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BIOGEOGRAPHICAL SURVEY OF THE ANTS OF THE ISLAND OF SAN SALVADOR, BAHAMAS

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ABSTRACT

Forty-one species of ants are now known from San Salvador. No species is restricted to the island, all are widely distributed in the West Indies. The lack of endemism, combined with evidence provided by other groups of organisms, suggests that the native ant fauna arrived relatively recently. The ant fauna is depauperate compared with that of sites in Florida, and lacks 26 species reported from the western Bahamas. Sixty-seven species of ants are now known from the Bahamian Archipelago. Fourteen species of exotic ants occur on San Salvador; they are concentrated in disturbed areas and most seem rare or absent in native plant communities. More species are expected to invade the island in the future. Comparing the San Salvador fauna of ants, wasps, and butterflies with the fauna of sites in Florida shows that different insect groups differ in their response to the island effects that have determined the diversity of the insect fauna of San Salvador.

INTRODUCTION

The island of San Salvador is of special interest faunistically because of its isolation. It is presently separated by a deep channel from other islands, a channel that persisted during the Pleistocene when many other islands were linked by the large emergent Bahamas banks. It is distant (about 350 km) from the islands of the Greater Antilles, which seem to have been the sources of most of the biota of the eastern Bahamas. Similarly, the distance between San Salvador and major population centers, combined with a lack of easily exploited natural resources on the island, have kept both trade and habitat modification to a relatively low level. Even the areas that were once in extensive crops (sugar cane) have largely succeeded to native vegetation. San Salvador is therefore an excellent place to look for a primeval Bahamian ant fauna.

San Salvador is also a good survey site for pragmatic reasons. The Bahamian Field Station attracts ecologists working on a great variety of projects, so that a faunal survey is likely to have immediate applications to other studies. Field research on San Salvador is also greatly facilitated by the amenities provided by the Bahamian Field Station.

METHODS

An initial survey for ants does not involve quantitative sampling, but requires visits to a complete array of habitats, best defined as plant communities. The plant communities chosen for study in this project are these described by Smith (1993). The general ant hunting methods, which are based on ten years of ant survey in Florida, are: visual inspection of the ground and vegetation; breaking open dead wood, dead twigs, and hollow plant stems; turning over objects on the ground; searching in arboreal bromeliads; extracting ants from leaf litter, using a modified Berlese funnel. A Towne's trap was used to capture winged ants in coppice forest. It is probably more important to be persistent than methodical in such a study: ants were also collected around lights during breaks in the symposium programs, adhering to the author's body when ant flights coincided with pre-sunrise jogging, and while waiting for airplanes (the author was waiting, and perhaps the ants as well - see discussion of exotic ants below) at the airport. The survey was conducted 7-11 June 1991 and 11-19 June 1993. Most species of ants were identified by the author. Dr. Philip Ward (University of

California-Davis) identified the *Pseudomyrmex* species. Taxonomic and nomenclatural problems (there are several) are not discussed here, but will be covered in a forthcoming manual of the ants of San Salvador. Voucher specimens are in the collections at the Bahamian Field Station, San Salvador; Archbold Biological Station, Florida; Harvard Museum of Comparative Zoology, Massachusetts.

RESULTS AND DISCUSSION

Numbers of Ant Species on San Salvador

Forty-one species were found during this study (Table 1). Several kinds of evidence suggest that the ant inventory is approaching completion.

1. The number of newly-encountered species dropped sharply during the study: 31 species were found during the first four days, no new species were found in the last two days of intensive work.
2. Only two species were collected only once; all other species were collected several times or many times.
3. The habitats of some "expected" ants were known from studies elsewhere. *Crematogaster sanguinea*, for example, occurs regularly in bromeliads on Andros Island, *Pseudomyrmex mexicanus* is easily found in large dead twigs in Florida, *Wasmannia auropunctata* is common in moist disturbed areas in Florida and elsewhere. This kind of information allowed directed search for particular species.
4. Trips to different parts of the island did not yield any "new" ants.
5. The collecting methods are productive elsewhere. For example, during a recent trip to a scrub site in Glades Co., Florida, I collected thirty-eight species in about two hours-almost as many species as were found in twelve days on San Salvador.

