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EXOTIC ANTS OF THE FLORIDA KEYS
(Hymenoptera: Formicidae)

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ABSTRACT

A survey of ants (Hymenoptera: Formicidae) in the Florida Keys produced 84 species, including 29 exotics. This high proportion of exotics is probably due to several factors: habitat disturbance, a long history of commerce, and a climate suitable to a large number of tropical synanthropic species. Origins of Keys exotics: 17 Paleotropical, 12 Neotropical. Evidence outside Florida supports the impression that most tropical tramp ants originate in the Old World. Nine species of exotics are rare or localized in the Keys; there are several alternative reasons why exotics might be rare. Some native species may have been displaced. Berlese funnel samples of cryptobiotic species support the general impression that exotics are pervasive in the Keys. There are several reasons why it is important to monitor invasions by exotic ants. TABLE I: list of exotic ants of the Keys. Appendix A: Notes on species previously considered native. Appendix B: Notes on species whose nativeness is somewhat suspect.

INTRODUCTION

The Florida Keys give the impression of having been set up for the benefit of exotic ants. The Keys are a series of small islands, with a long history of commerce before any control of ant-infested materials. Most of the habitats are more or less disturbed, making them vulnerable to synanthropic ants. Before humans set up their pan-tropical transport service, there was little access for tropical ants, and the islands probably had empty or inefficiently occupied niches for tropical ants. The resulting massive and pervasive augmentation of the native fauna may be destructive, but it is also fascinating, like graffitti raised to an art form.

This paper describes the remarkable exotic ant fauna of the Keys, and attempts to describe the ecological significance of these ants.

METHODS

The methods used in the survey of exotics are not precise. Ants are highly aggregated in colonies, which are themselves often aggregated in certain sites or habitats. Ants are active, and more easily found under certain environmental conditions, which are not always identifiable and which vary from species to species. In such a situation sampling must be done on a huge scale if it is to show abundance or dispersion of a large number of species. Most of the survey work was qualitative, concentrating on finding as many species as possible at each site by inspection of ground and vegetation, breaking open twigs and plant stems, setting out various baits, checking lights on buildings and the surface of swimming pools, using Malaise traps and Berlese funnels. The work was done by several people (primarily by the author) between 1982 and 1989 during a general survey of the ants of the Florida Keys. An annotated list of species has already been published (Deyrup et al. 1988). Berlese funnel samples from tropical hardwood hammocks and coastal hammocks were collected in a way that allows some quantitative analysis. Separate samples of about 2 liters of leaf litter were taken from sites about 15 cm^2. The ant fauna and habitat information were listed for each sample. This procedure permits some correlation between habitat and fauna, and gives an impression of the prevalence of species within the habitat sampled. Species that occur together in such small sample areas can be said to have similar habitat requirements and some degree of mutual tolerance.

Voucher specimens of all species are in the collection at Archbold Biological Station.

Species	Origin*	Habitat**	Prevalence†	Apparency‡
Camponotus planatus	AN	TH	W	A
Cardiocondyla emeryi	OW	P	W	A
C. nuda	OW	P	W	A
C. venustula	OW	B	R	A
C. wroughtonii	OW	TH	R	C
Cyphomyrmex rimosus	NW	TH	R	A
Eurhopalothrix floridana	NW	TH	W	C
Hypoponera punctatissima	OW	P	W	C
Monomorium ebeninum	AN	P	R	A
M. floricola	OW	P, TH	W	A
M. pharoanis	OW	P	R	A
M. destructor	OW	P	R	A
Odontomachus ruginodis	AN	P, TH, CH	W	A
Paratrechina bourbonica	OW	P, B	W	A
P. guatemalensis	NW	TH	W	A
P. longicornis	OW	P, B	W	A
Pheidole flavens	NW	P	R	C
P. megacephala	OW	P	R	A
Pseudomyrmex mexicanus	NW	P, TH, CH	W	A
Quadristruma emmae	OW	P, TH, CH	W	C
Solenopsis invicta	NW	P	W	A
Strumigenys eggersi	NW	P, TH, CH	W	C
S. gundlachi	NW	TH	W	C
S. silvestri	NW	P, CH	R	C
Tapinoma melanocephalum	OW	P	W	A
Tetramorium bicarinatum	OW	P	R	A
T. caldarium	OW	P	W	A
T. simillimum	OW	P	W	A
Wasmannia auropunctata	NW	P, TH, CH	W	C

