The Army Ants

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[With 2 plates]

The Dorylines, one of the eight major subfamilies of ants, range throughout the Tropics and sub-Tropics of the world. They have survived very successfully from early Tertiary times, or at least 65 million years, on the basis of the unique combination of a nomadic behavior pattern with a fully carnivorous way of life. All that we now know about these ants and their relatives supports Wheeler's (1913) surmise that an exclusively carnivorous diet could not have persisted together with a fixed nest unless colonies were to become very small. In the ponerine and myrmecine subfamilies, which presumably are direct offshoots of the doryline ancestor, a largely carnivorous diet is widely characteristic as are fixed nests, but in species following this pattern small colonies are the rule (Haskins, 1951). But in doryline evolution the problem of large colonies and a carnivorous diet has been solved through a nomadic pattern of existence.

The dorylines have an impressive reputation of long standing as marauding insects, typified by Wheeler's (1913) characterization of them as "the Huns and Tartars of the insect world." General descriptions of their interesting temporary nests or "bivouacs" were available in the earlier literature, and from the observations of Savage (1849) and Vosseler (1905) in particular on the African species of *Dorylus* (*Anomma*) and of Sumichrast (1868), Belt (1874), Müller (1886), Bates (1863), and others on the New World ecitons, it seemed that in all probability the nomadic way of life must characterize the entire subfamily.

Reading this literature in 1930, as a psychologist interested in problems of "instinct," I was at once struck by the impressive breadth of the *Eciton* problem and by the fact that no real solution had been found. On preliminary consideration, the prevalent hypothesis of food exhaustion (Vosseler, 1905) seemed doubtful to me as an explanation of nomadism in these ants, yet no good alternative presented

itself in the literature. This problem seemed to represent an excellent opportunity for studying "instinct" in a social insect, and I had been looking for a widespread group pattern evidently influenced in fundamental ways by hereditary mechanisms.

Because Barro Colorado Island, the Smithsonian Institution's Canal Zone Biological Area, is a relatively undisturbed area of tropical forest in which representative Central American forms such as army ants are accessible for investigation, this situation afforded the best opportunity for carrying out basic phases of the research. In 1932, in my first investigation (Schneirla, 1933) on the Island, the phenomenon was appraised and a tentative solution was formulated. This was strengthened into a theory in three subsequent investigations on the Island (Schneirla, 1938). Now, after completion of eight investigations on the Island with other studies elsewhere in Central America (Schneirla, 1949; Schneirla and Brown, 1950, 1952), it is possible to offer a systematic account and interpretation of the behavior and biological characteristics holding not only for the terrestrial species of *Eciton* on which these studies have concentrated but probably to an appreciable extent for dorylines in general.

Gradually, through this work, an appreciation developed of what the "instinct" problem entails for one who would investigate it in the natural situation. The term, after all, is just a word representing our concept for a behavior phenomenon characteristic of the species; "adaptive" in that it fundamentally benefits species survival, and somehow basically dependent upon the genetic nature of the insects themselves. But the solution of a behavior pattern such as the raiding and nomadism of army ants as a complex system of activity, and an understanding of its hereditary basis (in this case what has kept the pattern predominantly in operation in this subfamily of ants for more than 65 million years) is not likely to fall readily into our hands. Rather it requires us to investigate the entire way of life of the animal, both in its behavioral or psychological and its biological aspects. This is a suggestion of the problem I have pursued with the army ants as material and Barro Colorado Island as base.

Probably more than one-tenth of the more than 140 species known for the three genera which constitute almost all of the tropical American dorylines are represented by colonies on the Island. Some ten of these species are encountered with considerable frequency, particularly the terrestrial *Eciton* (*Eciton*) species, *E. burchelli* and *E. hamatum*. These species are correctly termed "terrestrial" in that their daily raids are predominantly carried out and their temporary nests are typically situated on the surface of the ground or even in the vegetation. Studying them, we learn something of the characteristics of less accessible subterranean species as well.

The German term "Wanderameisen" emphasizes the roaming life which the ecitons lead. The branching columns of species like *Eciton* (*E.*) *hamatum* and *Eciton* (*H.*) *crassicorne* and the swarm or column of *Eciton* (*E.*) *burchelli* and *Eciton* (*Labidus*) *praedator* are frequently encountered in the forests of the Island, and one may be sure the ants issue from a temporary colony "bivouac" somewhere in the general vicinity. But finding colony headquarters is never an easy matter. Without observing the correct clues one may follow the column in the wrong direction, away from the home site, a mistake easily made in the afternoon particularly. Even if by dint of sharp eyesight, some agility, and some luck we are able to follow the column in the correct direction, it is possible under certain conditions to pass the actual bivouac without noting any signs of its presence. The ordinary task of column-following is made interestingly more difficult by the fact that each species—the golden-yellow *hamatum*, the darkish-brown *burchelli*, the reddish-black *praedator*, and others— in its own way is color-camouflaged and merges readily with ground colors in the typically dim light of the forest. The course usually is a rough one: through tangled masses of vines with prickly palms as occasional hazards, wild pineapple thickets and a variety of natural mazes formed around fallen trees, up and down steep ravine banks and across elevated bridges formed by lianas, the army ants go readily but not always the human investigator. The main center of raiding and hence the base columns run most frequently through the heaviest growth. There the living prey is most plentiful, and so it is there the advance raiders turn most readily in response to movement and odors from their insect booty, and it is there the human investigator must go if he would follow them.

We find *Eciton* colonies by hiking the trails to intersect the raiding lines, then by tracking down the colony base by following the columns. This means that the trail system of the Island has been an indispensable asset to searching for and studying *Eciton* colonies in a systematic way. Almost without exception even our short-term studies of ecitons must begin with the bivouac, and almost the only way to find this home site is to follow *in* the raiding columns. In other parts of the Tropics, where trails and roads tend to run outside the forest by human preference, one follows the stream beds in survey work, and the going is considerably slower. In a one-man investigation of 6 months on the Island in the dry season of 1946 (Schneirla, 1949), I worked with 30 colonies of *hamatum* and nearly 20 of *burchelli*, studying two colonies continuously for more than 4 months, and other colonies over shorter intervals—a schedule hardly feasible in a forest other than that of Barro Colorado Island lacking a central system of trails. The techniques of finding and working with army ants depend upon these basic paths first of all.

A major behavioral and biological problem in this investigation has been the nature, basis, and adaptive properties of that most peculiar of insect nests, the *Eciton* bivouac. As mentioned before, *Eciton hamatum* and *burchelli* may be properly termed "terrestrial" species because their raiding and their bivouacking are carried out mainly above ground. Without any active excavating and without any manipulating of fallen materials, colonies of these species form a domicile with their own bodies. A typical bivouac of *Eciton hamatum* is shown in plate 1, upper, a cylindrical mass hanging as most of them do from the underside of some projecting surface to the ground. In addition to the sides or under surface of logs, other typical places are the spaces between buttressed tree roots, masses of brush, or even the undercut banks of stream beds or the overhanging edge of a rock. In the "nomadic" phase of its activity cycle, a colony in these species forms a new bivouac of this kind each evening, somewhere in the outlying area of the day's raid, and these tend to be open clusters similar to the one represented.

The characteristic *Eciton* ability to cluster their bodies, as well as the manner of clustering, depends first of all upon an anatomical characteristic, the opposed recurved hooks present on the terminal tarsal segments of the worker's legs. These hooks may be seen in plate 1, lower, and figure 1. The first ants to settle in a new place catch into a rough or soft surface by means of their tarsal hooks, or rather are pulled into this anchored position as newcomers run upon them as they stand and stretch them out in a hanging position. In fact the hooks are really anchored by the added weight of others that have crawled down over the body of the first ant, fixing it in place and soon immobilizing it.

In the nomadic phase a new bivouac cluster is formed at the end of each further day of raiding, and this is a most interesting event to watch. In the advanced and most complicated stages of raiding in the afternoon, caches of booty tend to be formed at each busy junction of raiding trails, increasing in size as more and more ants are knocked around and forced out of traffic. As darkness comes and raiding ceases, such clusters grow. Events become increasingly complex at these places as an exodus develops from the old bivouac, and the crowding and complications of traffic, with the tendency to stop and cluster when progress is impeded in darkness, account for the starting of hanging clusters from elevated ceilings near such places, generally at several of them before one nears completion as the new bivouac. As each new cluster begins, the initial slender hanging threads may become ropes which extend to the ground, depending upon a continued flow of traffic to the place. As the ropes continue to grow they are joined together into a single columnar mass. At

first this mass is small in diameter, but as more and more ants pour into it the wall spreads outward from the center, and so a symmetrical cylinder results. Since *Eciton* bivouacs typically grow from the top downward, first in hanging ropes, then joined together as they increase in length, the diameter tends to be largest at the top, and the mass usually tapers inward toward the bottom. *E. burchelli*, in which the workers seem to be stronger in their bivouacking processes, can form taller bivouacs from a surface to the ground, or pouches when the clusters form higher up. I have seen bivouacs of this species at heights of 20 meters or more from the ground, as in the hollows of great trees. The more frequent forming of elevated bivouacs by *burchelli* than by *hamatum* may be due to the fact that the former species extends its raiding masses into trees in far larger numbers and more frequently than does *hamatum*.

