THE FUNCTIONAL SIGNIFICANCE OF DIMORPHISM IN THE AFRICAN ANT, *OECOPHYLLA*

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Among the common and notorious ants of tropical Africa, Indomalaya and Papua are those belonging to the genus *Oecophylla*. They are conspicuous because of their moderately large size, abundance on domesticated plants such as mango and coffee, and aggressive habits. Their propensity for tending scale and other insect pests renders them economically important. Their habit of swarming over the incautious person who brushes accidentally against a tree dominated by them and biting viciously, causes them to be ranked among the numerous tropical pests. Of general interest is their habit of using their own larvae as silk-producing shuttles to bind together green leaves of which the nest is formed.

The variation in size of the workers was well known and they were therefore classified among the numerous polymorphic ants. The extent and significance of the variation had gone unnoted. Upon measuring 100 workers from each of three colonies taken in the Anglo-Egyptian Sudan in 1939, however, a true dimorphic condition was revealed which had gone completely unrecognized. This dimorphism was not the usual type in ants where the maxima has a markedly larger head than the minima and is called a soldier caste. In an article ('46) show-

ing the condition by figures and graphs I speculated "when the extremes of workers are obvious, as in the maxima and minima *Atta,* the rôle of each is similarly obvious. Perhaps there is a similar division of labor in *Oecophylla,* the smaller workers caring for the brood, the larger workers holding leaves together in nest making, defending the nest, etc."

As biologist to the Central African Expedition of the American Museum of Natural History, led by Dr. James L. Clark, I had an opportunity to revisit Africa in 1948 and test this speculation. The division of labor correlated with the dimorphic condition was strikingly verified. To summarize, it was determined that only the maxima foraged from the nest while the minima stayed within it, caring for the brood and not leaving the nest unless it itself was disturbed.

The distribution in Africa of *Oecophylla* lies largely between 15 degrees North Latitude and 15 degrees South Latitude with an extension southward along the Indian Ocean coast. The records obtained on the expedition were largely from the central part of this range and are probably representative of the situation in Africa. One species, *longinoda Latreille,* with several subspecies or "varieties" represents the genus in Africa. Prior to Wheeler's great work on Congo ants ('22) the large workers were known to most people as the subspecies or race *longinoda,* the smaller workers as the subspecies or race *brevinodis* André. This long-time failure to recognize the conspecificity of the different sizes was responsible for such suspicious listings as that of Stitz's (1916) of both "races" from the same locality. Wheeler himself, though aware that the two were the same species, was unaware of the implications of these variations in size. All of the chief describers of African ants erected new forms on color alone, Santschi ('28) being the latest, calling them variously, varieties, races or subspecies. These are not correlated with dimorphism and more careful study in the field will be necessary to determine whether they are valid or not and what rank they deserve. Some, at least, are merely normal color variations within the species. The only myrmecologist speculating at all on the variations appears to be Santschi ('35, p. 279) who records the species from the Belgian Congo with the note "Le tube ne contenait que des ♀ de petite taille: serait-ce une variété ou un nid commençant?" The specimens were doubtless neither a "variety" nor the workers of the first brood but the normal minima caste and his restraint this time was fortunate.

Records and Observations

The following specific records and observations are arranged by localities starting with Kenya and proceeding west. All are in 1948.

Mombasa, Kenya, February 11. At the height of the long dry season in mid-afternoon, when very few ants or other insects were to be observed, workers were taken thirteen miles north of this ancient Indian Ocean seaport. No intensive search for the nest could be made in the limited time available. Only the maxima caste was seen and this consisted of workers crawling slowly in the shade, over the dry and dusty leaves beneath two large mango trees and on the trunks themselves. The ants doubtless nested beyond reach in the trees.

