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The vanished plague ants (Hymenoptera: Formicidae) of 19th century Bermuda

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Abstract

Several 17th and 19th centuries accounts from the Atlantic islands of Bermuda (32° N) describe enormous plagues of ants whose species identities have never been satisfactorily determined. Whereas there are few clues to the identity of the 17th century plague ants, earlier authors proposed four primarily tropical ant species as possible candidates for the 19th century plague ants: *Monomorium destructor* (JERDON, 1851), *Monomorium pharaonis* (LINNAEUS, 1758), *Pheidole megacephala* (FABRICIUS, 1793), and *Solenopsis geminata* (FABRICIUS, 1804). None of these species, however, fit the firsthand accounts very well. Searching the collections of several major museums, I did not find any ant specimens from Bermuda dating from before 1900. However, reanalyzing published accounts, I propose that the 19th century plague ants were a *Lasius* species. *Lasius niger* (LINNAEUS, 1758) was the only ant species reported from an 1873 expedition to Bermuda, and the first ant from Bermuda identified to species. However, this recorded ant may actually have been some similar *Lasius* species, e.g., *Lasius grandis* FOREL, 1909, currently the most common ant on the Atlantic islands of Madeira (33° N) and the Azores (37 - 40° N), or *Lasius neglectus* VAN LOON & al., 1990, now a widespread pest species in Europe. Since 1873, no *Lasius* species has ever again been reported from Bermuda. It is possible that the *Lasius* of Bermuda were driven extinct by later invading ants. Bermuda's small size, relatively flat topography, and scarcity of intact natural habitat may have afforded the resident *Lasius* insufficient refuge against the onslaughts of invasive exotic ants.

Key words: Atlantic islands, Bermuda, exotic ants, Lasius grandis, Lasius neglectus, Lasius niger, pest ants.

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Introduction

Over the past 500 years, there have been many accounts of tremendous ant plagues in different parts of the world. For example, between the 16th and 18th centuries, several tropical West Indian islands were wracked by a series of ant plagues (WHEELER 1926). Recently, WILSON (2005) examined historical records of these West Indian ant plagues. Based on accounts of the ants' appearance, behavior, ecology, and impact, WILSON (2005) concluded that the ant species most likely responsible for these ant plagues were the big-headed ant, *Pheidole megacephala* (FABRICIUS, 1793), and the tropical fire ant, *Solenopsis geminata* (FABRICIUS, 1804).

On the Atlantic islands of Bermuda (32° N), two ant species have had great population explosions during the 20th century. *Pheidole megacephala*, first recorded in Bermuda in 1889 (DAHL 1892), was by far the dominant ant species there in the early 20th century (HASKINS 1939). In the 1940s, however, the Argentine ant, Linepithema humile (MAYR, 1868) arrived in Bermuda and quickly overran much territory, driving back P. megacephala. Pheidole megacephala, however, persisted, and ever since these two species have been contesting ever-shifting battlefronts between mutually exclusive territories that together occupy most of the land area of Bermuda (HASKINS 1939, HAS-KINS & HASKINS 1965, 1988, CROWELL 1968, LIEBER-BURG & al. 1975, WETTERER & WETTERER 2004). All other ant species in Bermuda are currently rare and/or inconspicuous, and it is uncertain whether any of these remaining ant species are native (WETTERER & WETTERER 2004).

Several dramatic accounts describe earlier ant plagues in Bermuda, in the 17th and 19th centuries. In an attempt to identify these plague ant species, I searched through several ant collections, including those of the American Museum of Natural History in New York, the Academy of Natural Sciences in Philadelphia, the Bermuda Aquarium, Museum and Zoo, the Bermuda Department of Agriculture, the British Natural History Museum in London, the US National Museum in Washington DC, Harvard University's Museum of Comparative Zoology, Oxford University's Natural History Museum, and Yale University's Peabody Museum. I was unable to find any pre-20th century ant specimens from Bermuda (see WETTERER & WET-TERER 2004). In the present study, I analyzed all accounts of the 17th and 19th century plague ants in Bermuda with respect to appearance, behavior, ecology, and impact, to evaluate which ant species were the most likely candidates for the great ant plagues of Bermuda.

