ARMY-ANT LIFE AND BEHAVIOR UNDER DRY-SEASON CONDITIONS

4. FURTHER INVESTIGATION OF CYCLIC PROCESSES IN BEHAVIORAL AND REPRODUCTIVE FUNCTIONS

T. C. SCHNEIRLA AND ROBERT ZANES BROWN

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 95 : ARTICLE 5 NEW YORK : 1950

ARMY-ANT LIFE AND BEHAVIOR UNDER DRY-SEASON CONDITIONS

ARMY-ANT LIFE AND BEHAVIOR UNDER DRY-SEASON CONDITIONS

•

4. FURTHER INVESTIGATION OF CYCLIC PROCESSES IN BEHAVIORAL AND REPRODUCTIVE FUNCTIONS

T. C. SCHNEIRLA
Curator, Department of Animal Behavior
The American Museum of Natural History

ROBERT ZANES BROWN
School of Hygiene and Public Health
The Johns Hopkins University

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 95 : ARTICLE 5 NEW YORK : 1950

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Volume 95, article 5, pages 263–354, text figures 1–8,
plate 16, tables 1–3

Issued December 27, 1950

Price: $1.25 a copy

CONTENTS

INTRODUCTION

THE TYPICAL PATTERN of activities in the New World dorylines, or army ants, under the presumably optimal conditions prevalent in the tropical rainy season is a strikingly regular phenomenon. Previous investigations have shown (Schneirla, 1938, 1944a) that in each colony of the *Eciton* (*Eciton*) species studied, three closely interlocked sets of events are involved regularly and persistently through the rainy months, namely: (1) the production of very large (20,000+ individuals), all-worker broods at regular intervals of about 35 days from batches of eggs laid by a single colony queen; (2) the occurrence in each colony of two very different activity phases in regular alternation: a nomadic phase in which large daily raids and nightly changes of bivouac occur, and a statary phase in which raids are low in vigor and the colony does not change its nesting site; and (3) processes of trophallactic interaction between brood and workers whereby the given colony receives a high or a low energizing effect in its population according to the developmental status of its brood or broods.

Before any intensive dry-season studies of the phenomenon had been undertaken, the supposition was that these regular and cyclic processes prevalent in eciton colonies in the rainy months must be subject to a considerable reduction or distortion, or even to a suspension, during the dry period (Schneirla, 1948). This prediction found its basis in the extent to which behavioral and physiological functions in most insects are influenced by weather and food conditions (Uvarov, 1928, 1931; Wigglesworth, 1939). If the desiccation tolerance of the ecitons were fairly low, as scattered evidence indicated, and if colony food supply were greatly reduced as a result of a marked drop in the accessible population of forest arthropods, which the carnivorous army ants take as their booty, the pattern should be disrupted or fail for two reasons. There might be a direct environmental inhibition of extra-bivouac activities of the workers, or colony activity might be kept near a minimum because of a reduction or failure of regular prolific brood production which would reduce very radically the energizing of mass worker activities. Incidental suggestions of reduced or suspended doryline activities in dry months are to be found in the literature (Vosseler, 1905; Wheeler, 1912).

These considerations were inadequate as a preparation for the fact, discovered subsequently in two field investigations during the dry months of different years, that the ecitons are able to pass through this season with much the same pattern of reproductive functions and colony behavior as prevails in the rainy season. Among more than 20 colonies of four *Eciton* (*Eciton*) species studied in southern Mexico in the 1945 dry season (Schneirla, 1947), all cases fitted the nomad-statary cycle in their brood and activity conditions at time of discovery. In a more intensive investigation of particular colonies in Panama during the dry season of 1946 (Schneirla, 1949), no real exceptions to the pattern were found in more than 50 cases involving two species of *Eciton* (*Eciton*). One colony ('46 H-O) was found at an advanced stage of dissolution in which the workers held a dead queen, and comparable cases were created through experimental intervention. Thus with only a suggestion of a limited loss of army-ant colonies under dry-season conditions, the available evidence clearly indicated that a continuation of the nomad-statary cyclic pattern is typical in *Eciton* (*Eciton*) species throughout the year, in both rainy and dry seasons.

Because no broods other than all-worker broods (all very large) had been discovered in the rainy months (Schneirla, 1933, 1944a, 1944b) and because of inferences from circumstantial evidence (Schneirla, 1949), broods containing the sexual forms (males and queens) had been anticipated as appearing at some time in the dry season. One non-worker brood was found in southern Mexico in 1945, and 11 such broods were found in Panama in 1946. As far as could be ascertained, these broods were composed only of males, numbering fewer than 3000 in any case, or only about 10 per cent as numerous as the population of the usual all-worker brood (Schneirla, 1948). Only one colony

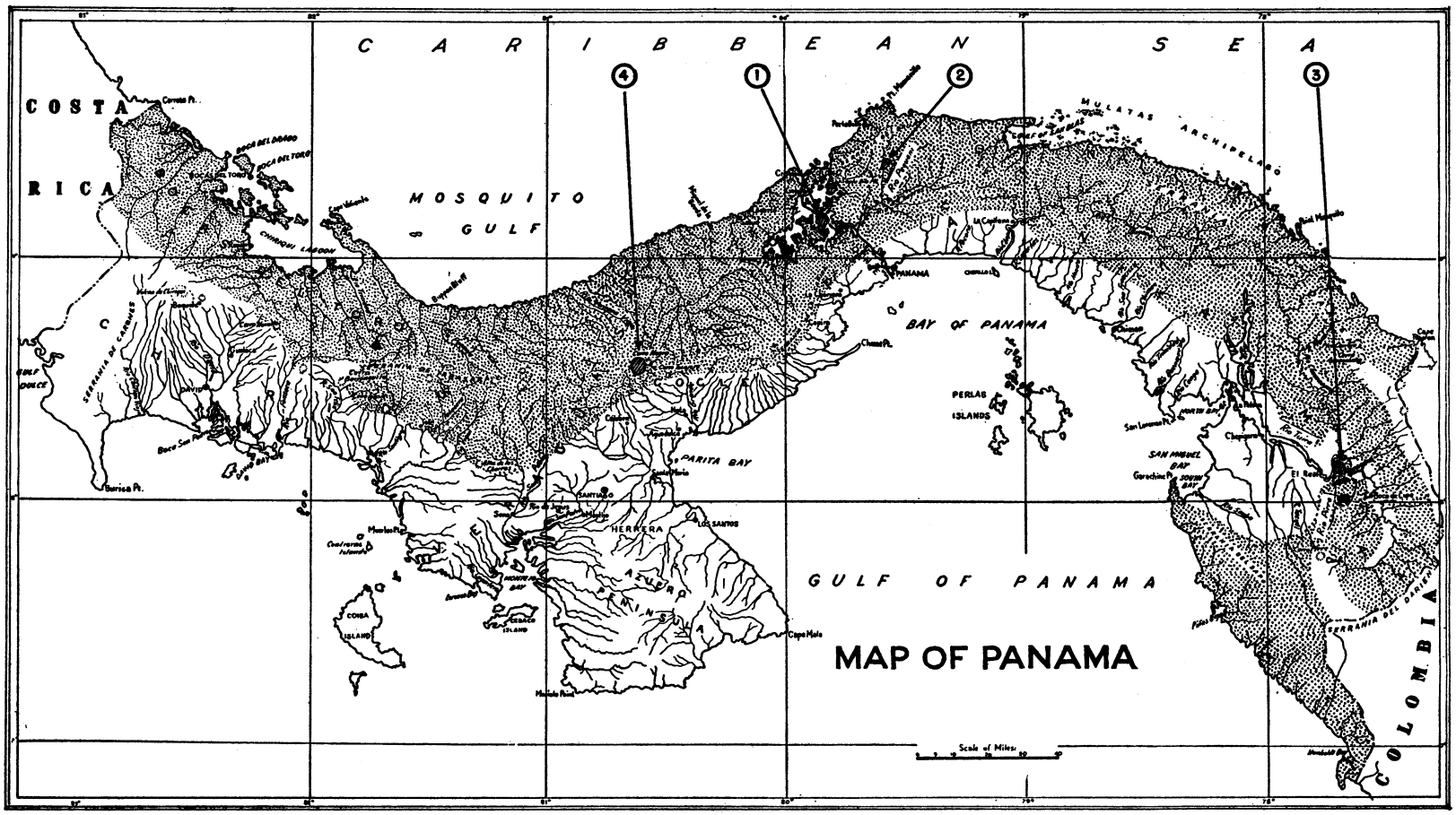


FIG. 1. Map of the Republic of Panama to show the principal areas of study in this investigation. 1. Barro Colorado Island. 2. Pequeni-Boqueron River district. 3. Darien districts. 4. El Valle district. Stippling indicates humid terrain of the Lower Tropical Zone. Adapted from Goldman (1920).

was found with a supernumerary queen, the circumstances of whose origin were unclear, although this colony ('46 B-I, *E. burchelli*) had been studied rather closely through the entire preceding nomad-statary cycle. This case appeared to resemble one in which Wheeler (1921) had discovered, in a colony of *E. burchelli* with a brood of "a few hundred" nearly mature male pupae, two females which he suspected to be young and infertile on the basis of their coloration and fresh appearance. The present study was begun near the end of a Panama rainy season, with the object of discovering how the unique eciton queens are produced, in view of the possibility that they might appear in distinct broods earlier in the dry season than the described male broods.

The investigation was designed to combine an intensive resurvey of army-ant dry-season conditions in a part of Panama previously worked in both seasons of the year, with contrast studies to be carried out in other areas in Panama at different stages of the season. The object was not only to study further the seasonal adjustments peculiar to these ants, but also to compare in detail such adjustments in the two species previously studied. A principal question concerned the clarity and regularity of the nomad-statary cycles and the duration and variability of their two principal phases in the two species. Another concerned the typical condition and variation of the eciton bivouacs or temporary nests during both phases of the cycle, from ecological and behavioral standpoints.

The study of colony activities and reproductive functions in this investigation provided the basis not only for a contrast of such processes in the two seasons and in the transition period from rainy to dry weather, and of events involved in the appearance of the sexual forms, but also for a further examination of the cyclic character of the activities. We were interested in obtaining records on the duration of both nomadic and statary phases in the cycle for each of two species of *Eciton* (*Eciton*), for comparison with corresponding records obtained in the 1946 dry season and also for an examination of variations within these phases during a given season. One question concerned the possibility of throwing further light upon the causation of the cycle itself, i.e., whether the periodic gravidity of the queen which is its pacemaker (Schneirla, 1944a) is governed largely or wholly by processes intrinsic to the queen, or to extrinsic causal events. The present investigation thus constituted a continuation of comparative studies on the behavior patterns of two species of *Eciton* (*Eciton*), with emphasis upon certain specific problems centering around the dry-season adjustments of these ants.

GENERAL PLAN OF THE INVESTIGATION

The plan was to study *Eciton* activities and biological conditions in the latter part of a rainy season, during the transition from rainy to dry weather and during the ensuing dry season. At Barro Colorado Island, Canal Zone, the scene of investigations carried out in other years (area 1, fig. 1), particular colonies of two selected species were to be studied in detail (as to colony behavior, nest and brood conditions) over considerable periods of time, and as many other colonies as possible for shorter intervals. In three other sections of Panama (areas, 2, 3, and 4), respectively to the north, east, and west of area 1, survey studies were to be made during the transition from rainy to dry weather (area 2), during the dry season at the estimated height of sexual-brood production (area 3), and later in the dry season (area 4).

LOCALITIES OF INVESTIGATION

The principal part of this project carried out at Barro Colorado Island in the Panama Canal Zone, area 1, was supplemented by short survey studies of about two weeks each in three other sections of Panama selected because of the variety of forest terrain represented and because of their geographical relationship one to another.

In area 1, Barro Colorado Island, the work involved all sections of the seven-square-mile area of forest except the southwestern part in which only a limited amount of investigation was done. In general, the scene of principal activities shifted less according to a preconceived plan than to an opportune study of colonies most useful from the standpoint of the aims of the project. An effort was made to include studies involving all

the principal types of terrain and forest cover on the island.

Area 2, the forested country between the Pequeni and Boqueron rivers, lies above Madden Lake, and to the north of Barro Colorado Island. This area might be described as lying on the inland side of a shallow pass or dip through the Atlantic Range. This feature may be emphasized by the fact that the Las Cruces gold trail, over which the Spaniards traveled in Colonial times from Panama City to Porto Bello on the Caribbean side, passed directly through the area in which we studied eciton activities. From the hydrographic station at Candelaria on the Pequeni River as base, the study was carried eastward to the Peluca station on the Boqueron River, and from an intermediate point southward to the confluence of the Boqueron and Pequeni rivers.

In area 3, the survey was centered around areas of forest regions southeast of El Real, to the east of the Pirre River at a point about 20 miles south of El Real, and southward from Yavisa to the Tuira River, with the Yavisa-Pinogana trail mainly as the base line (area 3, fig. 1; see Breder, 1946).

In area 4, a survey was conducted to the northeast of El Valle, a mountainous region immediately north of the continental divide on the front range of mountains 45 miles southwest of Panama City and 25 miles north of the Pacific coast. The mountains, ranging up to 2600 feet in height, are heavily forested, but the valleys, where most of the search for eciton colonies was carried out, are broken by many small cultivated areas.

GENERAL TIME SCHEDULE

The investigation in area 1 was begun on November 7, 1947, in order to give a picture of conditions prevailing during the last month of the rainy season. This season ordinarily ends in this area of Panama about December 15, and conditions in 1947 fitted the average very closely. When we left the island on December 10 to visit area 2, a change to dry weather was impending. The studies thus began with a survey of rainy-season conditions during five weeks in area 1, which lasted to nearly the end of rainy weather in that district.

Between December 10 and December 20, 1947, we were absent from the island, working in the Pequeni River-Boqueron River district (area 2). With the exception of this interval, at least one of us was present on Barro Colorado Island and engaged in field study there at all times from November 7, 1947, to March 21, 1948.

From February 14, 1948, to February 27, 1948, the senior author was engaged in making a survey of eciton conditions in area 3, the localities in the Tuira-Chucunaque River district of Darien in eastern Panama. His companion on this trip was Dr. Graham Fairchild of the Gorgas Memorial Institute, Panama City. The camps used as bases for study in this area were established in the following order: forest in the vicinity of El Real, for two days; south of El Real up the Pirre River, for three days; a return to the El Real area, for three days; then finally to the Yavisa district, for two days.

From March 2 to March 14, 1948, the junior author was engaged in a survey of the El Valle district to the west of the Canal Zone (area 4). His companion on this trip was Dr. Robert A. Johnson, Oneonta State Teachers College, New York, who was engaged in a study of the ant birds. In this survey the Campana forest closer to Balboa on the east also was visited.

The investigation was closed on Barro Colorado Island on March 21, 1948.

The time schedule in the study of colonies investigated for longer or shorter periods is given in figures 2 and 3.

METHOD AND PROCEDURES

Method and procedures were similar in general to those employed in the Barro Colorado Island investigation in 1946 (Schneirla, 1948, 1949). A synchronization of individual efforts in the 1948 study made possible an extension of the investigation along more specialized lines.

The basic study in area 1 involved (1) regular daily patrolling to discover the maximal number of new colonies of *E. hamatum* and *E. burchelli;* (2) the investigation of behavorial (raiding situation, colony movements) and biological (brood conditions, queen's condition) circumstances in colonies under continued or short-term study; (3) the taking of records on bivouac ecology in

certain colonies under continuous study, including readings of temperature conditions within the bivouac and of temperature and humidity conditions external to the bivouac; (4) the preserving of brood samples taken at intervals of two to three days as regularly as possible from the colonies under protracted study, and from all colonies under study for limited periods; (5) varied procedures described below and in the section concerning brood-development processes (pp. 331 ff.). In the shorter studies carried out in areas 2, 3, and 4, the method was essentially that of a patrolling schedule designed to discover the greatest possible number of colonies for the study of colony behavior, the taking of an adequate brood sample, and the capture and preservation of the colony queen. When possible, particular colonies in the survey studies were kept under observation for two or more days before a brood sample was taken and the colony queen removed. The duration of study possible for each colony is given in the colony protocols (pp. 276–317) and is represented in figures 2 and 3.

The most consistent patrolling was carried out between the hours of 8:00 A.M. and 2:00 P.M., in a schedule that depended upon the number of colonies under continued study that had to be visited and "worked" on the given day. The hours after dusk in the evening generally were used for tracing the bivouac-change movements of colonies currently on record and for appropriate studies of night-time eciton activities. The afternoon hours as a rule were used for the examination and preservation of material, marking eciton queens, completing records and taking necessary photographs, and carrying out laboratory observations and tests.

The discovery of new colonies and the study of their behavior and condition were important parts of this investigation. If time permitted, the raiding systems of newly discovered colonies were traced to the bivouac, so that records of the status of raiding (e.g., for *E. hamatum:* three-trail system or one-trail system, extent of trail development from bivouac), location, and condition of the bivouac could be made. As adequate a brood sample as possible was taken when conditions (especially bivouac location) permitted. Whenever feasible, the colony queen was removed for examination or study at the laboratory (see below).

Because the spatial distribution of the brood (or broods) in the colony bivouac cluster differs in a regular way according to developmental stage, with a central concentration early in the larval period and a progressively wider spread of the brood towards the periphery as maturity is approached, sampling procedures had to be adapted to growth stage if samples were to be at all representative of the brood population. In sampling worker broods, generally no more than 250 individuals were taken from the bivouac at one time, and samples were taken at intervals of two or three days. Thus in cases such as colonies '48 H-1 and B-II, from which samples were taken at intervals through most of the larval growth period, a total of less than 10 per cent of the entire brood population was extracted from the bivouacs for preservation. In the case of sexual broods (i.e., of male and fertile female types) sampled in area 1, only about 10 individuals were taken at a time during larval development, and during pupal development only two or three were taken at a time. Because the fertile female types were outnumbered about 400 to 1 by males in the sexual-brood population, ordinary sexual-brood samples were very likely to contain only males, and special measures discussed later in this paper were required to find the female types.

Most of the samples from worker broods and all of the samples from sexual broods were kept alive in humid air vials until they could be immersed in a modified Bouin's solution for fixation in the laboratory. After having been in the fixative for 24 hours, the material was washed in 70 per cent alcohol containing 2 per cent glycerin. This material is to be used for growth studies which incidentally will be useful as a means of checking the field estimates of nomadic stage or statary stage in colonies studied only for short intervals.

When a colony was first discovered, the functional queen was removed for examination. In most instances she was taken to the laboratory for measurement (especially of gaster dimensions) and was returned to the colony within 24 hours. After December 7,

the queens of virtually all colonies discovered on Barro Colorado Island were marked in individually distinctive ways, by clipping one or two tiny nicks in the exoskeleton at the overlapped posterior edge of the tergal plates of the abdomen (see pl. 16, fig. 1). This was done in the laboratory while the queen was lightly etherized. The nicks were made with iridectomy scissors in such a way that the infolded and contracted membrane beneath the given plate of the gaster was not punctured. The queens all recovered within a few minutes from the principal effects of ether and all of them appeared to be in good condition when returned to their colonies. Twenty queens of *E. hamatum* and 10 of *E. burchelli* were thus marked in distinctive ways (see table 3) and all except one (H-19) were received in the normal manner when returned to their colonies. In this way the colonies with marked queens could be identified when encountered later, and "new" colonies could be differentiated from colonies previously under study. About one-fourth of the colonies with marked queens were reencountered and identified one or more times. It was very probable that this number would have been larger had more time been available after January 15 for patrolling, locating bivouacs, and extracting queens for identification.

Among the colonies studied on the island, only five were deprived of their queens (for preservation) near the end of the study. However, in areas, 2, 3, and 4, the captured queens were all preserved in modified Bouin's fluid, with the exception of three which were preserved in 10 per cent formalin for study of their fat bodies.

Notes were kept on the location and characteristics of both nomadic and statary bivouacs. Systematic records were taken in numerous cases of the conditions of humidity and temperature in the vicinity of the bivouac and of temperature within the bivouac. These records were supplemented by five-day hygrothermograph records obtained with two Bristol recording instruments used in experimental and control pairings to obtain tracings from representative situations in the forest (e.g., ridge top and ravine bottom) and from situations occupied by *Eciton* colonies (e.g., the log interior occupied by colony '48 H-12 when statary). These results are to be reported in a later paper.

ACKNOWLEDGMENTS

The principal travel and field-subsistence expenses of this project were supported through a contract (505 T, 164–468) with the Office of Naval Research, Human Ecology Branch, Biological Sciences Division. Continuing histological studies of preserved material have been supported in part through a renewal of this contract with the Office of Naval Research, and in part through a grant from the Committee for Research in Problems of Sex, National Research Council, to the Department of Animal Behavior, the American Museum of Natural History. A grant from the Penrose Fund of the American Philosophical Society covered the travel and subsistence expenses of one assistant. Through the generosity of Dr. Caryl P. Haskins, the services of Dr. Ernst Enzmann were available for the field investigation.

We wish to express our gratitude to the many friends who advanced our work in various ways. Mr. James Zetek, Custodian of the Canal Zone Biological Area, aided with arrangements in his characteristically efficient way. Mr. G. E. Matthew, Chief, Section of Meteorology and Hydrography, Panama Canal, and members of his staff, were helpful with suggestions about field arrangements and the calibration of instruments, and Mr. W. H. Esslinger and the personnel of the Hydrographic Station at Madden Dam gave us valuable aid in connection with the Pequeni River trip. Drs. Graham Fairchild and Harold Trapido of the Gorgas Memorial Institute kindly cooperated in arrangements for the Darien trip, on which Dr. Fairchild made a most cooperative traveling and camp companion. The officials of the Elliott Steamship Line kindly permitted us to travel from Panama City to El Real, Darien, on one of their coastwise boats. To Sr. and Sra. Pablo Othon, thanks are due for their generous hospitality during the stay of Drs. Fairchild and Schneirla at El Real. To Dr. Walter Clark of the Kodak Research Laboratories in Rochester, New York, and to Mr. C. C. Soper and Mr. Paul Hermle of the Kodak Tropical Research Laboratories in

Panama, we are grateful for advice and suggestions concerning technical problems in field photography. Dr. Robert A. Johnson of Oneonta State Teachers College, New York, studied the behavior of ant birds in connection with our project, and cooperated with Mr. Brown in carrying out the El Valle survey.

The drawings for text figures 1 to 8 were made by Mr. Walter Holmquist of the Illustrators Corps of the American Museum of Natural History.

RESULTS

COLONY RECORDS[1]

THERE FOLLOWS a summary in chronological order of the records of colonies studied on Barro Colorado Island. Résumés of the respective colony protocols are presented here, in which the facts concerning behavior conditions, brood production, and other circumstances of colony life during the interval of study are reduced to the minimum compatible with clarity. These records may be examined in relation to figures 2 and 3, in which is a graphic summary of the time relationships as concerns period of colony study, the activity phases involved, and the brood production of the respective colonies.