Although I am generally satisfied with this survey, I would be amazed if no more ants were ever added to the San Salvador list. Exotic species will probably continue to invade, especially if plants with soil are imported. Some "tramp" species spread slowly, and may already be present in small populations that were not detected. There could also be native species that escaped my attention. In Florida there are soil-dwelling species that I have found in only a tiny fraction of the thousands of litter extractions done for the Florida ant survey, and there may be equally rare ants on San Salvador. Even if there are a few elusive species yet to be found on San Salvador, there is no doubt that the island truly has a depauperate ant fauna. South Florida mainland sites have many more ants: Archbold Biological Station, which is much smaller and has much less habitat diversity than San Salvador, has 105 species of ants.

There are several kinds of island effects that can lead to a depauperate fauna. In this case, I believe that the most important factor is the direct effect of isolation, which has prevented many ant species from reaching the island. An indirect island effect that can eventually result in a depauperate fauna is the replacement of a rich endemic fauna of vulnerable species by a small group of exotics. Examples of this are known from the Galápagos (Lubin, 1984), and Puerto Rico (Wheeler, 1910), and there are also examples from continental sites, such as Texas (Porter & Savignano, 1990). There is indirect evidence that this has not happened on San Salvador, as discussed below in the section on endemics. There is still less evidence that the relationship between island size and species diversity has any relevance to the ants of San Salvador. The total Bahamian ant fauna, compiled from the literature, fits nicely on an area-diversity curve, but this was done by the biogeographically questionable expedient of combining the areas of all the Bahamian islands (Wilson, 1988). San Salvador has far too many ants to fit the curve, even ignoring the fact that much of the interior of the island is actually water and should not be included in area calculations.

Comparisons with Other Bahamian Islands

There are only a few published records of

Table 1. Ants from San Salvador

Brachymyrmex obscurior
Brachymyrmex minutus
Camponotus ramulorum
Cardiocondyla emeryi, OW
Cardiocondyla nuda, OW
Crematogaster steinheili
Cyphomyrmex minutus
Dorymyrmex pyramicus niger
Hypoponera opaciceps
Hypoponera opacior
Monomorium ebeninum
Monomorium floricola, OW
Odontomachus ruginodis
Paratrechina longicornis, OW
Pheidole flavens
Pheidole megacephala, OW
Pheidole sp.
Pseudomyrmex cubaensis
Pseudomyrmex pallidus
Pseudomyrmex seminole
Pseudomyrmex simplex
Pseudomyrmex subater
Quadristruma emmae, OW
Rogeria curvipubens
Solenopsis abdita
Solenopsis corticalis
Solenopsis geminata, NW
Solenopsis globularia
Solenopsis invicta, NW
Solenopsis sp. 1
Solenopsis sp. 2
Strumigenys eggersi, NW
Strumigenys gundlachi, NW
Tapinoma litorale
Tapinoma melanocephalum, OW
Tetramorium bicarinatum, OW
Tetramorium simillimum, OW
Trachymyrmex jamaicensis
Trichoscapa membranifera, OW
Xenomyrmex floridanus
Zacryptocerus varians

OW = Exotic, Old World tropics
NW = Exotic, New World tropics

ants from San Salvador, but the western Bahamas have been studied more carefully. Marion Smith (1954) provided a list of thirty species from the Bimini Islands, based on what appears to have been an intensive collecting effort by Mont Cazier and others from the American Museum of Natural History. William Wheeler (1905, 1934) collected Bahamian ants and compiled literature records; most of this work dealt with New Providence and North Andros Islands, resulting in lists of 37 and 34 species, respectively. A few additional records were provided by Ward (1985) and myself (unpublished). A survey of all the faunal lists provides two insights into the San Salvador ant fauna.