17th century accounts of plague ants in Bermuda

Three early 17th century accounts described major ant problems in Bermuda. A manuscript of uncertain authorship written circa 1619 (ten years after Bermuda's first settlement) reported serious insect plagues: "a certain Indian bugge called, by a Spanish appelation, a caca-roche, the which, creepeinge into chestes and boxes, eate and defile with their dung (and thence their Spanish name) all they meet with; as doe likewise the litle aunt, which are in the summer time in infinite numbers" (LEFROY 1882). In 1624, Capt. John Smith, of Virginia Colony fame, wrote

that in Bermuda: "the little Ants in summer time are so troublesome, they are forced to dry their figs upon high frames, and anoint their feet with tar, wherein they sticke, else they would spoile them all ere they could be dryed" (with "they" and "their" referring successively to the settlers, the fig frames, the ants, and the figs; from KEVAN 1981). A letter from Bermuda dated 1625 includes another brief mention of pest ants: "as for ants and wormes that distroy the fruits it is a common thing in all the Spannyshe and Canary vyneyards that flyes and vermine would destroye all if painfull and diligent p.vencon were not vsed wherefore we pray you be not discouraged in that" (from KEVAN 1981).

19th century accounts of plague ants in Bermuda

Two mid 19th century accounts described an ant plague in Bermuda that began around 1842. HURDIS (1897, published posthumously by his daughter) wrote of a great plague of ants in a passage dated 10 October 1848:

"During the last seven summers this part of Bermuda has been infested with Ants to a fearful degree; not only did they teem on the streets and highways, so as to render it impossible to walk without destroying numbers, but hill and dale, and even the dwellings of men were equally alive with this insect pest.

"Dense columns of them might be seen travelling up and down every tree, and great was the havoc they occasioned among young Pigeons and Poultry, nor did full-grown domestic rabbit escape their deadly attack, and pigs are sometimes destroyed by them.

"In the present summer we have happily escaped this enormous nuisance, the legions of Ants being reduced within reasonable bounds. The cause of this extraordinary decrease is entirely unknown to me.

"There are two species of Ant in the Bermudas – the one very small, and *supposed* to be a native insect; the other (*Formica*) larger, and said to be an importation from the West Indies. The later prevails in Hamilton and the surrounding neighborhood, where the former has disappeared.

"If we bear in mind the original formation of the Bermudas, it must be evident that no insect can be indigenous to them.

"Every housekeeper, gardener, and all who deal in articles of food, are keenly alive to the destructive habits of the Ant. Nothing appears to escape their active search, and whether it be meat, milk, sugar, honey, cake, or fruit, the ingenuity of the owner has to be exercised, in order to save the same from utter destruction.

"The Ant appears to have a natural repugnance to common whale oil, for which reason it is generally used by the native and others as a protection against these annoying depredations. Store-room tables have their legs placed in tin or leaden cups filled with oil; shelves made to hang from the ceiling have their iron supports passing through tin funnels of the same; and iron meat hooks are guarded in a similar manner. It is only by these means that any article of food can be considered safe from these marauders.

"Finding the Ants one morning disposed to attack a bottle of honey, I placed the same (a common wine bottle) in a soup plate on a sideboard, carefully filling the plate with water. On returning to the room a short time afterwards I found the bottle swarming with Ants, and on a closer inspection, was greatly surprised to find a column of those insects passing and re-passing on the surface of the water, between the rim of the plate and the bottle of honey in the centre. This they appeared to do with perfect ease, merely wetting their feet in the operation, or, in other words, absolutely walking on the water.

"There is another peculiarity in the habits of the Ant which deserves to be mentioned. If a couple of Snipe have been shot in the marshes, and are destined as a present to some friend, to save them from the Ants during the night they are suspended by a single thread from the upper part of an open window, and, notwithstanding this precaution, they will be found covered with Ants in the morning, while others continue to descend the long and slender passage of communication. Are we to ascribe this property of discovering food to the power of scent?

"The Ant is also very destructive to rabbits, whether old or young. The hutches should be made to stand on legs, by coating which with tar from time to time the inroads of this destructive pest may be kept in check" (HURDIS 1897: 324-326).

JONES (1859) quoted almost all of the above text, with some small editorial changes, taken from the then unpublished work of Hurdis. JONES (1859) also added information from Hurdis not included in HURDIS (1897), that offer some additional clues to the identity of the pest ant. In addition to mentioning that the ant "infests the Bermudas in legions during the greater portion of the year," JONES (1859) quoted Hurdis as follows:

"There are two species of ants in the Bermudas, one of which is about the size of the common ant of England, and is supposed to be an importation from the West Indies: the other is a much smaller insect, which I have observed only among the islands in the Sound.

"The ant is also very destructive to the domestic rabbit, to poultry, and young pigeons, to caged birds, and to all sick animals; and man himself, when in a helpless state, is sometimes attacked by it.