The ecology of the *Eciton* bivouac is a complex and devious problem. We have tried to understand why *Eciton* bivouacs, seen in the daytime, generally are found with appreciable overhead shelter, in places less exposed to sunlight and more humid than elsewhere in the general environment. The answer does not seem to be that the first ants to cluster have hit upon a good site through direct sensory discrimination of atmospheric differences. At the time when the clusters are actually forming in the evening, various places in the general forest have an equal and minimal illumination and are nearly alike in their temperature and humidity. Investigation of the process leads us to the conclusion that the optimal character of the bivouac is achieved accidentally and indirectly. This is suggested by the fact that the bivouacs are formed near trail junctions, which are established under daylight conditions, when environmental differences in light and dryness have some effect upon the behavior of the ants, causing them to avoid places of extreme stimulation. Also, the bivouacs typically hang from elevated surfaces, which are likely to afford some protection to the cluster when it is exposed to the general environment on the following day.

The interior of the bivouac, where the brood is sheltered and the single colony queen rests, offers an impressively stable environment to these more susceptible members of the community as well as a central resting place for the worker population. The hanging cluster traps a cubic area of atmosphere which does not reach the extremes of temperature and dryness attained by the general forest environment, but in general is somewhat cooler and drier at night and somewhat warmer and more humid during the day. This result is achieved rather indirectly, on the whole, although mainly as a result of worker behavior. The indirectness may be suggested first of all by the fact that, when resting, workers cluster more closely together at night in

reaction to the lower temperatures of the forest at that time, the bivouac walls become tighter and better conserve heat produced internally (by the brood in particular). Conversely, after dawn, when increasing light excites growing numbers of ants to leave the bivouac walls, as the raid grows, this wall thins out, usually develops small apertures, and is undercut at the bottom. The effect is to increase the internal air circulation as well as to cool the atmosphere in the interior through evaporation so that the internal temperature of the bivouac does not rise to the height reached by midday in the environs. The incubation properties of the bivouac represent an important factor in *Eciton* life, for with less regular atmospheric conditions in the nest, the stages of brood development could not have their typical regularity in timing. More than a limited irregularity in these biological processes would surely have important distorting effects in the *Eciton* activity cycle.

An *Eciton* colony is a complex organization that contains in its regular membership not only a fertile queen and a great horde of neuter females or workers, but also an immense brood of developing individuals (usually all workers), and in addition many non-insect guests or "ecitophiles" (beetles and others) ranging to parasitic forms. The *Eciton* workers, which carry on the raiding and other labors of the colony, make up most of the social unit and may number into some hundreds of thousands as in the case of *Eciton burchelli*. Colonies of *Eciton hamatum* usually are much smaller than those of *burchelli*, and probably average not much more than 150,000 workers. In strictly subterranean species, such as *Eciton praedator* and *Eciton crassicorne*, the populations seem to be larger on the whole, judging especially from the durations of the emigrations.

A population component of great importance in *Eciton* life is the brood, which is always present at some stage of development in any functional colony. Without their broods, these colonies cannot exist very long. Throughout the year, at fairly regular intervals, the population of the colony is increased by the emergence of successive great new broods, which virtually always consist entirely of workers. In the case of *Eciton hamatum* we have counted more than 40,000 individuals in a single all-worker brood, probably the typical brood size for that species. Single broods of *Eciton burchelli* are much larger, approaching twice the size of those of *hamatum*.

Of course the colonies do not continue to grow indefinitely by the addition of new broods. There are at least two measures of population control exerted in the normal environment: one, losses involved in the daily raiding forays, in which great numbers of workers are lost in combat with insects whose nests are pillaged; the other, natural hazards such as exposure to environmental extremes, particularly

in the dry season. The result is that on the whole, during most of the year, the majority of colonies do not change greatly in size, notwithstanding the regular addition of large worker increments from new broods.

There is one major departure from the annual series of all-worker broods. In the last months of the rainy season, evidently a time of exceptional plenty for most colonies of army ants, many *Eciton* colonies seem to increase their colony populations very appreciably. There often follows a further exceptional occurrence, namely, the production of a bisexual brood consisting of a great many males and a very few queen individuals. Such broods occur most frequently in the first third of the dry season. Through an intricate process which we have studied in some detail, production of the sexual brood leads to a two-way division of the colony, another process of importance in population control.
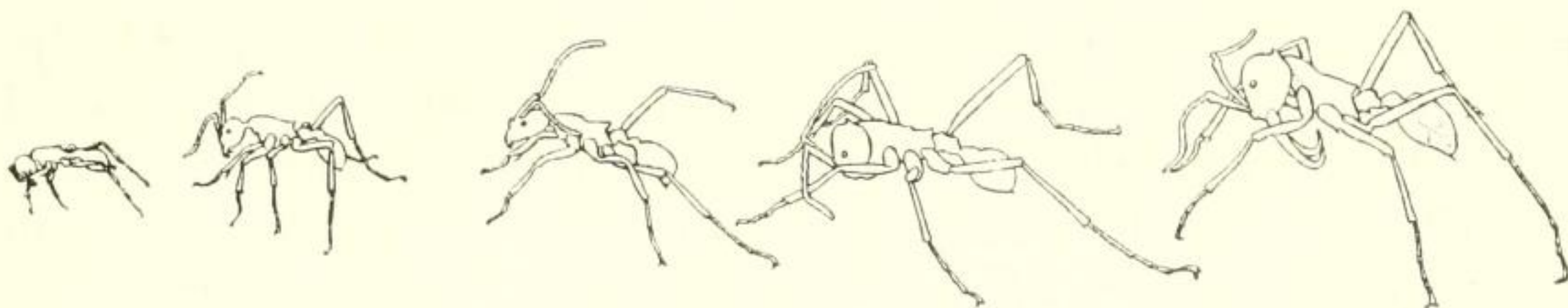

FIGURE 1.—Representative workers from the population series of an *Eciton hamatum* colony. Differences in size and structure through the population are represented here by individuals arbitrarily selected from the minim and major extremes and the intervening 20-percentile points. Body lengths: minim worker, 2.9 mm.; major worker, 9.9 mm.

The ecitons exhibit in an outstandingly regular way that important social characteristic, polymorphism—the occurrence of morphological differences through a population of one sex, in this case the female sex. The workers present differences in both size and form. The main differences are shown in figure 1. The worker series from the largest through the intermediate to the smallest size is not a broken series of radically different types but a smooth and gradual one on the whole. The five worker types of *Eciton hamatum* shown in the figure represent arbitrary steps in a regular series ranging from the smallest or minim workers (about 2.9 mm. in length) to the largest or major workers (about 12 mm. in length). The largest workers have disproportionately large heads and anterior bodies, an anatomical peculiarity which ends, as in a burst of glory, with the enormous head and mandibles of the major workers. These individuals are characterized by their huge sickle-shaped mandibles and by the great strength which can be exerted in closing and holding them shut. The jaws, together with the stings and poison glands, make the major workers formidable foes of any intruders into bivouacs or raids.

It seems probable that the entire membership of any *Eciton* all-worker brood is the product of fertilized eggs of essentially equivalent genetic constitution and that the principal difference in the conditions of their development depends upon the amount of food received. Statistical evidence is available indicating a different growth rate for the larvae of minim, intermediate, and major workers. It would appear that the differences are established very early, and probably depend first of all upon the order in which the eggs are laid, with the first-laid eggs having an initial advantage which is thereafter maintained to produce major-worker types, those laid later in the series a disadvantage resulting in successively smaller castes. Major workers are the first to mature as larvae and to spin their cocoons and first to emerge from their cocoons as mature pupae, with degrees of difference to the extreme of the minim workers, which are last in these respects in both *hamatum* and *burchelli*. In the development of an *Eciton* all-worker brood there appears to be a trend toward an extreme emphasis on underfeeding, since the typical curve of body-length variations in the brood population is skewed somewhat toward the smallest sizes. The conditions that influence brood development normally appear to be closely similar for successive worker broods in the same colony or for worker broods of different colonies, judged from our population studies on broods and adult populations.

