FINAL OBSERVATIONS ON *PHEIDOLE MEGACEPHALA* AND *IRIDOMYRMEX HUMILIS* IN BERMUDA*

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INTRODUCTION

Pheidole megacephala (Myrmicinae) and *Iridomyrmex humilis* (Dolichoderinae) are two well known invasive pest species of ants which, within approximately the last century and a half, have achieved almost worldwide distribution within the tropical to semi-tropical habitats available to them. Both are extremely aggressive and are capable of displacing native ant faunas on an impressive scale. Thus *P. megacephala*, originating probably in middle Africa, radiated extremely actively in both the Old and New Worlds as a "tramp" species, and by 1852, judging by Heer's vivid account (Heer, 1856) it had thoroughly occupied, among many other western European locations, the island of Madeira, exterminating a very large fraction (if not all) of the indigenous ant fauna.

Iridomyrmex humilis, the "Argentine Ant" was first reported from Buenos Aires in 1866, and described by G. Mayr in 1868 (Skaife, 1951, p. 7) (it may well have originally been indigenous to Brazil). By 1882 it had found its way (likewise as a "tramp" species exploiting human transport) to Madeira, which it occupied, in competition with the resident *P. megacephala*. It was a successful "occupation", and by 1898, according to Stoll (1898) *P. megacephala* had completely disappeared from the Island, leaving *I. humilis* as the sole ant reported. Nothing is known of further details of the explosive interaction between these species in this limited island environment.

P. megacephala reached Bermuda at least as early as 1902 (Dahl, 1902), where it behaved essentially as in Madeira, displacing the greater part of the indigenous ant fauna and "blanketing" the Islands. By the time that one of the authors made a survey in 1927, its situation as a ubiquitous field and house ant closely resembled Heer's account of it in Madeira seventy-five years earlier.

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It was therefore of particular interest when *Iridomyrmex humilis* was noted in Bermuda in 1953, the original focus having been reported at Waterville in Paget, where it was probably introduced with nursery stock. By late 1953 seven new foci had been identified, and the invader was well on its way to challenging *P. megacephala* for "possession" of the Island (Crowell, 1968). In 1955 the Bermuda Department of Agriculture officially recognized *I. humilis* as a "major economic pest", and roadside surveys were conducted by the Department, under the direction of I. W. Hughes, tracing its expansion from 1955 to 1959.

In 1959, and twice in 1963, Haskins and Haskins (1965) conducted "point surveys" which indicated that by that time *Iridomyrmex* had occupied a large part of the Island and was actively replacing *megacephala* in many districts widely dispersed throughout Bermuda. At that time these authors raised the question of whether the ultimate outcome of this competition would be complete elimination of one of the species (probably *P. megacephala*), as occurred in Madeira, or whether a long term "permanent" but shifting equilibrium would result.

The 1959/1963 survey was followed in 1966 by a more complete one by Crowell (1967), undertaken in the same basic mode as the previous ones, and including a summary of earlier surveys. Finally, the most complete survey to date was accomplished by Lieberberg, Kranz, and Seip (1975) in 1973, again using methods basically similar to those of the preceding censuses. Thus a fairly complete picture was achieved of the interactions of *humilis* and *megacephala* over nearly two decades. So far as we are aware, no detailed surveys were made, so it seemed that a final one should be undertaken, thirty-three years after the first official report of the arrival of *I. humilis*. That effort is the subject of the present note.

METHODS AND RESULTS

In some respects this last survey was disappointing. So much land in Bermuda has been committed to building and to "artificial withdrawal" in other developments eliminating or greatly modifying many of the sites included in the earlier surveys, and the density of motor traffic has so much increased that any repetition of the surveys in the older "roadside observation" mode was not only deemed impracticable, but would have been unrepresentative, in our view.

Therefore, recourse was had to a different procedure. Ten specific sites were selected which has been censused in the 1963 Haskins survey and in the surveys of Crowell and Lieberberg *et al.* and are still relatively unmodified physically, and a careful examination made of these. It was hoped that a survey of this kind would be adequate to answer at least the general questions posed above. In Table I the data for those sites are presented for the 1963, 1966, 1973, and the current surveys. The data from Crowell were by necessity under-represented, because, unfortunately, the early Department of Agriculture surveys which he reports proved difficult to compare reliably with later ones, and because the maps in his publication have been so reduced as to be difficult to interpret reliably, but the extensive accounts in his text are wholly consonant with the other material, and highly informative.

Table II presents a summary of the shifts in distribution of *P. megacephala* and *I. humilis* at the ten selected sites as recorded by the surveys, proceeding from east to west in the Islands.