"During the heat of summer, millions of these insects make their appearance upon every road and pathway, and sometimes invade the dwellings of men in such multitudes, as to become an intolerable nuisance. Every tree, and almost every bush then teems with its black columns, ascending and descending in the great occupation of obtaining food."

This quote is of interest in that it specifies the size of the ant, and it is the only mention of the pest ant's color: black. In England, the name "common black ant" usually refers to *Lasius niger* (LINNAEUS, 1758). JONES (1859: 116) also made his own observations on the ants of Bermuda:

"The Common Ant (*Formica*), of the Bermudas swarms in countless myriads throughout the hot season, and makes sad havoc among the naturalist's specimens, during the drying process; but should a univalve, or crustacean, have to be cleared of its fleshy inhabitant, certain are we that a more sure method could not be resorted to, than to place the specimen within reach of these never weary scavengers; but a short time would elapse ere every particle would be consumed, save and except the shelly covering, which, by simple process, would be prepared for the cabinet."

Possible identities of the 19th century plague ants in Bermuda

There are few clues to the identity of the 17th century plague ant, except that it was small, it swarmed both inside and outside houses, and it attacked drying fruit. Many pest ant species fit this description. No earlier authors have speculated on the identity of the 17th century plague ant of Bermuda, and I too will refrain. Four ant species have been put forth as possible candidates for the 19th century plague ants in Bermuda (WHEELER 1906a, MCCALLAN 1948). There are strengths and weaknesses with each of the four candidacies.

WHEELER'S (1906) candidates: Monomorium destructor and Solenopsis geminata

WHEELER (1906a) proposed that the 19th century pest ant in Bermuda reported by HURDIS (1897) may have been either *Solenopsis geminata* or *Monomorium destructor* (JERDON, 1851), "but whether he refers to one of these or to some other species, it is certainly of interest that no such species can be recognized among those enumerated by subsequent writers... we must conclude that it has since become extinct or, at any rate, so rare as to have escaped the notice of subsequent collectors."

Monomorium destructor is known to have great, localized population explosions followed by crashes. For example, MAYOR (1922) described a tremendous outbreak of *M. destructor* on subtropical Loggerhead Key (25° N) in the Florida Keys. Much like the early descriptions of ants in Bermuda attacking mammals, MAYOR (1922) wrote of *M. destructor* on Loggerhead Key:

"So voracious are these insects that we are obliged to swing our beds from the rafters and to paint the ropes with a solution of corrosive sublimate, while all tables must have tape soaked in corrosive sublimate wrapped around their legs if ants are to be excluded from them. These pests have the habit of biting out small pieces of skin, and I have seen them kill within 24 hours rats which were confined in cages."

Amazingly, the population of *M. destructor* on Loggerhead Key has completely disappeared. No later survey of Loggerhead Key found *M. destructor*. Instead, the island is now dominated by *P. megacephala* (WETTERER & O'HARA 2002).

Monomorium destructor is primarily a tropical species. Although it has never been reported from Bermuda, it is known from a few locales at the same or higher latitude, including sites in Australia (Fremantle, Sydney, Adelaide, Melbourne; CLARK 1941), the Middle East (Palestine, Israel, Libya, Syria, Lebanon, Tunisia, and Iraq; AN-DRÉ 1881, EMERY 1908, CRAWLEY 1920, MENOZZI 1934), and the southern US (WHEELER 1906b). Unfortunately, M. destructor is a poor candidate for the Bermuda plague ant for several reasons. First, it is yellow and brown in color, and this does not match the descriptions of the black Bermuda plague ants. WHEELER (1906a) did not cite the account by JONES (1859) and was probably unaware of his description of "black columns" of ants. In addition, M. destructor workers seem too small to be described as being the size of the common ant of England. Finally, outbreaks of *M. destructor* tend to be very localized. I know of no instances where this species reached plague proportion over a wide area.

WHEELER's (1906) proposal of S. geminata as the plague ant in Bermuda has more strengths and fewer weaknesses as the proposal of M. destructor. Solenopsis geminata workers show high intercolony differences in coloration, ranging from red-orange with dark brown in the rear of the gaster, to nearly uniform brownish black (TRAGER 1991). Known as the "tropical fire ant," it has a painful sting and readily attacks vertebrates, including people. WIL-SON (2005) considered S. geminata to be the most likely candidate for a great plague ant of some tropical islands of the West Indies. However, as its common name suggests, this species in primarily tropical, and is known from only a few locales at the same or higher latitude as Bermuda, including sites in the southern US (CREIGHTON 1930, Francke & al. 1983, Jouvenaz & al. 1977, Lobdell 1930), Cyprus (COLLINGWOOD & al.1997), Greece (COL-LINGWOOD 1993), and New Zealand (MAYR 1876). However, in none of these temperate areas is S. geminata known as a serious pest. In addition, workers in S. geminata colonies are extremely variable, and would seem unlikely to be described as being the size of the common ant of England. Still, S. geminata cannot be ruled out as the pest ant of 19th century Bermuda.

