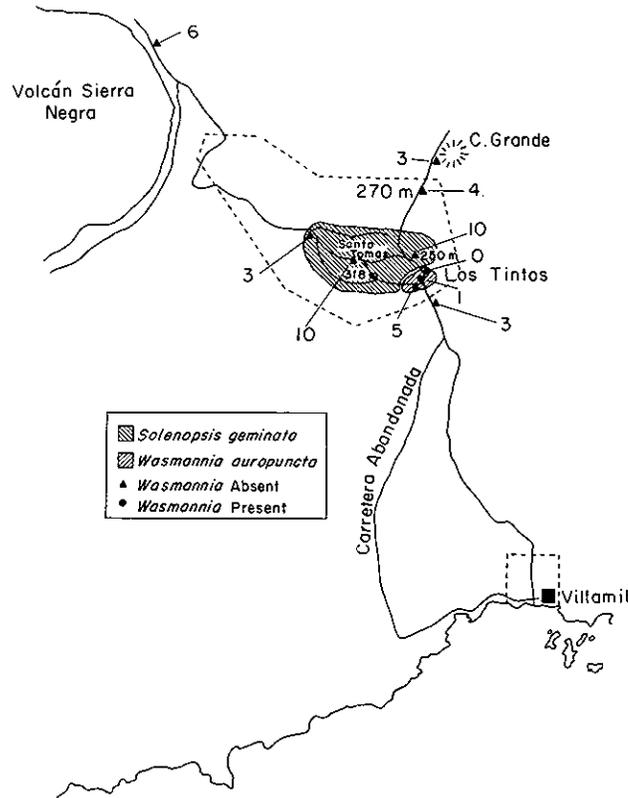


Figure 5. Map of the agricultural sector of Santo Tomás on Volcán Sierra Negra, Isabela Island, showing the distributions of *W. auropunctata* and of *S. geminata*. Numbers beside the symbols indicate the numbers of other species of ants collected at each site.

significant negative correlation between scorpion density and numbers of groups (i.e., queen-right nests and groups of workers with brood) of *Wasmannia* ($r = -0.84, P < 0.05$). Along this transect, the density of scorpions decreased from $0.55/\text{m}^2$ (no *Wasmannia* groups) to $0.05/\text{m}^2$ (with 0.85 groups of *Wasmannia* per m^2).

At the Guayabillos and Trágica sites on San Salvador Island, both the numbers of species of insects caught in sticky traps and their overall abundances were lower in *Wasmannia*-infested areas than in non-infested areas (Table 3). The increase in numbers of individuals captured in traps (especially in tree-traps) at Trágica was due entirely to the emergence of large numbers of flies (Diptera) from a nearby temporary pond. At Trágica, 63.6% (54.2–72.9%) of the total captures were small flies, in comparison with 19.2% (9.5–29.2%) at Guayabillos.

Certain species may actually benefit from the spread of *Wasmannia*, including nest inquilines such as the spider *Ischnothyreus* sp. (Oonopidae) and some plant-feeding species of Homoptera that produce honeydew and are tended by *Wasmannia* (Silberglied, 1972). In the transition zone of Santa Cruz Island, we found a significant positive correlation ($r = 0.48, P < 0.05$) between the numbers of *Wasmannia* and the numbers of coccids (Homoptera, Coccoidea) on 10 branches

Table 2. Displacement of a scorpion, *Hadruioides maculata galapagoensis*, and two species of spiders, *Theridion calcynatum* and *Tidarren sisypoides*, by *Wasmannia* at Guayabillos on San Salvador Island A, Numbers of 20 m² plots that contained scorpions in adjacent areas with and without *Wasmannia*. B, numbers of *P. galapageium* trees with spiders (both species combined) in adjacent areas with and without *Wasmannia*. (Fisher's exact probability test was used in both instances)

| A | | Scorpions | | | P |
|------------------|--|-----------|--------|-------|-------|
| | | Present | Absent | Total | |
| <i>Wasmannia</i> | | | | | |
| Present | | 7 | 18 | 25 | 0.004 |
| Absent | | 18 | 0 | 18 | |
| Total | | 25 | 18 | 43 | |
| B | | Spiders | | | P |
| | | Present | Absent | Total | |
| <i>Wasmannia</i> | | | | | |
| Present | | 0 | 25 | 25 | 0.009 |
| Absent | | 17 | 8 | 25 | |
| Total | | 17 | 33 | 50 | |

each of five trees each of *Croton scouleri*, *Scalesia pedunculata*, *Psychotria rufipes* and *Psidium galapageium*.

DISCUSSION

For island faunas in general, the 'faunal coefficient', or the slope of the logS/logA curve, falls within the range of $z = 0.3-0.4$ (Gorman, 1979). Possible reasons for the low faunal coefficient observed for Galápagos ants based on 1981-82 collections ($z = 0.114$) are: (1) the islands are still poorly sampled and more species of ants remain to be discovered, particularly on the larger islands; (2) the island fauna is not yet fully saturated and larger islands in particular have fewer species than expected, and (3) most of the species are 'tramps' which have been able to colonize most of the islands. Perhaps a similar case is that of the Hawaiian Islands, where $z = 0.16$ (calculated from Wilson & Taylor, 1967) for an entirely introduced ant fauna of 36 species. The high proportion, in recent collections, of 'tramp' species that are newly recorded for the Galápagos suggests that the islands have the potential to sustain a higher diversity of species of ants than is currently present.

