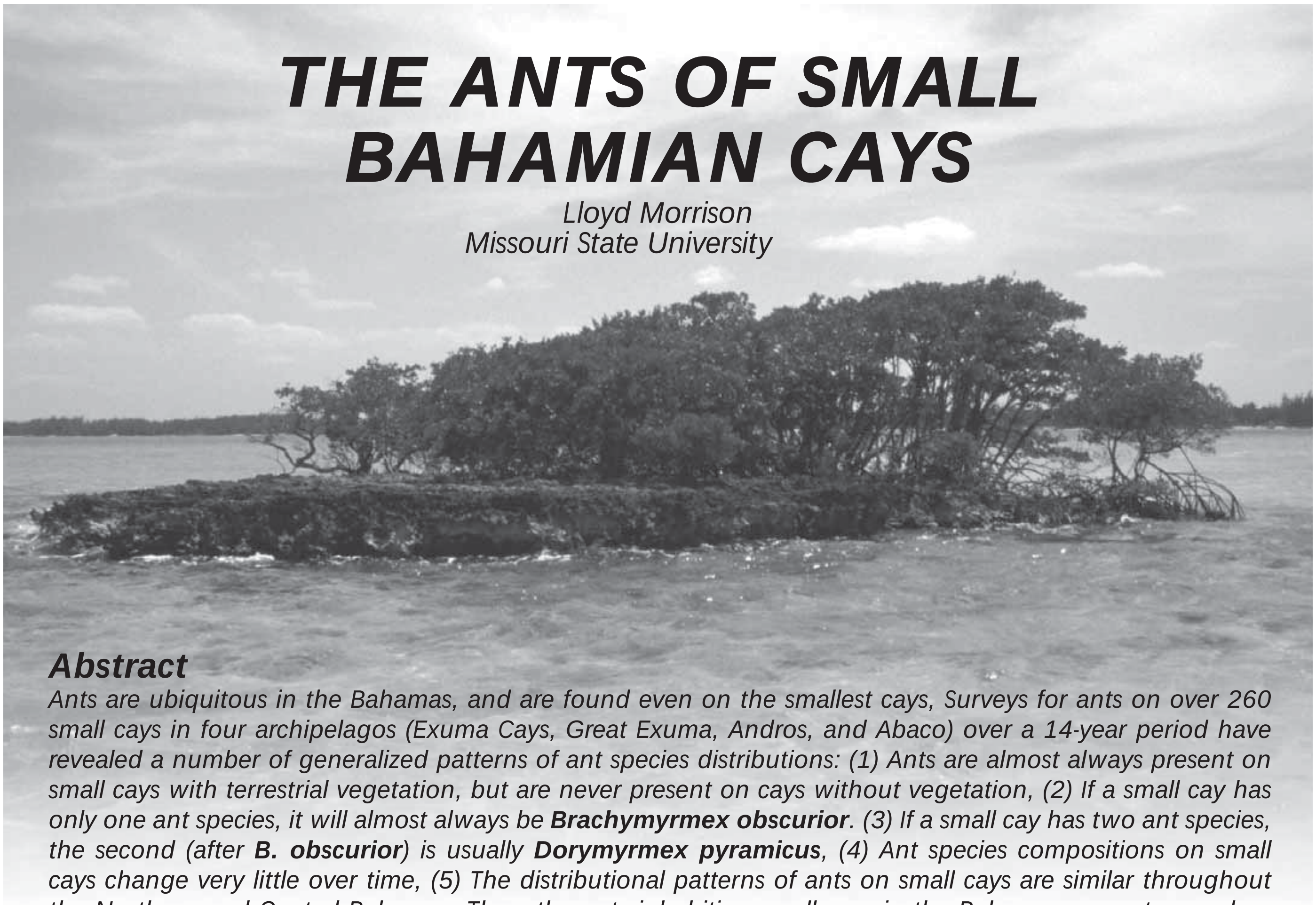

# THE ANTS OF SMALL BAHAMIAN CAYS


*Lloyd Morrison*
*Missouri State University*



## Abstract

*Ants are ubiquitous in the Bahamas, and are found even on the smallest cays, Surveys for ants on over 260 small cays in four archipelagos (Exuma Cays, Great Exuma, Andros, and Abaco) over a 14-year period have revealed a number of generalized patterns of ant species distributions: (1) Ants are almost always present on small cays with terrestrial vegetation, but are never present on cays without vegetation, (2) If a small cay has only one ant species, it will almost always be* ***Brachymyrmex obscurior****. (3) If a small cay has two ant species, the second (after* ***B. obscurior****) is usually* ***Dorymyrmex pyramicus****, (4) Ant species compositions on small cays change very little over time, (5) The distributional patterns of ants on small cays are similar throughout the Northern and Central Bahamas, Thus, the ants inhabiting small cays in the Bahamas are not a random assortment of the larger species pool in the region, but rather a very predictable subset of species. The underlying mechanisms of these patterns appear to be largely associated with the presence and type of vegetation present, which in turn is dependent upon various physical variables such as island size, elevation, and exposure to winds, waves, and tides.*


## Introduction

Ants are common and important components of many tropical and subtropical ecosystems (e.g., Hölldobler and Wilson 1990), and the Bahamas are no exception, Ants have been collected and species lists published for most of the larger and a number of the smaller islands in the archipelago (Wheeler 1905, 1934, Mann 1920, Smith 1954, Deyrup 1994, Deyrup et al. 1998, Morrison1998a), While such lists for the larger islands are likely to underestimate true species richness due to limited collecting effort, these collections do reveal the diversity and ubiquity of Bahamian ants.

Ants are frequently found in marginal or 'inhospitable' habitats (Hölldobler and Wilson 1990), and the Bahamas contain thousands of small cays representing such potential ant habitat. Elsewhere I have described the metapopulation dynamics of ants inhabiting these small cays, focusing on rates of immigration and extinction (Morrison 1998b, 2002). In this contribution, I