MCCALLAN's (1948) candidates: Monomorium pharaonis and Pheidole megacephala

MCCALLAN (1948) footnoted a description of early ant plagues in Bermuda with "Monomorium pharaonis or/ and Pheidole megacephala (?)," but gave no rationale for this speculation. McCallan's (1948) proposals of Monomorium pharaonis (LINNAEUS, 1758), or/and Pheidole megacephala seem to have little merit. Monomorium pharaonis is similar in appearance and many of its habits to M. destructor. However, it seems to be a very unlikely candidate because it is almost exclusively an indoor pest. Pheidole megacephala fits some of the descriptions of the plague ant in Bermuda. In fact, P. megacephala showed a population explosion on the Atlantic island of Madeira at about the same time as the 19th century ant outbreak in Bermuda (HEER 1852). In addition, P. megacephala still swarms in streets and in the countryside in parts of Bermuda (WETTERER & WETTERER 2004). It is found in great numbers in trees and it is a common house pest. Unfortunately, it is the wrong color and size. It is brown (with a somewhat lighter thorax) and strongly dimorphic, with very distinct minor and major workers. In addition, I know of no reports of this ant attacking live vertebrates.

New candidates: Lasius species

WHEELER (1906a) overlooked one ant species reported from Bermuda that seems to be a very good candidate as the 19th century plague ant, *Lasius niger*, the first ant identified to species from Bermuda. KIRBY (1884) reported only one ant species collected by the HMS Challenger expedition in April 1873, a species he identified as *Formica nigra* (= *Lasius niger*). Although FABRICIUS (1804) had moved this species from *Formica* to his newly established genus *Lasius*, SMITH's (1858) catalog of ants at British Museum still listed this species as *Formica nigra*, and KIRBY (1884) used this old name as well. KIRBY (1884) noted that this species was "probably introduced" and that "the specimens do not appear to differ from the ordinary European species."

Alternatively, the 19th century pest in Bermuda may have been some other *Lasius* species. One strong candidate as a plague ant in Bermuda is *Lasius grandis* FOREL, 1909, a species often misidentified as *L. niger* (e.g., see WETTERER & al. 2004, in press). Another possible candidate as plague ant is *Lasius neglectus* VAN LOON & al., 1990, a species apparently from Asia Minor that has recently spread through much of Western Europe (see SCHULTZ & SEIFERT 2005).

The three candidate Lasius species, L. niger, L. grandis, and L. neglectus, are the correct size and color to be the 19th century plague ant of Bermuda and are known to reach very high densities. WHEELER (1910: 11) called Lasius niger "the commonest of all our ants" in North America. WILSON (1955) wrote that in Europe, L. niger is often the overriding local dominant of the ant fauna under a variety of ecological conditions. Lasius niger is considered the most important pest ant in England (CORNWELL 1978). On the Atlantic island of Madeira (33° N), at about the same latitude as Bermuda (32° N), L. grandis is by far the dominant ant species in virtually all non-arid parts, from seashore to mountaintop, and it is a major agricultural and household pest (WETTERER & al., in press). Lasius grandis is also the most common ant on the Atlantic islands of the Azores (37 - 40° N; Wetterer & al. 2004). Lasius neglectus is currently a major pest in many parts of Western Europe (see SCHULTZ & SEIFERT 2005).

Lasius niger, L. grandis, and L. neglectus are omnivorous and commonly scavenge on dead animal material (WILSON 1955; pers. obs.). All three are known as household and outdoor pests and commonly tend Hemiptera in trees (WHEELER 1910, FOREL 1928, WILSON 1955). Only one feature of the published description of the Bermuda plague ants is not known for Lasius. I could find no published records of Lasius species attacking live vertebrates. It is certainly possible that the reports of the ants attacking vertebrates were exaggerated (e.g., see WETTERER in press). Alternatively, the 19th century ant plague in Bermuda may have involved two ant species, including a Lasius species and a second species that attacks vertebrates.