DISCUSSION AND CONCLUSIONS

The first conclusion from these data is clear and unequivocal: Thirty-three years after the first reporting of *I. humilis* in Bermuda, *P. megacephala* and *I. humilis* still coexist in strength there. Secondly, the earlier surveys have noted a consistent slowing in the rate of expansion of *humilis* as the territory has become saturated, and an increasing tendency for the patterns of distribution of both species to form an interdigitating, mosaic-like pattern, reminiscent of the patterns of mosaic distribution of three species of *Lasius*, two of *Myrmica*, and one of *Formica* described by Brian (1977) for a long-occupied British garden site. This tendency, together with the slowing expansion of both species, was noted particularly in the survey of Lieberberg *et al.* Both developments appeared to have progressed further in 1986. They may well suggest an approach to "saturation" of the environment.

The "equilibrium", however, is clearly an uneasy and shifting one, with ground being continually lost and regained by both species: a feature also emphasized in the earlier surveys. It will be noted that, in the current tabulation of sites, only two, Spittall Pond Reserve and Ireland Island, have remained in consistent "possession" of one species (*P. megacephala*) throughout the whole period.

Table 1. Combined surveys of ten sites occupied by *Pheidole* or *Iridomyrmex* (or both) between 1963 and 1986 (sites which have remained physically basically unmodified over that period) suggesting competitive shifts in occupation over that time.

SITE	1986	1973	1966	1963
1. ST. DAVID'S HEAD (GREAT HEAD PARK)	<i>I. humilis</i> only	Area where <i>I. humilis</i> and <i>P. megacephala</i> coexist		
2. MULLET BAY ROAD AND FERRY ROAD (ST. GEORGE'S ISLAND)	<i>I. humilis</i> only	Mixture of <i>I. humilis</i> and <i>P. megacephala</i>	<i>I. humilis</i> and <i>P.</i> <i>megacephala</i> shifting lines with greatest area occupied by <i>humilis</i>	<i>P. megacephala</i> (sparse)
3. LEAMINGTON CAVES	<i>I. humilis</i> only	Area where <i>I. humilis</i> was replaced by <i>P. megacephala</i>		<i>I. humilis</i> only
4. KNAPTON HILL INTERSECTION	<i>I. humilis</i> only	<i>P. megacephala</i> , re- placing <i>I. humilis</i>		<i>I. humilis</i> only
5. KNAPTON HILL ROAD AND HARRINGTON HUNDREDS	<i>I. humilis</i> only	Area where <i>I. humilis</i> has been replaced by <i>P. megacephala</i>		<i>I. humilis</i> only
6. CHRISTCHURCH/ BRIGHTON HILL	<i>I. humilis</i> only	Area in which <i>P.</i> <i>megacephala</i> has re- placed <i>I. humilis</i>		Mixture of <i>I. humilis</i> and <i>P. megacephala</i>
7. SPITALL POND RESERVE	<i>P. megacephala</i> only	<i>P. megacephala</i> only		<i>P. megacephala</i> only

SITE	1986	1973	1966	1963
8. HAMILTON: NEWSTEAD	<i>I. humilis</i> ; <i>P. megacephala</i> (mosaic, predominantly <i>humilis</i>)	<i>I. humilis</i> only		<i>I. humilis</i> only
9. WRECK ROAD	<i>P. megacephala</i> only	New <i>I. humilis</i> focus. Area where <i>I. humilis</i> has been replaced by <i>P. megacephala</i>		Mixture of <i>I. humilis</i> and <i>P. megacephala</i>
10. IRELAND ISLAND	<i>P. megacephala</i> only		<i>P. megacephala</i> (sparse)	

*Of the ten localities recorded, only these two (Spittall Pond Reserve and Ireland Island) have remained unchanged (both with *P. megacephala* only) throughout the twenty-three-year observation period.

Table II. Representative shifts in distribution.