focus on generalized patterns of ant distribution on very small cays, and address the possible underlying mechanisms, I pose the question of whether the ants inhabiting small cays are simply a random assortment of the larger species pool in the region, or a deterministically derived subset of species. In other words, it is possible to predict which species of ant one may find on a small Bahamian cay with a large degree of accuracy? Furthermore, will such a prediction, or its accuracy, differ among the various archipelagos of the Bahamas?

## Methods

The data in this paper are derived from surveys of ants on 264 small cays in four Bahamian archipelagos (Exuma Cays, Great Exuma, Andros, and Abaco), conducted from 1989 to 2003 (Table 1). For the purposes of this paper, I define a small cay as any island with < 1,000 m$^2$ vegetated area (including islands with no vegetation).

*Table 1. Bahamian cays surveyed for ants.*

| Archipelago | No. of cays surveyed | Years surveyed |
|---|---|---|
| Exuma Cays | 129 | 8 (1989-1994, 1998, 2003) |
| Great Exuma | 36 | 5 (1998-2002) |
| Andros | 59 | 3 (1990, 1999, 2003) |
| Abaco | 40 | 1 (2003) |

In the Exuma Cays, the study area included the 13.5 km island chain between O'Briens Cay to the north and Bitter Guana Cay to the south. The study area at Great Exuma included small cays around George Town, including both the north side of the main island in Elizabeth Harbour, and the south side over the shallow banks. The study area at Andros included the small islands lying offshore the main island of Andros, between Nicholls Town to the north and Staniard Creek to the south. The study area at Abaco included small cays in the tidal creeks along the western coast of Great Abaco Island, south of Marsh Harbour, in the region from Snake Cay to Iron Cay.

The cays at Andros tended to be lower in elevation, with less steeply sloping sides, and experienced more tidal inundation than cays in the other archipelagos. These conditions often resulted in relatively large intertidal mangrove communities; intertidal mangroves were rare on small cays in other archipelagos. The cays at Abaco were better protected from wind and waves than those in the other archipelagos, and tended to have more vegetation cover and higher plant species richness for their size compared to cays in other archipelagos.

