SOME ECOLOGICAL CHARACTERISTICS OF ANTS IN NEW GUINEA RAIN FORESTS[1,2]

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INTRODUCTION

The purpose of the present paper is to describe in a preliminary way the ecology and local distribution of the ant fauna of the Papuan rain forests and in so doing to introduce several classificatory systems that can be employed in future descriptive ecological work. The account is entirely descriptive and comparative in nature. The author has not attempted to accomplish an intensive analysis of any aspect of the "community organization," and indeed it is probably true that no such analysis could be undertaken without thorough autecological studies of many individual species over a period of years. Nevertheless, there are several good reasons for presenting the available material in a compendious form, however fragmentary may be the accounts of individual species. First should be mentioned the extremely poor condition of our

present knowledge of the biology of most of the genera and species that make up the huge Papuan faun. Beyond the early account of the ecology of New Britain ants by Dahl (1901), there exist only a few scattered, incomplete references to individual species, and these are usually appended to taxonomic studies. In any broad consideration of the evolution of adaptation and behavior of the world ant fauna, this scarcity of information on the Papuan fauna has always formed a major gap. Further, ants are an influential part of the biotic environment of most animal species in New Guinea, as they are in most tropical rain forest areas. Knowledge of the biology of at least the dominant ant species should form an important part of the background of future rain forest ecological studies, including further autecological studies of ant species. Finally, and perhaps most importantly, summaries of community ecology of the type proposed here will serve the purpose of contributing to comparative studies of faunal structure in different zoogeographic regions. Information relating to relative abundance and the

extent and nature of local adaptive radiation is essential to the future ecological refinement of zoogeographic studies.

The taxonomic basis of part of the present work, along with a gazetteer of collection localities, has been given in a series of earlier publications (Wilson 1957a, 1957b, 1958a, 1959; Wilson and Brown 1956, Brown and Wilson 1957, Brown 1958). The ecological studies reported in the present paper were centered in a tract of primary lowland rain forest located between the Busu and Bupu Rivers, east of Lae, Mandated Territory of New Guinea. At the time of the author's visit, during April and May, 1955, this area was especially favorable for the study of the endemic ant fauna. In the previous year the first bridge strong enough to support motor vehicles had been built across the Busu River, and the road from Lae extended into the rain forest beyond. The South Pacific Lumber Company was in the process of cutting tractor trails in all directions through the forest and had made considerable headway in high-grading the largest trees. Both virgin forest tracts and new clearings were accessible for ground collecting, while the trunks and tops of freshly felled trees could be examined in quantity for arboreal ants.

The ant fauna of the Busu-Bupu area is perhaps the richest ever recorded for a single locality anywhere in the world. While the lack of reliable taxonomic revisions in several large and critical genera make an exact count impossible at the present time, it has been estimated that at least 59 genera and 172 species occurred within a few square kilometers in the collection area (see Table I); exhaustive collecting would probably increase the species count to well over 200. This fauna far exceeds those of the better known temperate localities. To cite an example, Dr. Mary Talbot has recorded 22 genera and 67 species in a diversified area of fields and woodland at the Edwin S. George Reserve in southern Michigan. (Talbot, pers. commun.). The Reserve covers 2 square miles, or approximately 5 square kilometers, and is therefore comparable to the area studied at the Busu River. Dr. Talbot considers the fauna at the Reserve to be unusually rich for a locality at this latitude, and her coverage is undoubtedly much more nearly complete than my own at the Busu River. Localities in the southern United States do not harbor notably richer faunas than that at the Edwin S. George Reserve. Van Pelt (1956), for instance, recorded a total of 30 genera and 76 species during a careful survey of the 8-kilometer square Welaka Reserve in central Florida. It is therefore evident that the Busu-Bupu

TABLE I. Composition of three local ant faunas

Genus	NUMBER OF SPECIES		
	Lower Busu River, New Guinea	Welaka Reserve, Florida (A. F. Van Pelt)	E. S. George Reserve, Michigan (M. Talbot)
PONERINAE			
Amblyopone	..	1	1
Anochetus	2	..	..
Brachyponera	1	...	..
Cryptopone	2	..	..
Diacamma	1	..	..
Ectomomyrmex	2	..	..
Gnamptogenys	1	..	..
Leptogenys	3	1	..
Mesoponera	1	..	..
Myopias	6	..	..
Odontomachus	3	1	..
Platythyrea	1	..	..
Ponera	6	3	1
Prionopelta	1	..	..
Proceratium	..	2	1
Rhytidoponera	3	..	..
Trachymesopus	3	1	..
CERAPACHYINAE			
Cerapachys	4	..	..
DORYLINAE			
Aenictus	2	..	..
Neivamyrmex	..	2	..
PSEUDOMYRMECINAE			
Pseudomyrmex	..	2	..
Tetraponera	3	..	..
MYRMICINAE			
Adelomyrmex	1	..	..
Acidomyrmex	1	..	..
Ancyridris	1	..	..
Aphaenogaster	2	7	4
Cardiocondyla	2	3	..
Crematogaster	6	5	2
Dacetinops	1	..	..
Dilobocondyla	1	..	..
Heptastruma	1	..	..
Kyidris	1	..	..
Leptothorax	..	2	7
Lordomyrma	3	..	..
Meranoplus	1	..	..
Monomorium	1	2	1
Myrmecina	3	1	1
Myrmica	..	..	6
Oligomyrmex	2	..	..
Pheidole	15	6	..
Pheidologeton	1	..	..
Podomyrma	5	..	..
Pogonomyrmex	..	1	..
Pristomyrmex	3	..	..
Rhopalomastix	1	..	..
Rhopalothrix	3	..	..
Smithistruma	..	7	1
Solenopsis	1	6	1
Stenamma	..	..	3
Strumigenys	12	1	..
Tetramorium	..	3	..
Trachymyrmex	..	1	..
Triglyphothrix	1	..	..
Vollenhovia	2	..	..
Xiphomyrmex	1	..	..
Incertae sedis	3	..	..
DOLICHODERINAE			
Conomyrma	..	2	..
Hypoclinea	..	1	4
Iridomyrmex	5	2	..
Leptomyrmex	2	..	..
Tapinoma	..	1	1
Technomyrmex	1	..	..
Turneria	2	..	..