It is very probable that the emergence of the major-worker type is a strategically important factor which made possible the evolution of these *Eciton* species as terrestrial forms. In the deep forest environment that evidently prevailed throughout tropical America in late Jurassic times, a condition very probably congenial to the evolution of surface-living social insects, there also existed vertebrates like the anteaters and the coatis in particular which might have curbed this emergence of the *Eciton*, except for the appearance of an effective protective measure such as the major workers. Anteaters, and particularly the terrestrially and arboreally active tamanduas, are very numerous in the Barro Colorado forest, yet never have I seen one of them molesting an *Eciton* bivouac. The large and delicate brood inside the exposed temporary *Eciton* nest would be a very palatable find for the tamanduas and no doubt for the coatis also, were it not for these major workers with their formidable bites and stings.

Notwithstanding their effective equipment, the majors, because of their clumsy oversized foreparts and unwieldy mandibles, play a minor role in the normal work of raiding. As they trudge the trails, they are characteristically shunted to the side by the more agile travelers of smaller castes. These last, and particularly the intermediate workers, are the normal killers of prey and carriers of booty. Far from accompanying as "officers," as Belt (1874) thought, and direct-

ing traffic, the major workers often stand around or blunder in the paths of others. But although their function in traffic appears to be mainly negative and indirect rather than specifically directive, it is an important function, since collisions and traffic blocks incidentally play a contributory role in the development of *Eciton* raids and the emigrations which occur as their sequels. Although the major workers never are seen carrying anything, the submajors normally carry larger booty objects, and are particularly effective in carrying the large male larvae when these are present in the colony. On the whole, booty objects are carried, roughly, in relation to size by the workers, with the smallest burdens carried by the minim workers. Workers, major and submajor, as well as the largest intermediates, play a particularly useful role in the construction and maintenance of the bivouac. Because of their long legs and well-developed tarsal hooks, these individuals become strong parts of the substructure in the temporary nest, and normally can hold together under external disturbances such as wind or rain.

It is plain that polymorphic differences in the *Eciton* worker series account for a corresponding relative specialization as in many other ants. The intermediate workers are prominent in activities outside the bivouac and do the bulk of the effective raiding. Because of their size, moderate proportions, and agility they are better suited for ferreting out, attacking, and transporting booty, and laying down chemical trails and traveling on them through varied and difficult terrain, than are the largest and smallest castes. On the other hand, the *Eciton* minors are an asset in transporting and feeding the brood, particularly when it is in the egg and earliest larval stages. When a colony has a brood of eggs or very young larvae, these generally are found in large boluses in the center of the bivouac, surrounded and permeated by minim workers. So these diminutive workers, which presumably received the least amount of food and were most stunted of all in their own larval brood, come into their own as mature workers through being physically best suited for the early transport and feeding of the young brood, a function of critical importance in colony life.

The pillaging activities of the dorylines mark them as a unique subfamily among ants—one with a constant predatory challenge to the environment. Two principal types of raiding pattern are found, exemplified by the column-raiding *Eciton hamatum* and the swarm-raiding *burchelli*, and apparently expressed in degrees of difference through the dorylines. The most arresting and dramatic raids are those of the swarms that are formed daily by *burchelli* colonies (fig. 2). The *burchelli* forays grow much larger than the somewhat similar mass raids of *praedator*, and cause far more commotion in the forest.

For an *Eciton burchelli* raid nearing the height of its development in swarming, picture a rectangular body of 15 meters or more in width and 1 to 2 meters in depth, made up of many tens of thousands of scurrying reddish-black individuals, which as a mass manages to move broadside ahead in a fairly direct path. When it starts to develop at dawn, the foray at first has no particular direction, but in the course of time one section acquires a direction through a more
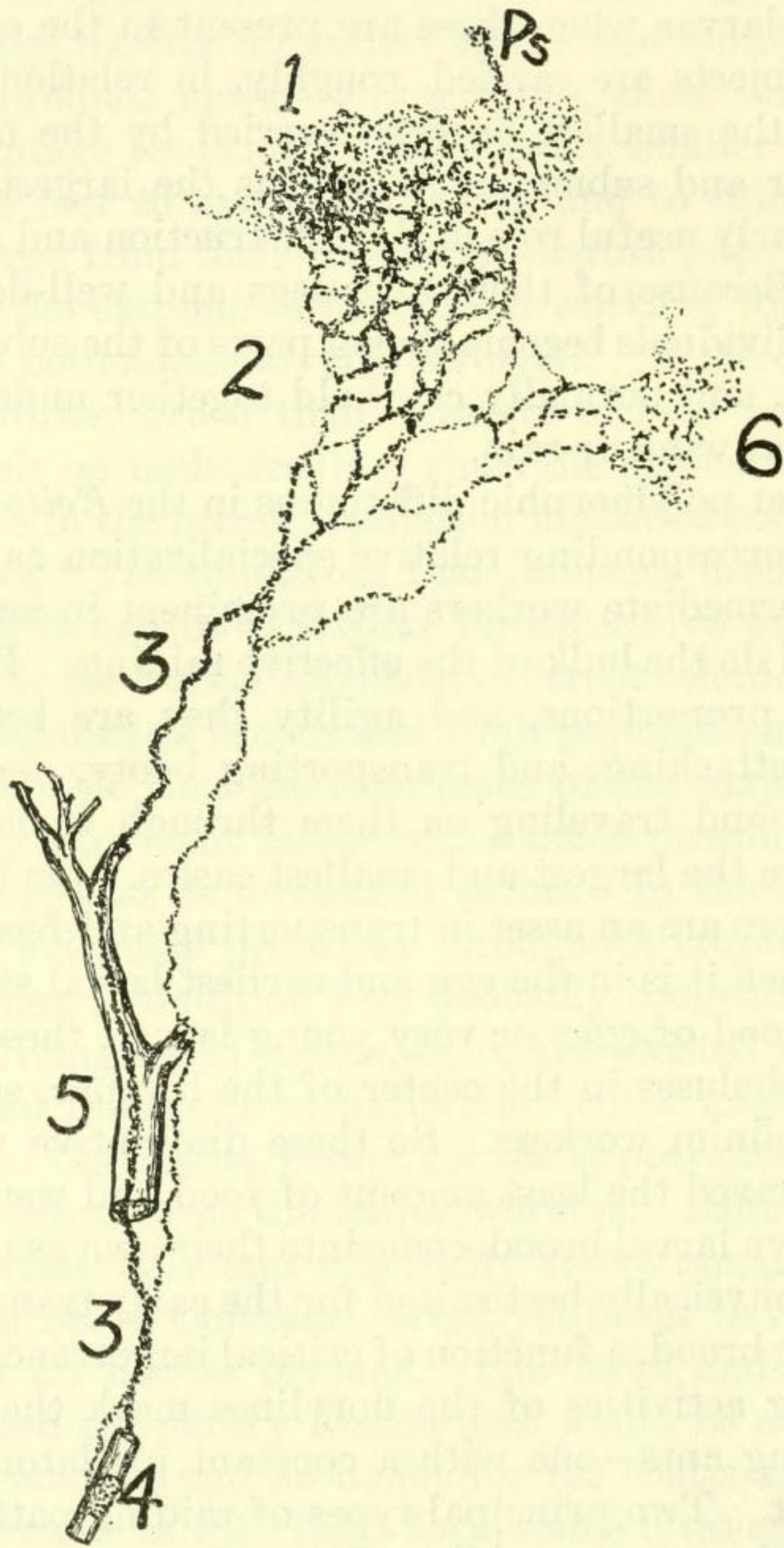

FIGURE 2.—Diagram of an *Eciton burchelli* nomadic-phase raid at 11 a. m., after about five hours of raiding. 1, Swarm (now approximately 70 meters from the bivouac and about 15 meters wide); Ps, pseudopodic advance column; 2, fan-shaped mass of consolidation columns; 3, principal column (the alternative column disappeared within the following hour); 4, the bivouac, within a hollow log; 5, remains of large fallen tree, a spot thoroughly raided by the swarm about 2 hours previously; 6, a subswarm recently formed by division of the main swarm.

rapid advance of its members and soon drains in the other radial expansions. Thereafter this growing mass holds its initial direction in an approximate manner through the pressure of ants arriving in rear columns from the direction of the bivouac. The steady advance in a principal direction, usually with not more than 15° deviation to either side, indicates a considerable degree of internal organization, notwithstanding the chaos and confusion that seem to prevail within the advancing mass. But an organization does exist, indicated not only by the maintenance of a general direction but also by the occurrence of flanking movements of limited scope, alternately to right and left, at intervals of 5 to 20 minutes depending upon the size of the swarm.