Baits were used to attract ants. The number of baits was proportional to the log(area) of each cay, and ranged from 6 to 50. Baits consisted of ~one gram of finely ground tuna in vegetable oil (to provide proteins and lipids) and ~one gram of honey (to provide carbohydrates), and were placed in petri dishes painted white, which facilitated ant identification. Baits were left out for 45 minutes, at which time all ant species present at the baits were recorded. Surveys were always conducted between 8am and 6pm.

Because relatively few ant species inhabit these cays, accurate field identification of most species was possible. Specimens of morphologically similar congeners were collected and later identified in the lab to verify field identifications. Reference specimens have been deposited in the Bohart Museum of Entomology at U.C. Davis.

Some of the larger cays contained ants that were not attracted to the baits used (at least not diurnally). These species foraged primarily arboreally or nocturnally. Most of the ants that were frequently attracted to baits nested in the substrate, as opposed to the vegetation, and my focus is primarily upon these species. Visual surveys and hand collecting were employed at times to determine which species may be present but missed by the baiting. Such collecting for arboreally nesting species is necessarily destructive and inefficient, as habitat is destroyed in the process. Species that nested arboreally were usually not present on most of the smaller cays (which lacked the appropriate vegetation, except for mangroves), and do not affect the conclusions relating to cays with one or two species. For species that were attracted to baits, the sampling method was very effective (Morrison 1998b).

## Results and Discussion

A number of generalized patterns of ant distribution on these small cays are apparent:

Generalized pattern #1: Ants are almost always present on small cays with terrestrial vegetation, but are never present on small cays without any vegetation.

There were several plant species that usually grew in the intertidal zone: the red mangrove (*Rhizophora mangle* L.), the black mangrove, (*Avicennia germinans* [L.] L.), the white mangrove (*Laguncularia racemosa* [L.] Gaertn. f.), the glasswort (*Salicornia virginica* L.), and the saltwort (*Batis maritima* L.). The substrate on which these species were rooted was frequently submerged at high tide, Cays that contained some or all of these plant species and no others were regularly inundated at high tide. Thus, for the purposes of this paper, I consider these as 'intertidal' species, and plant species that are usually rooted on substrate that remains dry at high tide as 'terrestrial' species.

The vast majority of cays with terrestrial vegetation contained ants (>94% in three of the four archipelagos) (Table 2), The few vegetated cays that lacked ants contained relatively little terrestrial vegetation (9 of 12 had

*Table 2. Incidence of ants on small cays in relation to vegetation, Cays with only intertidal plant species or no plant species never contained ground-nesting ants (although some may have contained ants nesting in the intertidal vegetation; see text).*

| | Vegetated Cays* | | | |
|---|---|---|---|---|
| Archipelago | No. of cays | No. with ants (%) | No. of cays with only intertidal species | No. of cays with no plant species |
| Exuma Cays | 89 | 86 (96.6) | | 40 |
| Great Exuma | 36 | 36 (100.0) | | |
| Andros | 28 | 21 (75.0) | 17 | 14 |
| Abaco | 35 | 33 (94.3) | 5 | |

* "Vegetated" refers to terrestrial vegetation as defined in the text, and excludes the intertidal species listed in the text.

< 5 $m^2$ vegetated area), No ants were found on any cays that completely lacked vegetation, At Andros, where intertidal mangroves were common on some cays, arboreal ants often lived within dead twigs. These ant species are not included here, as I focus on species nesting within the substrate or in terrestrial vegetation.

This pattern indicates that the ants inhabiting these cays must feed on resources that are terrestrially-based (autochthonous), rather than marine-based (allochthonous). A relatively diverse assemblage of arthropods (including representatives of 10 orders) is able to exist on small Bahamian cays that have no terrestrial vegetation (Morrison 2005). The base of food webs on such islands must be ultimately derived from the ocean. Yet Bahamian ants are apparently not able to survive on resources obtained from the marine environment either directly (e.g., marine algae washing ashore) or indirectly (i.e., preying upon other arthropods that feed on such marine algae).Many ants are generalist feeders, and feed on plants directly or indirectly (i.e., upon herbivorous insects). (Ants nesting in mangroves presumably prey on herbivores of the mangroves.) Ants have been reported from islands completely lacking vegetation near Puerto Rico, although these islands had relatively large nesting seabird populations (Heatwole et al. 1981).

