Reprinted from Ecology, Vol. 24, No. 3, July, 1943
Printed in U. S. A.

NOTES AND COMMENT

PARABIOSIS IN NEOTROPICAL "ANT GARDENS"

The famous psychiatrist and myrmecologist, Professor August Forel, coined the term "parabiosis" in 1898 to denote the association between two species of ants living together in Colombia which he had found during 1896. Workers of the two species (*Dolichoderus debilis parabiotica* Forel and *Crematogaster limata parabiotica* Forel) formed common files to and from feeding grounds and a common nest, although they maintained separate chambers for their brood. This symbiosis differs from the more common type whereby compound nests of several species are formed, in which the chambers of each may anastomose with those of the other but are not confluent. In such cases the ants do not associate together and are frequently hostile. Parabiosis differs from another commoner association where ants of one species live with another in varying degrees of parasitism.

Ule described in 1901 what he called ant gardens which he had studied the previous year in Brazil. These gardens were balls of earth around small trees at variable heights above the ground from which grew a definite flora of small plants belonging to the families Araceae, Bromeliaceae, Gesneriaceae, Moraceae, Piperaceae and Cactaceae. Invariably the balls of earth were inhabited by one of several species of ants (*Camponotus femoratus* Fabr., *Azteca traili* Emery, *A. olitrix* Forel, *A. ulei* Forel). His far-fetched later conclusions that the ants deliberately sowed the seeds of the plants in earth which they brought up from the ground to make the balls were correctly criticized by Wheeler ('21).

Wheeler also showed that in British Guiana these ant gardens with the same or a similar flora were commonly inhabited by two species of ants, the *Camponotus femoratus* and Forel's *Crematogaster limata parabiotica*, living together in parabiosis. His paper contains a valuable review of Forel's, Ule's and Mann's examples of parabiosis in Colombia and Brazil.

In 1935 I was able to examine the ant gardens in exactly the same part of British Guiana where Dr. Wheeler's studies were conducted. During that year and the next, I found similar ant gardens in two countries not hitherto known to contain these ants and their gardens, Venezuela and Surinam. In addition to finding the *Camponotus* and *Crematogaster* so associated, a third member of the biocoenose was discovered, a tiny yellow species of *Solenopsis*. The greater complexity of the biocoenose was also shown by the discovery of phorid flies ovipositing in the adult worker ant bodies and the finding of a peculiar larval insect and adult weevil in one garden.

Camponotus femoratus, the largest and principal worker of the ant garden, was described by Fabricius in 1804 (*Syst. Piez.* p. 397) and in 1862 by Roger (*Berl, Ent. Zeitschr.* 6: 284). It is recorded only from the basin of the Amazon in Brazil and from the junction of the Cuyuni and Mazaruni rivers in British Guiana. The following records in my collection are new:

Venezuela: Rio Araturi and SE border of Orinoco Delta, Feb. 6 and 8, 1935 (N. A. W.).

British Guiana: Forest Settlement, Mazaruni R., Aug. and Sept. 1935 (N. A. W.); 22½ mi. west of Kartabo Point, 7·ix·1935 (N. A. W.); Oronoque R. of Courantyne drainage, July and Aug. 1936 (N. A. W.); Waikarabi Creek, Barama R., 28·iii·35 (J. G. Myers 5023); Mataruki, Upper Essequebo R., 5·xii·35 (J. G. M. 5835); Upper Essequebo, 1·xii·35 (J. G. M. 5788); Watershed between Essequebo and New R., 6·xii·35 (J. G. M. 5841).

Surinam: Above Wanoceri Falls, Courantyne R., 14·vii·36 (N. A. W.).

Trinidad, B. W. I.: Maracas Valley, 23·iii·35 (N. A. W.); Rio Claro, 3·i·35 (N. A. W.).

My records are all from tropical rain forest. The ants, however, were found in various types: swamp rain forest, white sand thin forest and virgin greenheart forest (*Ocotea Rodioei* (Schomb.)) in B. Guiana; both high forest and largely cultivated forest of a cacao plantation in Trinidad; Guianan rain forest and mangrove (probably *Rhizophora mangle* L.) in Venezuela. This ant was called "Warumuri" by an intelligent Arawak Indian guide and helper in B. Guiana.