TABLE I—(Continued)

Genus	NUMBER OF SPECIES		
	Lower Busu River, New Guinea	Welaka Reserve, Florida (A. F. Van Pelt)	E. S. George Reserve, Michigan (M. Talbot)
FORMICINAE			
Acanthomyops.........	..	.	4
Acropyga..............	3	..	..
Brachymyrmex.........	..	1	1
Camponotus..........	8	5	5
Calomyrmex...........	1	..	..
Echinopla.............	2	..	..
Formica..............	..	3	12
Lasius................	..	..	8
Nylanderia...........	6	2	1
Oecophylla...........	1	..	..
Opisthopsis...........	1	..	..
Paratrechina..........	..	1	..
Plagiolepis............	2	..	..
Polyergus.............	..	..	1
Polyrhachis...........	15	..	..
Prenolepis.............	..	1	1
Pseudolasius..........	1	..	..
TOTAL GENERA.....	59	30	22
TOTAL SPECIES.....	172	76	67

area, and other favorable lowland rain forest areas in New Guinea, contain faunas that are larger by a factor of 2 to 4 than those of most comparable local areas in the United States, a comparison that probably extends as well to the temperate zones of Europe and Asia.

Such a comparison of the sizes of local faunas, emphasizing as it does the traditional richness of the faunas of tropical forests, invites further comparisons of a more fundamental nature. Are the larger tropical faunas ecologically more diversified, and if so, in what way, and by how much? Are certain adaptations more marked in the tropical forest, as opposed to the temperate forest, *i.e.*, do a higher percentage of genera and species exhibit them and in a more exaggerated fashion? Has a general "complexity factor," involving an increased number of potential competitors, predators, and nest-food niches, had a demonstrable effect on the evolution of the fauna? In time it is hoped that we can profitably inquire whether a consideration of the adaptation itself, along with the peculiarities of local areal distribution in the rain forest, might not provide a clearer understanding of why tropical rain forests contain such large faunas and have served historically as the centers of major evolution in this group of insects.

STRATIFICATION IN THE BUSU RIVER FOREST FAUNA

Stratification of the fauna is well marked in the Busu forest. While each species is locally distributed in a pattern peculiar to itself, with a high degree of interspecies discordance obtaining, it

has been found convenient for purposes of broad description of the ant habitats to recognize three arbitrarily delineated strata. These are characterized in the sections below.

Ground stratum. This division comprises the species that nest in the soil, leaf litter, and all rotting wood on the ground, up to and including the largest rotting logs. The great bulk of both species and individual colonies live here, and relatively few of the species ever leave it to forage in the arboreal zones. On the other hand, a notably larger percentage of true arboreal-nesting species, including such abundant forms as *Iridomyrmex scrutator* (Fr. Smith), *Oecophylla smaragdina* (Fabr.), and *Polyrhachis (P.) erosispina* Emery commonly forage on the ground to swell the number of species occurring there. As might be expected, the available nesting sites in the ground zone are tremendously varied and the ecology of its resident species far more complex than is the case in the arboreal zones. A more detailed description of this stratum will be given in a later section.

Low arboreal stratum. Including species nesting in herbaceous and shrubby ground vegetation, the C-stratum of trees, and the first several meters of the trunks of larger trees. A small number of species nest primarily or exclusively in this zone: *Diacamma rugosum* (Le Guillou), *Lordomyrma* sp. (891),[3] *Iridomyrmex cordatus* (Fr. Smith), *Calomyrmex laevissimus* (Fr. Smith), *Polyrhachis (P.) erosispina* Emery, and several species of *Polyrhachis (Myrmhopla)*. Up into the low arboreal zone come two ground-nesting species to do most or all of their foraging: *Platythyrea parallela* (Fr. Smith) and *Meranoplus spinosus* (Fr. Smith). Some ground-nesting forms are incidental visitors, *e.g.* *Odontomachus simillimus* (Fr. Smith) and *Tetramorium* spp., while many high-arboreal species descend into the low arboreal zone commonly, *e.g.* *Podomyrma* spp., *Oecophylla smaragdina* (Fabr.), *Polyrhachis (Cyrtomyrma)* spp., and *Camponotus (Colobopsis) vitreus* (Fr. Smith). This is the most sparsely populated of the 3 zones, with respect to both nesters and incursive foragers.