In multiple linear regression analyses, plant species number was found to be the best predictor of ant species number in the Exuma Cays (Morrison 1998b). Plant species number was a superior predicted over other island variables—such as area, distance, and elevation—frequently thought to be important in determination of insular species richness (e.g., MacArthur and Wilson 1967, Whittaker 1998). This emphasizes the importance of plants to the ants inhabiting these small cays.

*Table 3. Ant species most likely to be found on one- or two-species cays.*

| **Archipelago** | **Exuma Cays** | **Great Exuma** | **Andros** | **Abaco** |
|---|---|---|---|---|
| No. of times indicated species is the only species/no. of cays with only one species: | | | | |
| *B. obscurior* | 48/49 (98.0) | 2/5 (40.0) | 9/9 (100.0) | 16/18 (88.9) |
| *D. pyramicus* | 0 | 2/5 (40.0) | 0 | 0 |
| *Crematogaster sp.* | 0 | 1/5 (20.0) | 0 | 1/18 (5.6) |
| *B. minutus* | 1/49 (2.0) | 0 | 0 | 0 |
| *Pheidole sp.* | 0 | 0 | 0 | 1/18 (5.6) |
| No. of times indicated species is one of two coexisting species/no. of cays with only two species: | | | | |
| *B. obscurior* | 29/29 (100.0) | 17/18 (94.4) | 5/5 (100.0) | 10/10(100.0) |
| *D. pyramicus* | 24/29 (82.8) | 16/18 (88.9) | 4/5 (80.0) | 2/10 (20.0) |

Generalized pattern #2: If a small cay has only one ant species, it will almost always be *Brachymyrmex obscurior.*

*Brachymyrmex obscurior* is a small-bodied ant that is apparently well suited to the extreme, marginal environments of these small cays. When only a single ant species was found, it was B. obscurior 93.7% of the time (averaged across all cays) (Table 3). *Brachymyrmex obscurior*