* Origin: OW=Old World tropics; NW=New World tropics; AN=Antillean

** Habitat: TH=tropical hardwood hammock; CH=coastal hammock; P=peridomestic, parking lots, etc.

† Prevalence: W=widely distributed in Keys; R=restricted distribution

‡ Apparency: A=easily seen in open; C=cryptic

RESULTS AND DISCUSSION

Number and Proportion of Exotic Species

Listing and counting the species would seem the last and easiest part of a survey, but there are problems even in so mundane a task. There are some difficulties with nomenclature, but these are trivial, as they do not affect the numbers of species, only the name appearing on the list. There are cases in the genera *Brachymyrmex, Camponotus, Conomyrma, Crematogaster,* and *Pheidole* in which species now classified as 1 may be 2 or more. Resolution of these problems might increase the list of species (including natives) from the Keys by as many as 6 species, but this would not greatly influence the general picture. A much more serious problem is that as many as 13 species of neotropical ants now considered native (having immigrated without human help) could actually be exotic.

The rules for determining whether a species is exotic are not always easily applied, in spite of efforts to set uniform standards (Whitehead and Wheeler 1990).

Of the 29 species that I consider exotic (Table I), 25 were previously considered exotic because of their regional taxonomic affinities,historical

records, or distributional anomalies. The evidence for the 4 additional species is compiled below (Appendix A), and shows some of the reasoning that can be used in difficult cases. The reasons for my uneasy feeling about the native status of several other species are presented in Appendix B. In the future it should be relatively easy to recognize newly arrived exotics because we finally have good baseline data on the ant fauna of south Florida. There is no reason to believe that the redistribution of tropical ants is even slowing down.

The known ant fauna of the Florida Keys includes 84 species, of which 29 (34%) are exotic. This seems an extraordinary high degree of exoticism, and one might be tempted to associate it with the vulnerability of islands to invasions by exotics. An extreme case of this is the Hawaiian Archipelago, with 42 species of ants, all exotics (Huddleston and Fluker 1968). When mainland Florida is considered, however, there appears to be a more general trend toward a higher proportion of exotics in the south. In Alachua county, a northern county that has been well-surveyed for ants, there are 17 exotics out of a fauna of 110 species (15%) (Johnson 1987). In Highlands County, a south-central county that I have studied intensely, there are 25 exotics out of 125 species (20%). In mainland Dade County, a moderately well-studied county adjacent to the Florida Keys, 32 out of 88 species are exotic (35%), a higher percentage than in the Keys themselves. The whole south end of Florida is a rather recently-constituted tropical area, and perhaps incompletely exploited by ants that arrived from the north. More important, this area is suitable for a large number of tropical synanthropic ants. There are many more tropical than temperate synanthropic species, so temperate areas tend to accumulate fewer exotics. These ideas could be tested by examining the ant fauna of disturbed sites in large mainland tropical areas.

Biogeography of Exotic Ants of the Florida Keys

There are two aspects to the biogeography of the exotic ants in the Keys. The first is the general distribution of the species, their geographic origins, the means and reasons for their expansion. The second aspect deals with the patterns of distribution in the Keys and the reasons for these patterns, a topic that leads directly into a consideration of the ecology of the species. The general distribution and the Keys distribution do not need to be closely related: some pantropical, ecologically aggressive species are rare or highly localized in the Keys, while other species that have no global reputation to speak of are abundant and widely distributed.