High arboreal stratum. Including species that nest in the upper trunks and canopy of the A- and B-stratum trees. Within this zone ants nest primarily in epiphytes (*Iridomyrmex scrutator* (Fr. Smith), *Polyrhachis (Myrma) andromache* Roger, *Camponotus papua* Emery), abandoned termitaria (*Crematogaster* sp. (909). *Camponotus*

[3] Accession numbers are given in those cases where identifications to species cannot be made. They correspond to series on deposit in the insect collections of the Museum of Comparative Zoology.

(*Colobopsis*) (*vitreus*), preformed cavities in live wood (most or all species of *Podomyrma* and at least one undetermined *Iridomyrmex*), and dead twigs (*Turneria* spp.).[4] Many of these species limit their foraging activity to the high arboreal zone (*e.g. Turneria* spp.), while others forage all the way to the ground. One species, an apparently undescribed *Pheidole* (*Pheidolacanthinus*) (accession number 925), nests both in this zone (in tree holes) and in the ground zone (large rotting logs), while appearing to forage exclusively in the arboreal zones. It is unique in this respect among the ants studied.

FURTHER DESCRIPTION OF THE GROUND STRATUM

Soil residents. The ground stratum contains 2 distinct major divisions. First can be distinguished the ants that nest in the soil exclusively or extend their nests from the soil into rotting logs. Relatively few rain forest ants nest primarily in the soil. Among these exceptional forms is *Cardiocondyla paradoxa,* which digs to about 20 cm in the earth and constructs a single entrance gallery concealed by leaf litter. *Rhopalothrix biroi* Szabó, on the single occasion a colony was found, was nesting in shallow galleries in the soil beneath a large rotting log. *Acidomyrmex melleus* (Emery) develops enormous colonies that penetrate deep into the soil and heap up massive earthen domes, which are turret- or castle-shaped following recent excavation. *Odontomachus simillimus* (Fr. Smith), *O. papuana* Emery, and species of *Leptomyrmex* nest primarily in the soil, but on occasion colonies have also been found in large logs in a late stage of decomposition. *Acropyga moluccana* Mayr and *Pseudolasius breviceps* Emery are primarily ground dwellers that extend their nests up into late-stage rotting logs. The single colony of *Leptogenys optica* found occupied a similar nest form.

Among ground-nesting ants few species nest or even forage beneath rocks. Only two species, *Cryptopone butteli* Forel and *Pheidole* (*Electropheidole*) *cervicornis* Emery, are found nesting in this situation. Workers of a few species of *Ponera* were found foraging beneath stones, but in each case were more abundant in adjacent open leaf litter. Fewer than 10% of rocks on the floor of the Busu forest had ants nesting or foraging under them. This is in marked contrast to the forests of the temperate regions of the world and in a lesser degree to the montane forests in New

Guinea, where stones tend to be the favored nesting sites.[5]

Residents of small pieces of rotting wood. The densest concentration of nesting ants, both in number of colonies and actual biomass, is to be found in small pieces of rotting wood on the ground, at the "zorapteran" and "passalid" stages of decomposition (see below). Included are entire small logs and variously shaped fragments of wood up to approximately 8 cm in diameter Genera that nest primarily or exclusively in this situation include *Ponera, Brachyponera, Prionopelta, Mesoponera, Myopias, Rhytidoponera, Cerapachys, Pheidole, Tetramorium, Xiphomyrmex, Oligomyrmex, Myrmecina, Pristomyrmex, Adelomyrmex, Triglyphothrix, Strumigenys, Kyidris,* and *Dacetinops,* all belonging to the subfamilies Ponerinae, Cerapachyinae, and Myrmicinae.

The prevalence of ponerines, cerapachyines, and myrmicines in small pieces of rotting wood is a conspicuous feature of rain forest ecology and is deserving of further careful study. It appears to the author that there are at least 3 reasons why the nest site might be so favored: (1) the pieces of wood tend to maintain uniform and favorable conditions of temperature and humidity, (2) extensive stable preformed cavities exist, not so likely to be disturbed by burrowing insects and earthworms as galleries excavated in the soil and large logs, (3) a dual habitat for foraging is available, consisting of both the rotting wood and the immediately surrounding soil and leaf litter layer.

Residents of large rotting logs. Logs with diameters greater than approximately 8 cm contain a proportionately light concentration of resident ants, possibly because they are deficient in features (2) and (3) above. The species normally occurring there comprise a fauna well demarcated from the soil and small-log faunas. They tend to confine their foraging to the interior of the logs, rarely venturing out onto the ground or into the arboreal zones. Conversely, non-resident ant species rarely penetrate into the larger logs. Species characteristic of this micro-habitat include *Myopopone castanea* (Fr. Smith), *Trachymesopus stigma* (Fabr.), several small *Pheidole* species, *Solenopsis* (*Diplorhoptrum*) *papuana* Emery, and species of *Vollenhovia*.