The huge sorties of *burchelli* in particular bring disaster to practically all animal life that lies in their path and fails to escape. Their normal bag includes tarantulas, scorpions, beetles, roaches, grasshoppers, and the adults and broods of other ants and many forest insects; few evade the dragnet. I have seen snakes, lizards, and nestling birds killed on various occasions; undoubtedly a larger vertebrate which, because of injury or for some other reason, could not run off, would be killed by stinging or asphyxiation. But lacking a cutting or shearing edge on their mandibles, unlike their African relatives the "driver ants" these tropical American swarmers cannot tear down their occasional vertebrate victims. Arthopods, such as ticks, escape through their excitatory secretions, stick insects through repellent chemicals, as tests show, as well as through tonic immobility. The swarmers react to movement in particular as well as to the scent of their booty, and a motionless insect has some chance of escaping them. Common exceptions, which may enjoy almost a community invulnerability in many cases, include termites and Azteca ants in their bulb nests in trees, army ants of their own and other species both on raiding parties and in their bivouacs, and leaf-cutter ants in the larger mound communities; in various ways these often manage to fight off or somehow repel the swarmers.

The approach of the massive *burchelli* attack is heralded by three types of sound effect from very different sources. There is a kind of foundation noise from the rattling and rustling of leaves and vegetation as the ants seethe along and a screen of agitated small life is flushed out. This fuses with related sounds such as an irregular staccato produced in the random movements of jumping insects knocking against leaves and wood. This noise, more or less continuous, beats on the ears of an observer until it acquires a distinctive meaning almost as the collective death rattle of the countless victims. When this composite sound is muffled after a rain, as the swarm moves through soaked and heavily dripping vegetation, there is an uncanny effect of inappropriate silence.

Another characteristic accompaniment of the swarm raid is the loud and variable buzzing of the scattered crowd of flies of various species, some types hovering, circling, or darting just ahead of the advancing fringe of the swarm, others over the swarm itself or over the fan of columns behind. To the general hum are added irregular short notes of higher pitch as individuals or small groups of flies swoop down suddenly here and there upon some probable victim of the ants which has suddenly burst into view. These flies cannot be feeding to any extent, for they rise again instantly. Very probably they are ovipositing on the prey, with their eggs subsequently carried along incidentally into the bivouac where those unconsumed with the booty may develop along with the *Eciton* brood. Now and then, in a laboratory nest containing *burchelli* workers and larvae, I have observed maggots that may be the young of these flies. It is probable that their entire life cycle is intimately intermeshed with that of the *Eciton*.

No part of the more prosaic clatter, but impressive solo effects, are the occasional calls of antbirds. One first catches from a distance the beautiful crescendo of the bicolored antbird, then closer to the scene of action the characteristic low twittering notes of the antwren and other common frequenters of the raid. For locating swarm raids these are most useful clues as a rule, since the birds ordinarily are to be heard at or near the scene of action from the time of first morning light when the raid begins. However, the calls are not an infallible clue to the raids by any means, for in the respective mating seasons of the different species, they may be heard almost anywhere in the forest *except* around the *Eciton* swarm raid. In collaboration with our investigation of 1948, Dr. Robert Johnson carried out an intensive behavior study of the antbirds attending *burchelli* swarms (Johnson, 1954). The birds do not feed upon the ants except accidentally— rather they feed on the flushed-out insects which are snatched up by them in quick flight from nearby perches. In between these captures the birds utter a characteristic call. Their music and actions are an inseparable part of this forest phenomenon.

Burchelli raids have the characteristic form represented by an example in figure 2. In the morning, from shortly after its beginning at dawn, the size of the mass increases through a steady stream of recruits from the bivouac entering along the consolidation trail through the fan of columns to the swarm. By midmorning (in the nomadic phase), with the swarm perhaps 90 meters or more from the bivouac and more than 15 meters wide, outgoing traffic has decreased and the principal trail is dominated by a thick procession of returning ants, mainly booty-laden, moving toward the bivouac. The haul—forest invertebrates of many descriptions, fragments of arthro-

1. A typical cylindrical bivouac of *Eciton hamatum* (colony '46 H–D) hanging from a log to the ground. This bivouac appears as it was found, except for some clearing away of vines and rubble around the cluster for the photograph.

2. Closeup of a small portion of cluster wall in a bivouac of *Eciton hamatum*. Note that most of the ants hang head downward, a feature due to the placement of their tarsal leg hooks.

PLATE 2
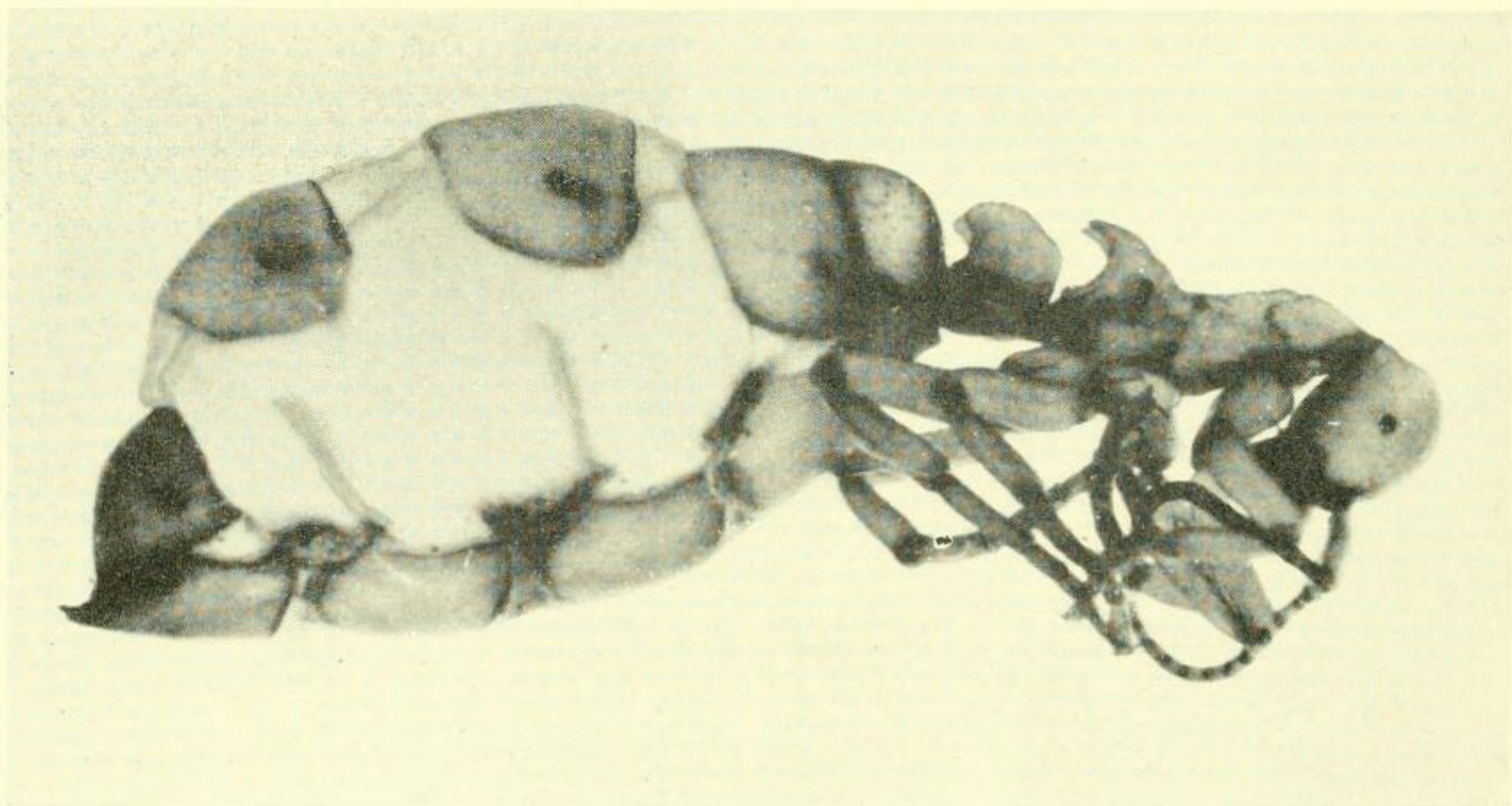
Queen of *Eciton hamatum* in the contracted condition (above) and the physogastric condition (below). The queen is physogastric only for a few days in the early and middle part of the statary phase; otherwise she remains in the contracted position.

pod bodies, and items of insect brood—is rushed along in the clutches of workers in the heavily thronged, 3- to 5-cm.-wide columns. The variety of captures, from tarantula femurs to ant eggs, gives evidence of the wide tribute levied by the swarmers upon forest life.

In his population studies of forest-flora life, Dr. Eliot Williams (1941) was impressed by the capacity of the ecitons to deplete the small life of a raided locality. One day, early in his investigation, when he laid down his quadrat frame on a hill near the Barbour-Lathrop trail, prepared to scoop up the soil and its faunal contents for a biological census, he was perplexed at the paucity of living things discovered. Other trials in the vicinity turned out similarly. The mystery was explained when we compared notes and I recalled that on the previous day an *Eciton praedator* swarm had worked that hillside.