Table 1 shows origins of the 29 listed exotics. The only origins designated are Paleotropical, Neotropical, and Antillean; in a number of cases more specific origins are debatable, as ants were stowing away centuries before the inception of myrmecology. There are 16 Paleotropical species, and 13 Neotropical, including 3 Antillean. This could be interpreted in more than one way, for example, one could say that the nearer the tropical region, the fewer species it contributes to the Keys fauna. This is not a useful view, as it ignores the fact that the nearer the area of origin to the target area, the more difficult it is to establish whether species from that area arrived independently, or were assisted during the 400 years before there were any baseline faunal studies. It would not be surprising, however, if the Old World Tropics has contributed almost as many exotics to Florida as the New World. In the Hawaiian study (Huddleston and Fluker 1968) only 2 of the 42 species originated in the New World. *Solenopsis geminata* seems to be the only widespread past species from the Neotropics, though *Wasmannia auropunctata* could easily be in the early phases of a pantropical explosion. I can find no analyses of synanthropic or exotic ants in mainland tropical areas. Until there have been further studies, especially including cryptobiotic species, we will have only an impressionistic view of the pantropical exotics, but the impression of almost total domination by Old World species makes sense because of the relatively large extent and heterogeneity of Old World Tropics (a greater diversity to draw from) and the long history of large-scale human disturbance in the Old World, resulting in adaptation by more species of ants to man-modified environments.

It is easy to assume that exotic species once established, spread relatively rapidly, and there are certainly many examples of this, in the Keys as elsewhere. Even without these examples, one

might reason that a species is unlikely to become established in a new region unless it has some clear ecological advantage. The chancy process of colonization by the first small population under new ecological conditions would seem to be by far the most difficult test for a species, and all further challenges would be easily overcome. It is surprising therefore, that 9 or the 29 exotics appear to be rare or highly local. There are conditions that might cause a pattern of rare exotics, and some species might fit these situations.

1. Exotic species might be caught by a survey in the early stages of expansion, with only a few established beachheads. *Pheidole megacephala* was found in a few places on Key West and in a huge extended colony at one site on Key Largo. It is an aggressive species that dominates the lowland ant fauna of some tropical islands (Hölldobler and Wilson 1990). This species was not found by Wilson in 1964. *Monomorium ebeninum*, a Bahamian species, was found as a cluster of thriving colonies (or an extended colony) in a Key largo parking lot. *Cyphomyrmex rimosus* (see Appendix A) seems to be moving south in Florida, with only a few records from southernmost Florida, and only one from the Keys.
2. Some ants may be at the other end of an invasion cycle, and are now dwindling in the face of some kind of ecological resistance. *Tetramorium bicarinatum*, which was common in the Keys 20 years ago (D.S. Simberloff, *pers. comm.*) may be an example of this. This same species shows a curious "relict" distribution elsewhere in Florida.
3. Exotic species might also be rare because there are only small patches of suitable habitat. The infamous *Solenopsis invicta* may be, unlikely though it might seem, an example of this. This species does not seem to thrive in maritime situations in Florida, or in coarse, excessively drained soils, habitats that are excellent for *Solenopsis geminata* (discussed in Appendix B)
4. Some exotics with poor competitive ability might persist for a long time at low levels if there is a constant supply of unoccupied habitat. Dacetine ants that exploit disturbed habitats might offer examples of populations slowly filling an ever-expanding universe of disturbed and degraded habitats in Florida. There are 4 exotic dacetines in the Keys, one of which, *Strumigenys silvestri*, appears to be rare and localized.
5. Some apparently rare species might be more abundant than they seem, but difficult to find without some sort of specialized sampling method; this hypothesis is hard to refute. *Cardiocondyla wroughtonii* could be an example of this.
6. It may come as a relief to learn that the author does not have a hypothesis to fit every rare or localized ant: *Monomorium destructor* is spectacularly common on Key West, where it has been present for at least 20 years (Wilson 1964), but is rare or absent elsewhere on the Keys and on the mainland.