A microsere involving the resident ant fauna is well marked in large rotting logs in the Busu forest and other lowland rain forests in New Guinea. In the following sections I have at-

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[4] Based on a study conducted on Espiritu Santo, New Hebrides, where *Turneria* are among the dominant ants of the lowland rain forest. At the Busu River these ants were rather scarce, and no nests were found.

[5] This generalization evidently holds for most or all of the tropics. I have found ants relatively scarce under rocks in rain forests in Vera Cruz, Mexico, and Ceylon, while W. L. Brown and A. C. Cole (pers. commun.) have made similar observations in Assam.

tempted a description of this microsere in which 5 arbitrary stages are recognized, each with a significantly different association of ants.

I. "Scolytid stage." The tree has only recently fallen. The wood is no longer "green," but the bark adheres as firmly as to the living tree. Ants are quite scarce, and probably include some species that normally reside in the living tree. No ants were definitely associated with this stage in the Busu forest, but species of *Podomyrma* very likely occupy it to some extent. It has been noted that in the arid eucalyptus woodland of Western Australia *P. adelaidei* (Fr. Smith) frequently nests in abandoned cossid burrows in logs of this stage.

II. "Cucujid stage." The wood is just beginning to rot, and fungal activity is particularly evident under the bark, which can be peeled away in large strips with a knife. Beetle tunnels are common in the subcortical areas, but there are no large frass-filled cavities available for occupation by ants. Ants are nevertheless fairly abundant in whatever cavities exist. Species apparently favoring stage II in the Busu Forest include one of *Pheidole* (933) and two of *Solenopsis* (*Diplorhoptrum*) (931, 1028). In other lowland New Guinea localities species of *Iridomyrmex* and *Nylanderia* are occasionally found here. Although not measured, temperature and moisture within the occupied cavities appear much more variable than in similar cavities in logs at later stages of decomposition.

III. "Zorapteran stage." The wood is considerably softer and can be torn out in large pieces with an ordinary digging tool. The bark is still intact but can easily be pulled off in large pieces to reveal extensive subcortical cavities partly filled with frass. In these cavities abound arthropod groups, including collembolans, mites, isopods, symphylans, campodeids, japygids, and representatives of various beetle families. In New Guinea, zorapterans appear to be limited to logs in this stage of decomposition and are often among the dominant arthropods there. Passalid beetles have begun to infiltrate, but are not nearly so common as in the following (passalid) stage. Ants are extremely abundant and include chiefly *Myopopone castanea* (Fr. Smith), *Trachymesopus stigma* (Fabr.), *Cryptopone motschulskyi* Donisthorpe, *Ponera pruinosa* Emery, and several species of *Vollenhovia* and *Nylanderia*.

IV. "Passalid stage." The wood is thoroughly rotten and can be crumbled easily in the hands, while the bark is fragmenting and sloughing of its own weight. Passalid beetles are among the dominant larger insects. The ant fauna is mostly restricted to several species that also occur in the preceding stage, notably *Ponera pruinosa* and one or two species of *Nylanderia*. The other species characteristic of the zorapteran stage are much less common in the passalid stage and evidently in the process of dropping out. As mentioned already, certain soil-nesting species of *Odontomachus* and *Leptogenys* sometimes occupy passalid-stage logs secondarily, while *Leptogenys optica* may penetrate them from nests located primarily in the soil.

V. "Staphylinid stage." The bark has mostly or entirely fallen off, and the entire log may be covered with moss or herbaceous plants. Wood adjacent to the ground has deteriorated to the point of mingling with the soil. Ants characteristic of the preceding (passalid) stage are no longer present, or at the most occupy large pieces of wood that still approximate the general conditions of that stage. The truly characteristic ants of this stage are species of *Acropyga* and *Pseudolasius* that have extended their nests up from the soil.

Several additional notes on the rotting log habitat must be added here. First, it should be mentioned that small logs, branches, twigs, and other fragments of wood pass through decomposition stages similar to those just described for large logs but much less distinct. Smaller pieces of wood in stages equivalent to III and IV, contain the largest number of resident species of any rain forest microhabitat and probably the highest concentration of individual ants. These wood fragments are especially favored by nesting ants when they are partly or wholly buried in moist, well-aerated leaf litter.

Logs of all sizes are seldom at any given time uniformly in one stage of decay, but rather through differential rates of decay, they form mosaics of wood in several decomposition stages. For example, stage V typically contains sizeable fragments of stage IV wood with its distinctive ant fauna. Moreover, not all species of trees pass through a microsere precisely as described. In some the bark falls off rapidly, before the wood has rotted much, and as a result there is no proper "zorapteran stage." In others the converse is true; the wood rots and begins to crumble before the bark breaks, and large central cavities form. This, incidentally, is the type of log preferred by wood-nesting *Leptomyrmex*, which need spacious preformed chambers.