In all, 32 colonies of *E. hamatum* and 20 colonies of *E. burchelli* were on record, most of them for intervals of more than two days, and some for considerably longer times. It is highly probable that there are no more than two or three cases in the two species in which the same colony has been assigned more than one symbol through the failure of identification at a second encounter. Colony '48 H-5 of *E. hamatum*, which may be the same as colony H-24, is an example. Even in the case of colonies in which the queens were unmarked and no physical identification existed, clues were available in the circumstances of activity phase and brood phase coincidence and (less dependably) in the topographical relationships. However, because of the fact that we were able to mark the (single) colony queens in the majority of cases, it was possible to identify most of the colonies represented in this report as distinctive cases. As minimal census figures, which undoubtedly understate the eciton population of these species on the Island, one may say that there were on Barro Colorado Island during the period of this investigation at least 30 colonies of *E. hamatum* and 20 colonies of *E. burchelli*.

The records of colonies studied in the Pequeni River, Darien, and El Valle areas (areas 2, 3, and 4) are summarized at the end of the section on colonies studied in area 1.

AREA 1: BARRO COLORADO ISLAND, CANAL ZONE,[2] NOVEMBER 7, 1947, TO MARCH 21, 1948

COLONY '48 H-1, *E. hamatum:* When found on November 6, 1947, to the southwest of Barbour Trail, station 9, this colony was in the early part of a nomadic phase. Two large worker broods were present: a newly emerged brood of callow workers and a second brood in the early larval condition. Large daily raids, generally of three systems, with nightly changes of bivouac, were the rule until November 20. The successive movements took the colony through a roughly elliptical course, approximately 600 meters on the long axis (fig. 4). The bivouac clusters were all in the open, usually beneath objects such as a log, crossed vines, and the like. Typically the changes of bivouac got under way late in the afternoon and had reached their advanced stages by 8:00 or 9:00 P.M.; a few were nearly completed at that time. The queen was observed on the nights of November 7, 10, 14, and 19, running along the route of emigration in a crowd of workers, always in a contracted condition and healthy in appearance. On November 20 the larvae were mature and spinning was observed. The exodus that evening reached somewhat beyond the terminus of the day's raiding on one of the three trail systems to a point where at 9:30 P.M. clusters were forming in various places beneath the heap of tangled

[1] COLONY SYMBOLS: Colonies studied on Barro Colorado Island are designated by symbols from '48 H-1 to '48 H-32 in *E. hamatum* and from '48 B-I to '48 B-XX for *E. burchelli*, representing serially the chronological order of discovery in both cases. Comparable designations are used for colonies studied in the other areas, with the addition of a capital letter to indicate the area: P, area 2 (Pequeni River); D, area 3 (Darien); and V, area 4 (El Valle), i.e., from PH-1 (or DH-1 or VH-1) for *E. hamatum* and from PB-I (or DB-I or VB-I) for *E. burchelli*. To distinguish these colony records from those of investigations in other years, each symbol begins with the abbreviation '48.

[2] See the contour map of Barro Colorado Island prepared by the 11th Engineers, Office of Departmental Engineer, Panama Canal Department, United States Army.

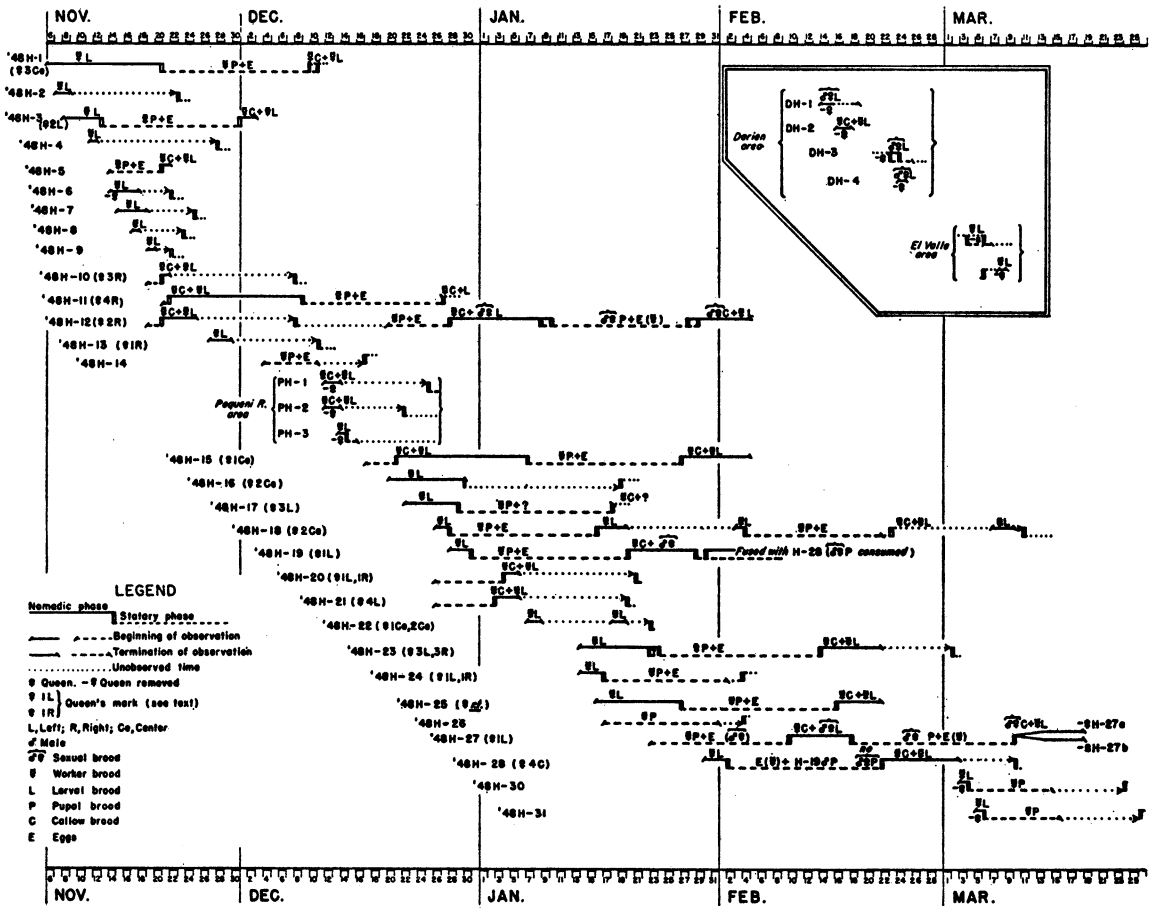


FIG. 2. Diagrammatic representation of the records of colonies of *E. hamatum* studied between November 6, 1947, and March 25, 1948. Colonies '48 H-1 to H-31 were investigated on Barro Colorado Island. The records of colonies investigated in the Pequeni-Boqueron River district are represented after the record of colony '48 H-14; those of colonies investigated in Darien and El Valle are represented at the upper right side of the diagram.

branches of a large fallen palm tree. The bivouac was finally settled later in the evening within the vegetation bordering the clearing in which the fallen tree lay.

The statary bivouac established on the night of November 21 and occupied until December 10 was an exposed cylinder formed between two tree trunks that lay parallel, one above the other, within the thick vegetation bordering the open area. Because of the position of the logs, the bivouac was at a height of about 90 cm. from the ground. In the spinning, which continued for two or three days, workers carried larvae to various places on the top of the lower log, up to a distance of 4 meters from the bivouac cluster. During the 19-day tenancy the bivouac shifted gradually along the log until finally it was about 50 cm. from its first position. This may have been a reaction to the radiation of heat from the fallen tree clearing, especially at midday, when the sun's rays beat directly upon unshaded ground within 1 meter of the initial position of the bivouac. The gradual shift in position took the cluster at angles somewhat away from the border of the clearing. After November 20, only single-system raids were seen; on a few of the statary days after November 23 no raiding occurred.

On December 9 at noon, just before leaving the island on the Pequeni River trip, we examined the H-1 bivouac with the aid of ether. The large, essentially mature brood of

pupal workers, all still enclosed in cocoons except for a minority of emerged majors, was distributed throughout the lower two-thirds of the bivouac cylinder; a second brood of very early larvae was massed together in the upper center, with the queen near by and above the brood. The queen, in the contracted condition, was taken to the laboratory, where she was marked distinctively (3-C). When she was returned to the colony, that evening, the ants had reclustered beneath some palm stalks on the ground close to the former bivouac position. Nothing more was seen of this colony.

In the period of observation, colony '48 H-1 completed nearly a full cycle of one nomadic and one statary phase, after the typical pattern of the species. Two broods of workers were produced, and a third worker brood was in the early larval condition when the study ended. The queen was in good condition and active when returned to the colony.

COLONY '48 H-2, *E. hamatum:* On November 7, 1947, this colony was found southeast of Barbour Trail, station 5, in a broad, curtain-like bivouac against one side of a stump, from which a large three-system raid had developed. From the appearance of the two large broods, one of callow workers and one of early worker larvae, which were present, the colony was judged to be in the first or second day of a nomadic phase. (Tested in the laboratory, these larvae were found less reactive and motile than were those of colony H-1, which was estimated to be in the third day of a nomadic phase.) The bivouac change of that evening took the colony to a new site approximately 350 meters away. Roughly one-third of the young larval brood was removed (without ether) on the following day, when a vigorous three-system raid was in progress. The queen could not be found. Disturbance of the bivouac early in the afternoon may have hastened the bivouac-change process, for the site was found vacated at 7:20 P.M., and no trace of the emigration column could be found. The colony was not seen thereafter, unless colony H-19, found on December 27, was actually H-2. As may be seen from figure 2, their phases were closely similar.

This colony presented the typical situation of early nomadic activity, with a brood of newly emerged callow workers and one of early worker larvae.

COLONY '48 H-3, *E. hamatum:* When first discovered on November 8, near Lutz Trail, station 2, this colony occupied an irregular open bivouac formed around the lower branch roots of a stilt palm. A large brood of nearly mature worker larvae was present, distributed widely through the cluster. That evening the bivouac site was changed in a move of about 120 meters. From the new cluster, which was within one end of a raised hollow log, a two-system raid developed on November 9. At 7:30 P.M. traffic was homeward bound on both principal trails, and no bivouac change occurred. Another two-system raid developed on the following day. The cluster was then somewhat withdrawn into the interior of the log, and signs of cocoon spinning were observed among the larvae. At 7:00 P.M., a bivouac change was under way, to a site beneath the base of a small tree 40 meters distant. On November 11 another two-system raid developed, further spinning was observed in the brood, and at 8:40 P.M. the colony was found midway in a bivouac change to a new site 150 meters distant. Here the cluster was almost completely covered by the arched shell of a hollow log, from which a two-system raid developed on November 12. On that day, cocoon spinning by mature larvae apparently reached its height. At 9:00 P.M. that evening this site was found completely vacated, and searching disclosed that the colony had moved a distance of 50 meters into a hollow tree on the bank of upper Lutz Creek.

The statary bivouac was almost completely enclosed within the hollow base of the large buttressed tree, where the lower part of the bag-shaped cluster could be glimpsed through small inter-buttress apertures. Small single-system raids were observed on the following days. On December 1, the bivouac cluster, previously pulled up a few centimeters, was lowered so that it reached the ground, and cocoon opening was well under way. This activity apparently reached its height on December 2, when a vigorous two-system raid occurred. That evening, when the colony moved a distance of 85 meters, most of the callow workers had emerged.

The first nomadic bivouac was formed in a low recess between two root buttresses of a small tree. In the late morning, after a moderately vigorous two-system raid had developed, this bivouac was examined without ether. At that time the callow workers were all free of their cocoons, and in the upper part of the bivouac were found a few large packets containing very young larval workers. The queen, in the contracted condition, was removed for examination and marking (3-L). When the queen was placed near the bivouac-change column moving southward at 7:05 P.M., she was readily received by the workers. At the time the colony was more than half removed from the site. The movement, towards Fossil Creek, was completed without complications. This colony was not seen again, as far as identification was concerned.

Colony H-3 was observed during the last five days of a nomadic phase, during a statary phase of 19 days, and in the early part of a further nomadic phase. One brood of callow workers was produced, and a further worker brood in the early larval condition was present when the study ended. A tendency to occupy physically enclosed sites was observed during the last few days of the nomadic phase, to a somewhat greater degree than is usual in the species.

COLONY '48 H-4, *E. hamatum:* An exceptionally small colony, probably numbering no more than 40,000 workers, was found at 12:00 noon on November 12, 1947, in an open cluster under brush in the thicket south of the Tower clearing. At that time only one large and one small trail system could be found, the large system with a major trail division at 80 meters. The smaller system disappeared from use during the noon "siesta" interval. The colony possessed a brood of recently emerged callow workers, as well as a brood of early larvae, massed in the center of the bivouac. While raiding was going on vigorously, the bivouac cluster seemed to be composed almost exclusively of callow workers. A single queen was found in the bivouac, in the contracted condition. This queen was returned to the colony, unmarked, after a brief examination. The bivouac-change movement of that evening was not observed, and on the following day the colony could not be found. This colony appeared to be functioning effectively in the nomadic pattern despite its unusually small size.

COLONY '48 B-I, *E. burchelli:* When found on November 12, this colony was bivouacked in the vicinity of Wheeler Trail, station 24. It was in the hollow interior of a large tree at one side of a large knot-hole about 1 meter from the ground. A completely enclosed brood of mature worker larvae entering the prepupal stage was found well distributed through the cluster. On that day a large swarm raid was in progress. However, during the following days smaller raids were the rule, and on some days (e.g., November 16, 17, 20, and 21) no raids occurred. Raids developed daily on November 22 and thereafter, with an increasing intensity, until on November 29 after much the largest raid of the series the colony moved off westward in the evening. This movement was not traced.

Colony B-I evidently had been statary only a few days when found, judging from the condition of its brood and from the fact that it passed 18 days in the given hollow tree site before moving away.

COLONY '48 B-II, *E. burchelli:* This colony was found on November 19, in the area of Zetek Trail, station 6, clustered about 3 meters from the ground, largely within the interior columns of an old strangler-fig tree. A fairly large swarm raid had developed at the time. Empty pupa cases were in evidence on the ground below the bivouac, and the accumulation increased on the following three days with signs of an acceleration in cocoon opening. When the colony moved from the site on the night of November 22, its large mature pupal worker brood had been nearly all removed from cocoons.

On November 22 and the following days, the swarm raids were all large, and the evening bivouac-change movements usually covered distances of 130 meters or more. A tendency was observed for an early completion of the movements; for example on November 23 at 7:00 P.M., the end of the bivouac-change column already was 40 meters from the day's bivouac site, and on November 24 at 7:10 P.M. it was estimated that half of the colony had reached the new bivouac site. In these first days of nomadism, the presence of a further brood in the early

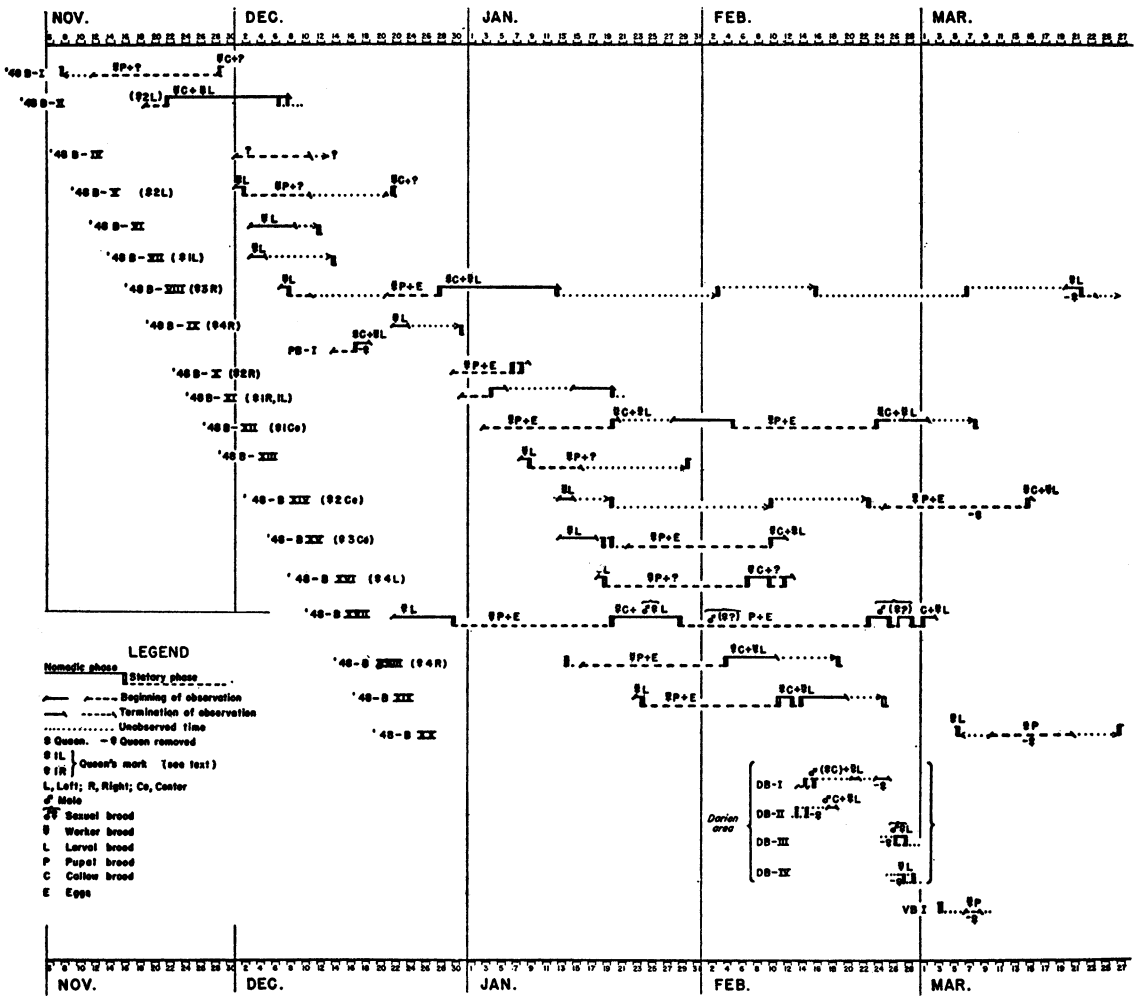


FIG. 3. Diagrammatic representation of the records of colonies of *E. burchelli* studied between November 6, 1947, and March 27, 1948. Colonies '48 B-I to B-XX were investigated on Barro Colorado Island. The records of colonies investigated in the Darien and El Valle districts are represented below, and the record of colony PB-I (Pequeni-Boqueron River) follows colony '48 B-IX.

stages of larval development was established. The queen was removed from the colony for 12 hours during the night of November 24, after having been picked up from the tail of the bivouac-change column. She was marked (2-L) at the laboratory, and next morning was received normally by the colony. On December 4, with the larval brood close to maturity, the colony was clustered in a half pouch against the north side of a large tree about 6 meters from the ground.[1] The bivouac-change movement of that night took the ants (more than 10 meters up) into the interior of a hollow tree 65 meters to the south. It was a surprise to find no trace of the colony when the site was visited at 9:00 P.M. on the evening of December 5. The colony must have moved away early that evening, for it could not be seen in the former bivouac position, and careful searching in the vicinity on December 7, 8, and 10 did not

[1] A tamandua anteater was seen on this same tree, at one time only about 1 meter below the B-II bivouac. In thousands of bivouac observations made during several seasons, this is the only instance of the kind. The animal was not seen consuming any ecitons nor did it appear to molest the bivouac.

bring it to light. Presumably, a statary phase began on December 7.

This colony completed a statary phase with the emergence of a large brood of workers, and passed through a regular nomadic phase (very probably 14 days) in which a further large worker brood developed to larval maturity.

COLONY '48 H-5, *E. hamatum:* On November 14 this colony was discovered in a wide cylindrical bivouac established well under the broad base of a large fallen tree, in a sun-exposed natural clearing near Barbour-Lathrop Trail, station 9. A large brood of pupal workers, still unpigmented, was found well distributed through the cylinder. The colony remained in this spot only one week more, staging a one-system raid on each day except November 17. On November 21, with a single-system raid in progress, the bivouac was examined in the early afternoon. Approximately one-third of the pupal worker brood had been removed from cocoons, and in the center of the bivouac was found a single bolus of early worker larvae. When the site was next visited at 7:35 P.M. that day, the colony was gone and no trace of columns could be found in the vicinity. The surface beneath and around the former bivouac site was strewn thickly with empty pupa cases.

This colony finished a statary phase in the typical manner, with the emergence of a large brood of callow workers, and a further brood of very young worker larvae was then present.

COLONY '48 H-6, *E. hamatum:* On November 14, when discovered near Shannon Trail, station 7.5, this colony occupied an open curtain bivouac beneath a log, and a large three-system raid was in progress. Well distributed through the bivouac was a large brood of worker larvae, somewhat more than half developed. The colony was studied during the next few days. Large raids developed daily, with nightly bivouac-change movements which generally carried over distances of more than 250 meters, usually to a new place close to the periphery of the day's raiding zone.

The movement that occurred on the night of November 17 was a long one, of more than 350 meters, which was not followed out to the new bivouac site owing to limited time. The queen was not removed for marking.

Colony '48 H-6 was passing through a regular nomadic phase, with a large brood of larval workers in an advanced stage of development.

COLONY '48 H-7, *E. hamatum:* This colony was discovered on November 15, occupying an open bivouac at the base of stilt palm roots, near Barbour-Lathrop Trail, station 3.5. A large brood of worker larvae in the intermediate stages of development was found, well distributed through the bivouac, with larger individuals graduated successively farther towards the periphery and smaller individuals towards the center, as is typical at that stage. The colony was kept under observation for four days, during which a large three-system raid occurred on each day and an extensive bivouac-change movement each night.

Colony '48 H-7 was passing through the intermediate part of a regular nomadic phase, with a large brood of larval workers about midway in development.

COLONY '48 H-8, *E. hamatum:* On November 17 this colony was found in the area of Barbour-Lathrop Trail, station 15, bivouacked in an irregular cluster around a mass of lianas. The brood consisted of worker larvae, estimated to be two-thirds advanced towards maturity. A vigorous raid was in progress in two well-developed trail systems. The bivouac-change movement of that night was not followed; the next day the colony was gone from the site.

Colony '48 H-8 exhibited regular nomadic behavior and brood condition, and was evidently somewhat past the midpoint of a regular nomadic phase.

COLONY '48 H-9, *E. hamatum:* When it was found on November 18, in the area of Van Tyne Trail, station 2.5, this colony had formed a large elongated cylinder beneath crossed lianas. A large brood of nearly mature worker larvae was distributed throughout the cluster. When the bivouac was probed lightly with a machete to examine its contents, the entire structure fell apart readily, as is characteristic of bivouacs of colonies with nearly mature worker larvae. The colony

was not located in the vicinity on the following day.