Wasmannia has successfully invaded a number of different habitats in the Galápagos Islands, displacing other species of ants and at least some other arthropods as well (see also Clark *et al.*, 1982; Meier, in press). Clearly, *Wasmannia* has not had the same impact in all other parts of its range; in lowland monsoon rainforest in Panamá, it occurred together with numerous other species of terrestrial ants at densities of 0.05-0.13 nests per m² (Levings & Franks 1982). Likewise, on Cocos Island (Costa Rica), *Wasmannia* co-occurs

Table 3. Comparison of insects caught in sticky traps at two sites on James Island. Shown are total numbers of species and individuals of all taxa captured in aerial traps and in tree traps at each location. χ^2 tests with equal expected values were used to compare captures at sites in *Wasmannia*-infested and non-infested areas

| Location | Aerial traps | |
|-----------------|--------------|------------------|
| | No. species | No. individuals |
| Guayabillos: WA | 28 | 66 |
| Guayabillos: WP | 13 | 21 |
| | $p < 0.02$ | $p < 0.001$ |
| | $p < 0.01$ | |
| Trágica: WP | 9 | 32 |
| | $p < 0.001$ | |
| Location | Tree traps | |
| | No. species* | No. individuals* |
| Guayabillos: WA | 34 | 107 |
| Guayabillos: WP | 24 | 46 |
| | ns | $p < 0.001$ |
| | $p < 0.05$ | |
| Trágica: WP | 21 | 133 |
| | ns | |

*All ants excluded from totals of species and individuals. WA, *Wasmannia* absent; WP, *Wasmannia* present.

with 22 other species, although the spatial relationship between *Wasmannia* and these other species has not been described (Hogue & Miller, 1981). The rapid expansion of this ant in the Galápagos may be due, on the one hand, to a suite of behavioural and ecological characteristics which give *Wasmannia* certain advantages over other species of ants in dispersal, colonization and competition, and on the other hand, to the nature of the native Galápagos invertebrate fauna and particularly that of the relatively species-poor native ant fauna.

Dispersal

Wasmannia has efficient short-range terrestrial dispersal. The nests contain numerous queens (more than 100 queens were found in a nest of c. 24 000 workers; L. Endara, pers. comm.) and new nests are started by 'budding', i.e. one or more queens move out on foot with a complement of workers and establish a new nest (Hölldobler & Wilson 1977; pers. obs.). *Wasmannia* nests are shallow, and workers and queens will relocate readily. Long-range dispersal is effected by human commerce and perhaps by rafting; small nests may be transported in the soil around plant roots and in produce (pers. obs.). Apparently, however, *Wasmannia* alates do not fly large distances and thus have limited self-propelled, long-range dispersal. Unlike alates of many other species of ants, those of *Wasmannia* were never trapped in aerial sticky traps, nor were they attracted to lights.

Colonization

Habitat requirements (temperature and humidity, nest sites) and food requirements determine successful colonization. *Wasmannia* is capable of nesting

in a wide array of substrates and in habitats ranging from semi-arid to humid (Spencer, 1941; Kusnezov, 1951). In the Galápagos, *Wasmannia* occurs in most habitats, but is most abundant in the moist transition and lower humid zones (Clark *et al.*, 1982; pers. obs.) and in habitats disturbed by man (pastures, fruit crops, villages). Its distribution does, however, appear to be restricted both geographically and altitudinally by extreme conditions of either high temperature and low humidity or low temperature and high humidity. Numerous dessicated groups of *Wasmannia* were found under rocks in open, treeless areas on San Salvador, particularly as the dry season progressed. On Santa Cruz Island, *Wasmannia* invaded the cool, wet *Miconia* zone during the hot season, but disappeared during the cold, wet season (Clark *et al.*, 1982; pers. obs.).

Wasmannia workers feed primarily on honeydew and invertebrates (scavenged or killed) (Clark *et al.*, 1982). Although honeydew appeared to be the major food item by weight (*ibid.*), when offered a choice of four baits (tuna, marmalade, sugar-water and milk), recruitment was consistently highest to the oil-rich tuna (I. de la Vega, pers. comm.). How dependent is *Wasmannia* on honeydew and nectar? The correlation between numbers of coccids and *Wasmannia* ants on four native tree species was noted earlier; one other tree species, *Hippomane mancinella*, had few or no coccids, and virtually no ants. In the arid zone on Santa Cruz I., *Wasmannia* fed on honeydew produced by coccids on *Opuntia echios* (Meier, in press). At Guayabillos, on San Salvador Island, *Wasmannia* foraged during the hot season almost exclusively on two species of trees, *Psidium galapageium* and *Castela galapageia*, both of which have abundant extra-floral nectaries. The presence of coccids, however, was not noted. While it is possible that *Wasmannia* would be less successful in areas with poor nectar sources and few coccids, the range of foods actually taken by these ants clearly establishes *Wasmannia* as a generalist or opportunistic feeder.