1. San Salvador has a relatively long list of ants, but this is probably an artifact of intensive collecting. There are only 5 species on San Salvador that are not reported from other islands. Three of these (*Q. emmae, S. eggersi,* and *T. membranifera)* are very small species that never emerge from leaf litter; they are widespread tramps, and undoubtedly occur elsewhere in the Bahamas. One species (*C. nuda*) is also a small widespread tramp species, usually confined to highly disturbed areas; it undoubtedly occurs on other islands. There are more species of tiny *Solenopsis* (*Diplorhoptrum*) on San Salvador than on other Bahamian islands, but since Wheeler seems to have ignored this group in his work in the Bahamas (it is a good group to ignore, as most species defy identification), the San Salvador list does not mean much. Smith (1954) lists three species (without assigning names) from Bimini; it is likely that the larger islands of the western Bahamas have at least four species.
2. While there may be no ants found only on San Salvador, there are many species that occur on other islands, especially Andros and New Providence, that appear to be missing from San Salvador (Table 2). This list includes both exotics (at least 7 species) and species I presently list as natives (19 species). Most of the native species are likely to have been derived from the Cuban fauna, and might have

Table 2. **Bahamian Ants Not Found on San Salvador**

Anochetus emarginatus	*Hypoponera punctatissima*, OW	*Pheidole androsana*
Camponotus bermudezi	*Leptothorax pastinifera*	*Pheidole punctatissima*
Camponotus culmicola	*Leptothorax androsana*	*Pheidole subarmata*
Camponotus fumidus lucayanus	*Leptothorax splendens*	*Platythyrea punctata*
Camponotus inaequalis	*Monomorium pharaonis*, OW	*Smithistruma nigrescens*
Camponotus triton	*Monomorium salomonis*, OW	*Strumigenys lanuginosa*
Crematogaster ashmeadi	*Pachycondyla stigma*	*Tetramorium lucayanum*, OW
Crematogaster sanguinea	*Paratrechina bourbonica*, OW	*Wasmannia auropunctata*, NW
Forelius pruinosus	*Paratrechina guatemalensis*, NW	

OW = Exotic, Old World tropics
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spread through the Great Bahamas Bank during the Pleistocene.

The combined list of Bahamian ants now includes 67 species.

Endemism Among the Ants of San Salvador

As I have stated above, there are no known endemic ants on San Salvador. Not only do the native species occur elsewhere in the Bahamas, but their distribution is even wider. Only 6 species are absent from Florida, and all species occur in the Greater Antilles (Kempf, 1972).

It is always possible that there were endemic species that were eradicated by human disturbance. Such disturbance not only included the destruction of forested areas, but also the importation of destructive exotics, especially ants. There is not likely to be any direct evidence of extinct species, but indirect evidence, provided by plant lists, argues against any extensive endemic ant fauna. There is a rich native flora of several hundred species, with no species or subspecies restricted to San Salvador and nearby islands (Correll and Correll, 1982). This seems remarkable, considering the long-term isolation of San Salvador.

The lack of an obvious group of endemic species on San Salvador would be easy to understand if the island had been colonized by land organisms relatively recently, and this is probably the case. At the end of the last interglacial, about 65,000 y.b.p., the sea level was 8-10 m higher than now (Pregill and Olsen, 1981), thus virtually eliminating the island. During the glacial maxima of the Pleistocene, only about 17,000 y.b.p., the Great Bahamian Bank emerged as a huge dry island (Pregill and Olsen, 1981) which, though not attached to San Salvador, could have served as a massive source of Caribbean dryland biota. San Salvador, emerging on its own small bank, would have been a relatively large target, perhaps 20 x 30 km, for dispersing organisms. As Pregill and Olsen point out, the composition of the native fauna of Caribbean islands is much more easily explained by climatic changes in the Pleistocene than by island size or even by the present degree of isolation.

Exotic Ants on San Salvador

So far, fourteen exotic ants, one third of the ant fauna, are known to be established on San Salvador. This might seem a high proportion of exotics, but it is no higher than in some places in Florida that have more than twice as many species as San Salvador (Deyrup, 1991). There are about fifteen widespread tramp ants in the West Indies that have not yet appeared on San Salvador, so the proportion of

exotic species is almost certain to rise.