Ecology of Exotic Ants in the Keys

Exotic ants occur in every habitat type on the Keys. On beaches and in mangrove area *Paratrechina bourbonica* and *P. longicornis* are especially common exotics. Almost universal in tropical hammocks are *Paratrechina guatemalensis, Camponotus planatus, Strumigenys gundlachi,* and *Wasmannia auropunctata. Pheidole flavens, W. auropunctata,* and *P. longicornis* are in disturbed areas everywhere. Elliott Key is something of an exception; although there were once extensive cultivated areas on the island, it now has no settlements other than the National Park Ranger Station, and it apparently lacks two of the commonest exotics (*Wasmannia auropunctata* and *Paratrechina guatemalensis*) found on the settled keys linked by U.S. highway 1.

Litter samples extracted by Berlese funnel provide some quantitative information on litter-inhabiting species. There are some interesting trends, and the 155 samples would seem to provide enough data for statistical analysis. As in many similar situations, however, such analysis would be a form of sophistry, as there were a number of uncontrolled variables, such as small differences in microhabitat, season of collection,

effects of current and recent weather (e.g.: moist weather brings up and disperses some cryptic subterranean species), and time elapsed between collection of sample and extraction of ants. Some results are summarized in the following table:

NUMBER OF SAMPLES

	Total	With Ants	No Ants	With Exotics	No Exotics
Elliott Key	42	32	10	12	20
Other Keys	113	95	18	52	43
Total	155	127	28	64	63

About half the samples (less on Elliott Key, more on other keys) have exotic ants. The exotics were not particularly concentrated in one or a few sites. No single species dominated the samples: 14 species were collected, and even the most common (*Quadristruma emmae*) appeared in only 20 samples. It is particularly interesting that *Wasmannia auropunctata*, which has invaded the Galápagos Islands, threatening many native invertebrates and even some vertebrates (Lubin 1984), is a relatively minor component of the Keys fauna, found in only 8 samples.

that exotic ants survive best in microsites that are generally favorable for litter-inhabiting ants, while the more unfavorable sites are occupied by natives adapted to the local unfavorable conditions.

It is hardly necessary to state that as exotic ants proliferated in the Keys there were no concerned myrmecologists documenting disarray in the native ant fauna. Species that are rare now may have been displaced by exotics, or they might have always been small peripheral populations at a climatically suboptimal extreme of their ranges. Mainland species absent from the Keys may have been eradicated, or they may never have occurred there. The best that can be done at this point is to list species that are very rare in the Keys, along with abundant exotics, usually congeners, that seem to have similar habitat preferences. The

Rare Native	Common Exotic	Habitat
Camponotus decipiens	*C. planatus*	Dead branches on large live trees
Odontomachus brunneus	*O. ruginodis*	Inland and coastal hardwood hammock
Paratrechina concinna	*P. bourbonica*	Debris in swamps and marshes
Paratrechina wojciki	*P. guatemalensis*	Hardwood hammocks
Smithistruma dietrichi	*Strumigenys eggersi*	
Strumigenys louisianae	*S. gundlachi*	Hardwood hammocks
	Quadristruma emmae	

There is no evidence that exotics occur in dense populations that exclude natives, or other exotics, from the site. In fact, of 45 samples that each contained only one ant species, only 8 had an exotic ant, while 37 had a native ant. The natives in these single-species samples varied widely, and there is no indication that any one native species is excluding exotics. The tendency for exotics to occur in more species-rich samples suggests to me that exotic species are all of more northern origin, with current distributions that extend at least to the north border of Florida.