FURTHER DESCRIPTION OF THE ARBOREAL STRATA

It is a noteworthy fact that the bulk of the arboricolous ant population nests in preformed cavities in living wood in the forest canopy. Ants

are scarce in small, hollow, dead twigs—only *Technomyrmex albipes,* a species limited to the forest border, is definitely known to use this kind of nest site at the Busu River. In striking contrast is the lowland rain forest fauna studied by the author at Pueblo Nuevo, Veracruz, Mexico, in 1953. Here large numbers of species of *Platythyrea, Pseudomyrmex, Paracryptocerus, Cyathomyrmex, Leptothorax,* and *Camponotus* form dense populations in dead twigs in the low arboreal zone. While exact counts have not been made, there can be little doubt that the arboreal fauna of Pueblo Nuevo, including, in addition to the forms just listed, live-stem dwellers such as *Azteca* and epiphyte dwellers such as *Crematogaster* and *Neoponera,* contains a significantly higher percentage of species (with reference to the total local fauna) than is the case at the Busu River. This relative species paucity in the arboreal fauna extends to all of Melanesia, and is particularly noticeable in the New Caledonian fauna.

A notable feature of the various faunal strata at the Busu River and other lowland localities in New Guinea is the tendency of workers to migrate downward during foraging. (The opposite may be true in other areas, such as New Caledonia). As noted previously, high arboreal species are abundant as foragers in the low arboreal zone and often penetrate to the ground zone, while low arboreal species commonly forage in the ground zone. Yet, despite the fact that the great majority of ant species nest in the ground zone, there is little foraging movement from the ground upwards. Few ground-zone residents forage into the low arboreal zone, and to my knowledge none ever reaches the high arboreal zone. Furthermore, the tendency for migration is extended even to within the ground zone itself. It has been noted that small-log dwellers normally forage out into adjacent soil and leaf litter, but true ground-nesting species are seldom encountered in rotting logs.

THE ECOLOGICAL DISTRIBUTION OF SPINESCENT SPECIES

During the present study an attempt was made to correlate degree of worker spinescence, *i.e.,* the number and size of spines on the body of the worker caste, with habitat preference or other particularities of behavior. My previous conception, held in common with a few other students of ants, was that conspicuous spinescence is to a degree associated with arboreal life. Actually, no such association was found in the New Guinea rain forests. On the contrary, the high arboreal

species are noteworthy for their reduced spination. Two of the 3 known high arboreal myrmicine genera, *Podomyrma* and *Dilobocondyla,* are spineless, while the third genus, *Crematogaster,* has propodeal spines of only moderate size. *Cyrtomyrma,* the dominant of the *Polyrhachis* subgenera in the high arboreal zone with respect to both species and biomass, has greatly reduced spines. All of the other high arboreal species, including members of *Tetraponera, Iridomyrmex, Turneria,* and *Camponotus,* are spineless.

The maximum development of spines is in fact seen in species that nest in the ground and low arboreal zones and forage in the open. Examples of extremely spinescent groups that fit this rule include subgenus *Planimyrma* of *Aphaenogaster,* subgenera *Pheidolacanthinus* and *Electropheidole* of *Pheidole,* and *Ancyridris,* most or all of which nest and forage in the ground zone; *Arnoldidris* and *Polyrhachis* subgenus *Chariomyrma,* which nest primarily in the ground and forage in both the ground and low arboreal zones; and *Polyrhachis* subgenus *Myrmhopla,* which nests and forages almost exclusively in the low arboreal zone. In cryptobiotic ground-dwelling species, *i.e.* those that forage mostly or entirely underground or inside rotting logs, there is a tendency for reduction in spination similar to that seen in the high arboreal forms.

In short, spinescence appears to be associated not with arboreal habits *per se,* but rather with epigaeic foraging behavior. It seems probable that spines serve as a defense against predators and that they are reduced only when confining conditions of the environment such as the cramped quarters occupied by twig-dwelling species or the narrow trophophoric field used by subterranean species, make such armament disadvantageous.

A PRELIMINARY CLASSIFICATION OF FOOD HABITS

It is possible to classify the rain forest ants according to their most conspicuous food habit into the following rough categories: (1) specialist predators, (2) general predators, (3) pastoralists, (4) harvesters. By "conspicuous food habit" is meant the special case of what appears, on the basis of usually limited field observations, to be taking up most of the workers' time in food gathering. This is by no means necessarily the only food habit, as will be shown below.

Specialist predators. In the rain forests the following types of specialists were discovered: millipede predators (two undescribed species of *Myopias*), isopod predators (*Leptogenys triloba* Emery), collembolan predators (*Strumigenys*

spp.), predators on small, soft-bodied arthropods (*Rhopalothrix biroi* Szabó, *Strumigenys loriae* Emery),[6] predators on other ants (*Cerapachys opaca* Emery). Many of these ants are marked by peculiarities in mandible structure, which, at least in the case of the *Strumigenys*, has been demonstrated to have a direct relation to specialized hunting behavior. *Strumigenys* workers capture collembolans by striking them and lifting them off the ground with their exceptionally long mandibles. Ant species that are prey-specific are usually also exclusively predaceous, *i.e.*, do not scavenge or gather honeydew in addition. An interesting exception to this rule is the parasitic myrmicine *Kyidris yaleogyna* Wilson and Brown, which, in addition to hunting collembolans and other small arthropods with its host species, *Strumigenys loriae*, also attend coccids (Wilson and Brown 1956).