Juba, Anglo-Egyptian Sudan, March 20. Also at the height of the dry season. Maxima workers only were out, at 4:30–5:00 P.M., foraging up and down mango trees at the edge of the Nile River and on the shaded ground beneath. The ants did not forage over the sunny, dry soil where the surface temperature at 3:45 P.M. was 119° F, the shade air temperature being 99° F. The relative humidity in the shade over the soil surface was 19%. The previous Sudan records (Weber, '43) were also in part from mango trees and described insect prey (grasshopper, beetle, bee, ponerine ant) and myrmecophiles. When the nests were disturbed a rattling sound like dry peas dropping on a plate was made by them striking their bodies against the leaves and nests. The body vibrated up and down between their stationary, widespread legs.

Dungu, Belgian Congo, February 29. On various trees and foraging on the ground in mid-day. Only the maxima caste out. These were carrying prey consisting of other insects in the direction of the tree crowns. Several had a captive *Camponotus* ant spread-eagled on a tree trunk, grasping it by opposite legs.

Niangara, Belgian Congo, February 29–March 1. The *Oecophylla* were undoubtedly the dominant arboreal ants in this wooded town and may well have been the dominant insects since they were found wherever looked for. They nested abundantly in mango trees. Scores of nests were scattered over individual crowns and since adjacent crowns usually interbranched the limits of a single colony would be difficult to determine. The ants foraged freely over the ground. Since the weather was mild, and rain had fallen several days before, their activities were not particularly influenced by meteorological conditions. A heavy rain 3–5 P.M. March 1 naturally caused a suspension of activity outside the nests for a time. Since they were active long after dark and before dawn they were nocturnal here as they were found to be elsewhere.

Every one of the thousands of workers seen foraging on the trees and ground from numerous nests was a maxima. The minima caste was only found by actually collecting sample

nests. Their existence would never have been suspected from casual collecting. The functions of the maxima were foraging for food and protecting the colony. The minima tended the brood in the nests and probably also the scale insects feeding on the leaves forming the nests; they were also seen to tend adult males and drag them about when the nest was disturbed. While both were aggressive, it was only the maxima that was effective or had the usual opportunity since the minima were confined to the nests many feet above the ground. The maxima rapidly crawled up the trouser legs or coats and viciously bit the unprotected skin. When biting they were hard to dislodge. No particular reaction followed the bites, however.

The food was found to consist chiefly of the carcasses of other insects and the secretions of scales. They also took pieces of fruit from our camp. Among the prey were termites, both the sexual forms from dissemination flights following the rains, and workers, when the ants had access to them. One such case was that presented when a truck wheel damaged a terrestrial termitarium and the ants took the opportunity to seize worker termites engaged in repairing the damage to their nest. These were later found many feet away and up in the arboreal ant nests. One nest had parts of four large and heavy sexual termites (*Macrotermes natalensis*?). These had been obtained from the ground and carried many feet away to the tree. At this time of year sexual forms were maturing. Probably many of the males had flown away at the time of the first rains several days before, following the long dry season which started in December.

Other arthropods associated with *Oecophylla* here were predatory Hemiptera with a coat of debris like the ant-nest debris, and a myrmecophilous spider. These were in a shelter of leaves attached by silk as in the true nests and housing scale insects only.

Bondo, Uele River, Belgian Congo, March 14. Nesting on a coffee tree of about twelve feet in height. There were scores of nests of variable ages on the bushy crown of the tree, which was in fruit. The ants bit painfully and were exceedingly aggressive. A myrmecophilous spider and tiny Coleoptera were in one nest. Male brood and adult males were present.

Of the large numbers of ants swarming over the tree and on the ground beneath, all were maxima. They were the brown form recorded also under Ndouti, French Equatorial Africa.

Zemino, Mbomu River, French Equatorial Africa, 5° N. Lat., 25° 10′ E. Long., March 4–8. A colony was nesting on a mango at the river band. One large nest at a height of seven feet which was examined had a large quantity of larvae with a few pupae. There was also prey consisting of dead worker ants of the genera *Odontomachus* and *Dorylus* (*Anommna*) and a female *Brachyponera sennaarensis* Mayr. A maxima was taken carrying part of a lepidopterous insect carcass. Large numbers of workers were out at 2:30–3:00 P.M. over the tree and forming dense files extending out over the ground beneath. All were of the maxima caste.