It is difficult to know how extensively the ecitons must cut into the population of small forest life. A *burchelli* colony is capable of heaping more than one measured gallon of booty in just one of its forward-area caches, and by conservative estimate there are 50 colonies of this species on the Island. The inroads of this and the numerous other *Eciton* species must constitute an important factor in the forest balance, operating against a rapid insect progeneration often cited as threatening to man.

Although *burchelli* swarms typically are larger than those of the subterranean *Eciton praedator*, the two species, both common on Barro Colorado Island, are similar in this respect: In both species the swarm advances broadside with alternate "flanking movements" as a rule, wheeling first to one side and then to the other. "Pseudopodic columns" extend similarly from the front and flanks of the mass in both, and in both there is a comparable fan-shaped complex of columns in the rear from which a single consolidation column leads to the bivouac.

Watching the swarm raids, first of all one gains the impression that movement in the mass is utterly confused, with ants here and there clustered in frenzied excitement, fighting and stinging their struggling captives, elsewhere scurrying about or moving in circuitous columns which appear to run in every direction. Nevertheless, appropriate analysis soon demonstrates convincingly that the swarm is effectively organized.

In these respects *Eciton* behavior represents a somewhat unique problem in social psychology, for no animal below man is able to function away from home in organized groups as sizable and at the same time as regular and complex in function as these swarms. For this reason I have found *burchelli* swarm organization worth investigating in some detail (Schneirla, 1940). It can be said that there are no leaders in these swarms except in a very temporary and limited sense, and that

not in the sense of human leadership; but the swarm at any stage is "directed" collectively in a complex manner through the activities of all ants participating in the raid (Schneirla, 1941).

Very different are the raids of *E. hamatum*, which I have studied as an example of the *Eciton* "column-raiding" pattern (Schneirla, 1933, 1938). This species is a frequent sight in the Barro Colorado forest. Operations in its relatively narrow files are marked by large, shiny, white-headed majors and smaller khaki-colored "soldadas," the former colliding frequently, the latter overrun frequently, according to the ebb and flow of traffic in two directions.

This species, also a true terrestrial *Eciton*, builds up and carries through its raids in the daytime, and typically emigrates after dark. In the morning, when one follows along in the direction taken by most of the booty carriers, and takes the correct turn at junction points, other things being equal he may be able to locate the bivouac. There are other cues, useful although far from infallible, such as the fact that the base of a "Y" junction usually is on the bivouac side. If no booty carriers are seen, and the junctions are irregular, the problem is more difficult. In the afternoon, and particularly in late afternoon, booty carriers are likely to be numerous, but usually they seem to be traveling in equal numbers in the opposite directions, and the bivouac seems to be hidden behind a screen of farflung and confused lines of traffic.

The answer is found when the raid is studied as a developing phenomenon. For this the columns must be traced out at regular times during the day, and transitions investigated appropriately. A *hamatum* column raid, like a *burchelli* raid, also generally begins at daylight with radiations in all directions around the bivouac, then soon becomes directionalized. But in this pattern, in the nomadic phase, two or more, frequently three, trail complexes develop, each with its principal trail leading from the bivouac to a peripheral zone of branching columns. The sketch in figure 3 represents one *hamatum* raid mapped at midmorning. Starting from the bivouac, we set out to follow one of the three main routes on which ants hurry to and from the bivouac. Booty-laden ants are almost all returning to the bivouac and for some distance the trail is followed by a single column, unbroken by branches other than short ones in places where the ants continue to raid up trees or in masses of vegetation. Earlier in the morning there were branch columns here in profusion, but most of these dropped from use once the area had been largely worked out. The single meandering base column is likely to continue outward for 50 meters or more, then to have a major division; and in all likelihood whichever branch we follow will have further divisions at shorter intervals as it is traced outward. In effect, the ants have established a complex spreading system of columns resembling a tree, in which a single trunkline from the

bivouac first divides into limb columns, which in turn divide and re-divide into branch columns, these finally into twig columns. The twig columns end in small scurrying groups of foragers.

The other main trail systems are similar, each with its base trail, its branching and rebranching secondary trails. They differ only in secondary details concerning the routes and distances, how much out-going traffic pours into each, and how much booty is returned. All these differences may influence which of these principal routes is to be taken in the eventual emigration of the evening.
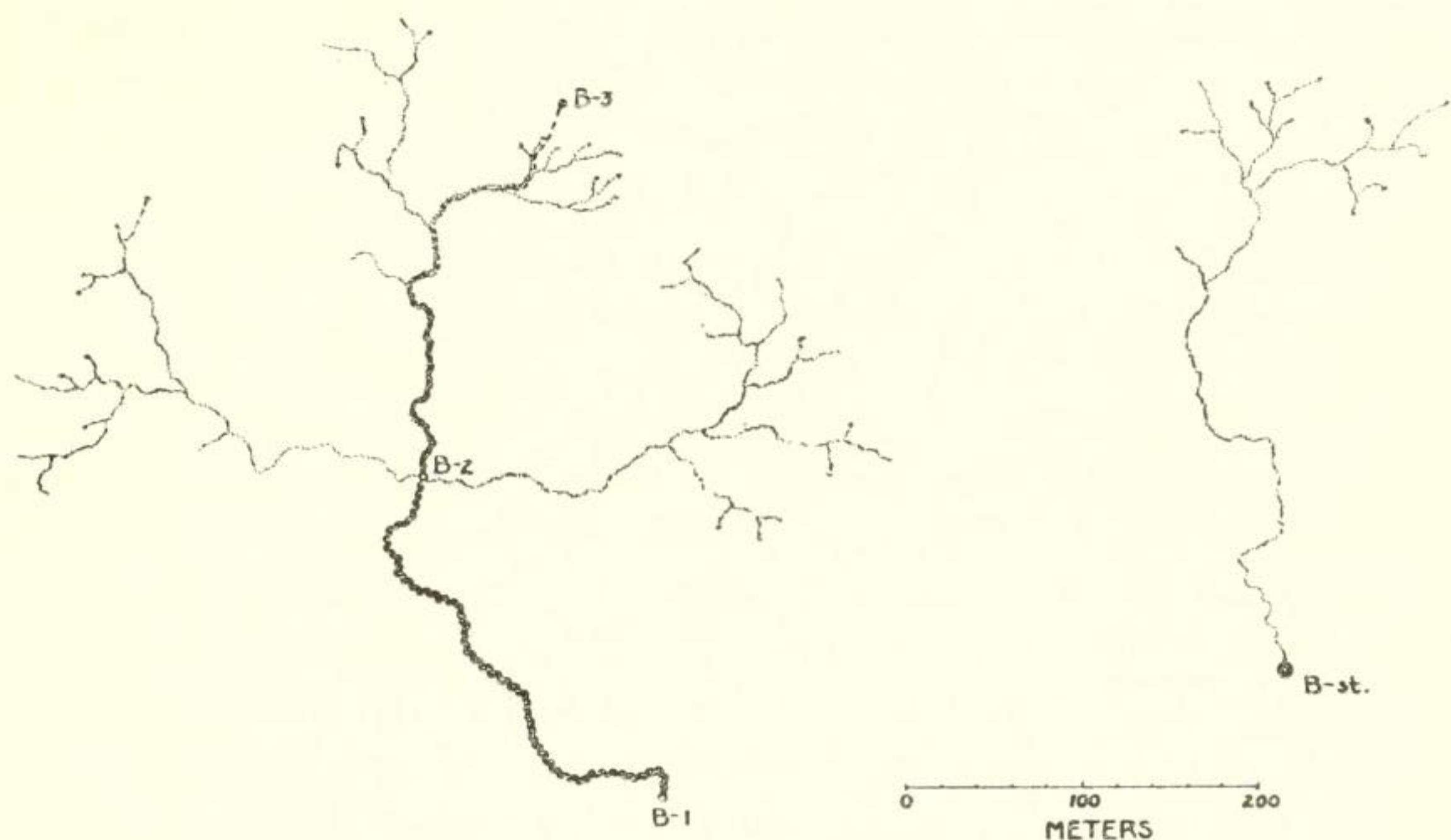

FIGURE 3.—*Left*, raiding and emigration in the nomadic phase: B–1, Wednesday's bivouac and emigration route to B–2, from which a complex 3-system raid developed on Thursday. Thursday evening the colony emigrated about 350 meters to the new place, B–3, from which a similar raid developed on Friday, and so on for 16 days, until the phase ended with the enclosure of the larval brood. *Right*, sketch of a raid in the statary phase, when the colony has an enclosed brood (passing through the pupal state) and is bivouacked in a hollow log or tree. Raids are much smaller than in the nomadic phase. The statary phase lasts 20 days and ends with the emergence of the pupal brood as new workers.

