

Observations of Nest and Colony Structure of the Neotropical Ant *Dolichoderus attelaboides* (Formicidae: Dolichoderinae)

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ABSTRACT

Two polydomous colonies of *Dolichoderus attelaboides* are described from Trinidad, West Indies at the start of the rainy season. One comprised four nests, the other five nests. Each nest was in a cylinder formed by a dried, rolled *Ischnosiphon arouma* (Marantaceae) leaf plugged at the ends with rough carton. Each colony had several hundred workers and some hundreds of brood. Three out of four nests from one colony had multiple dealate queens, in each case with just one showing developed ovaries. The other colony had no dealate queen in any nest, which may indicate that the colony was in a state of senescence. Each colony had alate adults and pupae, all queens. This finding is consistent with the hypothesis of split sex ratios. In each colony we also found several supposed prey items, as well as *Crematogaster* sp. workers and several limuoid beetles. These latter are presumably specialized myrmecophiles.

INTRODUCTION

Dolichoderus attelaboides (Fabr.) is a relatively large member of the worldwide ant subfamily Dolichoderinae. It is widespread in South America north of the Southern Cone, including the West Indian island of Trinidad (MacKay 1993). MacKay (1993:38) has summarized the sparse published biological information on this ant. It is mainly arboreal, found in forests and plantations, where it builds carton nests on above-ground vegetation. It is known to respond aggressively to disturbances of the nest.

Ischnosiphon arouma (Aubl.) (Marantaceae) is a common understory plant in some Trinidad forests. It has a single spray of large, long-stemmed undivided leaves. As these age and dry out, the petiole and leaf blade come to hang approximately vertical, and the leaf curls to form a durable cylinder that can be more or less closed along its length.

In May-June 2003, near the end of the dry season, we found two apparent polydomous colonies of *D. attelaboides*, each occupying several old *I. arouma* leaves. We describe here the structure of the nest and colony composition in this species.

MATERIALS AND METHODS

All observations are from the Arena Forest Reserve (10E 34N 61E 14W) in Trinidad, West Indies. This is a well-developed lowland secondary forest on well-drained soil.

The nest description is based on nine active and two old nests. To locate active nests, we supplemented visual inspection of dry, rolled *I. arouma* leaves with mechanical disturbance of plants, usually by rapping on stems with a stick. *D. attelaboides* workers tend to rush out of the nest after even a light disturbance. On locating the first nest of each colony, we examined all rolled *I. arouma* leaves in the vicinity, removing all non-nest leaves as we did so, to a radius of at least 5 m, as well as examining other understorey vegetation. We did not search in the ground layer. We then left each nest undisturbed for about 15 min, in order to allow alarmed workers to re-enter the nest, and bagged the nest, and froze it within two hours. All collections took place in the late morning. We later dissected each nest individually. The dealate queens were dissected and their ovaries examined for the presence of mature oocytes.

Callow workers and alate queens are readily

distinguishable from mature individuals by their lighter colouration. For present purposes, callows were diagnosed as having the femora and tibiae of the fore-legs yellowish-brown, versus dark red. As a supplementary character, the upper surface of the head, thorax and gaster is partly or entirely pale yellowish-brown in callows, versus uniformly dark in mature individuals.

As in most ants, pupal and adult queens are readily distinguished from workers by the much deeper thorax and the presence of wing buds, wings or wing scales.

Eggs were identified by their size and smooth surface, without apparent segmentation. However, we did not always take the time to definitely distinguish eggs from first-instar larvae, so that these are grouped together as "eggs".

Voucher specimens of *D. attelaboides*, collected by the authors as nest series 2117, are deposited in the Land Arthropod Collection of the University of the West Indies and at the University of Texas at El Paso.

RESULTS AND DISCUSSION

Nest Structure

Each nest in our study occupied a rolled dead leaf of *Ischnosiphon arouma*. The cylindrical space inside the leaf formed the nest cavity. Among active nests, this had a length of 12-14 cm and an estimated inner volume of 24-382 ml in our sample (Table 1).

Each nest cavity was closed below with a sheet of rough, dark

Table 1. Dimensions of nests A-D of colony 1 and nests A-E of colony 2 of *Dolichoderus attelaboides*.

	Nest								
	Colony 1				Colony 2				
	1A	1B	1C	1D	2A	2B	2C	2D	2E
Height (cm)	13.5	14.5	12.0	13.5	22.0	24.0	21.5	12.8	12.0
Inner diameter (cm)	2.0	2.7	3.5	1.5	3.5	4.5	2.5	4.5	6.0
Volume (ml)	42	83	115	24	212	382	106	255	339
Distance leaf base to upper sheet (cm)	0	12	2	10	6	4	1	14	9
Distance lower sheet to leaf tip (cm)	9	8	0	3	1	3	7	7	9

carton, the "lower sheet". It was partly closed above by an "upper sheet" of the same material. This latter always left a broad entrance hole, and in some nests the cylinder was hardly closed at all above. Only relatively neatly rolled leaves served as nest cavities, in our sample. The closure along the side was completed with additional carton joining the exposed leaf margin to the vane near the main vein. This carton formed a variable "side band" up to several mm wide, extending from the lower sheet to the upper sheet. In the one exception to this pattern, nest 1C, the upper sheet was complete, and a break in the side band near the top served as the entrance hole.