1. ST. DAVIDS HEAD:	1973: <i>megacephala</i> and <i>humilis</i> coexisting; 1986: <i>humilis</i> only
2. MULLET BAY ROAD AND FERRY ROAD (ST. GEORGE'S ISLAND)	1963: <i>P. megacephala</i> only (sparse); 1966: <i>humilis</i> and <i>megacephala</i> —shifting lines with greatest area occupied by <i>humilis</i> ; 1973 mixture of <i>humilis</i> and <i>megacephala</i> ; 1986: <i>I. humilis</i> only
3. LEAMINGTON CAVES	1963: <i>I. humilis</i> only; 1973: Area where <i>P. megacephala</i> has replaced <i>I. humilis</i> ; 1986: <i>I. humilis</i> only
4. KNAPTON HILL INTER-SECTION	1963: <i>I. humilis</i> only; 1973: <i>P. megacephala</i> apparently replacing <i>I. humilis</i> ; 1986: <i>I. humilis</i> only
5. KNAPTON HILL ROAD AND HARRINGTON HUNDREDS	1963: <i>I. humilis</i> only; 1973: Area where <i>P. megacephala</i> has replaced <i>I. humilis</i> ; 1986: <i>I. humilis</i> only
6. CHRISTCHURCH/BRIGHTON HILL	1963: Mixture of <i>P. megacephala</i> and <i>I. humilis</i> ; 1973: Area where <i>P. megacephala</i> has replaced <i>I. humilis</i> ; 1986: <i>I. humilis</i> only
*7. SPITTALL POND RESERVE	1963: <i>P. megacephala</i> only; 1973: <i>P. megacephala</i> only; 1986: <i>P. megacephala</i> only
8. HAMILTON-NEWSTEAD	1963: <i>I. humilis</i> only; 1973: <i>I. humilis</i> only; 1986: Predominantly <i>I. humilis</i> , but with small inter-spersed colonies of <i>P. megacephala</i>
9. WRECK ROAD	1963: Mixture of <i>I. humilis</i> and <i>P. megacephala</i> ; 1973: New <i>Iridomyrmex</i> focus, bordering on area of <i>I. humilis</i> and <i>P. megacephala</i> ; predominantly <i>I. humilis</i> ; 1986: <i>P. megacephala</i> only
*10. IRELAND ISLAND	1963: <i>P. megacephala</i> only; 1973: <i>P. megacephala</i> only; 1986: <i>P. megacephala</i> only

*Of the ten localities recorded, only these two (Spittall Pond Reserve and Ireland Island) have remained unchanged (both with *P. megacephala* only) throughout the twenty-three-year observation period.

In sum, these accumulated results would seem to give a fairly highly probable answer to the questions posed in 1965: the situation would seem to be one of equilibrium rather than slow replacement, at least on the time-scale involved.

Certain ancillary observations are of interest. Despite the near-saturation of the environment by the "tramp" species, other ants have regularly been reported, often now as cryptic rarities, in all of

the earlier surveys. The genus *Odontomachus*, (*insularis* and *brunnei*), present in later surveys, was reported from Bermuda by Dahl (1902), together with *P. megacephala* and was relatively abundant in 1927. It is now a rare form. Other long-term survivors include the genus *Brachymyrmex* (still relatively abundant in niches unoccupied by either tramp species) and the genera *Paratrechina*, *Cardiocondyla*, *Hypoponera*, and *Wasmannia*. Several of these are well known West Indian species, some themselves relatively invasive. So a number could represent relatively recent arrivals or successive reoccupations. Thus *Paratrechina* was first described by Crowell in his survey. On the other hand, a number seem to have been in Bermuda on a long-continuing basis despite the disturbances around them. In addition to *Odontomachus insularis*, for instance, *Hypoponera opaciceps* seems to have been recorded as early as 1902, and *Wasmannia auropunctata* was recognized by the Department of Agriculture and Fisheries of Bermuda as early as 1950 (Crowell, 1968).

In the course of their 1963 survey, Haskins and Haskins visited a number of the small islands in the Great Sound, including Hinson, Darrell, Ports, Long, and Hawkins, all at that time undeveloped and unoccupied. In all of them, pure and dense stands of *P. megacephala* were found, with no trace of *I. humilis*. This is probably not surprising, given the "budding" mode of colony propagation typical of *I. humilis*, in which young queens in the polygynic communities, fertilized within the community, typically omit the nuptial flight and remain in the parental nest, migrating with worker groups to found new sub-associations. These islands in Great Sound and other similar ones do not seem to have been examined since. It would be interesting to do so again, especially in such a location as Five Star Island in Southampton Parish, lying very close to an area of the mainland heavily populated with *I. humilis*.

Finally, attention should be drawn to the fact that no account was taken in this last survey (nor perhaps in the others) of the possible effects of the use of insecticides on any of the sites. There seems no way to check this element with any certainty, but we believe it unlikely that it has been a significant factor, since none of the sites examined (with the possible exception of the immediate vicinity of Hamilton itself) included crop or garden areas. The great majority involved roadside verge-land or rough and unimproved brush areas.

a good part much exposed to wind and weather, especially in winter, which would be expected to minimize the effectiveness of sprays, especially against these largely subterranean insects.

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