Our camp was pitched under mango trees which were dominated by the ants. The long dry season had begun in December and no trace of rain fell in January. Showers on six days in February amounted to slightly over one inch (30 mm.). This season was broken by an inch (28 mm.) of rain March 3, a shower (8 mm.) March 5 and an inch and two-thirds (42 mm.) on March 6. The result was a great influx of winged insects to our lanterns in the evenings of March 6–8, the remainder of our stay here. Among these were the winged sexual forms of *Oecophylla* whose workers were busily engaged in capturing insects falling to the ground. Hordes of insects lost or damaged their wings or were otherwise incapacitated and at dawn the following morning the *Oecophylla* and other predators were still engaged in dragging away the remnants. The chief sufferers were male ants of various genera (*Dorylus, Crematogaster, Camponotus, Oecophylla,* etc.) and termite alates.

The ants evidently foraged twenty-four hours of the day. Only maxima were abroad and these slowly stalked about with their antennae directed stiffly forward with an angle of about 90° between them. The gaster, "knees" and tarsi were noticeably paler than the head and thorax. The whole tone of color was a brownish ferruginous. Other forms in the genus are markedly green.

Djema, French Equatorial Africa, 6° 5′ N. Lat., 25° 15′ E. Long. March 6. *Oecophylla* formed part of the ant fauna of the typical savannah vegetation which was liberally sprinkled with low, gnarled trees and bushes. North of here the savannah vegetation gradually thins out to the Sahara Desert. About 50 miles south on March 9 the ants were taken in a small area of gallery forest with much more humid edaphic conditions.

Barroua Village, French Equatorial Africa, 5° 30′ N. Lat., 24° 40′ E. Long., March 9. Maxima workers only, from a mango tree.

Rafai, French Equatorial Africa, March 10. Nesting in a mango tree. A nest at a height of seven feet was particularly neatly sewed together and contained workers and male adults with a very few larvae and pupae. The ants were tending scales on the green leaves forming the nest. The workers inside were mostly the minima caste of unusually small size.

Ndouti Village, about 60 miles east of Bangassou, French Equatorial Africa, March 10.

Gallery forest. A much darker and browner form than previously taken and darker than the Rafai form some miles east which lived in a region noticeably dryer and with less luxuriant vegetation. Only the maxima caste found.

Bangassou, French Equatorial Africa, March 12. Nesting in a coffee tree about twelve feet high and in numerous mango trees. Only the maxima caste seen foraging outside of the nest, up and down the tree trunks and on the ground below.

Conclusions

Dimorphism in the worker *Oecophylla,* consisting of maxima and minima castes, is clearly correlated with division of labor. The dimorphism involves chiefly the general size of the ant and the maxima has not evolved as far as the large-headed soldier in some other dimorphic ants. The maxima caste forages day and night as a predator on small arthropods and is a vicious and effective defender of the nest. It brings food into the nest to the minima brood. The minima caste remains within the numerous nests forming one arboreal colony and does not emerge until the nest is disturbed. It tends scale insects on the green leaves forming the nests and cares for the brood.

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Addendum

Dimorphism has recently been found in the other species of the genus, *smaragdina* (Fabricius) of Indomalaya. (Cole, A. C., Jr., and Jones, J. W., Jr., Amer. Midl. Nat., **39**: 641–651, 1948). Graphs from measurements of the workers show a bimodal curve similar to that of the African species. The measurements of the castes show that they are identical in size with their African congeners (thorax length of minima caste 1.26 mm.–2.01 mm. with greatest frequency 1.50–1.60; thorax length of maxima caste 2.16–3.30 mm., with greatest frequency 2.60–2.65 mm.).