General predators. This category includes species that accept a wide range of small animals as prey. Their mandibles are not specialized, they frequently appear individually clumsy in the capture of prey, and they often depend in large part on newly eclosed or crippled arthropods. Moreover, many species are secondarily scavengers, readily accepting dead animals as well as rotted or desiccated fragments. Collembolans form a large part of the diet of many of the smaller species. Probably a majority of the genera and species of rain forest ants belong in the general predator category. Examples include most or all of the species of such large and prominent genera as *Rhytidoponera, Ectomomyrmex, Podomyrma, Tetramorium, Xiphomyrmex, Myrmecina, Acidomyrmex, Pheidole,* and *Aphaenogaster (Planimyrma)*.

Pastoralists. This category comprises the species of *Acropyga* and *Pseudolasius,* which appear to devote most of their time to tending honeydew-secreting insects within the confines of their nests. *Crematogaster* and *Iridomyrmex* may also prove to belong to this category when their habits are better known, but in addition to honeydew these two genera depend in great part on dead insects and could as well be put in a special "scavenger" category.

Harvesters. Ants belonging to this category are relatively scarce in the rain forest. Examples include *Pheidole (P.)* sp. (1023) and *Pheidole (Pheidolacanthinus)* sp. (1065), both of which

[6] The feeding behavior of these species has been reported on in detail elsewhere (Wilson 1956, 1958c; Wilson and Brown 1956).

have been found with abundant seeds and seed fragments in their nests.

COLONY SIZE

In Table II are given estimates of colony size of one to several colonies of rain forest species belonging to a wide range of ant groups. These data represent rough counts of the adult workers, taken to the nearest 5 in populations of 30 or less, to the nearest 10 for populations between 30 and 200, and to the nearest 50, 100 or 1000 for populations of increasingly larger size. Care was taken to avoid incipient colonies and colony fragments. In nearly every case the mother queen was uncovered, and the workers were full-sized (nonnanitic). The estimates given, although representing either unique colonies or at most very limited samples, nevertheless in most cases probably do not deviate far from the actual species averages, since an attempt was made to choose typical nests or relatively common species on which repeated subjective estimates were made.

On the basis of these limited quantitative data, plus a much wider range of subjective impressions, a few preliminary generalizations can be drawn. Perhaps the most important is that most rain forest species have small to moderate-sized colonies. Colony populations do not often contain more than several hundred adult individuals, while mature colonies of less than 50 adults are common and typify many species.

In general, ponerines, cerapachyines, and myrmicines maintain smaller colonies than dolichoderines and formicines, a fact that has already been noted by past authors in other parts of the world. Arboricolous species tend to maintain larger colonies than terricolous ones, but this is of course partly a function of the greater concentration of formicines and dolichoderines in the arboreal zones.

Perhaps the most important single ultimate factor regulating colony size in the rain forest is limitation of nest space. As previously noted, the greatest number of species nest in small pieces of rotting wood on the ground, and are further limited to wood fragments in intermediate stages of decomposition. Unless the colony is dispersed through several wood fragments, which is exceptional, it is clear that its total size can be limited by living space alone. It would seem to be of considerable adaptive advantage for species living in this situation to control colony size and to