The tropical tramp species of San Salvador include ten species from the Old World tropics, and four species from the New World tropics (Table 1). The apparently anomalous high rate of invasion from the Old World has two logical explanations. The first is that New World tramps are not always easily recognized as tramps, because by the time there were any ant surveys these species had already been moved around and could not be distinguished from good natural dispersers. As mentioned above, all the supposedly native ants on San Salvador are more or less widespread in the Caribbean, and any of them could have been imported to the island in the last 300 years. Now that there is a baseline study of the ants, it should be possible to recognize as exotics (on San Salvador) other widespread Caribbean species as they appear on the island. The second reason for the preponderance of Old World tramps in San Salvador and elsewhere is that the Old World tropics cover an enormous area, with a great diversity of ant faunas, whose species have had the opportunity to adapt to man-altered ecosystems for many thousands of years.

The ecological impact of exotic ants on San Salvador is difficult to measure, again because there is no baseline information. My general impression is that exotics do not dominate areas of native vegetation on the island, with the exception of beaches, which may have conspicuous populations of *S. geminata* and occasionally *T. bicarinatum*. Disturbed areas, such as lawns, yards and some roadsides often support dense populations of *P. longicornis*, *S. geminata*, *P. megacephala*, and *M. floricola*, with other native and exotic species present as well. At present exotic ants probably have minimal effects on the native biota.

Some exotic species that seem benign now may have a more rapacious history. Many exotic organisms go through an explosive phase when first introduced, and may have profound, sometimes permanent effects on native biota. *Solenopsis geminata* seems to have gone through such a phase on various Caribbean islands. The accounts of the period have a Munchausenesque flavor, but there are enough of them to indicate that a dramatic phenomenon actually occurred. Some of these accounts were compiled by Frank Cowan (1865), who describes a plague of ants in Hispañola and Jamaica in the early 1500s, spreading to Barbados in 1760, Martinique in 1763, and Grenada in 1770.

> *Barbados, Granada, and Martinique suffered more than any other islands from this plague. Granada especially was reduced to a state of the most deplorable desolation; for, it is said, their numbers there were so immense that they covered the roads for many miles together; and so crowded were they in many places that the impressions made by the feet of horses, which traveled over them, would remain visible but for a moment or two, for they were almost instantly filled up by the surrounding swarms. Mr. Schomburgk assures us that calves, pigs, and chickens, when in a helpless state, were attacked by such large numbers of the Ants that they perished, and were soon reduced to skeletons when not timely assisted. It is asserted by Dr. Coke that the greatest precaution was requisite to prevent their attacks on men who were afflicted with sores, on women who were confined, and on children that were unable to assist themselves. Mr. Castle, from his own observation, states that even burning coals laid in their way, were extinguished by the amazing numbers which rushed upon them.*

There are more recent chronicles of swarming ants. William Wheeler (1910) describes two small islands off Puerto Rico, one of which was overrun by *S. geminata*, the other by *P. megacephala*. In the latter case, there seemed to be no other ants on the island. If Wheeler had been studying beetles or spiders he probably would have found these also affected by *P. megacephala*. The spread of *S. invicta* through the southern U.S. has provided a good opportunity for methodical studies of the impact of a dominant exotic ant (Porter and Savignano, 1990), and may give some idea of the past impact of exotic ants on San Salvador. As discussed above, San Salvador

may have had few endemic species to lose, but it could have lost native species that were more generally distributed in the Bahamas. It may not be possible to get an idea of what, if anything, San Salvador has lost because there are probably no Bahamian islands of similar isolation and habitat diversity that have escaped invasion by *S. geminata* and *P. megacephala*. The islands in the western Bahamas that have a number of species of ants not found on San Salvador also have *S. geminata* and *P. megacephala*, so the absence of some Bahamian species on San Salvador is probably not due to early ant invasions.