Crematogaster limata was described by F. Smith in 1858 (*Cat. Hym. Brit. Mus.* 6: 139) and the subspecies *parabiotica* by Forel in 1904 (*Zool. Jahrb. Syst.* 20: 683). Forel described two varieties later. The species and its forms are recorded from Brazil, British Guiana, Colombia and Panama. The following records in my collection are new:

Venezuela: SE border of Orinoco Delta, 6·ii·1935 (N. A. W.).

British Guiana: the Forest Settlement, 22½ mi. W of Kartabo Point and Oronoque R. records listed for *Camponotus femoratus* above.

Surinam: the Wanoceri Falls record listed above.

The hitherto unrecorded third ant in the biocoenose is tiny (2 mm. in extended length) and yellow in color. It belongs to a new species of *Solenopsis* near *S. helena* and *pollux* to which the name, *S. parabiotica* Weber, may be applied (Weber, '43). The ants were found in three gardens near the Forest Settlement, Mazaruni R., British Guiana and doubtless would

have been found in more, here and elsewhere, had more time been available for examination.

Description of the Gardens

The *Camponotus-Crematogaster* gardens are described by Wheeler as "varying from the size of a walnut or orange to that of a football," but larger gardens were seen at heights of 50–100 feet above the ground. These latter were not examined. Gardens of similar size were seen in 1935 in the same area and those which I examined varied in diameter from 6 cm. to 23 cm. Most were somewhat elongated, the largest being 66 × 23 cm. The average dimensions of five were 30 × 16 cm., being elongated about the branch or trunk of the tree and the development of new chambers could probably continue to a considerable extent up and down the stem. The height above ground of the five nests varied from 1.6 to 6 meters with an average of nearly 4 meters.

A garden on the Surinam side of the Courantyne River above Wanoceri Falls was 15 × 5 cm. but this was noted as smaller than most of the nests glimpsed while traveling up this river. A garden near the junction of the Oronoque and New Rivers in the far interior of British Guiana was 20 cm. in diameter.

Small plants commonly grow from the gardens. Ule collected from the gardens in Brazil inhabited solely by *Camponotus femoratus* the following: *Philodendron myrmecophilum* Engl., *Anthurium scolopendrinum* Kunth., var. *poiteananum* Engl., *Streptocalyx angustifolius* Meg., *Aaechmea spicata* Mait., *Peperomia nematostachya* Link, *Codonanthe uleana* Fritsch, and *Phyllocactus phyllanthus* Link. From gardens inhabited by three species of *Azteca* in Brazil he collected *Philodendron myrmecophilum* Engl., *Nidularium myrmecophilum* Ule, *Ficus myrmecophila* Warb., *Marckea formicarum* Damm., *Ectozoma ulei* Damm., *Codonanthe formicarum* Ule, and two undescribed species of Gesneriaceae. "These fourteen species belonged to such different families as the Araceae, Bromeliaceae, Gesneriaceae, Moraceae, Piperaceae and Cactaceae."

Those plants identified by Wheeler and Bailey belonged to the Gesneriaceae ("probably species of *Streptocalyx* and *Codonanthe*") and "an *Anthurium*, a *Peperomia* and a few Bromeliads."

One plant impressed me at the time as being particularly characteristic of these gardens and was seen not only at the Forest Settlement but also 22½ miles west of Kartabo Pt. in B. Guiana and in that part of the Orinoco Delta, Venezuela, belonging to Venezuelan Guiana (Fig. 1). An Arawak Indian referred to it by the name "Kobua." As many as six stems of what may have belonged to one plant would be growing from even the small gardens. Specimens in flowers (collected 3·ix·1935) were brought to Harvard University and submitted to Dr. L. B. Smith who pronounced them to belong to the species *Codananthe calcaratus* (Miq.). The flowers in life were white with a five-petalled tubular corolla and a pinkish or lavender throat which was spotted. The unidentified species of Gesneriaceae figured by Wheeler (p. 97) may have been this *Codonanthe*. The roots of this and other plants ramified through the carton of the gardens and served to assist in binding it into a firm nest. Ule maintained that the ants deliberately sowed seeds of the plants characteristically growing from the gardens but I agree with Wheeler in considering such behavior not proved. Rather it more safely may be considered that seeds of these plants, lodging at random in the gardens or accidentally carried in by the ants as they might any particle of similar size, germinate and develop because the garden affords a suitable environment. In this biocoenose the ants would profit by the root growth of the plants adding to the firmness of the nest while the plants would be protected by the ants from *Atta, Acromyrmex* and other arthropod pests.

