THE NEST OF AN ANOMALOUS COLONY OF THE ARBOREAL ANT *CEPHALOTES ATRATUS*

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One of the distinctive elements of the neotropical ant fauna is the heavily armored and spinose genus *Cephalotes* of forested areas. The workers have powerful, short and convex mandibles that enable them to gnaw out cavities in the trees for nests. Kempf (1951) lists the species *atratus* (L.) from Honduras to Brazil and northern Argentina and summarizes the known biological records. He has also synonymized *quadridens* De Geer with *atratus*. As thus known, the worker is characterized as 8 to 14 mm and black in color and the female about 20 mm and black. The male length is up to 14 mm and with head, thorax and penduncle black, gaster and appendages testaceous to dark ferruginous. Other characters of the castes are fully described by him.

Under the name of *Cephalotes atratus quadridens* the present colony has been alluded to briefly (Weber, 1938, 1947; Wheeler, 1937; Whiting, 1938) and a figure of one of the anomalous workers has appeared (Wheeler, 1936). No account of its biology or nest has hitherto been published. Observations on the colony were initiated on December 11, 1934 and terminated on October 4, 1935, during tenure of a National Research Fellowship in Biology.

It is one of two known ant colonies that contained unprecedented numbers of anomalous individuals. Both were discovered and observed by the writer in Trinidad, B. W. I. and the other (*Acromyrmex octospinosus* Reich) was the subject of the book by Dr. Wheeler (1937). The *Acromyrmex* anomalies were considered by him to be mosaics or gynandromorphs but were later (Whiting, 1938) tentatively characterized as intersexes and intercastes. Dr. Whiting suggested that the *Cephalotes* anomalies, called

gynandromorphs by Wheeler, may be female intersexes if not also intercastes. These colonies, which are in the author's collection, need to be restudied and the cause or causes of the anomalies remain obscure.

General Environment of the Colony

The colony was taken on the savannah grounds (elevation 63 feet) of the Imperial College of Tropical Agriculture in a saman tree (*Samanea saman* ((Jacq.) Merrill) of the Family Mimoseae, a large, umbrella-shaped tree native to Central America. The daily temperature extremes were close to 21-30° C. and annual rainfall some 70 inches.

The tree was separated by 18 meters of well-cropped grassy lawn from the nearest tree, a *Cassia grandis,* to the southwest. The next nearest tree was 48 meters south and was a saman which housed a normal *Cephalotes atratus* colony in a large branch. Another tree, a saman, was 82 meters southwest from the first and lacked a colony of this species. Nine meters south of the latter tree was a saman tree with a normal *Cephalotes atratus* colony. There were no other suitable nesting sites in the area. It was the habit of the ants of all colonies to forage over the grass adjacent to their trees, where some were taken by the giant marine toad, long known as *Bufo marinus* (L.) (Weber, 1938).

The Nesting Tree

The crown of the saman, fully 30 meters in diameter, had an estimated volume of the order of magnitude of 2000 cubic meters and branches on which the ants were found were up to 15 meters distant from the actual nest site. The leaves were bipinnate and large and closed just before sunset. Early in the dry season (January-May) the tree bloomed and late in February young fruiting pods appeared.

Branches of the tree touched those of the *Cassia* whose trunk was 18 meters from that of the saman. The branches met at a height of seven meters and served as a bridge for the ants. The *Cassia,* also with large, bipinnate leaves, was a young and vigorous tree with smooth bark and

appeared with similar but smaller fruiting pods. There was no nesting site available here for the ants.

The Nest

The original position of the nest was just within the trunk, at the place where a large branch had been sawed off on the north side some 12 years previously and at an elevation of three meters. In the drying of the cut surface an irregular crack had developed that was about 10 mm wide and a few centimeters long. Through this crack the ants gained entrance to an otherwise hard and sound trunk.

The ants gnawed a series of irregular tunnels and chambers in the tough wood, the chambers closest to the outside being some 2-3 cm in, the farthest about 30 cm. There was no regularity in the disposition or size of the tunnels and chambers, the latter being simply enlargements of the former. The nest resembled that of *Camponotus herculeanus* except that the alternating hard and soft layers of wood in northern trees were absent from this tropical wood and there were therefore no concentric excavations.

After the nest was excavated on March 3, April 27 and June 21 the surviving ants took refuge in the innermost tunnels. The wood here was so hard and tough that the ants eventually left it and for a month there was no indication of another site. Finally, on July 28, a worker was detected shortly before sunset crawling to an inconspicuous hole in a small branch at a point 10 meters distant from the trunk and three meters above the ground. The branch was 6 cm in diameter. A mass of ants of all castes was found in a cavity here that was about 20 x 2-4 cm. The opposite end of the cavity terminated in a small tunnel a few millimeters in diameter which was too small for a male or female ant but suitable for a small worker. The ants had either made this cavity or enlarged that of an *Azteca* colony.