COLONY '48 H-10, *E. hamatum:* The raids of a *hamatum* colony, judged from the column formation to be statary, were observed on and after November 15 in the general area of Wheeler Trail, station 13. The bivouac could not be found. On November 21 a vigorous three-system raid was found to the east of Wheeler Trail, station 14, and was traced to a large cylindrical bivouac beneath a low log. This was evidently the second day of a nomadic phase, judging from the fact that the bivouac was crowded with callow workers and a few were on the trails, and that near the upper center of the bivouac a large bolus of very young larvae was present. The queen was removed to the laboratory where she was marked distinctively (3-R). When returned to the bivouac on the evening of the same day she was reaccepted very readily when set down near a moving column at the base of the cluster. At 8:00 P:M. the colony was engaged in a bivouac-change movement towards the east.

This colony was localized in a general manner when it was passing through the last days of a statary phase, and its bivouac was found on the second or third day of the succeeding nomadic phase.

COLONY '48 H-11, *E. hamatum:* This colony was discovered on November 22 by tracing back a long column from terminal branches through its long unbranched base line (a typical statary pattern) to a bivouac concealed within the shell of a hollow log to the east of Fairchild Trail, station 0.5. Empty pupa cases scattered outside the log suggested that the colony was nearing the end of a statary phase. By the following morning the pupa cases had increased greatly in number, and the cluster had shifted about one-half meter until it was visible as a plug bulging from the open end of the log. On November 24 a large two-system raid developed, and during the bivouac-change movement, which occurred that evening over a distance of 140 meters to the northeast, it was ascertained that the entire large brood of mature pupal workers had emerged. Although most of these callow workers ran in the bivouac-change column, a few thousand of them (evidently the last to be removed from cocoons) were carried by workers. On the following morning, after an extensive three-system raid had developed from the first nomadic bivouac, which was an open cluster between buttressed tree roots, the contents of the bivouac were examined. In addition to the newly emerged callow workers spread through the cluster, a brood of very young worker larvae was found near the upper center. The queen, in the contracted condition, was sufficiently active to slip out of the bivouac when it was first broken open. She was at length discovered near the base of the bivouac under a small cluster of workers. After having been marked (4-R) at the laboratory, she was readily accepted when returned to the bivouac that evening. On each of the following days until December 9, there was a large raid (generally a three-system foray) with an extensive bivouac-change movement in the evening. The successive movements of the colony first took it in a meandering course along the northwest flank of the Fairchild Peninsula to a location in the vicinity of Fairchild Trail, station 14. Then on December 3 and 4 the colony reached the end of the peninsula, and subsequent movements carried it back towards the south in a somewhat zigzag course which at times brought the bivouac close to the shore of Gatun Lake. Although all these movements were over distances greater than 150 meters, most of them were completed before 9:30 P.M., with the exception of two which were interrupted and delayed by prolonged evening rains. On December 8 signs of spinning were observed among the worker larvae, then evidently mature, and that evening the colony moved 170 meters to enter the cylindrical shell of a log which lay on the lower bank of a creek to the east of Fairchild Trail, station 6.5.

The colony retained its position within this log as a plug-formed mass about 70 cm. from the lower and open end and was still at the site on our return to the island after an absence of 10 days (December 10 to December 20). A few relatively weak single-system raids were observed. On December 26 the colony had an extensive one-system raid in operation, and cocoon opening was under way. When the bivouac was examined at this time, a single mass of very young worker

larvae was found near the top center. The colony moved away that evening, an unwitnessed and unexpected occurrence, and on the following day could not be found.

This colony ended one statary phase and passed through a regular nomadic phase of 17 days and a statary phase of 18 days during the time of observation. Two large broods of workers were brought to maturity during this time, and a further worker brood was present in the early larval condition when the study ended. It is possible that the nomadic movement which terminated the study, coming as it did when only about one-fourth of the callow worker brood had emerged from cocoons, was set off prematurely through the additional excitatory effect introduced when the bivouac was artificially aroused on the afternoon of December 26 (cf. colony H-1, December 9).

COLONY '48 H-12, *E. hamatum:* This colony was found on November 19, about 350 meters southeast of Wheeler Trial, station 14, bivouacked in a compartment within a mass of rubble in the crown of a large fallen tree. The bivouac was located by tracing back from Wheeler 17, where the peripheral branches of a (statary-form) raiding system were found at 11:30 A.M., a long meandering column which had no branches within 150 meters of the bivouac. In the secluded bivouac cluster was found a large brood of well-advanced worker pupae, a few days short of maturity, widely distributed through the lower two-thirds of the cluster.

What was in all probability the same colony (judging from spatial relationships and condition) was found on November 23 in an open bivouac about 175 meters to the east of Wheeler 16. When the colony was found in early afternoon, there were two principal raiding columns from the bivouac, one of them divided within a few meters so that in effect there were three major trail systems. In the bivouac cluster (examined without ether), an irregular elliptical mass beneath vines in a dark niche, two broods were found: a large brood of callow workers, evidently very recently emerged (judging by their light color and by the fact that few of them were on the trails), and a large brood of very young worker larvae. The queen was removed to the laboratory for marking (2-R). When the site was next visited at 7:00 P.M., the colony was nearly four-fifths moved. The queen was readily received at the nearly deserted bivouac site; in fact it was not until after 30 minutes that she burrowed her way from under the mass of workers which had soon formed over her, and presently got moving in the emigration column. On November 24, this colony (identifiable through the queen's mark), was found in its bivouac 20 meters to the south of Wheeler Trail, station 18, clustered in a regular cylinder under one end of a large log. It was not seen again for more than one month.

On December 22 at 10:00 A.M. a *hamatum* colony was found bivouacked well back within the cavity of a large hollow log about 150 meters to the southeast of Shannon Trail, opposite station 3 (see fig. 4). At the time there was just one long column to the west, with terminal raiding branches near Shannon Trail. A large brood of enclosed and still unpigmented worker pupae was found well distributed through the bivouac. The queen was finally discovered in the upper rear part of the cluster (i.e., towards the closed end of the hollow), where she was surrounded by a thick mass of workers, mainly minor forms. She was in the nearly maximal condition of physogastry, and close by her were found numerous small strands of eggs. She was removed to the laboratory for observations on egg laying. To avoid unnecessary interference with the regular course of events, she was returned to the lower border of the bivouac cluster on the evening of the same day, when she was readily received by the workers. The bivouac was kept under general observation during the following days, when single-system raids in various directions were the rule. On December 27, the opening of some hundreds of cocoons was noted, an event which increased considerably in tempo on December 28, when a vigorous two-system raid developed. That evening, with virtually all of the pupae removed from cocoons, the colony moved off to the southwest.

On December 31, the colony was bivouacked in a large open cluster near station 6, Shannon Trail. An extensive three-system raid was in progress. Here the contents of the bivouac were examined. In addition to the large brood of callow workers, numbers

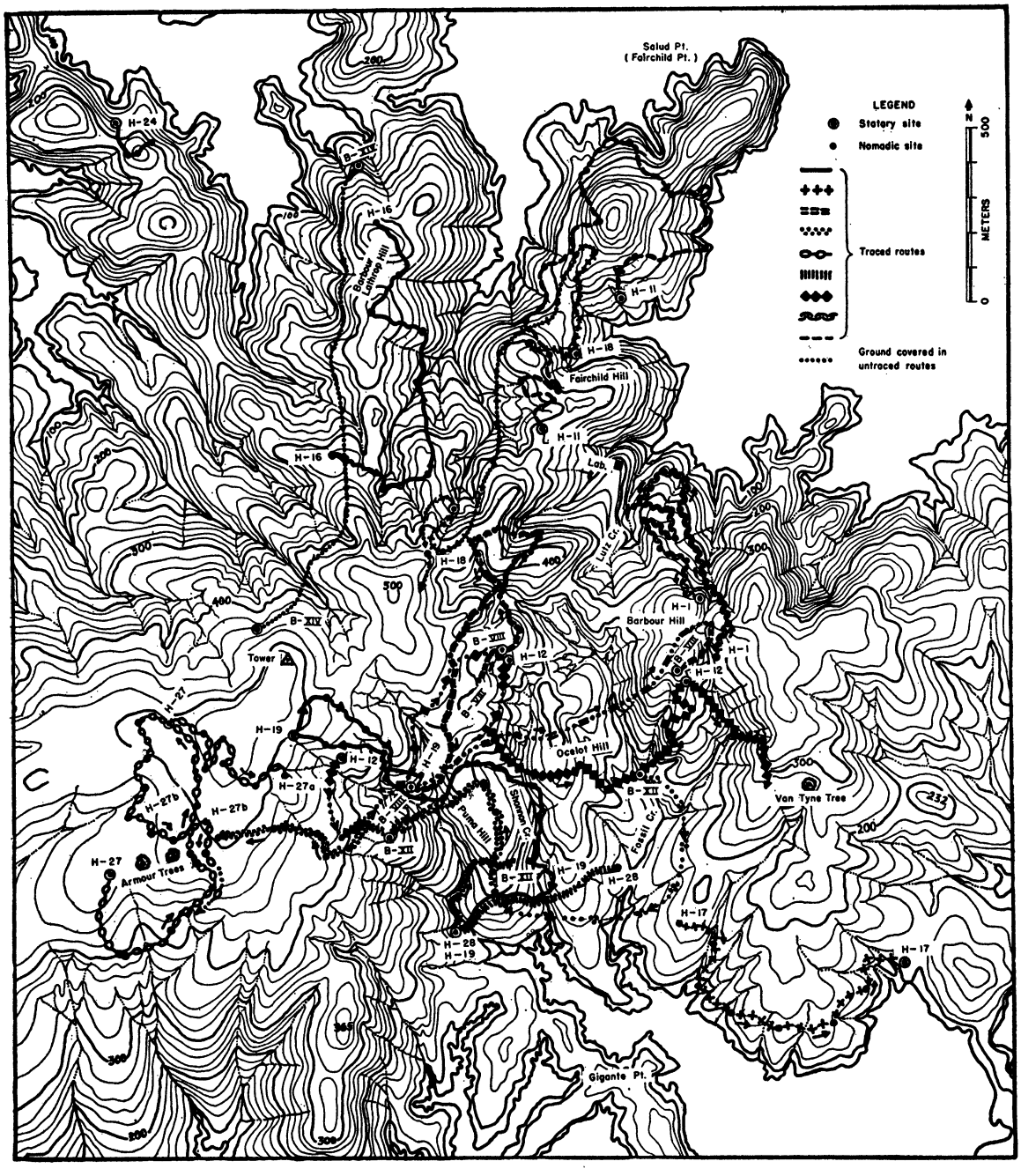


FIG. 4. Topographic map of a section of terrain in the central and northeastern part of Barro Colorado Island, to represent the movements of some of the colonies of *E. hamatum* and *E. burchelli* that were on record during the dry season of 1948.

of which were to be seen on the trails at considerable distances from the bivouac, a second brood in the larval condition was found. This brood was readily identified as a sexual brood (the first to be discovered during the 1948 dry season) by virtue of the relatively large size of the larvae, although a nomadic phase had barely begun. The queen was found contracted and in good condition. At 7:00 P.M. that evening the major part of the colony had moved from the day's bivouac, and a new cluster had begun to form at a site 160 meters to the southeast. After a very extensive raid on January 1, the colony again had moved completely away from its bivouac early in the evening, with the site vacated at 8:00 P.M. This movement was characterized by the formation of "flange clusters" bordering the column where it passed along vines and similar canalized places and by large, plate-sized aggregations of callows at some of the former trail junctions. At 7:40 P.M. the queen was observed moving along the trail in the midst of a dense group of excited workers. When seen early in the afternoon of January 2, the new bivouac (formed beneath a raised log-crotch at the stream edge below Shannon Trail, station 8) was notable for its bulk. This feature, increasingly marked on succeeding days, was an obvious consequence of the large and increasing body size of individuals in the sexual brood. The raid of that day was an extensive one on two highly developed trail systems, and the evening emigration took the colony more than 225 meters to the east side of Ocelot Hill. This movement also was characterized by the complete evacuation of the day's bivouac site before 7:30 P.M., and by an increasing prominence of "ant roadway" (Schneirla, 1948) sections along the line of travel, an expression of the increasing difficulty of moving the rapidly growing sexual-form larvae. The extent of the raid on January 3 is suggested by the fact that the ensuing emigration carried over a distance approaching 375 meters, with the colony crossing Fossil Creek at the cascades to form its new bivouac 50 meters to the east in the general direction of Barbour Trail, station 9. Incidentally, in crossing the deep rocky bed of the creek at this point the columns of H-12 passed within 2 meters of the statary bivouac of colony B-XII (*E. burchelli*), to which a heavy column of booty-laden workers was returning at the time (8:00 P.M.), and also by-passed numerous branching columns of *E. crassicorne* undergoing extension in the downstream direction through the evening. On January 4, an exodus was under way from the day's bivouac at 1:45 P.M. into the northwest section of a complex three-system raid. This continued persistently into an emigration. However, after raiding ceased at dusk, complications developed when a heavy centripetal return of former raiders developed, which blocked the exodus well short of the daytime periphery of raiding. As a result, at 9:00 P.M. the new bivouac began to form near a principal collision point about 125 meters from the bivouac of the day, i.e., at a point where the frontal meeting of outgoing and incoming columns forced a lateral "explosion" into an abandoned branch trail. Here the ants at length hit upon a shallow tree-stump cavity as clustering site.

After an extensive three-system raid on January 5, the emigration was well under way at 7:30 P.M., over the middle system towards the northeast, where at about 150 meters a cluster had begun to form in the eventual new bivouac site beneath a raised log. Events were similar on the following day, when the emigration took the colony about 100 meters farther to the north-northeast. In these last few movements, many complications occurred as a result of special difficulties involved in transporting the bulky larvae of the sexual brood. On January 7, there was a single raiding system to the northeast, over which an exodus had developed at 2:00 P.M. This movement, which involved the formation of a wide "ant roadway," took the colony just 40 meters to the northeast, where by early evening a large, curtain type of bivouac had been formed at the side of a log in the center of a thicket (site 1). Although the new bivouac appeared to be well established at 6:30 P.M., activities continued around the cluster and on the trail beyond, with the result that when site 1 was next visited on the morning of January 8, the ants were completing a movement of 25 meters farther downhill to the northeast, where the main section of the colony was clustered within the end of a raised hollow log (site

2). At 9:30 A.M. the movement was in its last stages, with a wide ant roadway still largely in place between sites 1 and 2. In this column near its end were seen throngs of ants, lugging along four large brown cocoons, notable in contrast to the fact that the remaining hundreds of sexual larvae seen were still unenclosed. (One of these cocoons, picked out for later examination at the laboratory, proved to contain a queen type of larva.) The colony remained at site 2, about 250 meters to the south of Barbour Trail, station 8, without any shift that night. On January 9, raiding was continued on the line to the east and northeast. From the early afternoon a ragged line of ants followed the trail (used January 7) uphill to the southwest, then after 8:00 P.M. a definite movement got under way, in which the entire colony moved to nearly the identical spot at site 1 in which the bivouac had been formed on the night of January 7.

On January 10, colony H-12 began a statary phase at site 1, bivouacked in a large half cylinder under the overhanging side of the big log, in deep thicket. At that time, cocoon spinning by male larvae, which had begun on January 9, was at its height. Until January 27 the bivouac remained at site 1, with only minor shifts in position, the raids were all single-system, and after January 14 raidless days were frequent.

On the morning of January 27, the eighteenth day at site 1, a series of events began which may be described as a gradual transition into nomadism and a beginning of colony division which, very probably because of experimental interference, was ineffective. These events, which occupied four days, were dependent upon the presence of a sexual brood at pupal maturity. Only their general trend will be sketched here. The events began on the morning of January 27, with the capture and removal of a callow queen from a miniature cylinder beside the bivouac at site 1. That evening another callow queen was seen (but not removed) at the lower border of the main bivouac at site 1. On this evening an exodus downhill to site 2 was observed, with a cluster forming in the log end, in which a further young queen was seen (but not removed). That evening, another young queen was seen at the lower right (east) border of the main bivouac. At the time the exodus to site 2 continued strongly. On January 27 and the following days, a complex raiding system developed to the east, based on the sub-bivouac at site 2. On January 28, the first males were removed in numbers from cocoons, and raiding occurred to the west and southwest from site 1; also the movement continued towards site 2, from which raiding continued to the east. In the evening, a sub-bivouac formed on the southwest line only about 8 meters from bivouac 1. At site 1, another young queen was captured from a separate cluster near the east side of the main bivouac cylinder. On January 29, the emergence of males was accelerated, the drift towards site 2 continued variably during the day, and a small raid extended towards the west from the sub-bivouac on that side. In the evening a new cylinder began to form about 20 meters farther out on the line to the west, the drift to site 2 gained headway, and there were indications that the majority of the male brood had emerged from cocoons. From site 2 a general movement to the southeast began, to a mammal burrow (site 3) 90 meters from site 2, in which thousands of ants were clustered in the evening. By afternoon on January 30 the extension from site 1 towards the west had disappeared, and only a thin file of stragglers was observed on the line downhill from sites 1 to 2, and thence to site 3. At the virtually abandoned bivouac site 1, two callow queens were found with scarcely a dozen workers, among heaps of empty cases.

Site 3 was now the center of operations on January 30, with raiding systems developed from it to the west and to the southeast. In the evening, oppositely directed emigrations were in full progress from this site, with alate males moving in both columns. On the line from site 3 uphill to the west, a moderate-sized cylinder had developed at 7:30 P.M. beside a small tree, and in this column at 7:30 P.M. a callow queen was observed in a goatee-shaped cluster of workers hanging from a vine only about 5 meters from site 3. The fate of this queen was not ascertained. A considerably larger exodus passed to the southeast from site 3, to a point across the deep creek bed where, about 40 meters from site 3, a large open bivouac cylinder (site 3a) had formed. On the following day, Jan-

uary 31, the westward extension from site 3 had disappeared by afternoon except for a few stragglers, and without any clusters. There was little traffic between sites 3 and 3a, but from site 3a two extensive raiding systems had developed. That evening the entire (reassembled) colony H-12 emigrated from site 3a about 130 meters to the southeast. The old queen of the colony (recognized by her mark) was observed in the last fourth of this movement, contracted and running freely in the column with a large entourage of excited workers following and crowding around her. (After the evening of January 31, no further callow queens were seen in H-12.) On February 1, 2, and 3, extensive raids developed, each ending in an evening exodus of 120 meters or more. When the bivouac was examined in detail on January 3, a large brood of very young larval workers was found massed in the upper center of the open cluster, and an estimated 1500 callow males hung in the walls and interior of the cluster. Thus far, no males had been observed in departure flights. When last observed on the evening of February 3, colony H-12 was engaged in an extensive movement which carried it close to the Van Tyne Trail, station 7.

During the time of study, which extended from November 19, 1947, to February 3, 1948, colony H-12 terminated a statary phase, passed through two complete nomad-statary cycles, and began a further nomadic phase. (The extensive movements of this colony, over a direct line of more than 1800 meters, are represented in fig. 4.) In this time two successive large worker broods were produced, as well as a considerably smaller sexual brood containing about 2000 males and only about six callow queens. Moreover, a great brood of worker individuals in the early larval stage was present when the study ended. Beyond doubt, all these broods resulted from eggs laid by the old queen which was marked at the outset and identified at the end of the study as the only queen surviving an inhibited colony-division process. This process, which centered around the appearance of a mature sexual brood, will be considered in a later paper dealing specifically with the subject of eciton colony division.

COLONY '48 H-13, *E. hamatum:* This colony was found on November 27, clustered in an open cylinder established well back underneath the branches of a fallen tree near the laboratory clearing. Two broods were present: a large brood of callow workers about three days emerged and a brood of very young worker larvae massed in the upper part of the bivouac at one side. A large raid developed during the day, and that evening the colony moved 110 meters to a site near the bank of Lutz Creek opposite Lutz Trail, station 1. On November 28 the colony was bivouacked in a triangular mass in the interspace between two buttressed tree roots. The cluster was examined at 8:30 A.M. (without ether), in order to remove the queen for marking (1-R). The young larval worker brood was found in long central festoons permeated by workers minor. The raid of the day was an extensive one. When the queen was returned to the bivouac at 7:15 P.M. an emigration was well under way to the southward, up the bed of Lutz Creek. This colony was not seen again.

Colony H-13 was found in the early part of a nomadic phase, with two large broods, one of recently emerged callow workers and the other of very young larval workers.

COLONY '48 B-IV, *E. burchelli:* On December 1, this colony was found in the area of Zetek Trail, station 6, its bivouac completely enclosed within a large hollow tree at a height of about 6 meters from the ground. At 10:00 A.M. there was a raid of relatively small dimensions, with the swarm only about 30 meters from the bivouac tree at the time. Only rather small raids were observed on various days thereafter, with no raiding on two of the six observation days preceding December 9, after which observations ceased for some days. When we returned to the island on December 20, there was no trace of the colony at the site. The tree was of hardwood without breaks in its shell, so that it was not possible to ascertain the presence of empty cocoons from the (presumed) emergence of a mature pupal brood.

This colony was observed during one week of a statary phase.

COLONY '48 B-V, *E. burchelli:* When this colony was first seen on the afternoon of December 1, it was bivouacked in a large

pouch cluster against one side of a big tree on the bank of lower Lutz Creek. The top of the long pouch was about 120 cm. up and its base scarcely touched the ground, a fact which with numerous other signs indicated a worker population considerably above the average in numbers. There was an extensive swarm raid to the north, with a secondary raid developing in the afternoon towards the southeast. A very large brood of essentially mature worker larvae was present, and during the afternoon and evening a considerable amount of larval cocoon spinning was observed in various places close to the bivouac. In the evening and early night the colony moved 160 meters to cluster within the central columns of a large, strangler-fig tree near the base of Donato Trail. In a condition of partial physogastry, with intersegmental membranes showing, the queen was removed to the laboratory and marked (3-L). On the following evening she was returned to the colony at the strangler-fig bivouac, where she was received in the normal manner.

When the colony was moving into the strangler-fig bivouac on the night of December 1, wide columns were seen in which larvae were carried to and fro between the base of the cluster (2 meters from the ground) and various places among the tree columns where spinning was in progress on scattered heaps of debris. The colony remained in this cluster at the fig tree until February 21, exhibiting small or only moderately developed raids in various directions, with occasional raidless days appearing after December 6. During the day on December 8, when no foray developed, the clusters could be seen only with difficulty, as they had withdrawn into the central interstices of the tree. On December 21, the ants staged a definitely larger raid than before, and large numbers of empty pupa cases littered parts of the tree and the ground below the bivouac. Unfortunately the site could not be visited that evening. On the next day the colony was gone, leaving a great litter of empty cocoons spread around below the former statary site.