Far from being merely soil brought in by the ants or lodged by wind or gravity among the roots, the material used in constructing the garden has a definite carton consistency like that fabricated by *Crematogaster* and *Camponotus* ants of many species or by some species of *Nasutitermes* termites (Figs. 1, 2). The base of the carton appears to be humus or decomposed plant remains adhering to the roots of epiphytes, the bark of the tree and in similar places in the neighborhood of the nest. As an ant carries such a particle in its mouth salivary secretions may well be absorbed by the material and assist in the cementing of it into carton. Soil lodged at random by the wind may be ruled out of consideration since winds and wind-blown dust are rare in rain forests; material lodged by gravity similarly is probably unimportant.

The ant chambers were highly irregular in form and size (Fig. 2). An occasional one would be as large as 40 × 10 mm. Partitions between chambers were thin so that a large proportion of the garden was available for nesting purposes. Chambers of the *Crematogaster* and *Camponotus* anastomosed freely while the *Solenopsis* nested in minute cells in the partitions and had entrances into the far larger chambers of the other ants. In one garden the *Solenopsis* chambers were found in central, basal and peripheral portions. In another garden their chambers were chiefly in the peripheral portions. In a third the cells were seen only between the carton and stems of plants growing from the garden. Generally speaking the medial chambers were largest and were occupied by the *Campo-*

notus but frequently small chambers of Crematogasters occurred here also. While cutting down one garden *Camponotus* workers ran off and upon investigation of the nest only Crematogasters were found. These had a huge number of females and much brood, the latter roughly separated in separate cells into piles of eggs, larvae and pupae. In this nest only comparatively small cells were present and it is possible that it was a new nest, perhaps an offshoot of one growing on a neighboring tree 60 cm. away, and that the Crematogasters had initiated it. Two weeks later another nest was found which was occupied largely by the *Crematogaster* and *Solenopsis* with few *Camponotus* workers present. It was thought at the time that the *Camponotus* might be moving to a nearby garden. In a third garden the Crematogasters were much more numerous than the *Camponotus* and occupied by themselves, in addition to the usual chambers throughout the nest, a little external mass of carton, on the outside of which dried leaves were attached.

FIG. 1. Ant garden attached to recently felled tree, containing *Camponotus femoratus* Fabr. and *Crematogaster limata parabiotica* Forel ants living in parabiosis. Characteristic plant growing from garden is *Codonanthe calcaratus* (Miq.). Forest Settlement, British Guiana. N. A. Weber, phot.

BEHAVIOR OF THE ANTS

Both the *Camponotus* and *Crematogaster* ants are aggressive, rushing forth from the nest as soon as it is disturbed and viciously attacking the intruder. The *Camponotus* are much the larger and have strong mandibles but no sting. Like other formicine ants they bite and curve forward the tip of the abdomen to spray the wound with formic acid so that a person may form a hasty impression of being stung. The *Crematogasters,* although small, are so numerous, active and vicious as to be as annoying as the *Camponotus.* They possess a sting too small

to pierce the human skin in most exposed places, unless given plenty of time, but a bite that may be felt. This aggressive behavior, however, is not always constant. In one nest the *Camponotus* ants were most aggressive, coming out to attack at the slightest disturbance, while the *Crematogasters* remained inside. When cutting down another nest the *Camponotus* ran from the vicinity and only *Crematogasters* were found inside.