Discussion

Some Lasius species appear to be the most likely candidate for the 19th century plague ants in Bermuda. It is surprising that no Lasius is now found in Bermuda. One possible explanation is that the resident Lasius in Bermuda were driven extinct by a later invading ant, perhaps Pheidole megacephala. Why, then, did the same thing not happen on the Atlantic islands of the Azores and Madeira? The answer may be that the Azores (2335 km²; 2351 m a.s.l. max. elev.) and Madeira (796 km²; 1861 m a.s.l. max. elev.) are much larger and have more varied topography than Bermuda (54 km²; 79 m a.s.l. max. elev.). Both the Azores and Madeira also retain extensive areas of relatively intact native habitat which may never have been invaded by exotic ants (WETTERER & al. 2004, in press). Bermuda's limited area, relatively flat topography, and scarcity of intact natural habitat may have afforded the resident Lasius species insufficient refuge against the onslaughts of later invading ants, such as P. megacephala.

Unfortunately, I did not find any *Lasius* specimens from Bermuda in any museum and thus was unable to evaluate KIRBY's (1884) identification of *L. niger* from Bermuda.

It is possible that the ants from Bermuda reported by KIRBY (1884) were not Lasius at all. CLARK (1930) reexamined some ant specimens evaluated by Kirby and considered his identifications and descriptions as "worthless." I remain hopeful of finding pre-20th century ant specimens from Bermuda that will help determine with more certainty the identity of the 19th century plague ants. One interesting possibility is to look at the stomach contents of preserved amphibian and reptile specimens collected in Bermuda. For example, specimens of the endemic Bermuda lizard Eumeces longirostris that were collected by JONES (1859) and described as types by COPE (1861) are at the US National Museum. Amphibian and reptile specimens of GARMAN (1884) appear to be in this museum as well. VERRILL (1902) mentioned "a few ants" found in guts of E. longirostris specimens. I expect additional potential sources of 19th century ant specimens from Bermuda also may be found in other museums in the US and Europe that would offer further clues to how and why ants that reached plague proportions in 19th century Bermuda have now vanished without a trace.

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Zusammenfassung

In etlichen Berichten aus dem 17. und 19. Jahrhundert wird von gewaltigen Ameisenplagen auf den Bermuda-Inseln im Atlantik (32° N) berichtet. Die Identität der Ameisenarten konnte nie zufriedenstellend geklärt werden. Zu den Ameisen der Plagen im 17. Jahrhundert gibt es überhaupt nur wenige Anhaltspunkte, zu jenen des 19. Jahrhunderts haben frühere Autoren vier, ursprünglich tropische Ameisenarten als Kandidaten ins Spiel gebracht: Monomorium destructor (JERDON, 1851), Monomorium pharaonis (LINNAEUS, 1758), Pheidole megacephala (FA-BRICIUS, 1793) und Solenopsis geminata (FABRICIUS, 1804). Keine dieser Arten passt jedoch wirklich gut zu den Berichten aus erster Hand. Meine Suche nach Ameisenpräparaten von den Bermudas aus der Zeit vor 1900 in den Sammlungen mehrerer großer Museen blieb erfolglos. Basierend auf einer neuen Auslegung der veröffentlichten historischen Berichte, stelle ich hier die Vermutung auf, dass es sich beim Verursacher der Ameisenplagen des 19. Jahrhunderts um eine Lasius-Art handelt. Lasius niger (LINNAEUS, 1758) war die einzige Ameisenart, die 1873 bei einer Expedition nach den Bermudas gefunden wurde, und gleichzeitig überhaupt die erste Ameise von den Bermudas, die auf Artniveau bestimmt wurde. Tatsächlich könnte es sich bei jener Ameise jedoch um eine andere, ähnliche Lasius-Art gehandelt haben, z.B. um Lasius grandis FOREL, 1909, die derzeit häufigste Ameisenart auf den atlantischen Inseln Madeira (33° N) und Azoren (37 - 40° N), oder um Lasius neglectus VAN LOON & al., 1990, heute ein weit verbreiteter Schädling in Europa. Bemerkenswerterweise wurde seit 1873 von keiner *Lasius*-Art von den Bermudas mehr berichtet. Möglicherweise ist *Lasius* auf den Bermudas von später eingetroffenen Ameisen ausgelöscht worden. Die geringe Flächenausdehnung der Bermudas, die recht flache Topographie und die Seltenheit intakter, natürlicher Lebensräume mögen unzureichend Rückzugsmöglichkeiten vor den Angriffen invasiver, exotischer Ameisen gegeben haben.

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