The small groups of ants in the outskirts are the pioneers, first to extend the raid into new territory, first to rush back, exciting ants in the rear, when booty is found. Occasionally each such group divides, as when it grows oversize or a natural obstacle is met, and a forking of the trail results. In the train of each of these "pushing parties" there is a two-way column joining its path with older routes in the rear and eventually with the bivouac, and thus all parts of the system are connected.

The *Eciton* raid travels on scent trails made by the ants them-selves—the basis of orientation in all *Eciton* raiding. The existence of a chemical trail on the path followed by every column may be

shown by simple tests such as displacing a leaf or other surface over which the ants run, which always disrupts traffic until the pathway unit is replaced or the break is rescented. The chemical trail is first laid by ants in the advance group, which indicate their entrance into new terrain by crawling slowly forward in a hesitant, meandering way. Each pioneer moves only a short distance beyond the end of the scent trail, but in this excited advance it rubs its abdomen against the ground, reflexly releasing a secretion (anal gland?) which starts a new section of trail. The trail is thus extended in relay fashion by a succession of individuals, each moving out only a few centimeters before returning to the rear. There are no particular "leaders" in the activity, but each newcomer contributes its bit to the roadmaking (Schneirla, 1941).

In a similar manner the path of a *burchelli* swarm is scented by pioneers operating all across the front of the swarm. The difference is that a *hamatum* pushing party usually contains only a few dozen individuals and a narrow trail is formed directly. The *burchelli* swarm is a large growing body of many tens of thousands, in its first advance scenting a broad pathway which is finally reduced to a relatively narrow trail when the swarm has passed far beyond. This striking difference in raiding patterns no doubt is the product of factors such as different olfactory sensitivity, glandular properties, and general level of excitability of ants in the two species.

Another important species difference concerns the nature of the prey. The relatively small raiding groups of *hamatum* do not make the clean sweep of small forest life that the swarmers achieve. Most of the *hamatum* booty consists of soft-bodied insect young, the larvae and pupae of other ants and wasps in particular. Only when their raids are largest and the foragers most excitable do they capture adult insects in any numbers. Normally, the occupants of invaded insect nests may even escape the column raiders by exploding in all directions from the nest exit at the first invasion, carrying their brood off before many of the raiders arrive on the scene. Well after the soldadas have gone, they return. But although the column raiders do not make as clean a sweep as the swarmers and are more selective in their captures, they are far from ineffective. Their multiple treelike systems usually cover an area up to 200° around the temporary nests to a distance of 300 meters or more, and great amounts of booty are taken. In all probability, it is the fact that their types of prey are largely different and competition only partial in this respect that has made possible the coexistence of these two species of wide-ranging carnivorous ants as terrestrial forms in the American Tropics.

There are two scenes that recur most vividly in my reminiscing about army ants. One is a great swarm raid in full swing with ant-

birds flitting about and calling from underbrush perches; the other is that moment near the end of a nighttime emigration when a previously monotonously plodding column begins to show an excited rushing about of workers, indicating that at last the queen is about to pass. The problem of *Eciton* nomadism has been a fascinating one to study.

That the dorylines are characterized by a nomadic existence has been known to science for more than a century, particularly from the observations of Savage (1847) on African driver ants, and Bates (1863), Sumichrast (1868), and others on the American forms. But the frequency of occurrence of the emigrations and their causes or, conversely, the cause of failures to move were quite obscure in the earlier literature. The dominant hypothesis was Vosseler's (1905) assumption that a colony moves on when it has exhausted the supply of prey around its temporary nesting place. The suggestion of Müller (1886) that a colony needs more food when it has a growing brood, and hence moves about more, although teleological, was much closer to what now appears to be the actual explanation. But nearly 50 years later it was possible for Heape (1931) and Fraenkel (1932) to conclude from the current literature that the doryline ants move on according to food scarcity and hence are a case of irregular "emigration." From what we now know, the dorylines emerge as a special pattern of true *migration*. In my first few weeks of work on the Island in 1932, findings indicated the existence of specific "nomadic" and "statary" conditions in the terrestrial ecitons, related to active and inactive stages respectively in brood development (Schneirla, 1933). Laboratory and field results increasingly supported a theory of cyclic nomad-statary phases, alternation of these opposite phases depending upon energizing of the worker population by successive broods in their active and passive stages of development (Schneirla, 1938).

Emphasis was first placed upon cross-sectional surveys and upon the study of the major turning points in the postulated cycle. A record of three complete cycles, accomplished by a colony of *E. hamatum* in somewhat more than four months, is sketched in figure 4. The first complete record of a cycle was obtained in 1936. Soon after my arrival early in the evening on August 5, I was fortunate enough to find a *hamatum* colony in bivouac just behind the laboratory, near Snyder-Molino 2, then in deep forest. From their almost concealed cluster located far beneath a large log, the ants were found at dusk pouring out in a single heavily thronged column in which were seen large numbers of newly emerged callow workers. Masses of callow workers were seen in the bivouac walls, and a considerable number of cocoons remained unopened. Almost all the cocoons had been opened that night before the colony completed its
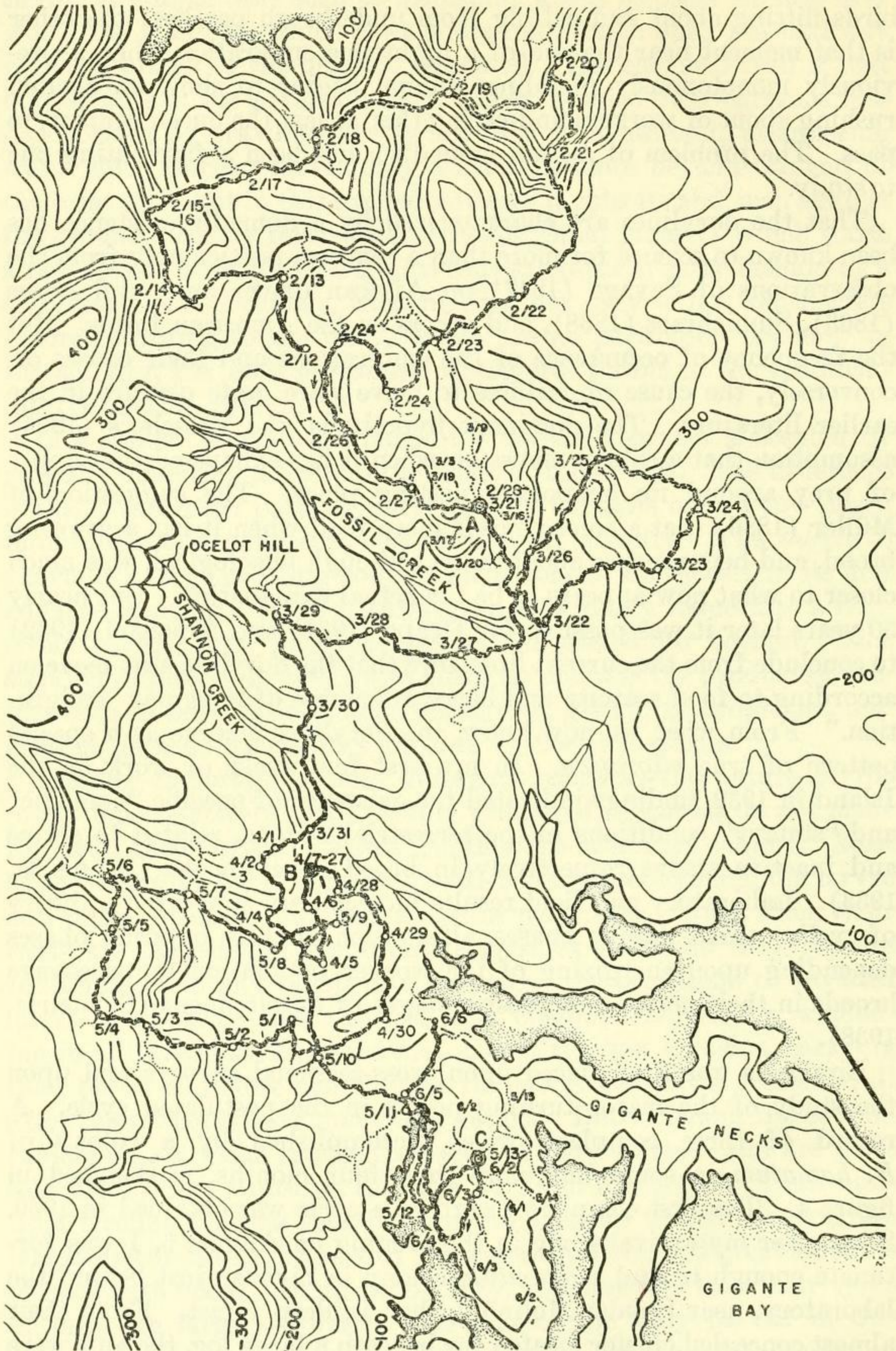
FIGURE 4.—Eastern portion of Barro Colorado Island mapped to show the itinerary (A, B, C), of colony '46 H–B (*E. hamatum*) during a period of 114 days, February to June, 1946. Double circles indicate successive statary sites; small circles indicate nomadic sites; double broken lines indicate successive routes of emigration; dotted lines indicate the principal routes of some of the daily raiding systems. Contour interval, 6.1 meters. Scale: length of the arrow indicating north-south direction (lower right corner) 300 meters.

movement to a site in Lutz Creek, and a great heap of empty cocoons around the vacated spot indicated that the colony had opened most of its brood at this place. Another clue to a long occupancy of the site was a whitened circular area on the rock exactly where the bivouac base had rested, evidently caused by the protracted action of *Eciton* chemicals.