Colony '48 B-V was found in the last day of a nomadic phase, after which it passed through a statary phase of 19 days while under observation. During this time the development of one large worker brood was completed; however, the presence of a further brood could not be ascertained.

Colony '48 B-VI, *E. burchelli:* This colony was under observation for six days from December 3 to December 8, during which it accomplished a regular succession of bivouac-change movements which took it from the vicinity of Fairchild Trail, station 10, to Fairchild Trail, station 5. Each of these movements followed an extensive swarm raid. The bivouacs were all exposed masses on the surface of the ground or close to it, except for the bivouac of December 4 which lined the interior of a hollow standing stump near a large opening at a height between 40 cm. and 140 cm. from the ground. A very large brood of larval workers was present, close to maturity, on December 8. Unfortunately the study had to be broken off on that day, presumably only a few days before a statary phase was to begin. Extensive searches of the bivouac on three successive mornings did not disclose a queen (although without much doubt one was present.)

Colony B-VI passed through six days of nomadic activity while under observation and was evidently close to entering a statary phase, with a larval worker brood which was nearly mature, when the study ended.

Colony '48 B-VII, *E. burchelli:* This colony was observed during two days (December 3 and 4), in which it passed close to the position of colony B-IV, in the area of Zetek Trail, station 6. The swarm raids of both days were very extensively developed, and each was followed by a bivouac-change movement directed southward in general. Both bivouacs were open clusters touching the ground. Two broods were present: a large brood of callow workers estimated (from their pigmentation and behavior) to be about four days emerged and a large brood of worker larvae in an early stage of development. The queen (contracted) was taken from the bivouac of December 4 for marking at the laboratory (1-L), and when returned that evening was received in a normal manner.

The colony evidently was approaching the end of its first week in a nomadic phase, judging from the condition of its two worker broods.

Colony '48 H-14, *E. hamatum:* This colony

was discovered at Armour Trail, station 12, on the afternoon of December 5, bivouacked in a low flat cylinder far beneath a large log. A single-system raid was in progress at the time. The bivouac contained a large brood of still unpigmented pupal workers. Considerable numbers of eggs were found in a few packets the size of hickory nuts near the upper center of the bivouac, and at the top rear of the cluster the queen was discovered in the midst of large numbers of workers minor. She was nearing maximal physogastry at the time, and when under observation in the laboratory during the day she laid between 1000 and 2000 eggs. She could not be marked. When she was returned to the colony that evening, a large cluster soon formed about her where she was set down at the lower border of the bivouac, so that her movement into the bivouac was a time-consuming process. On December 20, when we returned to the island, the colony was gone from the site.

When found, this colony was evidently passing through the intermediate part of a statary phase, with a large worker brood in the early pupal condition. The colony evidently completed its statary phase during the interval between December 10 and December 20.

COLONY '48 B-VIII, *E. burchelli:* When this colony (see fig. 3) was found in the area of Shannon Trail, station 4, on December 7, 1947, it was bivouacked in an irregular cluster in a mass of vines. In the bivouac was found a very large brood of essentially mature larval workers. There was no possibility of taking the queen at the time. An extensive raid occurred during the day, and in the evening the colony moved into the center of a large hollow tree to the east of Shannon Trail, station 3, where it was found on our return to the island on December 20. This statary bivouac was somewhere within the central hollow of the tree, evidently about 3 meters from the ground, judging from the behavior of successive foraging columns in mounting the trunk. All the observed raids from this site were relatively small ones. Raidless days also occurred.

Following a vigorous raid of two swarm systems, one beginning in the afternoon, on December 28, the colony left this site in the evening for a new location 200 meters to the north. The column was crowded with callow workers. From an examination of the new bivouac on the following day, it was judged that the colony had left its statary site with roughly one-fourth of its pupal cocoons unopened. These, mainly of workers minor, were largely opened on the one day. At this time, the presence of a further larger worker brood in the early larval condition was established. On the following days large raids were regular occurrences, all succeeded by nightly bivouac-change movements except on January 5. On January 2 a contracted queen was taken from the bivouac-change column. She was marked (3-R) and was returned to the colony on the following night, when she was received readily. Cocoon-spinning activities in the nearly mature larval brood were first observed on January 10. These activities increased on the following two days. It is an interesting fact that the bivouacs of January 11 and 12 were both noticeably more sheltered physically than at any other time since December 28. (The first of these was within a partially open hollow at the base of a tree, and that of January 12 in an elevated position, about 8 meters up, within a tall hollow tree.) From this position, in the vicinity of Balboa Trail, station 6, the colony moved again on the following evening, very probably in its last nomadic move of the series, judging from the condition of the brood, in which spinning activities were general. At its probable termination on January 12, this nomadic phase lasted 16 days, an exceptionally long nomadic interval for a colony of this species.

Colony B-VIII was next encountered on March 20, 1948, in the vicinity of Barbour Trail, station 9 (see fig. 4). Here it was bivouacked in a cylinder beneath the roof of a horizontally deep erosion cavity below the base of a tree. A large brood of mature larval workers was present, and cocoon spinning was going on extensively in countless small insect chambers and galleries within the clay bank behind the bivouac position. (The queen, approximately one-half of the brood, and about one-third of the worker population were removed for transportation to the Museum laboratory in New York, where the ants were used for circular-trail studies. The

queen's mark was clearly discernible, especially because of its prominent black edging.) Just 68 days had elapsed from the time this colony was last seen at Balboa 6 on January 12. In the meantime it had moved by an unknown route to a site located roughly 1200 meters in a straight line from the previous bivouac place.

The foray of March 20 was a large one, and that evening the remnant of the colony moved about 125 meters to establish itself about 7 meters up within a tall hollow tree. Without much question this marked the beginning of a regular statary phase. Unless the queenless colony succeeded in fusing with another colony when nomadism was resumed at the end of this phase (cf. Schneirla, 1949), dissolution must have set in then, after a few days of fairly regular activity, as in the case of colony '48 B-VI (Schneirla, 1949).

As for the collected part of colony B-VIII, workers, queen, and enclosed brood were placed in a cylindrical cage of fine-mesh wire in which they were taken by air to New York. In the subsequent history of this captive part of B-VIII, prior to its final degeneration through the effect of non-optimal conditions, two events are of particular interest. One was the death of the queen, who had remained among the workers from the time of her capture in the field. Her dead body, intact even to tarsal and antennal tips, was found among the workers on April 28, with the gaster contracted and no signs of membrane protrusion.[1] Another important event was the emergence of the unconsumed portion of the pupal brood, which occurred around April 30. This event greatly increased the level of activity in the thousands of remaining workers, which then began a vigorous circular column maintained almost continuously for somewhat more than 24 hours, in a large feeding area connected by a tube with the compartment in which the ants were clustered.

When originally found on December 7, 1947, this colony was completing a regular nomadic phase. It was on record through a statary phase of 20 days and a nomadic phase of about 16 days that followed. However, it escaped observation on what was probably the last move of this series, and was not seen again until March 20, 1948, more than two months later, when it was found at a considerable distance, engaged in the last stages of a nomadic phase. The time relations indicated that it had undergone regular cyclic changes in the meantime (see fig. 3). In a captured portion of this colony removed to the Museum laboratory in New York, the pupal brood (engaged in cocoon spinning on March 21) did not emerge as callows until April 30, an abnormally long time attributable to exceptional environmental conditions which retarded development.

COLONY '48 H-15, *E. hamatum:* This colony was found on December 20, 1947, by following back from its terminal branches a long single column which stretched nearly 200 meters to the bivouac place north of Snyder-Molino Trail, station 5. The bivouac was a low cluster formed well back under the shell of a moldy log. In the bivouac was a large, virtually mature brood of worker pupae, some thousands of which had already emerged from cocoons when the colony was found at noon.

The opening of pupa cases continued at an accelerated rate, and on December 21 a considerable increase in colony excitation was evidenced by the rise of an extensive raid on two trail systems, one of which branched into two sections close to the bivouac. The afternoon exodus started shortly before 2:00 P.M., and at 4:00 P.M. clustering had begun at a site 200 meters to the north, where the new bivouac formed. By 8:00 P.M. the previous (statary) site was deserted, ringed about by a thick pile of empty cocoons. In the bivouac-change column were seen hundreds of workers carrying newly emerged callow workers; however, no unopened cocoons were observed. On the following day the new bivouac, an exposed cylindrical cluster beneath a log, was found to contain a large brood of very young worker larvae, in addition to many thousands of recently emerged callow workers. The queen, in the contracted condition, was removed

[1] It seems improbable that this queen died while gravid. No eggs were seen, although the cluster of workers was inspected regularly through the glass cover of its laboratory nesting area. Under the conditions, it is doubtful that many eggs could have been laid by the queen, and consumed or otherwise disposed of by workers, without the occurrence having come to notice.

to the laboratory for marking (1-C). A large three-system raid developed during the day, and in late afternoon and evening the colony moved 160 meters to the south. This was the pattern of the following days, until on January 6 when the larval worker brood was mature the colony moved in the evening into a completely enclosed place within a hollow log close to Wheeler Trail, station 6. This site was occupied for 20 days, with minimal raids or no raids on given days.

On January 27, when the now mature pupal worker brood emerged as callows, the colony moved off to the southwest. In the bivouac was found a large brood of very young worker larvae. Extensive daily raids were the rule thereafter, with nightly bivouac changes generally covering a distance of more than 175 meters. These movements took the colony across Lake Trail and around Tower Hill. When it was observed for the last time on the night of February 4, the colony was engaged in a long movement westward from the area beyond Zetek Trail, station 3.

Colony '48 H-15 was at the end of a statary phase when found; thereafter, while under observation, it passed through a complete cycle of 17 nomadic days and 20 statary days, and had completed nine days of a further nomadic phase when observations ceased. During this period the colony produced two large broods of mature callow workers, appearing 37 days apart, and a further worker brood had passed its mid point of larval development at the end.

COLONY '48 H-16, *E. hamatum:* When this colony was found on December 20, it was established in an exposed cylindrical cluster beneath some tree roots near Miller Trail, station 6. There was a large larval worker brood approximately at its mid point of development. A large three-system raid was in progress. That evening, in the last stages of a bivouac-change movement of 210 meters to the south, the queen (in the contracted condition) was seen and picked out from her entourage in the emigration column. She was marked (2-C) at the laboratory. On the following day, the ants were back-tracking in a narrow file between the two bivouac sites and were also running on the raiding trails of December 20. Meanwhile, a large three-system raid had developed from the new bivouac. At 7:50 P.M. when the marked queen was set down near the bivouac of the day, she was received normally. A long bivouac-change movement then under way was completed, and next day there was no sign of back-tracking from the new bivouac site. On succeeding days there regularly occurred large raids, generally three-system, with successive nightly bivouac changes usually longer than 165 meters, in the course of which the colony moved in general northward along the Barbour-Lathrop Hill towards its end (see fig. 4). On December 30 the larval worker brood was close to maturity, and signs of cocoon spinning were to be seen around the open bivouac (located in the vicinity of Barbour-Lathrop 15). Unfortunately, the bivouac-change movement of that evening could not be followed, and on the following day the colony was searched for without success.

This colony completed 11 days of a nomadic phase, within which a larval worker brood developed to maturity.

COLONY '48 B-IX, *E. burchelli:* This colony was observed for one day only, on December 22, when it had a long, open, cylindrical bivouac beneath a log in the vicinity of Wheeler Trail, station 23, with a vigorous swarm raid in progress towards the west. A large brood of callow workers estimated at six days after emergence, and a further large worker brood in the intermediate phase of larval development, were present in the bivouac. Large numbers of the callow workers were found engaged in the raid, from the bivouac to the swarm front. The queen, found in the upper center of the bivouac, was taken to the laboratory for marking (4-R) and was returned at 8:00 P.M. to the colony. At that time the bivouac-change movement was well under way, and the queen was received in a normal manner when placed beside the main column. This colony was not seen again as an identified colony.

Colony B-IX had two worker broods, one of callows a few days old and a further brood of larvae near the mid point of development. From all the signs, the colony was near the seventh day of a nomadic phase.

COLONY '48 H-17, *E. hamatum:* On December 22, when discovered in an open bivouac about 100 meters east of Van Tyne Trail,

station 15, this colony was staging a large, three-system raid. A large brood of worker larvae somewhat past the intermediate stage of development was distributed widely in the bivouac. On that evening the colony moved more than 200 meters across Van Tyne Trail to set up its new bivouac close to a creek bank. On the following day, when a large raid was in progress, the elongated open bivouac cluster was examined without ether, and the queen was found in a contracted condition. After having been marked (3-L) at the laboratory, she was received in a normal manner when returned to the bivouac at 8:00 P.M. At that time the colony was engaged in a long movement of more than 210 meters to a point near the shore of Van Tyne Cove. Large daily raids followed, and successive evening moves took the colony on a somewhat irregular course along the shore of the cove towards the east, ending at a point 350 meters east of Harvard Trail, station 5, on the night of December 28 (see fig. 4). On the morning of that day, spinning had been observed in the brood of mature worker larvae.

The bivouac site occupied after December 28 was established beneath a wide mound formed by the massed branches of a fallen palm tree, in which the specific location of the cluster could not be discovered. The colony remained at this site, with only small raids or no raids on some of the days, until on January 18 a two-system raid was observed. The site could not be visited that evening, and the colony moved away unobserved. On the following day it could not be found in the vicinity. It was impossible to find empty cocoons in the mass of brush, to establish definitely the probable emergence of a mature pupal worker brood, and of course the presence of a further brood could not be ascertained.

This colony completed the last part of a nomadic phase, as well as a statary phase of 20 days, while under observation. A large brood of workers advanced from the mid larval into the pupal stage and presumably reached maturity as callow workers during this time. The colony was not seen as an identified colony after January 18.

COLONY '48 H-18, *E. hamatum:* On December 26 this colony was found in an open irregular cluster beneath a raised log, 25 meters to the west of Fairchild Trail, station 5 (see fig. 4). A mature brood of worker larvae was present. After a large raid on December 27, the colony moved 120 meters into the shell of a hollow log to the east of Fairchild Trail. Here signs of general spinning by larvae were observed, and a two-system raid of moderate proportions developed on December 28. That evening the colony again carried out a bivouac-change movement; however, this carried over only about 25 meters, again into the interior of a hollow log. At this site the colony remained for a considerable time.

On December 29 and following days, small, single-system raids were the rule; later raidless days became frequent. At length, on January 15 and 16, there were indications that the worker brood was being removed from cocoons, and on the night of January 16 at 9:00 P.M. the colony was found engaged in a bivouac-change movement. The new bivouac occupied on January 17 was located in the nearly closed basal hollow of a large tree, from which a three-system raid developed. After a long bivouac-change movement that evening, the new bivouac was formed below a brush heap where it was possible to establish the presence of a very young larval worker brood in addition to the large brood of worker callows. The queen was found in the upper center of the bivouac, in the contracted condition, and was taken to the laboratory for marking (2C-3C). When she was returned to the bivouac site on the same evening, she was received in a normal manner. At the time, a long bivouac-change movement was in progress, to a site west of Fairchild 8. Other work prevented continuing this record at the time.

Colony H-18 was next encountered near Wheeler Trail, station 5, on February 3, on the last day of a nomadic phase. (Very probably this marked the end of the phase begun on January 16.) The bivouac of the day was a low cluster beneath a raised log. Widely distributed through the long bivouac cluster was a mature brood of worker larvae, in which signs of spinning activity were observed. After a large raid during the day, the colony moved that evening through a distance of approximately 210 meters, into a

mammal burrow on the upper rim of the ravine bank 300 meters to the north of Wheeler Trail, station 5.

Next morning, on what proved to be the first day of a new statary phase, the queen was set down close to the mouth of the burrow that housed the colony and was received normally by the workers. At the time (about 10:00 A.M.) the ants were back-tracking in a thin file the entire distance to the previous day's bivouac, and were also found on the raiding trails of that day. On the following day, this back-tracking had ceased. On a later visit on February 21, the colony was found staging a moderately active raid. There were no signs of cocoon opening at the bivouac, although the pupal worker brood seemed essentially mature. The locality could not be visited on February 22, and on February 23 the colony was gone from the burrow and could not be found in the vicinity. It was considered most probable that the movement occurred on the night of February 22 (i.e., one day before it had been expected).

This colony was next encountered on March 7, stationed in an irregular bivouac under palm stalks, in the vicinity of Wheeler Trail, station 6. The bivouac contained a large brood of moderately advanced worker larvae, fairly well distributed through the cluster. The queen (her gaster somewhat distended) was removed to the laboratory for examination. That evening the colony moved across Wheeler Trail towards the south. On the following day at 9:30 A.M. the ants were back-tracking in thin files from the south (i.e., from the new bivouac site) to the former bivouac place and over the principal raiding trails of the preceding day. At 7:10 P.M. that evening, when the queen was returned to the scene, a file of workers was following the trail to the March 7 bivouac site. She was received normally, and at 8:30 P.M. neither queen nor workers were to be seen in the vicinity. Unfortunately, time did not permit tracking this colony through what were presumably the last few days of this nomadic phase, and it was encountered again only on March 12, when a file of workers was observed on the trail of March 7.

Colony '48 H-18 was first observed in the last two days of a nomadic phase, then in a regular statary phase of 19 days, after which the first three days of a further nomadic phase were observed. It was next found on the last day of what must have been the same nomadic phase. There followed a statary phase of 18 or 19 days, at the end of which the colony again passed from record. It was next encountered 14 days later, apparently in the last stages of the nomadic phase which had begun about February 22. During the time of the study, which carried from December 26 to March 8, colony H-18 completed two worker broods and had a further worker brood in the last stages of larval maturation when last seen. The queen, marked on January 18, evidently was in good condition and entering a further gravid episode when the colony was last seen.

COLONY '48 H-19, *E. hamatum:* When this colony was found on December 28, in the area of Balboa Trail, station 5 (see fig. 4), it was bivouacked in an open irregular cluster under a log. A vigorous three-system raid was in progress. In the bivouac was found a large brood of advanced worker larvae. The queen, fully contracted, was found in the upper center of the cluster. She was kept overnight in the laboratory, where she was marked (1-L). When returned at 10:00 A.M. on December 29 close to the new bivouac 150 meters distant, the queen was received in a normal manner. At the time, the ants were back-tracking on the trail to the bivouac of December 28. After a large, three-system raid had developed during the day, the colony moved 180 meters to the northwest. On the following day, with an extensive three-system raid developing, spinning was observed in the apparently mature larval brood. This activity became widespread in the afternoon and evening, when the colony moved 60 meters into what proved to be its statary site in a hollow log about 350 meters to the east of Wheeler Trail, station 14.

In this situation occupied on the evening of December 31, the colony formed a large cylinder under the overhanging roof of a large raised log. On December 31 and January 1, larval spinning continued on and within the log at various places to which larvae were carried by workers. On the following days the raids were all relatively small, single-system developments. It was observed after January 13 that the bivouac

cluster was extruded farther from the cavity of the log, until a position was occupied in which one side of the cluster was fully exposed to view. On January 18 opening of cocoons was observed, and the raid of the day was a two-system affair, noticeably more vigorous than before. Cocoon opening continued, until on January 20 after a considerably more energetic raid the colony moved away in the evening, with its callow worker brood altogether removed from cocoons.

On January 20 and thereafter the raids were all large, the bivouacs open clusters, and lengthy bivouac-change movements occurred in the evening and night. When the bivouac was examined on January 21, in addition to the large brood of callow workers, a young larval brood of a few thousand individuals of the male type was present. The queen was contracted and in good condition. With a succession of large daily raids, the colony in its regular evening bivouac-change movements first shifted from the vicinity of Balboa Trail, station 1, to Balboa station 6, then to the vicinity of Shannon Trail, station 9.5, which was reached on the evening of January 27. The raids began to be strikingly large and the booty haul very heavy; meanwhile, feeding activities involving brood became prominent around the bivouac and at former cache points along the trails during the evening movements.

On January 29, after nine successive moves, the colony bivouacked in a large, flat cylinder beneath the side of a huge log in the creek bed below Balboa 12. A large, three-system raid developed next day; however, the afternoon exodus was not very energetic, and new activities appeared to be developing at the bivouac which occupied large numbers of workers at the base of the cluster. About 10 clusters of workers, each the size of one's hand, were formed far back under the bivouac log, connected by wide columns with the main cluster. Although these could not be reached for examination, it was considered likely that such occurrences involved spinning by mature larvae of the queen type in the sexual brood, in advance of the males. This activity continued on the evening of January 29, when in the meantime all of the raiders returned to the bivouac and no emigration occurred. On January 30, a large raid developed, one system of which extended the lines of previous raiding trails (of January 28 and 29) down the ravine past American Museum Trail, station 3.5. This development was important for later events. Early in the afternoon the bivouac was examined, in an attempt to ascertain what part of the brood might be enclosed. Only naked larvae of the male type were seen in the accessible portions of the cluster. The old queen, partially physogastric (see pl. 16, fig. 1), was found near the top of the bivouac at the rear, within a bolus of workers minor. She was removed to the laboratory for observation, an event which was unfortunate for the stability of events in the colony, as developments proved.

Six hours later, at 8:00 P.M., the colony was found engaged in a movement over a distance of only about 7 meters, into the interior of the huge hollow log, where a wide, curtain type of cluster was forming against one wall. Here the colony later appeared to be well established. However, events that began on January 31 changed the picture radically. In the morning, some cocoon spinning was observed among male larvae, while a raid of moderate proportions developed, and back-trailing was seen on routes as far back as the bivouac of January 28. Meanwhile, cocoon spinning became general in the male brood. At some time during the night the colony began moving from the log, into a formerly developed trail which led southward across a hill towards the ravine at American Museum Trail, station 3.5. The movement was a very slow process, because of difficulties involved in dragging along the bulky male larvae, all now enclosed in the first thin sheath of their cocoons. Early in the afternoon of February 1, the colony queen (kept in the laboratory since early afternoon on January 30) was set down close to the column some meters from its end, now about 20 meters clear of the deserted bivouac log. (Thus, at the time, the entire colony was on the march, spread out along the chemical trail which extended across American Museum Trail, station 3.5, and beyond.) At 8:00 P.M., or about seven hours after the queen had been set down near the column, she remained in almost the same place beside the route. She appeared to be in good condition and capable of movement; however, each time she began to shift her posi-

tion, some of the workers would grasp at her legs and body, holding her effectively in place. Two dozen or more dead and maimed *hamatum* workers lay around her. In view of the stalemate that evidently prevailed concerning the queen in this situation, she was removed from the column and placed in an air vial, until another attempt to restore her to the colony might be made. In the meantime, the general movement towards the south had continued, so that now several meters of bare trail intervened between the place where the queen had been "sealed off" and the end of the column.