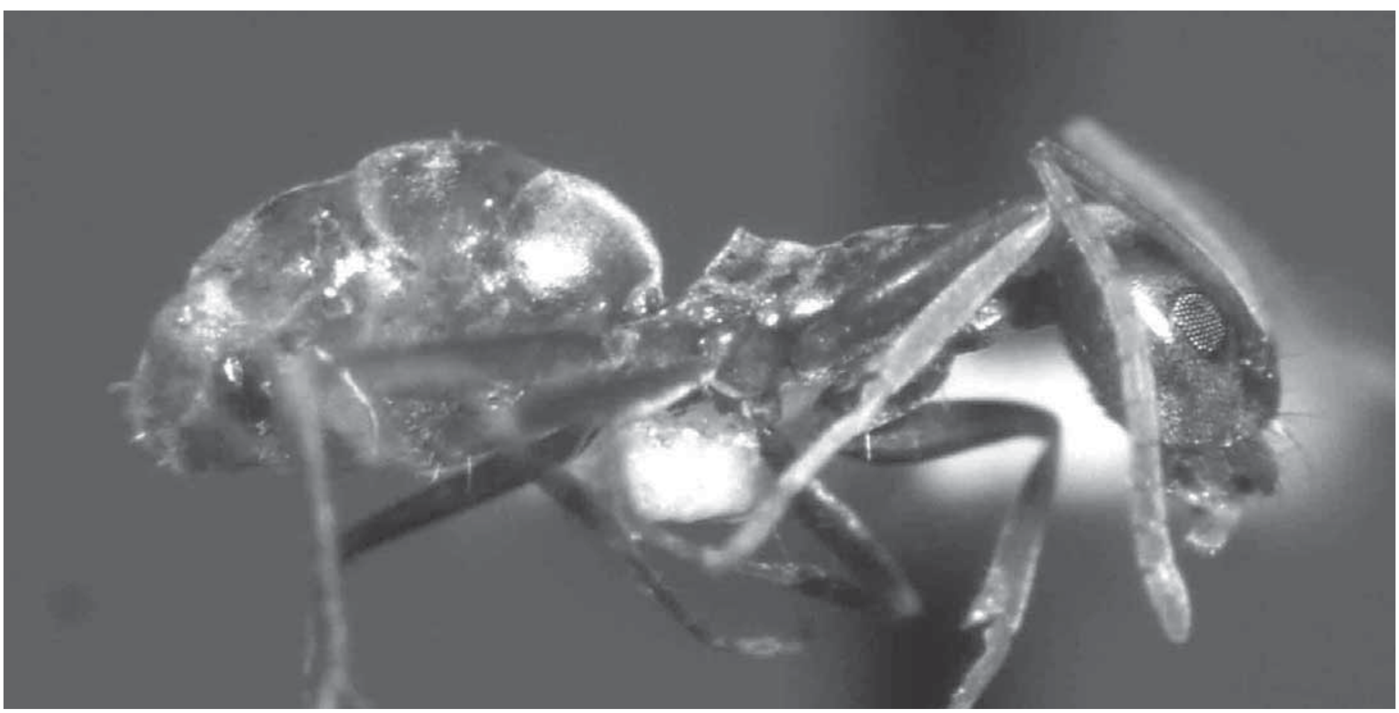

*Figure 1. Dorymyrmex pyramicus,*

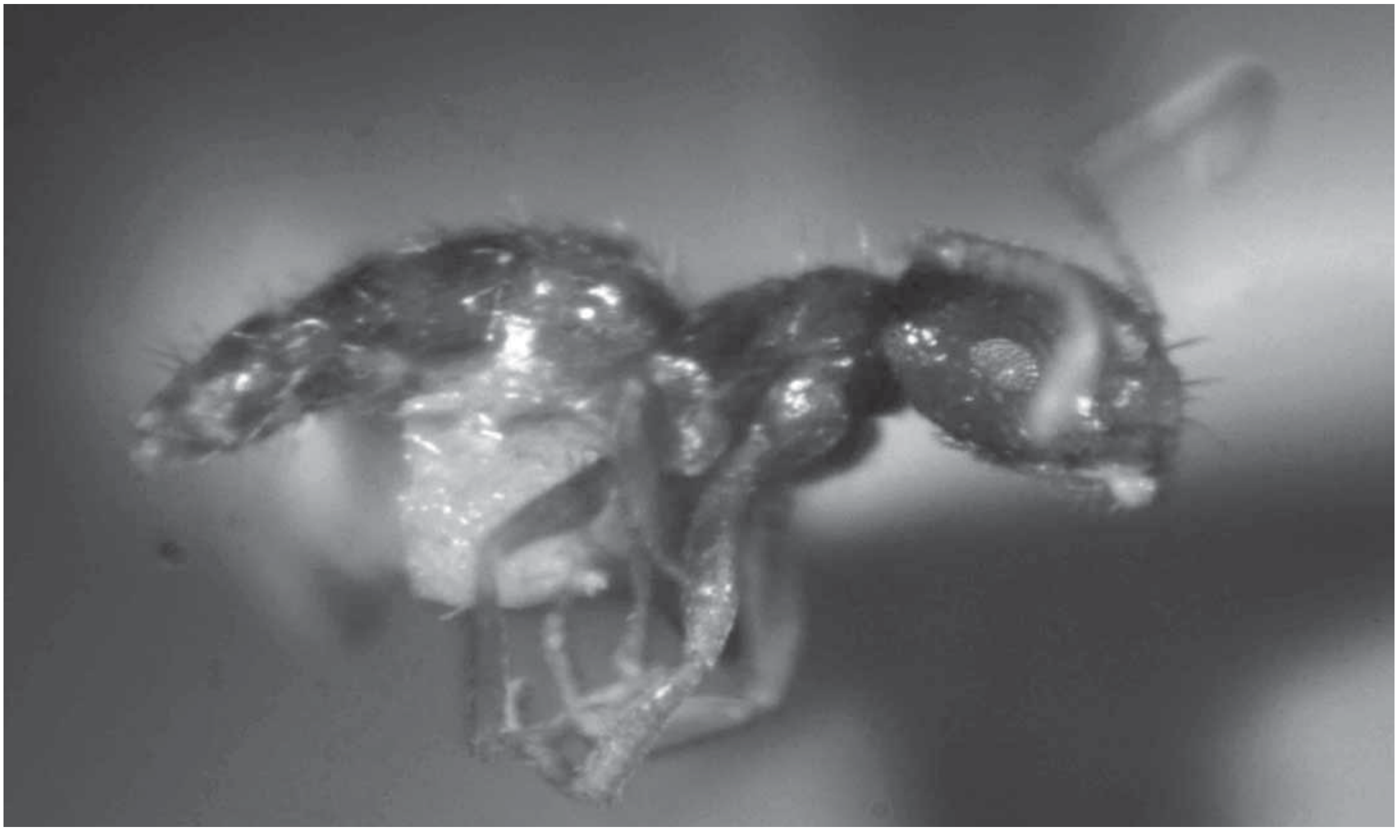

*Figure 2. Brachymyrmex obscurior.*

is found on the larger islands in these archipelagos, although it is not very common there (Morrison 1995) and seems to be largely restricted to marginal environments, particularly along the shore (personal observations). This suggests that, while being able to tolerate marginal conditions, *B. obscurior* is not a strong competitor against most other ants.

It is possible that several, closely related *Brachymyrmex* species exist on these small cays under this name. The taxonomy of the genus *Brachymyrmex* is in need of revision; the minute size of *Brachymyrmex* species makes identification very difficult, and many undescribed species are thought to exist (Creighton 1950, Deyrup et al. 1988, MacKay and Vinson 1989). Slight variations in coloration and eye size in what I consider as *B. obscurior* suggest that more than one species may exist under this name, although the observed differences were not pronounced enough to allow separation into distinct morphospecies. A second *Brachymyrmex* species that is relatively rare on these small cays, *B. minutus*, is easily distinguished from *B. obscurior*, Even if *B.* cf. *obscurior* represents a closely related species complex rather than an individual species, the ecological implications for these small cays are similar, as any species of this group would fill a similar ecological niche and interact with other ant genera in similar ways.