One garden with particularly aggressive *Camponotus* ants was cut down at eleven A.M. and placed on white sand of the thin forest floor, in a spot where the sun penetrated, in order to photograph. The sand was so hot that I could barely hold my hand on it and the intensity of the reflected sunlight was almost unendurable. Perspiration ran freely off me while merely standing in the clearing. The sun and heat quickly killed the *Camponotus* which fren-

FIG. 2. The same garden dissected. *Camponotus* ants leaving the garden and frenziedly crawling over the white sand were killed by the sun and heat in less than two minutes.

ziedly ran from the nest and exposed themselves on the sand. One worker which ran quickly from the nest over the sand started kicking on its back in 1¼ minutes and in another quarter minute was dead. Many other ants were killed in a similar interval.

Both species tolerate the *Solenopsis*. These tiny ants could walk unmolested by the larger species. None of the three ants was seen to attack another member of the trio, the *Solenopsis* treated the others as part of the environment while the larger ants acted as two castes of a polymorphic species.

Phorid Parasites and Other Members of the Biocenose.

Several nests in the Forest Settlement, Guiana area were seen parasitized by phorid flies.[1] These flies were seen to oviposit on both *Camponotus* and *Crematogaster* workers, temporarily paralyzing the ants. As the flies hovered over the ants, even some centimeters distant, the ants reacted in a characteristic manner. The *Camponotus* reared up on their legs or else vibrated jerkily as do *Lasius americanus* and many other ants. The Crematogasters generally up-ended their triangular gasters or else raised the fore parts of the body in a threatening manner. Neither ant manifested the frenzy or terror-like attitude of *Atta* soldiers and workers which have often been watched while attacked by phorids. The flies appeared to attempt oviposition on the petiole, or gaster, or junction between these segments. They ignored the tiny *Solenopsis* workers, which would probably not have enough food to feed the larval fly, and the brood of all three ants.

A myrmecophilous beetle was found in one *Crematogaster* cell which contained ant brood. This beetle, weevil-like in appearance, had numerous clavate, glandular-appearing hairs. In the same nest a peculiar larva was taken. Projecting from the pronotum were two dense circlets of clavate, glandular appearing structures. Interspersed were long hairs which also protruded in circlets from the dorso-lateral margins of each segment.

[1] Representative specimens are in the hands of Professor C. T. Brues for determination.

Summary

Forel in 1898 coined the term parabiosis to denote an association of two species of ants in Colombia which formed common files to and from feeding grounds and a common nest, although they maintained separate chambers for their brood. Ant gardens, balls of earthy carton formed by ants about trunks of trees, were described first by Ule in Brazil in 1901. One of several species of ants inhabited the gardens and a flora of certain small species of herbaceous plants always grew from them. Ant gardens were found in 1920 by Wheeler in British Guiana inhabited by two species of ants, *Camponotus femoratus* Fabr. which was taken in the Brazilian ant gardens, and *Crematogaster limata parabiotica* Forel which was one of the parabiotic species in Colombia. The author in 1935–36 found these gardens in Venezuela, British Guiana and Surinam inhabited by the same *Camponotus* and *Crematogaster* ants. In addition a third and minute ant, *Solenopsis parabiotica* Weber, was found living in the thin partitions between chambers of the larger species. Phorid flies parasitized the *Camponotus* and *Crematogaster* and two other myrmecophiles were found. The characteristic plant growing from the gardens was identified as *Codonanthe calcaratus* (Miq.). The aggressive behavior of the larger ants and the tolerance of all three towards one another are described.

Neal A. Weber

University of North Dakota

Bibliography

Forel, A. 1898. La Parabiose Chez les Fourmis. Bull. Soc. Vaud. Sc. Nat. **34**: 380–384.

Mann, W. M. 1912. Parabiosis in Brazilian ants. Psyche **19**: 36–41.

Ule, E. 1901. Ameisengärten in Amazonasgebiet. Engler's Botan. Jahrb. **30**: 45–51, 1 pl. (not seen).

Weber, N. A. 1943. The queen of a British Guiana Eciton and a new ant garden Solenopsis. Proc. Ent. Soc. Washington **45**: 90–91, Fig. 2.

Wheeler, W. M. 1921. A new case of parabiosis and the "Ant Gardens" of British Guiana. Ecology **2**: 89–103, 3 figs.