Next day the colony developed three extensive trail systems in a large raid in Lutz Valley. In the evening it emigrated over the principal trail of the central system and before 11 p. m. had mainly completed its new bivouac across Donato trail. This pattern of large daily raids and nightly emigrations was repeated during the next 17 days (a nomadic phase of 18 days), in which the colony moved in an irregular course to a site near Barbour-Lathrop 12. In the meantime a large new brood attained its full-term development. At the last nomadic site the spinning of cocoons by these mature larvae was in full swing, a process greatly assisted by workers laying the larvae on wood detritus and shifting them about at intervals (Beebe, 1919). Next day the first processes of enclosure seemed to have been completed for most of this brood. Now, clustered deeply under a large log on the hill east of Barbour-Lathrop 12, the colony remained for 19 days, a "statary" phase which coincided with the pupation of the current brood. Between August 24 and September 11 the bivouac shifted only about 25 centimeters farther beneath the great log. Daily raiding was always much less vigorous than in the nomadic phase, indicated by the use of only one trail system each day rather than two or or three as in the active phase (fig. 3). Each day after dusk the ants were found retreating into their bivouac, generally issuing in some other direction on the following day. In this way the colony "boxed the compass" in its successive raids from the statary site and managed to strike most sections of a circular area approximating 300 meters in radius.

These facts, first of all, oppose the hypothesis that colonies of this doryline species are forced to emigrate when they have exhausted the prey in a given area. For example, two days after this colony had left its site near Barbour-Lathrop 3 after a one-day stand, another *hamatum* colony stopped nearby and remained there 20 days, raiding in the area as it passed through a statary phase. If there was booty enough in this area to hold the second colony for that number of days, it is difficult to understand the moves of our record colony to its last two nomadic sites as based on scarcity of prey. It is similarly difficult to believe that the booty supply in the vicinity of the statary site was more plentiful than in other localities at which the latter colony remained only for a one-day stand in its nomadic phase—certainly not seventeen times more plentiful.

On the other hand, at the beginning of the study there was a precise coincidence between the emergence of a callow brood and the beginning of a nomadic phase of maximal activity and regular emigration; later the maturation and enclosure of a larval brood coincided with the passing of the colony into a statary phase of minimal raiding and no emigration; finally the colony entered a further nomadic phase when the latter brood emerged as callow workers. On the last day at the second statary site, circumstances were closely equivalent to those at the site vacated when the study began. On this day the colony staged a large 3-system raid, the mature pupal brood was released from cocoons, and the colony moved to a new site at the day's end. On the second emigration of this new phase, it was discovered that the colony had a new brood of very young worker larvae. It had come full circle in just 37 days after leaving the first site.

This coincidence of events in colony behavior and brood condition has been established as the rule not only for *E. hamatum* and *burchelli*, but also for related species. Surprisingly enough, the described nomadic-statary cycle occurs throughout the year, in both rainy and dry seasons, with an unbroken succession of overlapping broods and correlated activity cycles. This was confirmed by studies of 31 *hamatum* colonies and 19 *burchelli* colonies for various lengths of time in the dry season and early rainy season of 1946 (Schneirla, 1949) and of comparable series in these species for various lengths of time in a study extending from the late rainy season of 1947 through most of the dry season of 1948 (Schneirla and Brown, 1950). Colony '46 H-B of *E. hamatum*, while on record from February 12 to June 5, 1946, completed three full nomad-statary cycles and began a fourth (see fig. 4), as follows: Cycle 1, nomadic 16 days, statary 21 days, total, 37 days; cycle 2, nomadic 17 days, statary 20 days, total, 37 days; cycle 3, nomadic 16 days, statary 20 days, total, 36 days. This study ended after a further series of four nomadic days. In the course of the 49 observed emigrations in these three complete cycles, the colony moved from the area north of Barbour trail to the area of Gigante Point on the opposite side of the Island, an overland distance of 2 miles, and a total distance of somewhat more than 5 miles traveled in the successive emigrations. Throughout this entire time the correspondence of changes in colony activities and brood condition was exactly as we have described it for the colony studied in 1936. There was only a secondary difference in the duration of the phases, which in *hamatum* are most frequently 17 days in the nomadic phase and 20 days in the statary. *E. burchelli* is somewhat more variable in its nomadic phase, varying from 11 to 15 days. The statary phase of this species is less variable than the nomadic, with a mode of 21 days.

None of the hundreds of colonies in this species which have been studied at various times of year in these investigations has failed to show the described correspondence between brood condition and the colony activity pattern, with the exception of one natural case in which the queen had died and all semblance of the normal pattern characteristic of the species had disappeared. Such cases may be not infrequent, but extinction must be rapid, as indicated by our tests. Without further broods, as our field experiments show, regular nomadic function disappears in a colony, and the only way in which the worker population can be saved is by fusion with another colony of the species.[1]

The timing device of these recurrent and surprisingly regular cycles is no external event such as the lunar phases which influence rhythmic behavior in many other animals. Rather it lies within each colony, in the casual relationship between brood condition and colony behavior. An active larval brood as it grows provides more and more tactual and chemical stimulation to the adult workers, who are correspondingly responsive. (The nature of the intimate stimulative relationship normally prevailing between workers and brood has been demonstrated in laboratory observations and tests.) The brood thereby energizes the colony in an accelerating manner during its larval development. A great raid then ordinarily occurs each day, leading by complex stages into a colony emigration sometime after dusk. However, the essential increment of social stimulation vanishes abruptly when this larval brood matures and becomes enclosed in cocoons, and without it the level of colony excitement falls to a new low at which raids are always too small to provide a basis for emigration. Each statary phase ends when the emergence of a mature pupal brood as highly active callow workers suddenly raises the colony excitation level to a point at which the large daily raids and emigrations can occur. The hordes of newly emerged workers lose their initial excitatory effect after a few days of further maturation, whereupon they behave essentially like ordinary adult workers; however, in the meantime a new larval brood has reached a condition of high stimulative potency, so that a nomadic colony function continues without a break until this brood in its turn is mature, and so on.

Thus the key to periodic emigration evidently lies in the fact that when the colony is overstimulated with sufficient intensity and persistence, the population responds to environmental excitation at a high level of energy and participation. Each morning the initial stimulus

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[1] After the queen has been absent for more than a few hours, fusion can occur when the colony crosses paths with another of its species. This event throws interesting light on the normal adjustments of workers to the colony queen and upon the unifying effect of her odor in the colony (Schneirla, 1949).

to exodus is provided by daylight, but the invasion of the environment cannot exceed the low statary level unless an active brood provides the essential stimulative increment. During the morning the outgoing rush is diverted into trailmaking, capturing and transporting booty. It is normally depressed at midday in a kind of general "siesta effect," perhaps attributable to a combination of radiation, heat, and desiccation (Schneirla, 1949). When this temporary lethargizing effect disappears early in the afternoon, the exodus again bursts forth, but now advances rapidly along one or more of the established channels (Schneirla, 1938, 1944b), gaining such headway that no normal or accidental extrinsic or intrinsic change can halt it more than temporarily. Theoretically, the beginning of a raid in the morning marks the start of an emigration, but trail conditions and internal colony conditions are not propitious for a continued exodus until late afternoon. Then, when failing light at dusk brings raiding activity to a halt, foragers drain into the trails and actually augment the force of the exodus already under way. When this exodus has been completed by resettlement in a new place, the colony remains moderately quiet in the bivouac until daylight again acts upon it.

These statements are derived from studies of the terrestrial *Eciton* species. It is probable that the fundamental principle of brood stimulation as a hyperenergizing factor also applies to the subterranean species, doubtless with certain secondary variations in the mechanism.