By the evening of February 1, colony H-19 formed a lengthy column of ants struggling along with its brood of about 2000 partially enclosed male larvae (and perhaps also a few larvae of the queen type). This column was then more than 350 meters in length, and especially thick and complex in its last third where great difficulty was evidenced in transporting the huge, partially enclosed male larvae. Early in the day it had become apparent that H-19 would move into the two-day old trail of colony H-28, which crossed that of H-19 in the ravine below American Museum 3.5.[1]

From that area, where the former main raiding trails of the two colonies crossed, the H-28 bivouac-change trail (of January 29) led to the west, across another wide hill and towards the creek bed east of Wheeler Trail, station 25, where colony H-28 was bivouacked on February 1. The laborious movement of colony H-19 continued day and night until February 4, when, at about 9:00 A.M., the last of the H-19 ants with their huge brown cocoons (i.e., larval spinning continued en route) emptied into the newly established statary bivouac of colony H-28 in a cavity at the base of a tree. The general path of this shift, in relation to the trails of colony H-28, is shown in figure 4.

On the night of February 1, the H-19 queen was again set down beside the moving column at a point about 600 meters from the deserted bivouac. Kept in a moistened air vial since last exposed to the workers, she seemed lively and in good condition at the time. At 10:00 A.M. on the following day, she was picked out from a small group of workers holding her firmly in place in almost exactly the spot of release. Since results of the two trials indicated that she was unacceptable to most of her former colony, she was taken to the laboratory for preservation. In contrast, the queen of colony H-28, taken from her colony on January 30 close to the time the H-19 queen was captured, was received in a normal manner on February 1, when placed near her bivouac at about the same time the H-19 queen was set down near hers. The basis of this striking difference will be considered in a later paper dealing with the subject of colony division in the ecitons.

After the merger of colony H-19 with H-28 in the statary bivouac of the latter, the combined colony had two broods: the large, mature, larval worker brood of colony H-28 and the mature sexual brood of colony H-19, both newly enclosed in cocoons. A final check showed that during the statary phase a third brood, consisting of eggs laid by the H-28 queen, was produced. However, in the 20 days spent at this same location, the sexual brood of colony H-19 disappeared altogether, evidently through worker cannibalism, although the two worker broods of colony H-28 (i.e., the broods of pupal workers and of eggs) continued their normal development without any apparent complications. The colony fusion thus was one of workers alone, so far as the outcome was concerned.

Colony H-19 was initially observed in the last days of a nomadic phase, then passed through a regular statary phase of 20 days, followed by a special nomadic phase of nine days. Then, apparently by virtue of events set in course by the removal and detention of the colony queen at what evidently was a critical time, the colony engaged in a long movement of more than 600 meters into the trail system of colony H-28 and eventually fused with the latter colony. In the course of 39 days while it was under observation, colony H-19 produced a worker brood, also a sexual brood which was lost during its pupal stage through cannibalism in the joint H-19-28 bivouac.

COLONY '48 H-20, *E. hamatum:* On December 28 this colony was found bivouacked within a log shell in a thicket near Armour

[1] Without much question, the back-tracking of H-28 workers in the absence of their colony queen (see Summary and Discussion below) was an important factor in processes leading towards an eventual fusion of the two colonies.

Trail, station 11.5. A small raid was in progress, based on a long unbranched column to the southeast. Well distributed through the lower part of the bivouac was a large brood of fairly mature (partially pigmented) worker pupae. The colony remained at this site, staging small daily raids, until on the evening of January 4 it was found in a bivouac-change movement which carried southward 140 meters to a new site.

When the open bivouac of January 4 was examined, in addition to the large brood of newly emerged callow workers, a further large brood of worker larvae in the early stages of development was found. The queen, still slightly physogastric, was stationed within a cluster of workers minor in the upper center of the bivouac. She was kept overnight at the laboratory, where she was marked (2L-2R). On the following day at 4:00 P.M. the main part of the colony was found clustered 150 meters farther south, but from this new site the ants were back-tracking in a thin file to the site occupied on the preceding day, to the statary bivouac site vacated on the evening of January 3 and also into some of the former raiding trails radiating from that site. The queen was set down at the January 5 bivouac site, where a small cluster of workers had formed. She was received normally, and within an hour, after much variable movement and some reclustering, she was seen moving off towards the current bivouac in the midst of a large crowd of workers. On the following day no ants were seen on these trails, and the colony was not encountered again as an identified colony.

Colony H-20 was observed during the last week of a statary phase, in a secluded site typical of that phase. The phase ended with the appearance of a large brood of callow workers.

Colony '48 H-21, *E. hamatum:* Early in the afternoon of December 26, some branching columns were found in the vicinity of Shannon Trail, station 14. The slender base column from which they took their origin was traced back nearly 200 meters towards the west, where traffic dwindled away to nothing. Much the same result was obtained in early afternoon on December 27, and again on December 31, when similar lines were traced to their vanishing points northward of Fossil Creek and southward of Shannon 12, respectively. Because all three of these routes converged on the same locality, about 50 meters below American Museum Trail, station 5, it was considered possible that one and the same colony had carried out the series of raids from a statary bivouac site in the vicinity.[1] However, an extended search of the area on January 1 was unproductive. On January 3 in early afternoon, a much better-developed column of ants was traced southward across American Museum 5, and at length the bivouac was located at a point just 60 meters from the trail. The colony cluster was barely visible in its position far beneath the wide horizontal buttress of a fallen tree. Around the lower border of the cylinder of ants were heaps of cocoons, and there were other indications that the removal of a pupal worker brood was in its final stages. This colony finally had been located on the last day of a statary phase.

On the same day in the evening (January 3) the colony moved a distance of 110 meters to the north, where a cylindrical cluster was formed beneath a log on the hillside. When this bivouac was examined the following morning, two broods were found: a large and completely emerged brood of callow workers, and a further brood of worker types in the early larval condition, the latter massed in the upper part of the cluster. At the time, an energetic three-system raid was in progress. The queen (contracted) was taken to the laboratory for marking (4-L). In the evening the colony moved to the area of Balboa Trail, station 13. On the following morning the queen was returned to the new bivouac, where she met a normal reception. The colony was observed in large raids and further bivouac-change movements on two further days, after which observations were discontinued.

[1] The complete absence of traffic from the basal parts of the consolidation route of raiding, often within a distance of 40 meters or more from the bivouac, is a familiar characteristic of statary-phase raids during midday hours in the dry season. Previously reported considerations justify interpreting this aspect of colony behavior, which is almost never to be seen under rainy-season conditions, as an outcome of a deepened midday inhibition of activities at the bivouac through dry-season atmospheric effects (Schneirla, 1949).

This colony completed a statary phase with the appearance of a large brood of callow workers and was beginning a nomadic phase with a further worker brood in the early larval condition when the study ended.

COLONY '48 B-X, *E. burchelli:* When this colony was found on December 31, in the area between Van Tyne 10 and Harvard Trail, station 6, it was bivouacked in the center of a thicket. A rather weak swarm raid was in progress at 10:30 A.M. The bivouac was a large, oval, pouch-like cluster suspended from the lowest point of arc in a large looped liana which hung between two trees, with the bottom of the cluster about 80 cm. above the ground. Judging from the amount of debris (of wing covers and other inedible parts of arthropod bodies) scattered below the bivouac, the colony had been at this site for a number of days. A brood of mid pupal workers in cocoons was found well distributed through the lower two-thirds of the cluster, and in addition a few clusters of eggs, each the size of a hickory nut, were found in the upper center of the mass of ants. The queen, still somewhat physogastric with all intersegmental membranes showing, was found in the midst of a tight cluster of workers minor close to the new brood.

The queen was kept overnight at the laboratory for marking (1-R) and observation. In the meantime, the colony (whose bivouac had been thoroughly disrupted in the inspection of the preceding day) had shifted its site to form a new pouch-shaped cluster at the intersection of the large vine with a slender tree at a point fully 8 meters from the ground. The queen was set down at the base of this tree, at a point only about 2.5 meters from the former bivouac site and next to the base trail of the relatively small raid of the day. Within an hour, after much excited clustering of workers on the spot, the queen had moved up the tree into the midst of the new bivouac cluster. When the site was next visited on January 8, the colony was gone. It was not seen again as an identified colony.

Colony '48 B-X formed a statary bivouac which was rather unusual in its type and situation. The raids were relatively small during the period of observation, which evidently came roughly in the middle of a statary phase. Two broods were present, a mid pupal worker brood and a new brood of eggs which evidently had been completely laid when the queen was captured.

COLONY '48 B-XI, *E. burchelli:* A moderately developed swarm raid of this colony was found at 1:30 P.M. on January 3 in the area of Balboa Trail, station 9. The principal column of this raid was traced to a small hole in the base of a large tree into which the ants disappeared. That evening the colony was found moving from this tree over the principal raiding trail of the day to form an open cluster under a log in a brush heap about 75 meters distant. The column was thronged with newly emerged callow workers, and a few thousand worker-minor cocoons were carried along. When the bivouac was examined on the following day, in addition to the callow workers a large brood of very young larval workers was found in central strands. The queen (contracted) was removed and taken to the laboratory for marking (1R-1L). When the queen was returned on the following day, it was found to our surprise that the colony had not moved away, but had reclustered under the roots of the same tree about 1 meter from the former site. An extensive raid had developed, in addition to which the ants were back-tracking to the former hollow-tree statary bivouac site, and into trails radiating from it. That evening the colony moved completely away.

On January 15 this colony was found in an open bivouac in the area of Wheeler Trail, station 9. The queen (contracted) was observed in the bivouac-change column at 9:15 P.M., when the colony was in full movement to a new site about 150 meters distant. The new bivouac was a mass about 1 meter in length formed against the side of a dead tree, its bottom about 2 meters from the ground. The large brood of larval workers now appeared to be only a few days short of maturity. Large daily raids and nightly bivouac changes were observed, until the night of January 18, when the colony established a long cluster well underneath the sloping side of a large log. Here extensive cocoon spinning by the evidently mature worker larvae was observed, which continued with greatly increased frequency on the following day. Unfortunately it was not possible to check the site that evening; the

colony moved away and was not seen again as an identified colony. Judging from the prevalence of spinning activity in the brood, this was the last move of the series.

This colony was observed for a few days at the beginning and again for a few days at the end of a single nomadic phase of 16 days—rather long for a colony of this species. At the beginning of the study a large brood of callow workers was delivered, and when observations ended a further large brood of worker forms was just beginning its enclosure as mature larvae.

COLONY '48 B-XII, *E. burchelli:* A well-thronged column of *E. burchelli* was crossed on the night of January 3 (see notes on colony H-12) near the cascades of Fossil Creek. This column of homeward-bound raiders, many laden with booty, was traced to the bivouac cluster of the colony, established deep in a recess between two roots of a large, strangler-fig tree on the summit of the high creek bank. On the following day this bivouac was found to contain a large enclosed brood of worker forms in the early pupal stages. No raid occurred on that day. Visits to the site on January 5, 12, 15, 17, and 19 found the colony raiding each time; however, the raid of January 15 did not begin until early afternoon. Cocoon opening began on January 17 and reached its peak on January 19, when, after a large two-system swarm raid, the colony moved away in the evening over one of its principal raiding trails. Judging from the number of cocoons carried in the procession, nearly one-fourth of the brood remained unemerged at the time. The queen, still slightly physogastric, was removed from the bivouac-change column and taken to the laboratory overnight for marking (1-C). When she was returned to the site on the afternoon of the following day, the ants were back-tracking from the new bivouac to the fig tree, from which former raiding trails were also being followed. When the queen was set down close to the abandoned bivouac site, she was received in a typical manner, with much excited clustering of workers upon her. The new bivouac was not visited, and colony B-XII dropped from the record for a time.

This colony was again encountered on January 28, when it was found in an open bivouac in the area of American Museum Trail, station 3, roughly 600 meters in a direct line from the site left on January 19 (see fig. 4). The queen, taken from the bivouac for inspection, was found contracted and in good condition. The cluster contained a large brood of worker larvae, past the intermediate stage of development. Successive large daily raids and nightly bivouac-change movements were observed, in the course of which this colony moved up Puma Hill to the area of Balboa 10 and then shifted to the area of Wheeler Trail, station 18. The last three bivouacs of the nomadic series were: a cluster about 1 meter from the ground within the cleft of a lightning-split tree, a mass forming a plug near the end of a hollow log, and a cylinder formed within a fallen tree mass about 1.5 meters from the ground. On the evening of February 4, after an especially large raid, the colony moved 200 meters to enter the closed shell of a hollow tree. Here it remained, with minimal raiding, until February 24.

On the night of February 24 the colony moved just 40 meters to enter a hollow log. On the following day, when this log was opened, it was found that the colony had moved without having opened the cocoons of more than a relatively small part of its large brood of mature worker pupae. A further brood of worker larvae in a very early stage of development was also present. The callow worker brood emerged within the following three days, as nomadic activities continued. Colony B-XII was kept on record until March 2, through a series of large daily raids and nightly bivouac changes which occurred regularly. The single exception was a failure to move on the night of February 26, the third day after the statary bivouac had been abandoned. When the colony was last seen, on the night of March 2, it was in the area of Armour Trail, station 7, moving southward.

Colony '48 B-XII was on record from January 3 to March 2, in the course of which it shifted across a considerable part of the eastern section of the island into the central plateau (see fig. 4). Sixteen days of a statary phase and the beginning of a nomadic phase were observed; then the colony was rediscovered after a number of days when nearing the end of the same series, which ran the unusual length (for *E. burchelli*) of 17 days.

There followed a statary phase of 19 days, somewhat unusual in that the colony made its first nomadic movement before any large part of the mature pupal worker brood had been removed from cocoons. During the interval of 61 days it was on record, colony B-XII produced two large broods of mature workers, and a further large worker brood was passing through its early larval development when the study ended.

COLONY '48 B-XIII, *E. burchelli:* When discovered on January 8, this colony was staging a great raid of two swarm systems from its bivouac in the area of Harvard Trail, station 2. An unusually large brood of mature worker larvae was found well distributed through the bivouac, which was a large pouch hanging about 60 cm. from the ground in a thick mass of brush. Signs of extensive cocoon spinning were observed in the brood. Because of the high excitability of the workers, together with the thickness of the surrounding tangle, there was no possibility of finding the queen. The movement of that evening took the colony to the southward about 220 meters, where it formed a mass 1 meter from the ground in the cleft of a lightning-split tree. Here the colony settled, and raiding became minimal. About three days thereafter the colony moved upward within the same tree, to a point about 3 meters from the ground where it was completely enclosed within the tube of the hollow tree. Other work prevented maintaining the observations, and the colony was not identified again.

This large colony completed a nomadic phase and began a statary phase, with the enclosure of a large brood of mature worker larvae, in the manner characteristic of its species.

COLONY '48 H-22, *E. hamatum:* When discovered on January 8 to the northeast of Harvard Trail, station 3, this colony had an open bivouac against the base of a palm tree beneath a roof of rubble. An extensive three-system raid was in progress. A large brood of callow workers was found well distributed through the bivouac, and in addition there was a large brood of very young worker larvae in a single long mass near the upper center. The queen, situated behind the brood in the upper part of the bivouac, was taken to the laboratory for marking (1C-2C). She was contracted at the time. When she was returned on the evening of the same day and set down near the bivouac-change column, she was received normally by the workers.

Colony H-22 was rediscovered on January 18, in a bivouac situated only about 3 meters from the site occupied on January 8. The colony must have described a circuitous path in the intervening nomadic movements, but the coincidence of bivouac areas may have been due to the chance crossing and subsequent reëmployment of old chemical trails. The bivouac contained a nearly mature larval worker brood, well distributed through the cluster. The queen, in the contracted condition at the time, was removed to the laboratory for observation. Early in the afternoon of the following day, a file of ants was back-tracking through the former bivouac area. The queen was accepted readily when released near this column. The colony was not seen again as an identified colony.

Colony H-22 was observed near the beginning of a nomadic phase, and after 10 days was rediscovered when in the last part of the same phase.

COLONY '48 B-XIV, *E. burchelli:* On January 12 this colony was found in the area of Gross Trail, station 2, where it had formed a large irregular cluster under some palm stalks, with a smaller cluster about 60 cm. distant. A great brood of very young worker larvae was present, separated into numerous ball-shaped masses permeated by workers minor; also, there was a large brood of callow workers evidently a few days emerged. The queen, contracted at the time, was found in the center of a tight cluster of workers near the bivouac roof. A large raid of two systems was in progress. When the queen was returned on the following day after having been marked (2-C) at the laboratory, the ants were back-tracking from a new bivouac site to the southeast.

The colony was again encountered on February 25, this time near the center of the island where it had a statary bivouac at Lake Trail, station 2, 1800 meters in a direct line from the site of January 12 (see fig. 4). Here it was clustered within a standing hollow stump, where it formed a plug the bottom of which was approximately 1.5 meters from the ground, largely enclosed by the shell of the

stump at a point above a hole the size of a football. Samples of an enclosed worker brood (then nearing the intermediate stage of pupal development) were taken. Small raids were observed on March 1 and 3; on March 4, 6, and 7 there was no raiding at all. To capture the queen, the bivouac was examined with the aid of ether. The large pupal worker brood was found distributed throughout the lower three-fourths of the plug bivouac, and towards the top center of the cluster were found two packets, the size of walnuts, of eggs. The queen was also found near the top of the cluster, surrounded by a considerable mass of workers minor and smaller intermediates. She was somewhat more fully physogastric than had been expected, evidently not far past the peak of egg laying. Her mark was clearly identifiable as a prominent chevron. (At the laboratory she was Bouin-fixed for subsequent study.) On the following day the colony was found reclustered within the same stump. It finally moved away on the night of March 15, leaving a litter of empty pupa cases.

Colony '48 B-XIV was first observed with a young larval worker brood in what evidently was the early part of a nomadic phase. Then, 50 days later, it was found in statary condition about 1800 meters away, with a mid pupal brood which very probably represented the next in order to that present as early larvae on March 1. Also present was a new batch of eggs just being completed by the queen. The evidence suggests that between the first and the second observation periods, colony B-XIV passed through nearly two complete nomad-statary cycles in a regular manner.

Colony '48 B-XV, *E. burchelli:* When first observed at 3:15 P.M. on January 12, this colony was clustered below the overhanging bank of the creek below Lake Trail, station 5, with an extensive raid in progress. In a bivouac-change movement that night the colony moved about 150 meters to mass within the mouth of a mammal burrow. On the following day, with a large raid in progress, the bivouac was investigated without ether and was found to contain a large brood of worker larvae approximately intermediate in development. At 7:25 P.M. that evening, when almost two-thirds of the colony had moved away from the site of the day, the queen appeared in the column and was captured for marking at the laboratory (3-C). When she was returned to the new bivouac on the following day, the ants were found back-tracking to and beyond the deserted site of the previous day. On the following days large raids occurred, and a succession of nightly movements took the colony to the vicinity of Armour Trail, station 2. Here on January 17 it passed from observation for a time, having completed its movement away from the bivouac site of the day before the observer arrived at 8:00 P.M.

On January 22 this colony was found established in a statary bivouac in the vicinity of Zetek Trail, station 3.5. In the afternoon of that day, from some terminal branches and a swarm to the east of Armour Trail, a long column with a few branches was followed back more than 300 meters to a hollow tree. Here the colony was found massed within a partly broken trunk shell, about 2 meters from the ground. At 3:00 P.M. traffic was largely directed towards the bivouac, with more than half of the ants carrying morsels of booty. During the following days the raids became small, and frequent raidless days appeared. The colony moved from the site on the night of February 10.

The bivouac of February 11 was an open cluster, a long oval mass under a raised log. A large raid developed during the day. A large brood of emerged callow workers was found well distributed through the bivouac, and three walnut-sized packets near the top center contained a large brood of young worker larvae. The queen, in the fully contracted condition and with her mark plainly visible, was found in the upper part of the bivouac cluster. At this juncture the colony was released from observation.

During the 30 days in which this colony was on record, the latter part of one nomadic phase was completed, a full statary phase of 21 (or perhaps 22) days followed, and finally a further nomadic phase was begun. In this time one worker brood completed its larval and pupal periods, and a further brood in the early larval stage was present when the study closed.

Colony '48 H-23, *E. hamatum:* On January 14 when first seen, this colony was biv-

ouacked in an irregular open cluster under the root mass of a fallen tree, near Shannon Trail, station 4. In the bivouac were found a brood of callow workers judged to be about five days from emergence, and a second large brood of young larvae. The queen, taken from the upper interior of the cluster, was fully contracted at the time. She was removed to the laboratory for marking (3L-3R). A vigorous two-system raid was then in progress. That evening the colony moved about 145 meters to the northwest, where an open cluster was formed beneath a small log. On the following morning at 10:00 A.M. the ants were found back-tracking in a narrow file to the bivouac place of January 14 and on the former raiding trails from that site. The queen was received in the normal manner when set down near the bivouac of the day. That evening, after a large three-system raid had ended, the exodus was well under way at 6:30 P.M. At the time the last 10-meter section of column with the queen in its midst was leaving the bivouac site.

Large daily raids and nightly bivouac changes prevailed during the next few days. After January 18 there was a noticeable tendency to get into more secluded sites, with the last three nomadic sites being, in order: (1) the mouth of a mammal burrow; (2) the partially open basal cavity of a small tree; and (3) a mammal burrow opening beneath the overhang of a large root. In the last three moves a marked inertia was shown in beginning the emigration. Although the movement of January 18 was well under way at 6:50 P.M., that of January 19 was in a "trickling" condition (as far as movement from the bivouac was concerned) until after 10:00 P.M. (distance: 160 meters), that of January 20 was irregular at the bivouac until after 9:00 P.M. (distance: 95 meters), and that of January 21 did not become fixed in the direction of exodus until after 9:30 P.M. (distance: 110 meters).

The movement on the night of January 22 took the colony into a hollow log on the bank of Allee Creek to the east of Barbour-Lathrop Trail, station 1, where the ants remained until February 14. All raids that were observed were relatively small and were conducted essentially along single-system lines.

On the night of February 14, after a large raid during the day, the colony moved off to the east towards Lutz Trail, station 2, with its large brood of callow workers mainly emerged. On the following days the colony continued to stage large raids with nightly bivouac-change movements, some of them approaching 200 meters in length. The general course of the successive movements took the colony from the area of Lutz 3 across Donato Trail below station 1, then to the general vicinity of Donato Trail, station 5, where observations were discontinued with the bivouac-change movement of the night of February 21. It is notable that the bivouacs after February 15 tended to be established in rather enclosed situations, such as brush heaps, although colony behavior continued to be fully nomadic. The cluster of February 16 was almost completely enclosed within a hollow log, that of February 17 was established in a mammal burrow, that of February 18 was completely enclosed within the hollow base of a large tree, that of February 19 within a brush pile, that of February 20 only partially exposed within a hollow log, and finally on February 21 an open bivouac was established beneath a liana and against a tree.