Generalized pattern #3: If a small cay has two ant species, the second (after *B. obscurior*) is usually *Dorymyrmex pyramicus*.

When a small cay had two ant species, *Dorymyrmex pyramicus* was one of these on 74% of the cays (averaged across all archipelagos) (Table 3). *Dorymyrmex pyramicus* is larger and faster than *B. obscurior.* These two species compete strongly for the baits used, and likely compete for many other food types as well. *Dorymyrmex pyramicus* workers often find food resources first, but are displaced as *B. obscurior* workers arrive in greater numbers (Morrison 2006). Thus it appears that in spite of strong interspecific competition, these two species are able to coexist by virtue of the discovery-dominance trade-off that characterizes many ant communities (e.g., Holway 1999). Although *B. obscurior* may be dominant to *D. pyramicus* on these small cays, it is apparently not dominant to many of the ant species found on larger islands (as noted above).

The only exception to this rule was at Abaco, where *D. pyramicus* was one of a number of species that coexisted with *B. obscurior* on two-species cays. A probable explanation for this was that woody terrestrial vegetation was more likely to occur on the small, protected cays at Abaco, and support a greater diversity of ants. In addition to *D. pyramicus*, species that coexisted with B. obscurior on two-species cays at Abaco included representatives of *Camponotus*, *Crematogaster,* and *Pseudomyrmex*, which are all typically associated with woody vegetation on these small cays.