The nomadic "instinct" in these terrestrial army ants thus finds its basis in the dynamic, reversible, and repetitive relationship between reproductive processes and social behavior. Since the stimulative effect of the broods is the driving factor in the process, the *Eciton* cyclic pattern rests first of all upon the queen (pl. 2)—source of the immense broods. This curious individual is much larger than her sterile sisters, the workers, and wingless throughout life (Gallardo, 1920; Wheeler, 1925). The queen of *Eciton hamatum* is capable of producing more than 40,000 eggs in a single batch, all of them laid within about one week midway in each statary phase. In the *burchelli* queen, which produces even larger broods, Hagan (1954) has found a total of about 2,400 ovarioles, each judged capable of producing 20 or more eggs in a series. Since every brood is produced as a unit and is laid within a few days, its members pass through their successive developmental stages and reach full maturity almost in step. These are basic facts for the occurrence of the cycle.

Since the turning points in the colony activity cycle are correlated in a relatively precise manner with major changes in brood development, the pacemaker function must somehow depend upon whatever sets the queen at regular intervals from a resting condition to a further prodigious feat of egg production. The idea of an attunement

to some rhythmic environmental event such as lunar cycles at first seems attractive; however, in neither of the established *Eciton* species does the rhythm show any identifiable coincidence with any environmental periodicity. Moreover, numerous colonies studied simultaneously in 1946, 1948, and 1952 passed concurrently through very different stages of the cycle. This turns our attention to the organic process itself; however, the idea of a purely visceral rhythm or some other regular organic process endogenous to the queen as pacemaker has been weakened by evidence of her close dependence upon the external situation of the colony.

The nature of the controlling event has been clarified by studies of brood-adult relationship in the colony in relation to changes in the queen (Schneirla, 1949). When each successive brood approaches larval maturity, the social-stimulative effect of this brood upon workers nears its peak. The workers thus energize and carry out some of the greatest daily raids in the nomadic phase, with their byproduct larger and larger quantities of booty in the bivouac. But our histological studies show that, at the same time, more and more of the larvae (the largest first of all) soon reduce their feeding to zero as they begin to spin their cocoons. Thus in the last few days of each nomadic phase a food surplus inevitably arises. At this time the queen apparently begins to feed voraciously. It is probable that the queen does not overfeed automatically in the presence of plenty, but that she is started and maintained in the process by an augmented stimulation from the greatly enlivened worker population. Within the last few days of each nomadic phase, the queen's gaster begins to swell increasingly, first of all from a recrudescence of the fat bodies, then from an accelerating maturation of eggs. The overfeeding evidently continues into the statary phase, when, with colony food consumption greatly reduced after enclosure of the brood, smaller raids evidently bring in sufficient food to support the processes until the queen becomes maximally physogastric. These occurrences, which are regular and precise events in every *Eciton* colony, are adequate to prepare the queen for the massive egg-laying operation which begins within about one week after the nomadic phase has ended.

My theory, therefore, is that the queen is set off into each new reproductive episode in a feedback fashion by inevitable events in the colony activity cycle. It is a striking fact, however, that the instigating factor itself is an indirect outcome of events depending upon the queen's own function at an earlier point in the cycle.

Interestingly enough, this complicated set of events works out so that when the colony is emigrating nightly over a lengthy, rough, uneven route of 200, 300, or more meters in length, the queen is in a contracted condition and well able to withstand the trials of the

journey. Repelled by bright light, she never leaves the bivouac in the daytime, but is drawn from the cluster in the course of the nightly exodus and must then run the distance with a thick entourage of workers obstructing her variously in the frenzy of their excited activities. Throughout the nomadic phase the queen lays no eggs, and is in the condition shown in plate 2, upper, with contracted gaster. Tough exoskeletal armour plates, now overlapped closely, protect the vital part of her abdomen, and her powerful legs carry her over the most uneven paths, easily overcoming physical impedances in the difficult route despite being trammeled by her pellmell retinue of workers.

When the queen reaches one of the periodic climaxes in her existence and is delivering the enormous mass of eggs that she then produces, her gaster is so greatly distended with maturing eggs that the exoskeletal plates are forced far apart and the intersegmental membranes are tightly stretched between segments. Her gaster then may become 22 mm. or more in length (equal to her total body length in the contracted condition) and very bulky. Although the tightly stretched membranes of her gaster are very tough and tests show that the queen is able to walk about even when physogastric, carrying workers, undoubtedly a long run in an emigration would prove to be a great risk. But at such times, when the queen's condition makes her exceedingly vulnerable to jarring or abrasions, the colony is passing through a statary phase and no emigrations occur. The queen then remains at the center of a quiescent mass and has at least a week for undisturbed recuperation in the bivouac after the eggs have been delivered. This is all the more remarkable because it is an indirect outcome of her own rhythmic physiological processes.

Although most of the workers must have relatively short lives, our studies on Barro Colorado show that the normal function of a colony queen may be a long one. We have been able to keep queens on record by marking them permanently in a distinctive manner. With iridectomy scissors, one or two minute triangles of cuticle are cut from the edge of abdominal sclerites. The cut edges soon darken, so that the queens can be recognized readily when they are removed from their colony. Many recoveries have been made after several months, and a few after one year. The longest record thus far is that of a *hamatum* queen (colony '48 H–15), marked on December 23, 1947, and reidentified by means of her unique mark on April 3, 1952, nearly 5 years later. She was in vigorous condition and carrying out a normal reproductive function late in May 1952, when her colony was last seen. This queen therefore had a functional life of at least 4½ years, in which an estimated total of 45 broods (probably more than 1,800,000 individuals) had been produced. In 45 nomadic phases, with 16 emigrations each on the average, it is estimated that her colony traveled

at least 70 miles during the interval between marking and recovery. How much longer this queen may have functioned before the intervention of supersedure or normal death cannot be said.

How new colony queens are produced in the dorylines was a long-standing mystery (Wheeler, 1913, 1925). The specific solution for ecitons was obtained mainly through work on the Island. Almost all the broods produced at regular intervals in the colonies throughout the entire year are all-worker broods; however, at long intervals smaller broods of many males and a few queens are produced. Such broods arise most frequently in the first third of the dry season, apparently resulting from the initial effective impact of dry weather upon the queen (Schneirla, 1948, 1949). Apparently on Barro Colorado only a part of the colonies produce such broods in any one season. As an example, in a total of 52 colonies of *Eciton hamatum* and *burchelli* studied on the Island during 6 months in 1947–48, only four were found with sexual broods. These broods contained no workers, but only males and young queens (Schneirla and Brown, 1950, 1952). It is probable that the queen lays the usual number of eggs in such cases, mainly infertile eggs, but that in the early stages their number is greatly reduced. The total of individuals matured is roughly 1,500 males in *hamatum* and about twice that number in *burchelli*, with indications that only about six of the young queens emerge as callows. The normal nomad-statary process continues in a regular manner throughout the period of sexual-brood production, essentially as with a worker brood. The one difference is that the nomadic phase is shorter by nearly one week, depending upon a shorter period of larval development in sexual than in worker broods.

Through long-term studies on the Island, we have established the fact that a two-way colony division is the normal outcome of the production of a sexual brood by an *Eciton* colony. This process was investigated in detail on colony '46 B–I (Schneirla, 1949), colonies '48 H–12 and H–27 (Schneirla and Brown, 1950, 1952) and colony '52 B–I, which were studied through periods of 3 months or more in each instance, and in still other cases as well in the different years. Our results indicate that the sexual brood, from its early larval stage, has a strong attraction for a considerable section of the colony. Tests show that this unique attraction is based upon the distinctive odor properties of this brood. The effect leads to a counterattraction competing more and more widely with the drawing power of the regular queen, so that her position in the colony becomes somewhat ambivalent for large sections of the workers.

Colony division thus evidently develops through conflicting odor attractions which arise even while the colony still operates as a unit. The division process is more apparent when the fully developed young

queens emerge from their cocoons and receive the differentiated responses of workers, and it becomes an actuality when the males emerge a few days later. Emergence of the males sets off a maximum raid, somewhat more vigorous than with an emerging worker brood, and the colony moves off divergently on different raiding trails. Colony division thus may be understood as a special case of the initial emigration of a nomadic phase.

One difficult question concerns the fact that, although about six young queens normally emerge in a sexual brood, colony division never seems to produce more than two daughter colonies. The fact is that ordinarily only one of the young virgins can get established in a daughter colony—or two of them if the old queen is superseded. The entire process, including both the ascendancy of the successful queen and the rejection of the others, seems to be based on worker reactions to queen odors of different strengths and attraction, as well as on possible disturbance effects. As the two new daughter colonies move off divergently, each with its queen, the several unsuccessful young queens and perhaps also the discarded old queen are held behind ("sealed off") by workers in an interesting series of reactions which ends in their seclusion and final abandonment to the elements.

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