Within the period of study this colony completed a nomadic phase, then passed through a statary phase of 22 days, and was observed during the first eight days of a new nomadic phase when the record ended. The development of one large worker brood was completed, and a further worker brood produced during the statary phase was nearing its mid point of larval development when observations ended.

COLONY '48 H-24, *E. hamatum:* When found on January 14, this colony was located in an open bivouac in the area of Miller Trail, station 16. Although the size of the adult worker population was estimated to be considerably below the species norm, a brood of larval workers was present approximating the usual magnitude of such broods. This brood, within a few days of larval maturity at the time, was found well distributed through the bivouac. The queen was found in a brood-free zone near the top center of the cluster. In the contracted condition at the time, she was taken to the laboratory for marking (1L-1R). An emigration occurred

that evening; however, on the following day the ants were back-trailing in a thin file to the deserted bivouac site and beyond it into previously used raiding trails. The queen was received in the normal manner when she was returned, and towards evening back-trailing ceased as the emigration developed. When the last movement of the series occurred on the night of January 16, the brood appeared fully mature and signs of cocoon spinning were observed.

The statary bivouac site occupied after January 16 was a mammal burrow facing to the northeast, near the base of a hill in the vicinity of Miller 17. All raids observed were small ones, with sequences of raidless days. The colony was present on February 1 but was gone when the site was next visited on the morning of February 5. From the condition of the nearly mature pupal worker brood as observed on February 1, it was considered most probable that the colony had moved away on the night of February 3 or 4. From the pupa-case litter, it seemed that not all of the mature pupal brood could have emerged at the time of movement.

During the period of study, this colony passed through the last days of a nomadic phase and a subsequent statary phase of only 18 days. Because the colony was not observed in the last day of this phase, no reason can be advanced for the shortness of the phase in comparison with the duration characteristic of the species (see fig. 7). During the study, one large worker brood was brought from an advanced larval condition to pupal maturity. It cannot be said to what extent this brood had emerged from cocoons when the colony moved away, nor whether or not a further brood was present when the study ended.

On the basis of a close coincidence of activity and brood phases, and from its location when found, it is possible that this colony was '48 H-5, a colony last seen in the vicinity of Barbour-Lathrop 9, where it completed a statary phase with a movement towards the west on the night of November 20, 1947.

COLONY '48 H-25, *E. hamatum:* When this colony was first seen on January 16, it was staging a large raid and was located in an open bivouac in the Tower area, near Pearson Trail, station 2. After an extensive emigration of more than 300 meters that evening, the colony next day formed an open irregular cluster not more than 40 meters from the clustering site of colony B-XV, *E. burchelli.* Although friction occurred at several points between the extensive raids of the two highly active colonies, the difficulties appeared to be resolved through successive minor trail readjustments which evidently did not materially reduce the scope of raiding in either colony. When the H-25 bivouac was examined without ether on January 17, a large brood of approximately half-developed worker larvae was found well distributed through the cluster, and near the top of the mass was the queen, in a contracted condition. Examination showed that her right rear leg lacked tarsi altogether, and the distal end of the tibia was blackened, clearly from a local injury of some kind from which she had recovered.[1]

The queen was received normally when returned to the bivouac on January 17. For 10 days after the time of discovery, this colony staged large daily raids and nightly bivouac-change movements of considerable extent. In this time the colony shifted its successive bivouacs from the Tower area, first to the north and east across Shannon Trail near station 6, and then southeast and east across Ocelot Hill to a position on the hillside above Fossil Creek.

On the night of January 26, when extensive spinning was noted in the mature brood of larval workers, colony H-25 established a cluster beneath the partially open shell of a hollow log, on the east face of the hill overlooking Fossil Creek, about 450 meters east of Shannon 5. Here the colony remained, with minimal raiding, until the pupal brood completed its development and had mainly emerged on February 16.

With the emergence of the new callow worker brood on February 16, the colony entered a futher nomadic phase, in which it was kept on record during four successive days of extensive raids and nightly bivouac-change movements. During this time, its

[1] In contrast to the accounts of commonly finding Old World doryline queens in a somewhat mutilated condition, as though frequently dragged about by workers (Wheeler, 1921), the queens of eciton species are virtually always in perfect condition.

general route led first to the vicinity of Barbour 6, then bent around to the east along the face of the hill overlooking Fossil Creek.

While it was under study, colony H-25 completed a nomadic phase and a statary phase of 20 days, and when the study ended had begun a further nomadic phase. In the course of the record, one large worker brood developed to maturity and emerged as callows, and, at the last, another large brood of worker forms was in an early larval stage of development.

COLONY '48 H-26, *E. hamatum:* On January 17 this colony was found by our tracing back from its terminal branches a long unbranched column which extended for more than 300 meters from Barbour-Lathrop Trail, station 1, towards Allee Point. The colony was found bivouacked beneath a log in the midst of a fallen-tree mass. A large mature larval brood was present, and numerous signs of spinning were observable. The colony was kept under general observation, and circumstances indicated that it moved away on the night of February 4 or 5.

Colony '48 H-26 was on record during nearly all of a statary phase, in which a large worker brood developed to maturity. It was not possible to determine whether or not a further brood was present at the time the study ended.

COLONY '48 B-XVI, *E. burchelli:* On January 18 this colony was found in an open, irregular cluster under some palm fronds at the edge of a log in the vicinity of Lake Trail, station 3.5. A large brood of worker larvae was present, the maturity of which was indicated by the occurrence of spinning in numerous flat clusters of ants and larvae atop the log and on the log near by. The queen was found near the top of the bivouac cluster and was taken to the laboratory to be marked (4-L). That evening the ants moved 40 meters, mounted a hollow tree, and bivouacked within it at least 3 meters from the ground. When the queen was returned on the following day, the ants were back-tracking. She was received in a normal manner, with much clustering and great excitement as she finally mounted the tree.

The colony was under regular observation during its stay at this site, which ended on the night of February 7 with a bivouac-change movement over a distance of 150 meters into the ravine below Lake Trail, station 5. The first bivouac at the new nomadic phase was formed in a mammal burrow on the stream bank. Great numbers of unopened intermediate and minor worker cocoons were found, but it was not possible to locate a further brood (i.e., young larvae). The raid of February 8 was a large one, and in the bivouac-change column of that evening great quantities of bee and wasp pupae were carried along. Curiously enough, this movement carried only 7 meters up the steep bank, where the colony formed an open, blanket-like mass about 1.5 meters wide, supported here and there by leaves and by plants of the wild pineapple. Thousands of still unopened worker intermediate and minor cocoons containing mature pupae were observed when the large cluster was opened. On the morning of February 9, there was no sign of a foray even at 11:00 A.M., a decidedly abnormal circumstance for a colony in the nomadic phase. However, considerable quantities of booty were present in the bivouac, and the ants appeared to be busily engaged in feeding operations with callow workers. A raid developed in the afternoon, and that night the colony moved 20 meters uphill, at a lateral angle of 70 degrees on a 60-degree slope. Here the ants entered the base of a hollow tree, in which the cluster was nearly out of sight. The opening of cocoons continued. On February 10 no raiding foray had developed from this site by 10:00 A.M. However, on this day also a raid developed in the early part of the afternoon, and at 8:15 P.M. ants streamed back into the bivouac on the principal trail of the foray. No bivouac-change movement occurred. Meanwhile the opening of cocoons continued. On the following day, raiding began in the morning; however, once more at 8:30 that evening it was observed that traffic was directed predominantly inward towards the bivouac on the principal trail, and no bivouac-change movement occurred. From the signs, all cocoons were opened by that evening. On February 11 a moderately large raid developed; however, at 8:30 P.M. there were no definite signs of a bivouac-change movement. Unfortunately, the observer was taken away by other work, and the colony

moved off at some time that night. On the following day it was gone from the site and could not be found.

Colony '48 B-XVI, when first observed, was on the point of ending a nomadic phase with the enclosure of a large, mature, larval worker brood. There ensued a statary phase of 19 days, after which the colony moved off with the major part of its mature pupal brood still enclosed. This brood was not completely removed from cocoons until about three days thereafter. The behavior of the colony after the first nomadic day was rather exceptional, for after an initial movement of typical magnitude the colony staged a very short bivouac-change movement, passed two days with apparently subnormal raiding and no bivouac-change movements, then on the next evening carried out a bivouac-change movement with considerable inertia. Also, the bivouac of the third nomadic day, formed after a very short movement, was a "blanket-type" structure recalling that formed by colony '46 B-IV during its last days before dissolution (Schneirla, 1949).[1]

COLONY '48 H-27, *E. hamatum:* This colony was found on January 23, bivouacked within a hollow log in the vicinity of Armour Trail, station 9. From the condition of the brood, recently enclosed, the colony was judged to be in the third or fourth day of a statary phase. On occasional visits thereafter, small raids and raidless days were observed. On February 8, the colony began opening cocoons, an activity that reached its height on February 10, when after a large raid the colony moved in the evening to the south-southeast nearly 300 meters. Its itinerary is sketched in figure 4.

The first nomadic bivouac, an irregular cluster formed at the base of adjacent plants of wild pineapple, was examined on the following day (without ether). Near the roof of the main part of the cluster beneath the center of a pita leaf the queen was found, contracted and in good condition. In a number of separated strands in the central part of the bivouac was found a larval brood, readily identified as a sexual brood. The queen was taken to the laboratory where she was marked (1-L), and was readily received when she was returned that evening to the bivouac.[2]

On the evening of February 17, after eight successive days with large daily raids and regular nightly bivouac-change movements, the colony established itself in a hollow and partially buried log. Next day a considerable amount of milling around was observed among ants on the ground near the opening of the cavity in which the colony was housed. Spinning activity by mature sexual larvae was suspected (cf. H-12 and H-19); however, such activity must have been limited to a few individuals (mature queen larvae?), and no concrete clues of their identity were obtained.

The colony remained at this site for 21 days. On February 19 and 20 there were definite indications of a large-scale spinning of cocoons by mature male larvae, and on February 21 all the larvae appeared to have completed their outer envelopes. Thereafter the level of activity in the colony dropped, with small raids the rule and on some days no raids, until a reactivation occurred on and after March 5. The raids then became considerably more vigorous than before, and on March 5, 6, and 7, there were definite signs that at least three callow queens had emerged from cocoons. This event was followed by an evident reorganization of the colony, most clearly marked by the development of two (visible) hand-sized cylindrical clusters clearly separated from the bivouac, and one flat shallow cluster in the center of which a callow queen was visible, and which remained for more than two days. These

[1] It is unfortunate that this study could not have continued longer, for the available facts leave the basis of the somewhat abnormal behavior of colony B-XVI unclarified. The fact that neither a young larval brood nor a queen was found after the last "nomadic" phase began may have been due to their being overlooked because the bivouacs were difficult to search thoroughly, or, on the other hand, may have been an outcome of the queen's death early in the preceding statary phase (i.e., before any eggs were laid). It is improbable that an ordinary worker brood could have been overlooked. A further possibility is that a sexual brood in an early larval stage may have been present; such a brood might escape discovery in a colony of such magnitude.

[2] The H-19 queen, to which this mark had been given originally, had been removed from circulation and fixed in Bouin's solution on February 2, after two "sealing-off" episodes had occurred when she was reintroduced after a short absence from her colony.

events were followed within a day or two by the emergence of the male brood, a process which was well under way on March 9 and was completed late on March 10. The increase in raiding reached a peak on March 10, when there were three trail systems. On two of these, divergent outward movements began early in the afternoon and continued until the entire colony had been divided into two sections in separate bivouacs. The manner in which this colony division occurred, and in particular the role of the callow queens in the entire process, will be the subject of a later paper.[1]

On March 11 the two new colonies resulting from the fission of H-27 were clustered in exposed bivouacs located to the east and west of the statary bivouac site, and nearly 200 meters apart. Thereafter they functioned independently as colonies in the nomadic condition. They contained nearly equal sections of the brood of callow males (i.e., about 1000 alate males each) and of a further brood of very young worker larvae (i.e., about 12,000 worker larvae each). The eastern section, which will be referred to as H-27a, contained the "old" H-27 queen (distinguishable by her mark), unquestionably the queen responsible for producing the eggs of the early worker brood now divided between the new colonies. The western section contained a callow queen, readily distinguishable as a young queen by her light golden orange pigmentation. These two colonies thereafter behaved independently in a representative nomadic manner, except that section H-27a after its first nomadic day passed two days with somewhat weak raids and without bivouac-change movements before it left its first nomadic bivouac on the night of March 13, and H-27b passed one extra day without an emigration at its second nomadic site. Thus, directly after the complete division, both sections appeared to fall somewhat below the nomadic activity threshold for a day or two. Thereafter, in an eight-day interval following the complete fission, the new colonies behaved in a representative nomadic manner, each with large daily raids and nightly emigrations. In successive movements, H-27a reached the vicinity of Wheeler Trail, station 17, and H-27b reached the vicinity of Armour Trail, station 7, on March 19. The daughter colonies were then roughly 400 meters apart and proceeding more or less divergently (see fig. 4). Each colony was examined with the use of ether on March 19. The broods were similar, in that each of the colonies contained an estimated 600 to 700 alate males (i.e., some 300 of the original number had flown away by night; cf. Schneirla, 1948) and a further lot of young worker larvae estimated at close to 10,000 in H-27a and more nearly 15,000 in H-27b. Large samples of these broods were taken, as well as the single colony queens, which from previous inspections of bivouac-change movements were known to be the "old" queen in H-27a and a callow queen in H-27b. Both queens were fixed in Bouin's solution for eventual study.[2] The young brood of worker larvae in both colonies was actually the outcome of a division of a single brood which without question may be attributed to the "old" queen. It is to be expected that the young queen of segment H-27b would have begun to produce broods in due course of time.

During the period of investigation, colony H-27 completed a statary phase, passed through a nomadic phase of only eight days (with a brood of sexual larvae), then through a statary phase of 21 days at the end of which a colony division occurred. When the study ended the two daughter colonies produced through the fission of H-27 were each passing through the early part of a nomadic phase. H-27 first produced a large worker brood, then a sexual brood of approximately 2000 males and probably a few more than the three females of the queen type observed, and finally a large new brood of worker individuals which was divided between the two

[1] Indications were that only one callow queen survived, i.e., the one which became the effective queen of colony H-27b. Two callow queens were found "sealed off" by a few workers at the statary bivouac site when it was virtually deserted on March 11. The fate of others beyond these three could not be ascertained.

[2] A subsequent examination by Dr. Whelden revealed that the callow queen from H-27b contained large masses of sperm and therefore must have been fertilized at some time after her emergence at the statary bivouac, probably after nomadism had begun. The spermary receptacle of the "old" queen taken from H-27a also contained sperm to capacity.

daughter colonies when fission occurred. There is every reason to believe that the two sections of colony H-27 would have continued in typical function as independent colonies had they been permitted to retain their queens and young broods.

COLONY '48 B-XVII, *E. burchelli:* When discovered on December 29 about 100 meters to the north of Armour Trail, station 8, this colony was bivouacked at a height of 2 meters within the convoluted columns of a large, strangler-fig tree. A large brood of nearly mature worker larvae was present. No signs of spinning could be detected (however, such activities might have been overlooked quite easily under the conditions). After a rather vigorous raid, traffic on the principal trail continued as a variable and at times trickling movement to the south, which persisted until after 10:00 P.M. without a bivouac-change movement getting under way. Circumstances were similar on the following day, with an irregular traffic situation on the principal trail until after 9:00 P.M., when, however, a definite exodus began. On the night of December 31 the colony settled into the upper part (*ca.* 3 meters up) of a standing hollow trunk about 50 meters to the south of Armour 8, where it remained until January 20, with minimal raiding only. After a vigorous raid on that day, the colony moved away in the evening, with nearly one-third of its mature pupal worker brood still enclosed in cocoons. A moderately large raid was staged on the following day, and the opening of cocoons continued; however, the bivouac in the midst of a large brush heap could not be examined for other broods. A further move on the night of January 22 took the colony to a site in the area of Armour 5.5, where it clustered under the shell of a hollow log. Here it was ascertained that virtually all the new worker brood had emerged from cocoons; however, no other brood could be found. This last matter was clarified on the following day, when the open half cylinder of the new bivouac beneath the overhanging side of a large log was examined, with the result that a further brood, of larval males then 6 to 7 mm. in body length on the average, was discovered. On this and succeeding days, the raids became more extensive, and nightly bivouac-change movements occurred on which the formation of longer stretches of "ant roadway" became prominent. However, on January 27, for the first time since this nomadic phase began, the bivouac was established 1 meter from the ground within the columns of a strangler-fig tree. Two new facts of importance were now recorded. First, on January 27, the colony appeared to be very sluggish; the raid of the day was not large, and in the evening no bivouac-change movement occurred. Second, in probing the lower margin of the bivouac in order to pick out samples of the male brood with a minimal disturbance of the bivouac, the observer brought forth two fully formed cocoons which proved to contain mature larvae of the queen type.[1] At this time, the male brood was still entirely naked, barely showing the preliminary signs of cocoon-spinning activity.

On the evening of January 28, in the last movement of the series, the colony entered a hollow tree where it was clustered within the largely enclosed trunk about 1.5 meters from the ground. The raids until after February 17 were relatively small; in fact, on February 14, 15, and 16, raids were set off by artificial means after none had developed in the first half of the morning. Thereafter, a crescendo in extra-bivouac activity was noticed, and on February 20 a definitely augmented excitement was observed among workers at the base of the bivouac. (The cause of this local excitement in the bivouac could not be ascertained.) On the morning of February 21, cocoon opening was seen, and callow alate males with extended wings were taken from the top of the cluster. At the same time, a new and recently hatched brood of worker larvae was found, bunched in the upper center of the bivouac cluster. Despite the increasing level of daily raiding and an augmented excitement centering especially around cocoon-

[1] One of these enclosed mature queen larvae was put at once into Bouin's fixative; the other was kept alive for nine days in the laboratory among workers of the B-XVII colony (and some of their male larvae) in an artificial nest. This second queen individual was removed from its cocoon on February 4, when it was found to have metamorphosed into a fully pupated queen, still unpigmented except for the eyes. This specimen, the first queen pupa of the dorylines to be taken, was fixed in Bouin's solution for eventual microscopic study.

opening in the bivouac, no movement had occurred up to February 23. Routine periodic inspections of all principal trails from the bivouac were carried out at this time, in the anticipation that a colony division would occur in conjunction with the emergence of the male brood.

However, there was no fission of the colony as far as could be established, and no callow queens or signs of their presence (cf. colonies H-12 and H-27) were ever observed in this case. The colony moved away on the evening of February 23, with all or virtually all of its male brood removed from cocoons. Three successive bivouac-change moves occurred thereafter; then on January 26 the colony remained in its place without a movement. Two further movements took place, after which on February 29 there was another failure to move from the bivouac of the day. On March 2, with the colony operating close to Armour Trail, station 4, it was necessary to end this case study.

During a survey lasting 66 days, colony '48 B-XVII completed a nomadic phase with the enclosure of a mature larval worker brood, passed through a statary phase of 20 days in which this brood matured into callow workers, produced a sexual brood of an estimated 2500 males and two or more queens carried through larval development in a nomadic phase of just nine days, and then passed through an unusually long statary phase of 25 days in which this sexual brood completed its pupation. When the male brood emerged there was no division of the colony (and no individuals of the queen type were ever seen except for the two captured at larval maturity). Instead, the colony moved off as a unit with a further worker brood in the early stage of larval development. The first eight days of a new nomadic phase had been observed when the study ended. The mature functional colony queen (undoubtedly present) was not seen at any time during the study. The colony was not encountered as an identified case after March 2.

COLONY '48 B-XVIII, *E. burchelli:* This colony was found on January 16 through our tracing back the principal trail of a moderate swarm raid to the bivouac in the area of Armour 1. Here a cluster was found in the center of a lightning-split tree about 2 meters from the ground. Judging by the presence of a large heap of relatively fresh insect parts scattered on the ground directly below the cluster, the colony had been at this site for a few days prior to discovery. Raids were weak or absent on certain days until after February 1; then on February 2 there were signs of the removal of worker callows from cocoons. This activity increased in scope until on February 4, after a large raid, in the evening the colony moved away to the northwest. In the irregular open bivouac of the following day, perhaps one-fifth of the mature pupal worker brood was found still enclosed in cocoons. (The last of these, mainly worker-minor types, were removed as callows on February 6.) On February 6 a large new brood of worker larvae at an early stage of development was found in the upper center of the bivouac. On February 9 reexamination of the irregular open bivouac cluster of that day disclosed the young larval worker brood massed in the central core of the bivouac in long strands extending from the top nearly to the bottom of the cluster. The queen, in a contracted condition, was found near the top center of the bivouac. (She was taken to the laboratory, given the mark 4-R, then received a normal reception when returned to the colony in the evening.) Meanwhile the daily raids had been large ones, and nightly bivouac-change movements occurred which were all extensive, with the exception of that on February 8, which was forced into a relatively short raiding system begun in the early afternoon, and which carried over a distance of only 20 meters. Because of other work, it was necessary to close this study on February 10, when the colony had reached a point about 100 meters to the southwest of Lake Trail, station 2.

Colony '48 B-XVIII when found was in the early part of a statary phase, in which after 19 days of observation a large brood of callow workers was produced. Thereafter, seven days of regular nomadic activity were observed before the study had to be discontinued. At the time, a further brood of worker forms in the early larval stage of development was present.

COLONY '48 B-XIX, *E. burchelli:* This colony was found on January 23 in the vicin-

ity of Wheeler Trail, station 6, bivouacked in a deep, triangular root opening at the base of a hollow tree. In the bivouac was a large brood of mature worker larvae, perhaps more than half of which already had begun to spin cocoons. Although the contents of the bivouac cluster were spread around considerably during the examination at 10:00 A.M., the queen could not be found. That evening the colony moved 40 meters into the head of a large palm tree near Miller Trail, station 1, in which it remained until February 11.

On the evening of February 11, after a large raid, the colony moved 165 meters to form an open bivouac cluster in the area to the south of Wheeler Trail, station 7. Although the column was thronged with newly emerged callow workers, an estimated one-fourth of this brood was carried along in cocoons. The brood was not completely removed until February 14. No movement occurred on February 12, and on this and the following days a tendency rather unusual for the early nomadic condition in this species was observed. This was the formation of bivouacs in rather secluded places rather than as the usual exposed masses. For example, on February 13 a curtain mass was formed in a heap of rubble at the base of a hollow tree, on February 14 a largely enclosed cluster was established within one end of a hollow log, on February 15 the ants clustered within the base of a hollow tree, and on February 16 they massed within a water-eroded chamber in a stream bed. On February 18 the bivouac was an open cylinder formed beneath a tree root on a steep bank, and here for the first time in this nomadic phase it was possible to ascertain the presence of a further brood of worker larvae, then past the mid point of development. The functional queen could not be found. At this time, while it was operating in the area of Balboa 6, the colony had to be released from study.