TABLE II. Estimated nest population of selected species

Species	Locality	Accession number	Estimated adult population size
PONERINAE			
Prionopelta opaca Emery	Karema	595	20
Platythyrea parallela (Fr. Smith)	"	570	50
Rhytidoponera araneoides (Le Guillou)	"	3 accessions	50
R. laciniosa Viehmeyer	Busu R.	1002,1031	100,150
Gnamptogenys macretes Brown	Bisianumu	649	40
Leptogenys bituberculata Emery	"	663	300
L. diminuta (Fr. Smith)	Karema, Bisianumu, Nadzab	539,608,1087,1106	90-400
L. purpurea Emery	Tumnang	803,849	500,2000
Mesoponera papuana Viehmeyer	Busu R.	994	10
Diacamma rugosum (Le Guillou)	Nadzab, Didiman Creek	2 accessions	30,50
Cryptopone motschulskyi Donisthorpe	Bisianumu	626	20
Ectomomyrmex striatulus Karawajew	Karema, Wamuki	532,857	10,20
Myopias concava Willey and Brown	Busu R.	990	60
M. julivora Willey and Brown	"	905,1048	40,70
M. sp.	"	983	30
CERAPACHYINAE			
Cerapachys opaca Emery	Busu R.	921	100
C. polynikes Wilson	"	936	20
DORYLINAE			
Aenictus currax Emery	Karema	562	100,000+
MYRMICINAE			
Cardiocondyla thoracica (Fr. Smith)	Bisianumu	653	70
C. paradoxa Emery	Didiman Creek	703	50
Crematogaster (Orthocrema) elegans (Fr. Smith)	"	692	300
Cr. (Acrocoelia) subtilis Viehmeyer	Busu R.	909	5000+
Cr. (Acrocoelia) sp.	"	910	300+
Strumigenys bajarii Brown	Busu R.	969	400
S. frivaldszkyi Emery	Karema	594	15
S. mayri Emery	Bandong	1125	100
S. loriai Emery	Bubia, Busu R.	686,907	300,500
S. sp.	Busu R.	926	200
S. sp.	"	1008	50
Rhopalothrix biroi Szabó	"	987	50
Dacetinops cibdela Brown and Wilson	"	1058	10
Ancyridris sp.	"	956,973	10,15
Podomyrma sp.	"	1055	200+
Pristomyrmex sp.	Nadzab	1083	100
Adelomyrmex biroi Emery	Busu R.	935	10
Acidomyrmex melleus Emery	Bisianumu, Tumnang	2 accessions	5000+
Vollenhovia brachycera Emery	Karema	567	150
Aphaenogaster (Planimyrma) dromedarius Emery	Busu R.	908	100
Myrmecina transversa Emery	"	875	50
Meranoplus spinosus (Fr. Smith)	Ebabaang	821	150
Pheidole (Pheidole) sp.	Busu R.	1023	50
Pheidole (Pheidolacanthinus) spp. (several)	"		50-200
Pheidologeton sp.	Karema	591	3000+
P. sp.	Busu R.	874	5000+
DOLICHODERINAE			
Leptomyrmex fragilis (Fr. Smith)	Bubia	1061	350
Iridomyrmex scrutator (Fr. Smith)	Busu R.	several accessions	500-3000+
FORMICINAE			
Pseudolasius breviceps Emery	Karema	543,547	500,200
Acropyga sp.	Busu R.	906	1000+
Paratrechina (Paraparatrechina) pallida Donisthorpe	Bubia	684	500
Paratrechina (Nylanderia) sp.	Busu R.	972	200
P. (N.) sp.	"	1038	150
Camponotus papua Emery	Nadzab	1095	300
C. confusus Emery	Bisianumu	620	200
C. vitreus (Fr. Smith)	Busu R.	881	4000+
Calomyrmex laevissimus (Fr. Smith)	Bisianumu	609	250
Polyrhachis (Chariomyrma) hirsutula Emery	Bisianumu	629	150
P. (Chariomyrma) limbata Emery	Busu R.	937	100
P. (Chariomyrma) sp.	Bisianumu	605	30
P. (Cyrtomyrma) debilis Emery	Karema, Bubia, Bisianumu	556,603,1077	300-350
P. (Myrma) rufiventris Emery	Karema	586	200
P. (Myrmatopa) omyrmex (Donisthorpe)	Busu R.	1014	60

achieve the ability to rear through sexual broods with a small worker force.[7]

Beyond the immediate association between nest site and colony size, it seems safe to generalize that specialist predators tend to have the smallest colonies, while the largest colonies are formed by species that derive a large part of their diet from insect honeydew. This would seem on first examination to be a function of diversity and local abundance of food supply. Legionary species, e.g. *Aenictus* spp. and *Leptogenys purpurea* Emery, are exceptional in being able to maintain large colonies, since, despite their exclusively predatory habits, they are constantly shifting hunting grounds (Wilson 1958b).

Among the many rain forest species studied, monogyny appears to be the strong rule. In the exceptional cases where multiple queens are present, they rarely exceed 2 or 3 per colony. In the great majority of species the brood is not synchronized in its development, *i.e.,* it is spread at any given moment over most or all of the developmental stages, and there is no evidence for marked periodicity of oviposition. Notable exceptions

[7] The tendency for rain forest ants to nest in small pieces of rotting wood and the effects of this habitat choice on colony size, phenomena also noted by the author in tropical rain forests in other parts of the world (Ceylon, Mexico), have some important evolutionary implications. There is growing evidence at the present time to suggest that tropical rain forests, particularly those in the central continental areas of the Old World, are the chief evolutionary centers for most ant groups. Certainly at the present time the tropical rain forests, both in the Old and New Worlds, contain the highest concentration of species and basic phylogenetic stocks of any of the major vegetation zones. Wheeler's well known (1928) statements concerning the primary importance of desert regions are no longer supported by modern zoogeographic evidence. (cf. Bernard 1953, Kusnezov 1957). Under such circumstances the great favorability of the small-log habitat must have had considerable influence on the course of evolution of the ponerines and myrmicines. Moreover, it very probably played an important role in the early evolution of the Dolichoderinae and Formicinae, since it has recently been shown that *Aneuretus simoni* Emery, the sole living member of the related, primitive subfamily Aneuretinae, normally forms small colonies in fragments of rotting wood on the floor of rain forest (Wilson *et al.* 1956). A hypothesis worth considering is that many, perhaps most, of the phyletic groups of ponerines and myrmicines have passed through an evolutionary stage in which they were adapted primarily to life in the small-log habitat in tropical rain forests, and that, in radiating and penetrating new habitats, they have tended to conserve the modest colony size that characterizes most of these groups today. There is good evidence, on the other hand, to suggest that the small-log habitat is not primitive for ants generally. The most primitive subfamily of ants, the Myrmeciinae, represented by two genera limited to Australia and New Caledonia, consists in large part of soil dwelling species that frequently form large colonies containing thousands of workers.

include the legionary species just mentioned in the genera *Aenictus* and *Leptogenys*.