General Significance of Exotic Ants

Exotic ants are of particular significance for several reasons:

1. Ants are the dominant arthropods of tropical

ecosystems, and anything that changes the ant fauna is likely to affect many components of the ecosystem. It is important for conservationists to monitor ant invasions, as exotic ants, including inconspicuous species, could have major effects (often indirect) on native flora and fauna. As an example of this, the remaining trees of lignum vitae on Lignum Vitae Key (a botanical preserve) have been severely attacked by a scale that is tended and defended by the exotic ant *Wasmannica auropunctata* (M. Williams, *Pers. comm.*).

2.Any ecologist who is working on relationships between ants and other organisms needs to know which ants are exotic. There is nothing more embarrassing than postulating complicated coevolved relationships between species, only to discover one of the partners is just off the boat.

3. The organisms most likely to be directly affected by exotic ants are native species of ants. There appear to be no endemic ants restricted to the Florida Keys, and any replacement of native species does not affect global diversity. The ant fauna of older and more isolated groups of islands usually includes endemic species that are likely to be threatened by the combination of habitat destruction and introduction of alien ants.

4. Monitoring ant invasions is also useful as it may forewarn us of pest problems. We seem almost powerless to halt the invasion of exotic ants once they have made a beachhead, but at the very least we can take advantage of these invasions as inadvertent ecological experiments of the greatest practical and theoretical interest.

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LITERATURE CITED

Baroni, Urbani, C. 1978. Materiali per una revisione dei *Leptothorax* neotropicali appartenti al sottogenere *Macromischa* Roger, comb. (Hymenoptera: Formicidae). Entomol. Basilensia 3:395-618.

Brown, W.L., and W.W. Kempf. 1960. A world revision of the ant tribe Basicerotini (Hymenoptera; Formicidae). Studia Entomol. 3:161-249.

Deyrup, M., J. Trager, and N. Carlin. 1985. The genus *Odontomachus* in the southeastern United States (Hymenoptera: Formicidae). Entomol. News 96:188-195.

Deyrup, M., N. Carlin, J. Trager, G. Umphrey. 1988. A review of the ants of the Florida Keys. Fla. Entomol. 71:163-176.

Hölldobler, B., and E.O. Wilson. 1990. The ants. Harvard University Press, Cambridge. Pp. 732.

Huddleston, E.W., and S.S. Fluker. 1968. Distribution of ant species in Hawaii. Proc. Hawaiian Entomol. Soc. 20:45-69.

Johnson, C. 1986. A north Florida ant fauna. Insecta Mundi 1:243-246.

Lubin, Y.D. 1984. Changes in the native fauna of the Galápagos Islands following invasion by the little red fire ant, *Wasmannia auropunctata*. Biol. J. Linn. Soc. 21:229-242.

Wheeler, W.M. 1932. A list of the ants of Florida with descriptions of new forms. J. N.Y. Entomol. Soc. 40:1-17.

Whitehead, D.R., and A.G. Wheeler, Jr. 1990. What is an immigrant arthropod? Ann. Entomol. Soc. Amer. 83:9-14.

Wilson, E.O. 1964. The ants of the Florida Keys. Breviora 210:1-14.

APPENDIX A: SPECIES NOT PREVIOUSLY CONSIDERED AS EXOTIC

Camponotus planatus. This species has always been considered native in the Keys, and was widespread at the time of the first list of Florida ants (Wheeler 1932). It is currently the dominant ant of most hardwood hammocks in the Keys. Nests are usually in dead wood, and it is easy to imagine *C. planatus* rafting to the Keys. It has always been difficult, however, to explain the absence of *C. planatus* from tropical hammocks on the mainland without invoking some strict ecological requirements existing only in the Keys. During the last few years I have found isolated well-established populations in Sarasota, Tampa, and east Miami, and there are early records (Wheeler 1932) from Miami, Fort Myers, and Coconut Grove. This suggests that the species is not confined to the Keys by highly specific habitat or climatic requirements, and shows that the species is moved about by humans. If it had been established in the Keys for thousands of years, it would have almost certainly become widely distributed through suitable habitats in south Florida. There are no other Antillean ants that are common in the Keys and absent from similar habitats on the mainland.