At the beginning of these observations, the signs indicated that colony '48 B-XIX was close to the end of a nomadic phase. It is possible, however, that the colony would have moved on February 23 had the bivouac not been disrupted and the colony artificially excited by an extensive examination; hence the duration of the ensuing statary phase must be set at 18 or 19 days. During this statary phase a large brood of workers completed pupation, and when these emerged as callows a further nomadic phase began. During the first nine days of this phase there was one failure to move, and a definite proclivity was observed for entering secluded, ecologically sheltered bivouac sites.

COLONY '48 H-28, *E. hamatum:* When found on January 31, this colony was clustered in a rather small, irregular, exposed bivouac beneath some sticks and leaves near American Museum Trail, station 3. During the preceding two days, it had moved up to this position from the vicinity of Shannon 13. Although this colony was abnormally reduced in its worker population, a fairly well-developed raid of two trail systems had dedeloped. In the bivouac was found a normal-sized brood of nearly mature worker larvae, close to which was found the queen, in a contracted condition at the time. (Her faded appearance, with a more grayish yellow coloration than is typical, suggested that she might be elderly in comparison with functional queens of the species.) The queen was removed to the laboratory where she was marked (4-C). She was received in a normal manner when returned to the new bivouac on February 1. This bivouac, incidentally, was another exposed cluster of the flat "platter" type.

On February 1, with most of its now mature larval brood already partially enclosed, the colony moved in the evening into a deep recess at the base of a tree, located near the creek below Wheeler Trail, station 23. The single system raid on February 2 led to the south. In the meantime, a general movement of colony '48 H-19 had begun on February 1. This movement followed the removal of the H-19 queen as described in the protocol for that colony. The failure of the H-19 colony to receive its functional queen was in diametric contrast to the typical reception given the H-28 queen which had been removed and returned at about a corresponding time. Several hundred meters of this movement occurred over trails developed by colony H-28 during the last three days of its nomadic phase. A minimum of conflict between the colonies was observed, and for the most part both the H-19 workers and sexual brood were

received without particular difficulties in the H-28 statary bivouac. On February 4 this long movement was completed after it had been under way more than three days. Then the worker populations of the two colonies (with a mature worker larval brood and a mature larval sexual brood) were contained in the same bivouac. The colony, now an especially large aggregation of workers, remained in this place until February 22. Samples of the H-19 sexual brood were obtained with increasing difficulty as time went on, and after February 20 neither male cocoons nor other signs of this brood except empty cocoons were seen. The entire brood of the former colony H-19 must have been consumed, although the H-28 brood came through its pupal development essentially intact.

On February 22 there were signs of an unusual excitement around the statary bivouac site (for which no particular cause could be ascertained), and a large raid of three strong trail systems was developed. In the evening the entire colony moved off to a new site only 33 meters away, carrying along the greatest part of its mature pupal worker brood still enclosed in cocoons, a most unusual occurrence in *E. hamatum*. Cocoon opening on a large scale was observed during the next two days, and the callow worker brood appeared to have emerged entirely by February 25. Once begun on February 22, nomadic behavior continued, and for eight successive days, while the colony remained under observation, regular large raids and nightly bivouac-change movements were observed. On February 25, when the contents of the bivouac were examined, in addition to the large brood of nearly emerged callow workers, a further large brood of worker individuals in an early larval stage was found, but no signs whatever of males or callow queens. The "regular" H-28 queen was found in the contracted condition, easily recognizable through her distinctive mark, active and in good condition when observed during the course of an emigration. In the end, the fused colony constituted one of definitely more than average worker population, with a single queen and behavior properties typical of the species.

At the beginning of the study, colony '48 H-28, well below the species average in its worker population, was completing a nomadic phase. At that time a single mature brood of worker larvae was present. Through the removal of the queen of another colony (H-19) at a critical time, together with a chance intersection of chemical trails, that colony fused with H-28 so that the latter possessed two mature larval broods, one of worker and the other of sexual (male, and perhaps a few female) forms. During the statary phase the sexual brood was gradually eliminated through cannibalism, so that after 20 days, only the H-28 worker brood remained to emerge as callows. When the colony entered the ensuing nomadic phase, in addition to the new brood of callow workers it had a further brood of worker forms in the early stages of larval development.

COLONY '48 H-29, *E. hamatum:* When this colony was found on February 26 in the vicinity of Drayton Trail, station 1, it was clustered in a mammal burrow, entering a statary phase with a large pupal worker brood and with minimal raiding. Here it remained until after March 15, the last day of observation. On March 20 the site was found deserted, with large numbers of empty pupa cases scattered in the burrow.

Colony '48 H-29 evidently passed through 18 or more days of a statary phase, then moved off after a large part or all of a worker brood had emerged. The possible presence of a further brood could not be ascertained.

COLONY '48 H-30, *E. hamatum:* When this colony was found on March 4, it was bivouacked under the overhanging outer edge of a brush mass in the vicinity of Shannon Trail, station 7. An extensive three-system raid had developed, and in the bivouac was found a large brood of approximately mature worker larvae. That evening, a bivouac-change movement of about 160 meters took the colony into the ravine below Shannon 8. Up to 9:00 P.M. the ants were entering a large hollow log; however, later on they shifted to a mammal burrow about 40 meters farther downstream. The queen was observed in the latter section of the movement, in the contracted condition, and was captured for preservation. On March 5 and 8, backtracking was observed to the log in which clustering had begun on the night of March 5 and beyond it to the abandoned site of

March 4. On March 5 the statary bivouac of the colony, a plug formed in the outermost section of the mammal burrow, was investigated to ascertain the condition of the brood. Spinning activity was general among the mature worker larvae, and most of them were enclosed in thin envelopes. After the bivouac at the mammal burrow had been disturbed, the colony shifted in the late afternoon and evening of March 5 into a mass of brush a few meters away from the burrow opening, where it was observed a few days later and where it evidently remained to the end of the statary phase.

Colony '48 H-30 was found on the last day of what evidently had been a regular nomadic phase, with a large brood of mature worker larvae. On the first day of the statary phase a short movement of the colony was forced by ransacking the bivouac. Presumably this colony completed its statary phase, after which dissolution must have soon occurred, unless by chance a fusion with another colony became possible.

COLONY '48 H-32, *E. hamatum:* When this colony was found on March 5, it possessed a large brood of mature worker larvae and was bivouacked in a cavity below the roots of a tree in the vicinity of Barbour-Lathrop Trail, station 7. A well-developed raid of three trail systems was in progress, and in the evening the colony moved nearly 300 meters into a large hollow tree to the northwest of Barbour-Lathrop 5. In the course of this movement, the queen was observed in the column and was captured for preservation. At the time she was partially physogastric, evidently about to enter the first stages of an egg-production episode. On the following day, back-tracking was observed along the route from the hollow tree to the March 5 bivouac and beyond. The colony remained bivouacked in the hollow tree with typically reduced raiding, until some time after March 15, the last day of observation.

This colony completed a nomadic phase with the enclosure of a mature larval worker brood and had passed through the first part of a statary phase when last observed. It is probable that the removal of the queen led to the eventual dissolution of the colony after the statary phase ended, as was presumably also the case with H-30 (cf. '46 B-IV, Schneirla, 1949).

COLONY '48 B-XX, *E. burchelli:* This colony was found on March 10 near Armour 9, clustered within a standing hollow tree stump at a height of about 3 meters from the ground. From the litter of insect parts beneath the bivouac, the site had been occupied for a few days before discovery. The raids on this and following days were small. On March 12 the bivouac was thoroughly investigated with the aid of ether. Through the lower two-thirds of the cluster was scattered a large brood of recently matured worker larvae, about one-third of which (mainly workers major and larger intermediates) had the usual thick brown envelopes, the other half thin envelopes with signs of continuing spinning. This suggested that the colony had moved into the site on March 9 and perhaps March 8, but not before. The queen was found near the top of the bivouac, in the center of a thick cluster of workers huddled in a little pocket in the inner trunk wall. (She was in a nearly maximal physogastric condition. Although a careful search brought to light no eggs in the bivouac, this queen laid several hundred eggs during the eight hours she was kept alive in the laboratory prior to being preserved.) After the demolition of their bivouac, the ants reclustered inside the same stump close to their original place and were still operating small daily raids from the spot when last examined on March 19.

This colony while under observation passed through 10 days of a statary phase, very probably having been discovered only two or three days after this phase had begun. It was estimated that on March 19, from the condition of the pupal worker brood, the colony had roughly seven or eight days before the emergence of this brood would occur and nomadic activities would begin. Because the queen was removed, there is little doubt that this colony eventually suffered dissolution, unless a fusion with another colony of the species could have occurred by chance.

AREA 2: PEQUENI-BOQUERON RIVER SECTION, DECEMBER 11 TO 20, 1947

COLONY PH-1, *E. hamatum:* This colony was found at 11:00 A.M. on December 12,

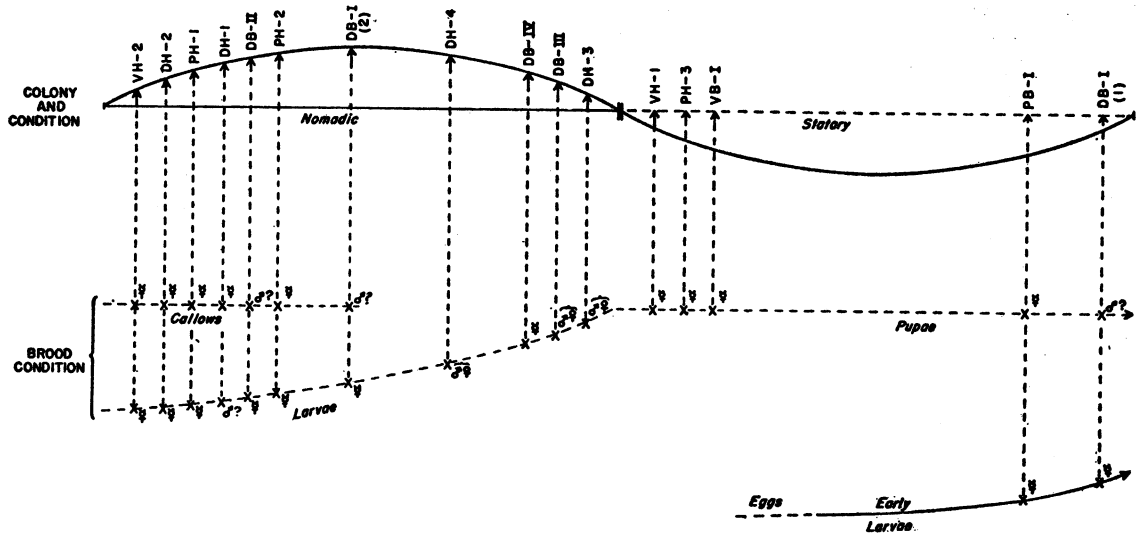


FIG. 5. Schematic representation of the concurrence of events in colonies of *E. hamatum* and *burchelli* studied in areas 2, 3, and 4 (cf. fig. 1). P, colonies in the Pequeni-Boqueron River district, area 2; D, colonies in the Darien districts, area 3; V, colonies in El Valle, area 4. Under Colony and Condition, the crest of the biphasic curve represents the nomadic phase of colony activity and the trough represents the statary phase. The colony symbols (H, *hamatum;* B, *burchelli*) designate the estimated stage of the cycle reached by each colony at the time of study. Condition of the brood or broods for the corresponding times in the respective colonies is indicated below. Brood symbols: ☿, worker brood; ♂ ♀, sexual brood; ♂?, sexual brood, queen forms not seen.

1947, bivouacked near the Las Cruces Trail about 4500 meters west of the Pequeni River. The colony formed an irregular bivouac beneath some splintered pieces of wood lying on the hillside. Two well-developed trail systems were in evidence. In the bivouac were found two broods, a large brood of callow workers probably three days after emergence, and a large brood of very young worker larvae, massed in a few long strands near the upper rear of the cluster. The queen was contracted and nearly escaped by running off on one of the raiding trails when the bivouac was opened. She was removed for preservation. During the next four days the ants were observed back-tracking along their trails in this vicinity, although the main part of the colony left the area on the night of December 12.

This colony was in the early part of a regular nomadic phase when investigated, with the typical combination of recently emerged callow worker brood and a second brood of worker larvae at an early stage of development. It is probable that colony dissolution did not occur until this nomadic phase and a subsequent statary phase had run their course.

COLONY PH-2, *E. hamatum:* This colony was found in an open bivouac in the upland hills about 4800 meters west of the Pequeni River, at 1:30 P.M. on December 12. (Its proximity to the area in which PH-1 was operating very probably was a matter of chance.) A large raid was in progress on three well-developed trail systems. The bivouac was a low cylinder under the head of a large log. In it was found a brood of callow workers estimated at about five days after emergence, not very different in pigmentation from adult workers. There was also a brood of young worker larvae estimated to be about two days more advanced than that of colony PH-1, somewhat more widely distributed through the bivouac than in colony PH-1. The queen was found near the upper center of the bivouac, in the contracted condition. She was removed for preservation. That night the

colony moved away; however, back-tracking occurred on the trails in this vicinity for about as long as in colony PH-1.

Conditions were much the same in this colony as in PH-1 at the time, as concerns clear signs of the early nomadic phase. However, colony PH-2 was two or three days more advanced in the nomadic phase than was colony PH-1.

COLONY PB-I, *E. burchelli:* This colony was found on December 13, bivouacked on a steep hillside about 2000 meters west of the Pequeni River. At 11:15 A.M., a moderately large swarm raid was found through localizing the calls of numerous ant birds, and the trails were traced back about 70 meters to the bivouac, which was within a large hollow tree at a height evidently more than 6 meters from the ground. On December 15, at 3:00 P.M., a raid was found just getting under way, clearly in an afternoon start from the fact that the swarm was poorly organized and had pushed only about 4 meters from the bivouac tree. On December 16 at 4:00 P.M. there were indications that the colony had staged a day-long raid of moderate size, in the return of ants in a fairly heavy column with considerable amounts of booty. On December 17 an extensive raid was in progress at 11:00 A.M., and a heavy return of booty to the bivouac tree was observed. That evening, the colony moved from its situation within the hollow tree to an open situation near by, where it was found on the following afternoon in a long curtain cluster beneath a root just 3 meters away from the tree base. A heavy raid was in progress at the time. In the bivouac was found a great brood of newly emerged worker callows, only a few thousands of them (mainly workers minor) still enclosed. A second brood of very young larval workers was found in a few small festoons near the upper center of the bivouac and well to the rear of the bivouac wall. The queen was found in a mass of workers minor and major, hanging from the under surface of the bivouac root in the central part of the cluster. She was in the nearly fully contracted condition at the time.

This colony was observed during the last five days of what appeared to be a regular statary phase. When observations closed, a nomadic phase was beginning, with the appearance of a large brood of callow workers and with a large new brood of early larval workers present.

COLONY PH-3, *E. hamatum:* When found on December 15, 1947, about 11:00 A.M., this colony occupied a bivouac near the crest of a hill saddle about 1500 meters west of the Pequeni River. There was a single raiding system, with a base trail essentially unbranched within 200 meters of the bivouac.

The colony was bivouacked near the partially open end of a large hollow log. In this bivouac was found a large brood of mature worker larvae already partially enclosed for the most part, and on top of the bivouac log were found two large spinning areas to and from which workers were busily engaged in carrying larvae. Our progressive breaking of the log shell in attempts to find the queen at length caused an extensive movement of workers carrying larvae away from the log in wide columns, with a resettlement presently beginning within another hollow log about 6 meters away. A cluster was finally brought out, from the roof of the first bivouac site, in which the queen was found. Her gaster appeared to be in a slightly distended condition, although without membrane protrusion. When introduced into Bouin's solution the severed gaster (unlike those of fully contracted queens) sank at once to the bottom of the vial, suggesting a partial advance towards physogastry. On December 16 the colony was found in the hollow log to which it had moved from the disrupted bivouac on December 15.

This colony was just entering a statary phase, most probably in the first or second day of that condition, with a large brood of mature worker larvae undergoing enclosure.

COLONY PC-A, *Eciton* (*E.*) *conquistador* Weber: The first of two colonies of this species, recently described (Weber, 1949) from specimens taken in this investigation, was found on November 15, 1947, about 1300 meters west of the Pequeni River, bivouacked within a hollow hardwood tree. The cluster was formed within the basal hollow of the tree, somewhere within 0.5 meter of the ground. At 11:30 A.M. the ants were raiding on a single trail system connected with the bivouac by a long basal column. Scattered debris below the hole through which the ants

entered the tree, mainly booty remnants such as empty pupa cases of various ant species, indicated a stay of some duration at the site. On November 16 the raiding seemed heavier than before, both on the line of the preceding day and on a new raiding system. Even after 9:30 P.M. that night a steady column of ants continued to return to the bivouac.

The raid of the next day was heavier and involved operations on two trail systems. Late in the afternoon a fairly thick column of ants passed outward from the tree on one of the principal columns, a sign of impending nomadism corroborated by the presence of callow workers in the column and huddled beside the route close to the tree. An effort was made to enter the bivouac, without success. It is probable that the use of ether in this operation blocked a movement of the colony which might otherwise have been carried out on this last night of observation.

Colony PC-A, from the signs, evidently had passed through a statary phase at this site. At the close of the observation there were indications that the colony was about to become nomadic.

COLONY PC-B, *E. conquistador:* This colony was found at 11:00 A.M. on November 15, 1947, at a point about 3 miles to the west of the site of colony PC-A. When discovered, the colony was raiding vigorously on three trail systems, each with a single base route to the bivouac, and large quantities of booty were coming in. The bivouac was a plug-shaped cluster within the interior of a hollow log and near the broken end, where the mass was partly exposed. A large brood of mature worker larvae was found distributed throughout the cluster, and numbers of these larvae were being transported to and from places on the surface of the log and within cavities in its wall where cocoon spinning was in progress. Despite a careful search, the queen could not be found; presumably she escaped into the inaccessible upper interior of the log. On the following day this colony was bivouacked at a point about 140 meters from the previous site, within the complete cylinder of a hollow tree from which the ants issued at a point about 3 meters from the ground. At 3:00 P.M. there was just one raiding system, with a single long base column extending from the bivouac tree, unbranched within 40 meters of the tree.

Colony PC-B evidently was in the final day of a nomadic phase when discovered, with all indications pointing to a regular statary condition as sequel. In all of the observed circumstances, in regard to brood conditions and colony behavior, these colony records of *E. conquistador* bear a general similarity to the conditions prevalent in *E. hamatum*.

AREA 3: DARIEN, REPUBLIC OF PANAMA, FEBRUARY 14 TO 27, 1948

COLONY DH-1, *E. hamatum:* This colony was found at 9:45 A.M. on February 14, in the forest to the southwest of El Real, about one-half mile from the Tuira River clearing. The bivouac was a single large mass formed as a modified cylinder beneath the crotch of a raised log, and fairly open to view. A three-system raid was in progress at the time. In the bivouac was found a large brood of callow workers, estimated to be not more than two or three days out of cocoons. In addition, a brood of larvae of the sexual form at an early stage of development was found in a few strands near the top of the bivouac at one side of center. About one-half of this brood was removed for preservation. The queen was found in the upper part of the bivouac cluster, about 20 cm. away from the position of the sexual brood. In the contracted condition, she was removed for preservation.

COLONY DB-I, *E. burchelli:* This colony was first encountered at 10:30 A.M. on February 14, 1948, in the El Real forest about three-fourths of a mile southeast from the locality of colony DH-1. At the time a large swarm raid was in progress, its advance body about 11 meters in width and operating at about 110 meters from the bivouac. The colony was massed in a deep, well-like cavity between two high tree buttresses, a depression entirely closed except for a long opening on top, not much wider than would permit inserting an arm. Two broods were present: a large sexual brood still in cocoons for the most part, with a few hundred alate males already emerged, and a large brood of very young worker larvae. No callow queens were

observed, and the functional queen was not found.

On February 20, what appeared to be the same colony, from all indications, was operating about 500 meters to the east of the DB-I location of February 14. The bivouac was a long cylinder below a small log which lay beneath the overhanging side of a huge log under a tight thatch of vines and limbs. Hundreds of alate males were found in the cluster, as well as a large brood of early worker larvae. No cocoons of sexual forms were present. As thorough a search as possible was made, but no queen was found. A moderately large swarm raid was in progress at the time.

This same colony, from all the circumstances, was encountered again on February 23, 1948, only about 120 meters to the northwest of the February 20 site. This time the colony was found within the closed shell of a tall hollow stump, about 1.3 meters from the ground. Brush round about was cleared, and after the cluster had been localized and ether appropriately applied, the stump was felled with machete and broken open carefully, and the contents of the bivouac were examined almost *in situ*. Some hundreds of alate males (considerably darker in pigmentation than on February 20) were found spread through the lower two-thirds of the plug-like cluster. A large brood of worker larvae was present, the smallest members of which were found concentrated in the upper center of the cluster, the larger sizes scattered rather widely through it. The queen, in a contracted condition, was found within a clump of workers near the top of the bivouac cluster. She was removed for preservation.

Colony DB-I evidently was encountered at three separate times, judging from spatial relations and from progressive differences in brood condition. When first encountered, the colony seemed to be nearing the end of a statary phase, with a sexual brood beginning to emerge and a brood of larval workers at an early stage of development. Six days later, when found at some distance from the presumed statary site, the colony evidently was operating on a nomadic basis, and apparently had lost nearly half of its alate males (presumably both through nightly flights and through colony division). When found once more, nine days after the initial encounter, the colony was not clearly nomadic in either situation or behavior, possibly because of the large segment of the larval worker and the alate male broods removed on February 20. On February 23, the functional queen (contracted) was found, definitely adult and not a recent callow. It is probable that, despite artificial interferences from repeated searching and from the removal of brood, this colony had operated largely on a nomadic basis for about one week, after the close of a regular statary phase and a possible colony division.

COLONY DH-2, *E. hamatum:* This colony was found on February 16, 1948, about 20 miles south of El Real, roughly 2 miles up a small branch of the Pirre River. A vigorous three-system raid was in progress. At 4:00 P.M. a thick column crowded with callows had advanced along one principal trail to a disance of 60 meters from the bivouac, crossing the river on the trunk of a great fallen tree as bridge. The bivouac was found under brush on the low bank of the stream, an open irregular cluster which contained, in addition to newly emerged callow workers, a very large brood of early worker larvae. The young brood was massed in three or four strands near the center of the cluster. The queen, found near by in a cluster of workers minor, was in the contracted condition. She was removed from the bivouac for preservation. The emigration was completed that evening, and next morning the colony was found in a new bivouac site more than 200 meters away. However, back-tracking continued during the following two days.

This colony was estimated to be in its first or second nomadic bivouac when discovered.