It is inevitable that more species of ants will invade San Salvador. Many species of ants move in landscape plants, especially if they are transported with soil. Even a single specimen plant of an orchid or bromeliad can have colonies of several species of hitchhiking ants. Air transport allows less hardy travelers to relocate as never before. On my first trip to San Salvador the airplane was invaded by queen *B. obscurior* and *S. invicta* as it stood in the airport in Fort Lauderdale. Several queens were still alive when we landed in San Salvador and were headed toward the door when I captured them. Not surprisingly, both these species were already present on San Salvador, but the episode demonstrates how readily species can relocate. Several exotics that are very abundant in South Florida are apparently absent from San Salvador; these include *Wasmannia auropunctata*, *Paratrechina bourbonica*, *P. guatemalensis*, *Hypoponera punctatissima*, and *Pseudomyrmex mexicanus*.

There are also native Bahamian species, such as species of *Camponotus* and *Crematogaster*, that would probably thrive on San Salvador. It is, however, difficult to predict which ants would have a large ecological or economic impact on the island. Species that are everywhere in south Florida could encounter unexpected resistance on San Salvador. The infamous *Solenopsis invicta* may be an example of a species that has failed to become securely established. One species, *Pheidole fallax*, which was collected on San Salvador by James Greenway in 1932 or 1933 (Wheeler, 1934) was not found in recent surveys, though it still occurs on some other islands of the Bahamas.

Ants as Representatives of Terrestrial Arthropods on San Salvador

The ant fauna of San Salvador can be briefly described as depauperate relative to mainland sites of similar habitat diversity, with a large proportion of exotics, most of which live in close association with humans. Does this pattern fit other terrestrial arthropods? There are only two matched sets of arthropods to compare, of which the best is the aculeate wasps. A complete list of wasps for San Salvador (Elliott, 1992) includes thirty species. This wasp fauna certainly fits the pattern of a depauperate fauna when compared to an unpublished Florida mainland site list (Archbold Biological Station) of 198 species. The pattern of exotics, however, does not agree at all: at neither site are there known to be any exotic wasps. The high proportion of exotics among the ants may be due to the fact that while ants are poor dispersers (queen ants are heavy bodied with deciduous wings) they are excellent colonizers, as a single female may produce enormous numbers of reproductives over her lifetime. Aculeate Hymenoptera, including ants, usually invest large amounts of care in each offspring, which usually improves the survival chance of each offspring but reduces the number of offspring. Queen ants, by delegating this care to workers, obtain the benefits of both parental care and high reproductive rate, making them good colonizers. Aculeate wasps, except for social species, are poor colonizers because their reproductive rate is low.

These considerations of mobility and fecundity allow the obvious prediction that the most diverse group of arthropods on San Salvador should be those with females that disperse readily carrying large numbers of eggs. Phytophagous groups might be favored, as the vegetation of San Salvador is notably diverse, with 524 species in 265 genera (Smith, 1993). The group fitting this profile is the butterflies and moths (Lepidoptera). There is some suggestion that species of Lepidoptera, or at least the butterflies, are relatively numerous on San Salvador. Nancy Elliott has provided an unpublished list of forty-one species,

(coincidentally the same number as the ants) most of which probably breed on the island, as the collecting effort has not been sufficiently intense to pick up many strays. This can be compared with butterfly lists from the Florida Keys (Minno and Emmel, 1993) and the Archbold Biological Station (Minno, 1992a), using information from species accounts to decide which species are breeding in the area. It is not always certain whether there is a breeding population in the area, so the numbers are probably not exact. The butterflies, ants, and aculeate wasps considered together show the patterns: if the San Salvador ratio of butterflies to aculeates were the standard, ABS would have about 150 wasps too many!

	Butterflies	Ants	Wasps
San Salvador	41	41	30
Florida Keys	73	83	-
Archbold Biol. Stat.	63	105	198

Since species of moths are likely to greatly outnumber butterflies, about 15 to 1 at the ABS (Minno, 1992b) and North America north of Mexico as a whole (Covell, 1984), even taking into account the fact that not all moth groups are as mobile as butterflies, there are probably several hundred species of moths on San Salvador.

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