Cyphomyrmex rimosus. There are two species of the genus *Cyphomyrmex* in the Keys. *C. minutus* is a long-time resident of south Florida, one of a number of Antillean species whose native status is impossible to prove or disprove. A second species, *C. rimosus*, has become abundant in north Florida (where there are no early records of *Cyphomyrmex*) and is now sympatric with *C. minutus* in south Florida, including the Keys.

Eurhopalothrix floridana. This species was described from Florida (Brown and Kempf 1960) and has been considered native. David Smith (USNM) recently discovered a damaged specimen, collected in Key West in 1887, in the Pergande collection. In spite of this history, *E. floridana* is almost certainly exotic in Florida. *E. floridana* occurs in Mexico (W.L. Brown 1985, *pers. comm.*) and other members of the genus are neotropical. It is a highly cryptic species that could easily have been carried about in nursery stock, but is very unlikely to have reached Florida by rafting. Although there are a number of native organisms in Florida that have disjunct populations in Mexico or the southwestern U.S., these species are almost always associated with xeric habitats, not the tropical hammocks and mesic woodlands where *E. floridana* occurs. There is fairly good evidence that the species has been expanding its range as it is now easily obtained in areas of north Florida where Van Pelt did extensive sampling with Berlese funnel in the 1950s.

Odontomachus ruginodis. The distribution of this species is uncertain outside of Florida and the West Indies (Deyrup et al. 1985). It has been present in the Keys at least since 1964 (Wilson 1964), and is common, especially in disturbed sites, on the southern mainland. Large, disjunct populations in Winter Haven and Sarasota, combined with a predilection for disturbed sites, give a convincing impression of an exotic species that is rapidly expanding its range.

Appendix B. Dubious Natives.

Brachymyrex obscurior. At least two species currently go by this name in Florida. Their dedication to disturbed sites and their ease of transport — one can readily obtain colonies in potted plants and pieces of sod — give this species the appearance of an exotic. When the taxonomy of the species complex is better understood it may be possible to determine the origin of the Keys form.

Leptothorax torrei. This species was only recently discovered in the Keys (Deyrup et al. 1988), and is otherwise known only from Cuba (Baroni Urbani 1978). It is a soil-inhabiting ant that does not seem well-adapted for rafting. Queens could have blown over from Cuba, but it seems more likely that the species was distributed in nursery stock in the early days of settlement in the Keys.

Pachycondyla stigma. This large ponerine has a pantropical distribution, and its original home is unknown. It does not give the impression of a species that has remarkable dispersal ability, but it does often occur under bark of dead

trees, which would help it spread by either rafting or commerce. It must have had assistance to achieve at least some of its enormous range through the tropics.

Platythyrea punctata. This is a neo-tropical species with an isolated population in south Florida. It does not appear to be a species likely to have independent long-distance dispersal, but colonies may occur in dead wood and could have reached Florida by rafting.

Pseudomyrmex cubaensis, P. elongatus. These species occur in dead branches and twigs, and could have reached south Florida by rafting. Since nests are often in small-diameter twigs or weed stems, the species could also have been transported readily in the days of massive and unregulated trade between the Keys and nearby neotropical areas.

Solenopsis geminata. This is known in the southeastern U.S. as the native fire ant, and it probably is a native species that migrated from the west long ago. Coastal, upland, and lowland populations of *S. geminata* look some what different, and the coastal form in particular may have been introduced during the documented invasions of *S. geminata* into the West Indies in colonial times.

Solenopsis corticalis. This species inhabits small twigs and grass culms, and seems a good candidate for dispersal by rafting. On the other hand it could also have easily arrived through commerce, even in fodder brought in during the early days of the cattle trade. It is otherwise known from Cuba, and not recorded from the U.S. until recently (Deyrup et al. 1988).