Interestingly, even though *D. pyramicus* is usually present on cays with two or three ant species, it is usually not present on small cays with >3 species (Morrison 1998b). Thus *D. pyramicus* is probably a relatively poor competitor relative to the overall ant fauna, although it is relatively common on the larger islands (Morrison 1998a).

Generalized pattern #4: Ant species compositions on small cays change very little over time.

In the archipelagoes where repeated surveys of small cays have been conducted over time (Exuma Cays, Great Exumas, and Andros), rates of turnover (immigrations and extinctions) for most species of ants are low (< 10% per year; <5% per year for *B. obscurior* and *pyramicus*) (Morrison 1998b, 2002). Turnover rates have been observed to increase somewhat due to increased recent hurricane activity, yet are still relatively low in an absolute sense (unpublished data).

These small cays, composed almost entirely of marine limestone, are riddled with small crevices and galleries that represent suitable habitat for the ground-nesting ants. It is likely that, when sea level rises, ants nesting within this limestone are able to survive in air-filled chambers or blocked off tunnels. I have observed an active nest entrance of *B. obscurior* within the intertidal zone on a small cay at Andros; the ants presumably block off the entrance at high tide. The activity of *B. obscurior* on the smallest cays at Andros all but ceases at high tide, when much of these small cays are submerged. It seems likely that ants nesting within the limestone substrate could survive a complete inundation of the cay, at least for a limited time. Arboreal species of ants nesting within hollow vegetation could also easily survive flooding of the islands (as long as the vegetation was not washed away).

Generalized pattern #5: The distributional patterns of ants on small cays are similar throughout different regions of the Bahamas.

Surveys of ants in the Exuma Cays, Andros, Great Exuma, and Abaco all revealed similar patterns of distribution, usually with the same ant species playing the same roles. It is possible that the southeastern Bahamas exhibit different patterns, since these islands tend to be more arid and have a different geological history. The Exuma Cays, Great Exuma, and Andros were all part of the Great Bahama Bank during the Pleistocene, whereas Abaco was separated by a deep water trough on the Little Bahama Bank. The southeastern islands of the Bahamas are derived from many smaller banks (Sealey 1985).

Although geologic history (particularly fluctuating sea levels) undoubtedly plays a role in determining current species distributions (e.g., Deyrup 1994), dispersal events in modern times have also shaped the current ant fauna of these islands. Most ants disperse naturally by mating flights of the reproductive castes, which may cover distances of 8 km or more and occur over water (Wilson 1971). Ants also stow away in cargo and ballast transported on ships, and occasionally aircraft. Numerous species of ants have been introduced worldwide this way (McGlynn 1999), and many ants in the Bahamas have been introduced from elsewhere (Morrison 1998a).Ants could easily travel via ships and planes among the larger inhabited islands, and then disperse by mating flights to the smaller islands nearby. Rafting on vegetation (Wheeler 1916, King 1962, Heatwole & Levins 1972) is another method by which ants could potentially reach uninhabited and unvisited islands too distant for mating flights.

As an example of the ability of ants to colonize small, remote islands (and further evidence of the ubiquity of ants in the Bahamas), consider the Scrub Cays, a group of small, low-lying sandy cays that lie 40 km from the Exumas Cays (the nearest island chain) and 60 km from Andros. Only one other island, Green Cay (which is also very small and remote) is present within a 40 km radius of the Scrub Cays. Exploratory surveys of these uninhabited cays in 1998 revealed that several species of ants (including *B. obscurior* and *D. pyramicus*) were present (unpublished data). These cays were almost certainly submerged when sea levels were higher, and may be of very recent origin, given the apparently unstable nature of such sandy cays. Passing yachtsman may occasionally visit these islands, but such visits are unlikely to introduce ants, and the species present presumably dispersed there naturally.

## Conclusions

The ants inhabiting small cays in the Bahamas are not a random assortment of the larger species pool in the region, but rather a very predictable subset of species. This subset appears to result from a deterministic process that depends to a large extent upon the presence and type of vegetation present, which in turn is dependent upon various physical variables such as island size, elevation, and exposure to wind, waves, and tides. The open water distances separating the small cays from each other and from larger islands do not appear to be a major barrier to colonization.