Embedded in the carton were abundant coarse fibres and occasional entire leaflets of *Pentaclethra macroloba* (Willd.) (Leguminosae), as well as apparent grains of soil. *P. macroloba* is a dominant tree in the Arena Reserve, where its leaflets form the main nest-closure material of another ant, *Anochetus emarginatus* (Fabr.) (L. Dempewolf, M. Cazabon and A. Roach, pers. comm.).

There was no inner partitioning of the nest cavity except in 1A. In this a dry leaf of another plant was found inside the nest, fixed in place with carton in such a way as to form an incomplete division between about the upper third and lower two-thirds of the cavity. The area above the partition contained mostly workers and brood, suggesting that it was being treated as a sort of fortuitous brood chamber.

Colony Composition

As we interpret it, Colony 1 comprised four nests (1A-1D) in two *I. arouma* plants about 2 m apart, while Colony 2 comprised five nests (2A-2E) in four plants with a maximum separation about 3 m. The close spatial association of nests within each of the two groups, together with a superabundance of apparently suitable, unused *I. arouma* leaves in the area around each group, supports this interpretation. Colony 1 was in an area of sparse *I. arouma*, while Colony 2 was in a broad, dense patch of this plant. The composition of each nest (Table 2) is assumed to be complete for all

phena except mature workers. It is likely that some of these were away from their nests at the time of collection.

A striking feature of each colony is the considerable similarity of composition among nests, with each phenon distributed approximately at random among the nests. In addition, the two colonies are similar to each other except in one conspicuous aspect: While Colony 1 had 17 dealate queens distributed among three of its four nests, we found no dealate queen in any part of Colony 2. Nests 1A, 1B and 1C each had one queen with developed ovaries, suggesting decentralized reproduction at the level of the colony. The presence in nest 1D of a badly mauled queen (presumably dead at collection) with wings chewed off is suggestive of reproductive conflict at some level, possibly with worker policing (Ratnieks 1988).

The apparent absence of dealate queens in Colony 2 is something of a puzzle, especially in view of the abundant young brood. The most obvious hypothesis is that we failed to find all nests. However, our search was extensive enough that any additional nest in an *I. arouma* leaf or other understory vegetation would have had to be at a considerable distance, with plentiful suitable nesting sites much closer at hand. In addition, it is noteworthy that not one of five known nests had any dealate queen, in strong contrast to Colony 1. An alternative hypothesis is that Colony 2 had been rendered queenless and was in a state of very early senescence, possibly with some reproduction by workers.

Each nest of each colony had new reproductive adults and pupae, but these were uniformly queens, with no sign of males. This is consistent with the hypothesis of split sex-ratios among colonies (Bourke and Franks 1995). It is less likely that males are produced later in *D. attelaboides*, both because this runs against the rule in social hymenoptera (Bulmer 1983) and because there were no male pupae in our colonies at a time when most nests already had more alate queens than queen pupae. Our results are also consistent with a burst of colony founding in the early wet season in this species.

Although the numbers of mature workers, callow workers and brood vary quite considerably among nests, ratios among mature workers, brood and callows workers are similar between colonies and reasonably uniform between nests of Colony 1. There is, however, no such consistent pattern among nests of Colony 2, which may indicate that it had recently lost (or slaughtered) its queens and was losing social cohesion, as suggested above.

As seen in Table 2, most nests contained small numbers of insects other than *D. attelaboides*. Some of these (omitted from Table 2) were probably or certainly prey, but nests also contained intact insects of two kinds that appeared to be nest symbionts. (Because all nests were frozen before examination, it can only be assumed that these were alive at collection.) It seems most likely that the *Crematogaster* ants were present as kleptoparasites. The term "nest symbiont" is applied loosely with respect to *Crematogaster*, as there was no indication that they nested together with *D. attelaboides*. Most nests also contained beetles with the typical limuloid form of several lineages of obligate myrmecophiles (Kistner 1979, 1982).

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Table 2. Composition of insects in nests A-D of colony 1 and nests A-E of colony 2 of *Dolichoderus attelaboides*.

	Nest										
	Colony 1					Colony 2					
	1A	1B	1C	1D	Total	2A	2B	2C	2D	2E	Total
Adults											
Dealate queens	2	8	7	0	17	0	0	0	0	0	0
Alate queens	11	8	4	2	25	3	6	19	5	12	45
Callow	4	7	4	2	17	3	6	14	4	7	34
Mature	7	1	0	0	8	0	0	5	1	5	11
Alate males	0	0	0	0	0	0	0	0	0	0	0
Workers	176	237	243	102	758	665	319	117	158	142	1401
Callow	120	126	92	35	373	251	93	12	16	16	388
Mature	56	111	151	67	385	44	226	105	142	126	643
Brood											
Queen pupae	3	10	0	1	14	4	1	1	0	1	7
Male pupae	0	0	0	0	0	0	0	0	0	0	0
Worker pupae	40	61	64	11	176	232	20	22	0	5	279
Larvae	22	70	35	38	165	72	42	26	20	29	189
"Eggs"	13	13	11	0	37	58	28	9	120	7	222
Total brood	78	154	110	50	392	366	91	58	140	42	697
Presumed nest symbionts											
<i>Crematogaster</i>	6	3	10	23	42	6	9	60	17	1	93
Limuloid beetles	2	0	1	0	3	6	6	0	2	0	14

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