Competition

Wasmannia might gain advantage over other species of ants by interference competition, predation, exploiting some resources more efficiently, or by all of these means (Clark *et al.*, 1982). There is evidence that *Wasmannia* displaces some species (e.g. *Pheidole williamsi*) by utilizing available nesting sites, while in other cases (e.g. *Conomyrma albemarlensis*, which has nests deep in the soil) competition may be for nectar and prey. While few encounters were observed at baits, *Wasmannia* recruited much faster and in larger numbers to food than did most other species and effectively prevented other ants from approaching baits (I. de la Vega, pers. comm.). *Wasmannia* workers were also observed to attack any foreign arthropod in the vicinity of the nest—other ant species (Clark *et al.*, 1982) as well as large scorpions and centipedes (*Scolopendra galapageia*).

Behavioral characteristics which may favour successful competition include mass recruitment to food, aggressiveness towards other ants (and possibly repelling other ants by means of chemical defenses, Howard *et al.*, 1982), and activity during both day and night (Clark *et al.*, 1982; I. de la Vega pers. comm.). The unicolonial social organization (Hölldobler & Wilson, 1977), with numerous small workers and interconnected nests, may ensure rapid transmission of information about sources of food throughout an extended

colony consisting of one or more main nests plus satellite groups of workers and brood.

Few species of ants overlap with *Wasmannia* in areas of high population density. Those that do so are all small ants which are either entirely hypogeic, nesting and foraging in the soil (*Solenopsis* spp. A and B), or partially hypogeic nesting inside rotting wood and foraging in the soil and leaf litter (*Strumigenys louisianae* (Roger) and *Hypoponera* spp.). In either case, there is little overlap in foraging and nesting habits between these species and *Wasmannia*.

Only one species of ant, *Solenopsis geminata*, may be a successful competitor of *Wasmannia*, at least in agricultural habitats. *Solenopsis geminata*, like *Wasmannia*, is a mass-recruiting species with large colonies and aggressive workers. Given these behaviours, and the fact that *S. geminata* soldiers and workers are considerably larger than the workers of *Wasmannia*, the latter may be unable to invade areas where *S. geminata* is already firmly established.

Some general predictions can be made concerning the outcome of interactions between *W. auropunctata* and certain elements of the native Galápagos fauna. The taxa most likely to be affected are transition and lower humid zone species (in areas of high *Wasmannia* densities); terrestrial or arboricolous species (broadly overlapping *Wasmannia* in habitat); species of small-medium body size and soft exoskeleton (susceptible to *Wasmannia* attacks); species lacking active defence mechanisms, such as chemical defences, or that rely on crypsis for defence (particularly those that rest under bark or stones); species lacking extended brood care; and insectivorous or nectar and honeydew feeders (overlapping in food requirements). Most spiders, for example, are insectivorous and have soft exoskeletons. Despite their large size, relatively hard exoskeletons and extended brood care, scorpions live under stones and debris and are rather sedentary. Furthermore, in view of the reduced diversity and abundance of insects in areas heavily infested by *Wasmannia*, it is likely that predatory arachnids such as scorpions and spiders will face a shortage of prey. The elimination of prey species by *Wasmannia* is the likely explanation for the observed absence from *Wasmannia*-infested areas on San Salvador island of *Tmarus stoltzmanni* Keyserling (Thomisidae), a crab spider that specializes on formicine and dolichoderine ants (*Camponotus* spp. and *Conomyrma albemarlensis*) (Lubin, 1983).

Species which should, to some extent, escape the deleterious influences of *Wasmannia* include strictly arid-zone adapted species on the one hand and high elevation, *Miconia* and fern-sedge zone species on the other (lower population densities of *Wasmannia*); hypogeic, aquatic, cavernicolous and wood or plant-boring species (non-overlapping micro-habitats); large species with hard exoskeletons or chemical defences (resistant to *Wasmannia* attacks); and primarily herbivorous species (non-overlapping food requirements).

SUMMARY

The little fire ant, *Wasmannia auropunctata*, occurs on five islands in the Galápagos archipelago. It is still in the process of expanding its range on at least two of these islands (Santa Cruz and San Salvador). At least 17 of the remaining 28 ant taxa currently known from the Galápagos are affected by the presence of *Wasmannia*. On Santa Cruz and San Salvador few other species of

ants co-occurred with *Wasmannia*, except at the edges of its distribution or in areas which it had only recently invaded. *Wasmannia* was also found to reduce population densities, or eliminate altogether, three species of arachnids (a scorpion and two theridiid spiders) as well as reducing the overall abundance and species diversity of flying and arboricolous insects at two sites on San Salvador. The mechanisms by which these species are displaced are currently being investigated.

Certain arthropods may escape the detrimental influences of *Wasmannia* through non-overlap of habitat and food requirements (as documented in the case of certain hypogeic ants), while others may actually benefit from the presence of *Wasmannia*, as appears to be the case for some coccids.

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