During the next two months eleven more auxiliary nests were found. The size varied considerably and all were in dead stubs of branches or in live wood. The mandibles of the workers were small and much time was required

to excavate. Some freshly excavated cavities contained scarcely a score of brood and with room only for a few workers. No auxiliary nests were formed in the *Cassia* tree.

Area Patrolled by the Ants

The entire crown of the saman was available to the ants. They crawled over every main branch and were frequently found on the most remote smallest twigs and leaves. They occasionally foraged over the grass at the base of the tree but not more than 3-6 meters away from it. The *Cassia* tree was also used, the ants gaining access over the long bridge formed by the intermingled branches. To prove that the ants were from the saman colony, workers on the saman were marked with yellow paint on the thorax, those on the *Cassia* trunk were marked on the gaster. One from the latter site was recovered later on the saman at a point where it had to traverse a minimum distance of 32 meters, whether by the grass route at the base of the trees or by the aerial bridge. Another ant was recovered a similar distance away on the saman. Marked ants from the saman were later taken at the base of the *Cassia* tree and on the *Cassia* at the aerial bridge site. Other *Cassia* ants were recovered in saman nests.

The total volume of foliage used by the colony was thus well in excess of the 2000 cubic meters of the saman crown and approached the volume of soil used by a large *Atta* colony. The area patrolled was not computable on the same basis as that of a terrestrial ant but ants of the colony were taken some 50 meters distant from each other, an indication of the diameter of the area.

The Colony

A. The Female

The female was discovered on April 27 after hours of chiselling into the hard wood on March 3 and later. She was in a small cavity with eggs and minima larvae and was removed to an observation nest, together with a few media workers firmly clinging to her and some other workers and brood. Within two hours she laid nine eggs. The workers assisted with egg-laying. As an egg would

slowly emerge a worker would grasp it and pull it away. She continued to lay eggs for two days; one laid on the 29th took 15 minutes to be completely extruded. On the 30th at 8:05 a.m. she was found to be lying on one side, with legs folded. The workers were licking her body and pulling her about. She showed no movements when she was isolated under the microscope, except of the terminal pair of gastric segments. These were rhythmically opening and closing the cloaca, an early cycle taking 20 seconds, later cycles taking longer. One lasted 25 seconds and consisted of 10 seconds of opening and 15 seconds of closing. The segments opened to a maximum of 0.7 mm which was easily equal to the length of one of her eggs. Twenty seven minutes after she was discovered in this condition the movements appeared to be in the nature of a retching and they later slowed down. Within three hours the cloaca was open more than it was closed and she was then returned to the observation nest. The workers immediately approached, explored her with their antennae, and licked her thoroughly as before. By 1 p.m. her terminal segments were still moving and an hour later she was preserved in 80% alcohol, where she floated despite an opening made in her gaster to allow the penetration of the fixative. Later sectioning showed that the ovary was normal and contained many eggs in all stages of growth. There was no sign of a double or binucleate egg.

All evidence pointed to the existence of the single female as the progenitor of this large colony. Her age probably dates from some time after the branch of the tree was cut off, 12 years earlier.

B. Brood

Eggs, larvae and worker pupae were found on the first occasion of opening the nest on March 3 and up to August 5. Soon after April 27 the ants largely abandoned the original nest site.

Media larvae were taken on September 15 and maxima to the 25th. Male pupae were taken on June 21 and were not again found until September 19 to 25. Adult males were taken June 21 — August 5 and two on September 25.

Alate females were found on July 28 and one on August 5. The September brood probably was the result of unfertilized eggs laid by the workers; some of these had fully developed ovaries containing eggs. The brood maturing through August 5 was probably from eggs laid by the queen up until her capture on April 27. The data suggest a maximum period of development from egg to worker of between 100 and 141 days and comparable periods for the sexual castes.

The first part of the worker pupa to take on the adult coloration was the eyes, as in *Cryptocerus varians,* then the tarsal claws and apices of the large spines and gaster. The head and thorax become black last. The pupa may move its legs and other appendages slightly when it is still a pale yellow in color. The pupa is aided from its white envelope by the adult workers licking and using the mandibles to pull at it. A callow worker, gray in color, could walk fairly fast when the nest was exposed in July.

Food of the Ants

The main source of food for the colony throughout the months of observation was the secretions of the membracid, *Adippe inconspicua* Fowler. From February through July these insects were on the fruiting pods of the saman and were being constantly tended by the ants. As the pods in most cases were many meters from the nest sites, much time must have been consumed by these slow-moving ants in travelling back and forth from the feeding areas. While the pods were young and succulent they bore large numbers of *Adippe* and their secretions at this time appeared to be particularly important as a source of ant food.

Workers that were foraging on the grass at the base of the tree gathered bird feces containing insect remains. Others dismembered a large, naked caterpillar lying freshly killed in the grass. The ants were often found to carry indeterminable bits of food but were at no time seen to carry recognizable plant remains.