DISCUSSION: ECOLOGICAL DIVERSIFICATION IN THE RAIN FOREST FAUNA

Considering the great taxonomic and distributional complexity of the New Guinea ant fauna, one is inclined to ask, to what extent is there a correlated ecological diversification? There are two aspects of such diversification that must be examined separately. First is the question of the maximum ecological amplitude attained by the fauna as a whole. Surprisingly, the New Guinea fauna does not at first glance appear to have much greater amplitude than a temperate fauna such as that studied by Van Pelt (1956) in Central Florida. In both areas are found, among others, extreme specialists, including exclusively arboricolous forms, army ants, collembolan-feeders and subterranean coccid tenders. Each area contains remarkable specialists the other lacks: New Guinea has myrmecophagous forms (Cerapachyinae), while Florida has fungus growers (Attini). In a north temperate zone, such as Dr. Talbot's study area in Livingston County, Michigan, the fauna appears to have fewer extreme specialists, but the difference is not great. There are arboricolous species, collembolan-feeders, subterranean coccid-tenders, and an impressive array of other major adaptive types in both areas. In the case of the Floridian fauna, it is true that many of the principal adaptive forms probably originated in forest centers in the Neotropical Region rather than in the Old World. However, this does not affect the main argument that many or most of the major adaptive types found in the New Guinea rain forests thrive in this temperate area as well. The comparison has not been carefully extended, as it should be, to the Neotropical rain forests, but there is abundant evidence in the literature on the Neotropical fauna to show that the generalization holds if the New World alone were considered.

But such forms of comparison, based simply on an enumeration of major adaptive types, can be misleading. The true distinction of the rain forest fauna appears to me to lie in the fact that its species have not only invaded principal niches, but saturated them as well. The arboricolous fauna can be considered typical in this regard. In central Florida a small number of species (16 according to Van Pelt) nest arboreally; these are confined almost entirely to dead hollow stems and favorable crevices in tree trunks. In the Lae area of New Guinea the arboricolous fauna is several times as large. Its specialized species live in a great variety of arboreal situations: live plant stems, dead stems, myrmecophyte pseudobulbs,

leaves bound together with silk, carton nests on leaves, and silken nests woven on the sides of tree trunks. The total arboricolous ant populations are, moreover, much denser in the New Guinea rain forests. The same considerations hold in even greater measure with respect to the Neotropical arboricolous fauna, which is phylogenetically closer to the Floridian fauna and hence more appropriate for such a comparison.

Local tropical ant faunas are usually adaptively more diversified and contain a larger number of species than local temperate faunas. Our information is not adequate to determine whether individual species in these faunas tend to be more specialized, but it is certain, and perhaps more significant, that a greater number of specialists coexist at any given time. This continuing richness is the source of the evolutionary vitality that characterizes tropical faunas. It can be conjectured that as a rule successful new major adaptive types of ants originate and achieve initial radiation in the tropical rain forests. If this is true, a "generally adapted" ant group would usually be one that has been notably successful in the tropical rain forests and hence is more likely to produce species that can penetrate adjacent temperate and arid regions secondarily.

SUMMARY

1. Local ant faunas in the lowland rain forests of New Guinea are among the richest in the world and contain approximately 2 to 4 times as many species as faunas occupying comparable areas in north temperate zones.

2. The largest number of species and colonies nest and forage exclusively in the ground zone (soil, leaf litter, and rotting wood on the ground). A smaller number nest in the forest canopy, while a third, still smaller faunal component is restricted primarily to the "low arboreal" zone, including C-stratum trees and the lower trunks of larger trees. Foraging tends to be downward: ground-zone species rarely leave the ground, while low—arboreal species commonly forage on the ground as well as in their own zone, and high-arboreal species often utilize all 3 zones.

3. Most terricolous species nest in small pieces of rotting wood, not exceeding 8 cm in diameter. A smaller but distinctive fauna inhabits larger rotting logs and stumps. True soil-nesting species are relatively scarce in the lowland forests but abundant in the mid-mountain forests above 1000 meters.

4. A rotting-log microsere is well marked in the resident ant species. The greatest concentration of species and colonies occurs in an intermediate ("zorapteran") stage of decomposition, during which there is an abundance of frass-filled cavities beneath a firm covering bark.

5. Worker spinescence is best developed in those species that nest in the ground and low arboreal zones and forage a great deal above ground. High-arboreal and subterranean species are notably non-spinescent, a trait presumably associated with the cramping conditions of their favored nest sites of trophophoric fields.

6. A preliminary classification of food habits is offered. The largest number of species and colonies appear to be general predators, accepting a wide variety of small animals (mostly arthropods) as prey. Specialist predators, pastoralists, and harvesters also occur but are less prominent.

7. Estimates of colony size of selected species are given. Colonies are generally small, usually containing no more than several hundred adults and often as few as 50 or less. This phenomenon seems at least in part to be associated with the generally confining nature of rain forest nest sites.

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