Although interspecific competition undeniably exists among these ants, it does not appear to be strong enough to affect species distributions on the small cays to a great extent. For example, there are no 'checkerboard' distribution patterns of mutually exclusive species (e.g., Diamond 1975, Cole 1983) that cannot coexist on the same island. On the smallest of these cays, it is possible to predict with a high degree of accuracy whether ants will be present or not, depending upon the presence of terrestrial vegetation, and furthermore which species will be present. This will vary somewhat among different archipelagos, but even this variability may be somewhat predictable depending upon the geomorphology of the islands and degree of protection from open ocean, which will in turn influence plant species abundance and diversity, to which the ants primarily respond.

Other studies have revealed patterns in the distribution of ants on island archipelagoes (e.g., Vepsäläinen & Pisarski 1982, Cole 1983). Like the Bahamian Cays, habitat suitability on small islands was an important factor in determining which species were present. Unlike the Bahamian Cays, however, interactions with other species were frequently found to be important. Working on mangrove islands in the Florida Keys, Cole (1983) reported that some species could not coexist on the same islands due to fierce interspecific competition. On islands in the Tvärminne archipelago of the Baltic Sea, Vepsäläinen & Pisarski (1982) also found evidence of interspecific interactions in determining ant species distribution patterns, but in this region many ant species were parasitic, and thus depended upon the presence of the appropriate host ants before colonization could be successful, (Parasitic ant species were not present on the Bahamian Cays studied.) Finally, like the Bahamian Cays, the islands of these archipelagos were well within mating flight range of the regional ant species pool (Vepsäläinen & Pisarski 1982, Cole 1983), so distance was not a barrier to colonization.

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*Appendix. Ants attracted to the baits used on small cays in the four archipelagoes, AB, Abaco; AN, Andros; EC, Exuma Cays; GX, Great Exuma.*

| **Species** | **Archipelago** |
|---|---|
| PSEUDOMYRMECINAE | |
| *Pseudomyrmex cubaensis* (Forel) | AN, EC |
| *Pseudomyrmex pallidus* (F. Smith) | EC |
| *Pseudomyrmex seminole* Ward | AB |
| *Pseudomyrmex simplex* (F. Smith) | AB, AN, EC, GX |
| *Pseudomyrmex subater* (Wheeler & Mann) | EC |
| MYRMICINAE | |
| *Crematogaster steinheili* (Forel) | AN |
| *Crematogaster* spp.[1] | AB, GX |
| *Cyphomyrmex minutus* Mayr | EC, GX |
| *Monomorium floricola* (Jerdon) | EC |
| *Pheidole flavens* (s.l.) Roger | AN, EC, GX |
| *Pheidole bilimecki* Mayr | EC, GX |
| *Pheidole* spp.[2] | AB, AN, EC, GX |
| *Solenopsis (Diplorhoptrum)* sp. | EC, GX |
| *Trachymyrmex jamaicensis* (Andre) *maritimus* Wheeler | AN, EC, GX |
| DOLICHODERINAE | |
| *Dorymyrmex pyramicus* (Roger) | AB, AN, EC, GX |
| *Forelius pruinosus* (Roger) | EC, GX |
| FORMICINAE | |
| *Brachymyrmex minutus* Forel | AN, EC |
| *Brachymyrmex obscurior* Forel | AB, AN, EC, GX |
| *Camponotus lucayanus* Wheeler | EC, GX |
| *Camponotus ramulorum* Wheeler | AB, EC |
| *Paratrechina longicornis* (Latreille) | AB |

1 Several undescribed *Crematogaster* species are apparently present in the Bahamas (Deyrup et al. 1998)

2 Several apparently undescribed *Pheidole* species were found across the archipelagos, Although Wilson (2003) recently revised North American Pheidole, not all Bahamian species were included. All un-named *Pheidole* were relatively rare on the small cays surveyed.