Myrmecophiles and Predators

The entire absence of myrmecophiles in this large colony

is noteworthy. Other common ants of the area that had a comparable colony size had a varied myrmecophilous fauna. Two phorid flies hovered over the nest while the brood collection of April 27 was being made and one apparently tried to ovoposit on a worker but both soon left. The integument was probably too dense for these parasites. On May 21 five workers were found in a motionless mass at the base of the tree under their nest. They were placed in a moist container to determine whether parasites would emerge but none did.

The marine toad, as noted before, fed on these ants and was the only predator observed. The stomachs of several ant-eaters (*Tamandua longicaudata* and *Cyclopes pygmaeus*), taken from nearby trees, did not contain remains of these ants.

General Behavior

The behavior of the workers underwent a marked change during the months of observation and collecting and seemingly as a result of this "persecution." At first they were aggressive, swarming over the hands and biting repeatedly. Their small mandibles could only pinch the human epidermis. Some workers fled but none freely dropped off the tree. Those which dropped off to the ladder or the clothes immediately climbed to where they could bite the exposed skin.

During July and early August they lost their aggressiveness to a large extent. By this time there were much fewer individuals and stimulation of one another would be reduced. Nevertheless, when a mass of workers would be encountered, as in exposing an auxiliary nest, the ants seldom attacked but fled.

By September the ants were so timid that, when one would be approached, it would instantly release its hold on the branch and drop to the ground from any height. It was noteworthy how often in their fall they might catch hold with their tarsal claws of a leaf, twig or hair on one's arm as they brushed by. The ants freely dropped off though one's fingers might be 15 cm. from them. Those that did not drop off ran quickly to the underside of the

branch. When the nests were exposed the ants remained motionless, appressed to the branch, or fled.

On September 14, 3:30 p.m., several small groups of ants were resting quietly on main branches of the *Cassia*. Their mandibles were not moving and they were not feeding. Aggregates like this at this time of day were not seen when the colony was larger. On October 2 a cluster of 31 was on the sunny side of the *Cassia* trunk at 8 a.m. They were watched for half an hour and showed no tendency to leave or to feed. For the most part they remained motionless but occasionally one would change position. On both dates the ants instantly dropped off when they were approached with the fingers.

At all times of the year activity outside the nest ceased shortly before sunset, when the saman and *Cassia* bipinnate leaves folded and drooped down, and was resumed at dawn.

Behavior with Brood and Membracids

When the brood was exposed during the first months many of the workers tried to carry it away. There was no division of labor on the basis of worker size or normal or anomalous morphology. An egg or small larva would be held by the middle, between the mandibles, and carried under the massive head. A larger larva or a pupa, however, would be grasped tightly towards one end and carried vertically in front of the worker or even inclined over the back. The workers assisted the callow from its pupal case by cutting this with their mandibles as noted earlier. When the brood was exposed in later and smaller auxiliary nests the same behavior was noted despite the change in aggressiveness.

The membracids were not defended nor taken away by the ants when attempts were made to collect both. At all times, when feeding membracids and ants were approached, the ants and the adult female membracids fled, the latter taking flight, while the nymphs were left unguarded.

Behavior of Anomalies

The anomalous workers behaved as normal workers. They were aggressive when the rest of the colony was

aggressive and fled when the others fled. Those most conspicuously anomalous were the maxima and these were nearly all collected in the first few months. They carried food to the nest, aided in dismembering a caterpillar and tended membracids. One with worker body and male genitalia stroked a membracid as would a normal worker; other anomalies were frequently on the pods. They carried brood, when the nest was disturbed, like normal workers. The anomalies also licked the female integument in the observation nest, a typical worker habit.

Anomalies with one or both of the curious ram's horn antennae (as in Wheeler, 1936, Fig. 1) were able to pursue a direct course and no clear asymmetry in motion was observed. The winged and apparently female anomalies behaved as did the workers and either bit quickly and repeatedly or fled.

The males, which were superficially normal, were uniformly timid, did not bite and either attempted flight or concealment.

Numbers in the Colony

Systematic collection of the colony was undertaken when the colony was discovered to be anomalous. By June 21 the totals were:

Apparently normal worker adults	7284
" " pupae	885
Anomalous worker adults	2919
" " pupae	201
Adult males	94
Male pupae	48
Queen	1
	11432

The July and later collections added 19 alate females, including eight anomalies, and several hundred workers.

Summary

A nest of the arboreal ant, *Cephalotes atratus* (L.), contained over 10,000 adults during a 10-month period of collecting. The workers at first were aggressive and

attacked freely. Later, apparently as a result of the systematic search and collecting, the ants became timid, dropping from the tree or running to the opposite side of the branch when approached. Finally the remainder formed on another tree into temporarily immobile small clusters. These remnants of an aggressive colony lacked the stimuli of the queen, brood and other workers that might be necessary to maintain their normal behavior. The colony was also noteworthy in containing large numbers of anomalies whose cause remains obscure.

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