COLONY DB-II, *E. burchelli:* This colony was found on February 18, 1948, in the area of the Pita River about 5 miles to the east of the Pirre River. At 10:00 A.M. a swarm raid of moderate dimensions was located by means of the calls of ant birds, and the principal column was traced back across the dry river bed about 90 meters to the bivouac site. The bivouac was a cylindrical cluster formed beneath two crossed logs in the center of a thick tangle created by two fallen trees. In the lower part and outer walls of the cluster were perhaps 600 alate males (estimated at

about five days after emergence), and in the upper center was a bolus of young larval worker forms, a young brood of exceptionally small population for a colony of *burchelli*. The queen, taken from the top center of the bivouac, was in the contracted condition, and her exceptionally light color (cf. functional queens of the species) suggested that she might be a young queen of the season, with a daughter segment of a recently divided colony.

Colony DB-II was in the early part of a nomadic phase when found, judging from the condition of its broods perhaps the fourth or fifth day of the phase. It is possible, in view of the somewhat "callow" appearance of the single queen together with the exceptionally small population size of the young larval brood, that this colony was a section recently divided from a base colony as a consequence of the appearance of a sexual brood.[1]

COLONY DH-3, *E. hamatum:* This colony was found on February 21 at 10:15 A.M. in the forest about 4 miles southeast of El Real. The entire raid proved to be highly expanded at the time, with three large trail systems. The bivouac was a huge half cylinder formed well beneath the overhang of a large log and beneath a great piece of bark, all within a low grotto formed by a thick mass of vines. The task of examining the bivouac was carried out in detail, with the clustered ants pulled out literally strand by strand. This operation, which lasted from 11:00 A.M. to 4:00 P.M., was effective because the workers clung very tenaciously to the large mature larvae of their sexual brood, and an evident lethargizing effect of high temperature (and bright light) prevailed once the roof of vegetation was removed and direct sunlight reached the bivouac. (This effect was maintained through the day by means of tinfoil sheets used as reflectors.)

The functional queen (slightly physogastric at the time) was found near the extreme left pole of the half cylinder, within the third of the bivouac which from front to rear was clear of sexual brood. The mature larval brood was gathered in the right two-thirds of the bivouac, from base to top, most of the large larvae held up among the clustered ants. Around the base of the bivouac both in front and in the rear were some small clusters in which larvae were evidently spinning cocoons in the wood dust. The male brood appeared to be essentially mature, but few of the male larvae had yet begun to spin. About 20 larvae which had already spun filmy envelopes were removed. These were found towards the back and lower part of the bivouac, some on the ground in worker clusters but a few held near the roof of the cluster. Most of these, 14 to be exact, proved to be the queen type of larvae.[2]

The entire brood was captured, with the exception of not more than 25 larvae which were carried off by workers at times when it could not be prevented. At camp the male brood was counted a second time, and was found to total 1317 individuals (only about half as large as the male brood of some colonies of *E. burchelli*, such as '46 B-III, for which counts have been made). If the queen larvae are added as well as the larvae that were carried away by workers, the total does not exceed 1350.

Colony DH-3 when found evidently was ending a nomadic phase with a brood of mature larvae of the sexual form, in which the few queen larvae found had begun to spin their cocoons. It is not possible to say whether or not the colony would have performed a further bivouac-change movement had it been unmolested.

COLONY DB-III, *E. burchelli:* On February 26 at 3:30 P.M., a swarm raid was found crossing a small dry quebrada about 4 miles south of Yavisa. This raid, the swarm of which then was about 115 meters from the bivouac, was traced back to an irregular cluster under the root mass of a small fallen tree within the overhang of a deep thicket. A sexual brood at the mature or nearly mature larval stage was found distributed through much of the cluster, but some of the larvae were found with workers in pockets in

[1] Histological examination of the DB-II queen by Dr. Whelden has disclosed a uniform densely tangled mass of sperms in her receptacle.

[2] An attempt was made to preserve these larvae alive, so that stages of development through pupation to the callow condition might be obtained for preservation. However, they were somehow prevented from pupating, presumably through the effect of being transported about in necessary travel, for, although they all completed regular cocoons, none passed through the prepupal stage.

the dry wood or in the soil, where they apparently were engaged in spinning. Under the conditions, a thorough examination of this brood was out of the question. As many brood samples were taken as could be gathered in the time available. The population of the sexual brood was estimated at a minimum of 2500. The functional queen could not be found. Because of other operations, the site was not revisited.

This colony evidently was entering or about to enter the statary condition when found.

COLONY DB-IV, *E. burchelli:* At 11:15 A.M. on February 27, near the Yavisa-Pinogana Trail 1 mile north of the Tuira River, a large swarm raid was encountered. The head of this raid proved to be about 105 meters from the bivouac. The colony was found clustered in a pouch-shaped mass at a height of about 70 cm. from the ground, formed around a vertical liana and also supported by some vines and bush stems. The queen was found at length, in a cluster of workers which had fallen to the ground. A large brood of nearly mature larval workers was present, widely distributed through the lower half of the pouch. In addition to the swarm system followed back to the bivouac, another had developed at 90 degrees to the first—altogether a maximal foray.

This colony, when found, evidently was passing through the last part of a nomadic phase, perhaps only a day or two removed from the statary phase. The functional queen was slightly distended at the time of capture.

COLONY DH-4, *E. hamatum:* At 2:30 P.M. on February 27, to the east of the Yavisa-Pinogana Trail and 5 miles south of Yavisa, a vigorous raid of *E. hamatum* was found working along the lower part of a fairly dry quebrada. This proved to be part of a complex trail system which had been developed to a distance of nearly 250 meters from the bivouac. The bivouac itself was finally discovered upstream in the creek bed above a vertical cliff about 30 meters in height (evidently a wide waterfall in the rainy season),[1] around which the principal column of ecitons traversed by mounting a steep series of terraces. Two other trail systems also took their origin at the bivouac. The colony formed a thick cylinder hanging from an elevated log end to the ground, with one side resting against the overhanging creek bank. A large brood of larvae of the sexual form about two-thirds mature was found well distributed through the cluster, in all parts of the bivouac except the side close to the bank. The queen (contracted) was located near or within the upper rear of the cluster.

This colony when found evidently was entering the last third of a regular nomadic phase. The bivouac was an open cluster and the raid was maximal in extent and vigor.

AREA 4: EL VALLE, REPUBLIC OF PANAMA, MARCH 5 TO 10, 1948

COLONY VH-1, *E. hamatum:* On March 6 this colony was found at a point about 3 miles north of El Valle, at an elevation of about 800 meters. In the late morning a weak single-system raid was in progress. The bivouac was found in a clearing of broken forest, mainly a chayote garden, about one-half mile from dense forest. The colony formed a very small cylinder only about 15 cm. in diameter at the top and 30 cm. high, within the base of a hollow stump. It was noted that the proportion of workers major was unusually high. A mature larval worker brood was present, mainly enclosed. The queen was contracted.

This colony evidently had very recently entered the statary condition. The reduced condition of its worker population suggested that it had been subjected to arduous conditions, very probably centering around the fact that it had become statary in a situation with poor cover and well outside the main forest.

COLONY VB-I, *E. burchelli:* This colony was found on March 7, 1948, only about 100 meters from the place at which colony VH-1 had been found on the preceding day, also in an area of scattered vegetation and sparse cover outside the forest proper. The bivouac was a pouch hanging within the center of a hollow log. At 9:30 A.M. the swarm raid had pushed out only about 30 meters from the bivouac, an indication of a low level of

[1] This stream was named Three Falls Creek by Breder (1946), who visited the area in 1924 in connection with an investigation of the herpetological fauna of Darien.

colony arousal. A brood of mature larval workers was present, nearly all of them enclosed in cocoons. The queen, slightly physogastric, was found near the upper center of the cluster.

This colony, like VH-1, was especially small for its species. Likewise, it was found outside the border of the forest, evidently at the beginning of a statary phase.

COLONY VH-2, *E. hamatum:* This colony was found on March 8, 1948, at a point 6 miles to the north of El Valle, bivouacked within a clearing (thickly covered with recently felled forest) about 45 meters from the forest edge. A moderately active two-system raid was in evidence. The bivouac was located in a mammal burrow beneath a fallen log. Two broods were present, one of recently emerged callow workers, the other of early worker larvae. The queen was contracted.

At the time of study, this colony evidently was in the early part of a nomadic phase, judging from its condition of raiding and the status of its broods.

CONFORMITY OF COLONIES TO THE NOMADIC-STATARY CYCLE

The nomad-statary cycle has been defined by Schneirla (1938) as the occurrence in eciton species of regularly alternating sequences of two distinctly different patterns in colony behavior and underlying biological conditions, as follows:

Nomadic phase
- Large daily raids, approaching maximum in development
- Colony moves nightly to new nesting site
- Brood present in larval condition, reaching maturity as phase ends
- Single colony queen remains non-gravid throughout phase

Statary phase
- Raids small, or do not occur on some of the days
- Same bivouac site (an especially sheltered one) occupied throughout phase
- Two broods present, one passing from larval to pupal maturity, the other produced in egg form somewhat before the middle of the phase
- Queen undergoes egg-producing episode early in phase

The present investigation represented an opportunity to test the validity of previous descriptions of the nomad-statary cycle (Schneirla, 1938, 1944a, 1944b, 1948) based upon studies carried out both in the rainy season and in the dry season.

The project was begun early in November of 1947, in order to study rainy-season conditions, the transition from rainy- to dry-season conditions, and conditions in the regular dry season, in sequence, in regard to the adjustments of the army ants. A principal aim of the investigation was to determine the prevalence of cyclic processes in colonies studied under different environmental and seasonal conditions in well-separated forested areas of Pamana. Another was to obtain evidence on the duration of the two major phases of the activity-reproductive cycle of these ants, not only with respect to the central tendency and degree of variation within each species, but also with respect to species differences.

The records of 1948 on these points may be compared with similar evidence obtained on Barro Colorado Island in the dry season of 1946 (Schneirla, 1949), to find whether or not there are any indications of differences from year to year in the cyclic processes of either species.

A further important object of the investigation was to compare the influence upon the cycle of the development of sexual broods in comparison with that of worker broods. If there are differences in the duration of corresponding stages in the development of these two types of broods, as the 1946 study indicated, such a comparison should throw light upon the relative importance of extrinsic factors and of factors intrinsic to the queen in the control of the cyclic changes.

An examination of the colony protocols summarized in the foregoing section of this paper and represented graphically in figures 2 and 3 shows that every one of the colonies studied in area 1 clearly fell into place on the nomad-statary schedule. This applies to both short and long records.

On Barro Colorado Island, 30 colonies of *E. hamatum* were on record for an average of 22 days, the longest studies extending over 83 (H-18), 73 (H-12), 40 (H-15), 39 (H-23), and 36 (H-25) days. Twenty-four of these

records involved at least a portion of one nomadic phase, and 22 involved at least a portion of one statary phase; 15 of the records involved at least one transition from a nomadic phase into a statary phase, and 14 involved at least one transition from a statary into a nomadic phase. Thus, as figures 2 and 3 show, all stages of the nomadic-statary cycle were involved in these records.

In all, 20 colonies of *E. burchelli* were on record on the island, for an average of 24 days, the longest studies extending over periods of 105 (B-VIII), 66 (B-XVII), 64 (B-XIV), and 61 (B-XII) days. Fifteen of these records involved at least a portion of one nomadic phase, and 16 involved at least a portion of one statary phase; nine involved a transition from a nomadic to statary, and seven involved a transition from a statary to nomadic phase. Much as with the cases of *E. hamatum* studied on the island, all stages of the nomadic-statary cycle were encountered in the records for *E. burchelli.*

The results are very clear. Every one of these colonies presented characteristics of behavior, brood condition, and condition of the queen (contracted or physogastric) which were well synchronized and in good agreement with some stage in the standard description of the nomadic-statary cycle based on the work of previous seasons, both wet and dry. The characteristics of raiding, nomadism, brood condition, and condition of the queen that deserve special mention in this paper are dealt with later. Figures 2 and 3, together with the foregoing protocols, show in a general way adequate for present purposes that all of the 50 island colonies of the two species investigated were functioning in terms of the nomad-statary cycle, and all but one of them while on record operated in the manner characteristic of its species. During all the periods of observation, whether long or short, no colony (except B-XVI) exhibited any signs of breaking from the typical pattern of the cycle, although colony differences appeared in the length of the cycle, which will be discussed presently. Because our queen-marking procedure introduced the possibility of reidentifying colonies on the island, in numerous cases in both species colonies were reobserved after non-observation intervals. From an examination of figures 2 and 3, it will be seen that all such colonies when rediscovered were operating much as would be expected had regular cyclic processes continued in the meantime. A rather striking case is presented by colony B-VIII which, after passing from the record in mid-January, was next seen late in March, then (as may be seen from fig. 3) in a condition indicating that nomad-statary functions had continued regularly during the 68-day interval.

The results summarized in figure 6 indicate that all of the 17 colonies taken in other areas of Panama also conformed to the cycle in essential respects. Of the three colonies of *E. hamatum* taken in the Pequeni River area (PH-1–3), two were in the early part of nomadic phases and one was just entering a statary phase when investigated. Of two colonies of *Eciton* (*E.*) *conquistador*, one was nearing the end of a statary phase and the other moved from nomadism into a statary phase while on record. The one colony of *E. burchelli*, colony PB-I, that was taken in this area was in a statary phase when discovered and passed into the nomadic condition a few days later. It will be seen from figure 5 that of four colonies of *E. hamatum* and four of *E. burchelli* captured in the Darien area in late February and early March, seven represented various stages of the nomadic phase, and one passed from a statary into a nomadic phase while under observation. Finally, of two colonies of *E. hamatum* and one of *E. burchelli* studied in the El Valle area during early March, one was evidently beginning a nomadic phase, one was nearing the end of a nomadic phase, and one had entered a statary phase when found. Among 15 cross-sectional studies in two species, as figure 5 shows, all colonies conformed to the nomad-statary pattern, and all appeared to be functioning in a regular and adequate manner when they came under observation. The fact that two of the colonies discovered in the El Valle area had rather small populations of adult workers was presumably due to their operating (when found) in sparse growth somewhat outside the border of heavy forest, in noticeably dry areas. Even so, in both colonies developing broods of typical population size were present, the queens were in good condition, and raiding activities were

under way at the time. In contrast, among the 30 colonies of *E. hamatum* studied on Barro Colorado Island, only two appeared to fall considerably below the species average in worker population. One of these colonies was H-4, which was found during late November before the rainy season ended; the other was H-28, found in February during the dry season.

The above results indicate very clearly that in the areas of study in Panama, during the terminal weeks of the rainy season of 1947, and in the dry season of 1948, the colonies of *E. hamatum* and *burchelli* functioned predominantly in terms of the nomad-statary cycle. The one possible variant colony among nearly 70 cases (colony B-XVI, *E. burchelli*) was operating regularly when discovered but may have deviated later because of some mishap introduced through human intervention, e.g., marking of the queen. This matter, however, could not be established definitely. If colonies clearly undergoing dissolution existed in the areas of study at the time of this investigation, searching did not disclose them.

To examine the possibility that colonies deviating seriously from the cycle may have existed in the areas of study at the time of survey, despite the fact that none were found, our results may be reviewed from the standpoint of when (i.e., in relation to the activity cycle) colonies were most frequently found.

Frequency of Discovery in Relation to Condition of Colony

In both *E. hamatum* and *E. burchelli*, there are differences in the development of daily raiding depending on whether a colony possesses a developing larval brood or one that is enclosed and in the pupal stage of development. In both the rainy and dry seasons, the difference is typified by the fact that in nomadic colonies of *E. hamatum* with larval broods there are formed each day three distinct, tree-like systems of trails, whereas in the statary phase (with an enclosed brood) only one trail system develops or on some days none (Schneirla, 1938, 1949).

On the possibility that the influence of a greater colony arousal upon raiding would operate to make the raid more prominent and more readily discovered, it seems worth while to learn how many colonies were encountered at each of the different stages of the activity cycle. Although finding colonies is in part necessarily a matter of chance, it is also clear that the likelihood of finding a colony depends to a considerable degree upon characteristics such as the number of raiding systems and the total arc of the raiding sector, the distance to which the raid has been pushed from the bivouac, the number of branches per raiding system, and comparable features that would appear dependent to a great extent upon the internal condition of a colony.

In table 1 the numbers of colonies of the two test species discovered during the 1946 and 1948 dry seasons have been totaled

TABLE 1

Day of Discovery in Relation to Activity Cycle

	1946	1948	Total	Colonies per Phase Day
	E. hamatum			
Nomadic phase				
Days 1– 4	8	7	15	3.7
Days 5–13	4	12	16	1.8
Days 14–17	10	10	20	5
			51	
Statary phase				
Days 1– 4	3	5	8	2
Days 5–15	2	4	6	0.5
Days 16–20	2	4	6	1.2
			20	
	E. burchelli			
Nomadic phase				
Days 1– 4	5	4	9	2.2
Days 5–10	3	4	7	1.2
Days 11–13	3	7	10	3.3
			26	
Statary phase				
Days 1– 5	2	8	10	2
Days 6–16	1	1	2	0.2
Days 17–21	3	4	7	1.4
			19	

separately according to the stage of the activity cycle at which each was found. Because many of these colonies were under observation for only a few days, their classification depends upon a judgment of status derived principally from the current condition of the brood or broods. Experience has shown that such judgments may have a practical maximum of about 10 per cent error, or about 1.5 days in the intermediate range of an activity phase but less near the beginning or end.[1] For each species, to simplify matters, each activity phase has been divided into three sections, consisting of short beginning and ending sequences of a few days, and an intermediate sequence about twice as long as either of the former.

In view of the fact that the statary phase is longer than the nomadic in both species, and considerably longer in *E. burchelli*, a more adequate index of discoveries than "daily total of colonies discovered" is "colonies discovered per phase day." In these terms, we see from the table that in *burchelli* twice as many colonies were discovered in the nomadic phase as in the statary phase, and in *hamatum* even a larger proportion was discovered when in the nomadic phase. Without doubt an important factor accounting for the greater proportion of nomadic discoveries in *hamatum* was the fact that the three raiding systems that typify the nomadic raid of that species almost always cover a sector of considerably greater arc, greater extent from the bivouac, and more branches, than do those of *burchelli*. In *burchelli*, on the other hand, characteristics such as the effective raiding sector and the number of branches do not differ quite so strikingly in the two phases as they do in *hamatum*. In *burchelli*, variations in the total population of the raid are reflected less in characteristics such as effective raiding sector than in features such as width of the swarm and length of the consolidation fan. The number and relative activity status of ants within these zones undoubtedly influence the concentration and sound production of ant birds, whose calls are an important cue to the presence of *burchelli* raids. Also, in *burchelli* the nomadic phase is shorter than in *hamatum*.

In the nomadic phase, more colonies of each species were discovered per phase day, within the short periods at the beginning and end of the phase, than in the long intermediate part of the phase. Clearly, the cues for discovery must be low in effectiveness after the first few days of the statary phase, but evidently rise within the final few days. This would be expected from the fact that raids are more frequent and are better developed during the first and last days of the statary phase than in the intermediate days of the phase, when the colonies seem more lethargic as a rule (Schneirla, 1949). In addition to their greater frequency, the raids of both species generally are larger during the first and last statary days, and tend to reach out much farther from the bivouac than in the intermediate days of the phase.

It is manifest that although cues dependent upon the relative expansion and vigor of a raid must influence the likelihood of discovery, such results may be taken only as rough indications of the activity condition or level of excitability of a colony. That frequency of discovery is only a crude and approximate indication of the "vigor" of a raid, and the number of ants participating, may be suggested by the fact that the extended single-system raids characteristic of the last days in the statary phase, despite their relatively thin traffic, especially in long basal stretches, were found approximately as often in both species as were the raids of the intermediate nomadic phase. It is probable that the latter, with their larger sectors, more numerous branches, and typically greater traffic, usually represent larger raiding populations than at any time in the statary phase.

These considerations suggested that a colony which has no brood and is in process of dissolution (as was colony '46 H-O, discovered in a condition of disintegration, with its queen dead) is less likely to be discovered than is a normally functional colony in the statary phase, and still less than a colony in the nomadic phase. Not only are the weak columns of such moribund colonies unlikely to be seen, but it is also probable that the

[1] Brood samples were taken from each colony studied which are available for a more exact check on preliminary estimates, to be carried out in connection with a study on the growth curve of eciton broods.

dissipation of the given colony sets in rapidly once effective unity is lost when queen and broods are gone. Hence under such conditions the time available for discovery is limited. It is possible that among the scattered instances of indistinctive columns which could not be tracked to bivouacs in our study, some may have actually pertained to colonies undergoing extinction. These considerations suggest that entire army-ant colonies may be wiped out under dry-season conditions, without such events coming to the notice of investigators. In other words, the colonies represented in our list of cases, virtually all of which were in conformity with the nomad-statary cycle and evidently adapting well to dry-season conditions, may not represent the entire range of possible colony situations in that season of the year.

Duration and Related Characteristics of the Major Activity Phases

When available results are considered, the existence of distinctive nomadic and statary activity and brood-production phases can be taken as well established for the two species of *Eciton* (*Eciton*) under study, for both the rainy and dry months of the year. Each of these phases has recognizable characteristics which differentiate it clearly from the other phase, so that even in the dry season, when more variation may exist in beginning and ending activity phases than is typical in the rainy months (Schneirla, 1949), the changes may be sufficiently clear as a rule to warrant a comparison of phase durations.

In this study, an effort was made to obtain a sufficient number of consecutive records for colonies of both species to permit a comparison of the length of nomadic and statary phases, and to compare the records for 1948 with those obtained in the dry season of 1946. The data for the duration of the two phases in 1946 and 1948 are presented in figures 6 and 7. The few instances in which judgments of phase duration may be considered somewhat equivocal will be considered later in this discussion.

In figures 6 and 7, appropriate symbols distinguish cases with sexual broods in the larval or the pupal condition from cases with worker broods, among colonies from which phase-duration data were obtained. We are interested here in examining the possibility that the principal activity phases may differ in duration according to the type of brood present in the colony.

In all, three nomadic phases were recorded in *E. hamatum* and one in *burchelli* when sexual broods in the larval condition were present. In *E. hamatum*, as may be seen in figure 6, these three phases were the shortest in a total of seven cases reported for the species in 1948, and in *E. burchelli* the single record of this kind was the shortest of five cases. All of the colonies settled consistently into the statary condition when the larval sexual brood was mature and spinning was under way, as is the case when worker broods are present. Hence the termination point of the nomadic phase seems to be synchronized directly with the time of larval maturation. It would seem that the shortness of the nomadic phase in both species when larval broods of sexual individuals are present is specifically dependent upon a shorter time for larval maturation in such broods than in worker broods.

It should be mentioned in this connection that when a sexual brood is present close to larval maturity, the colony may stop its nomadic movements altogether or may enter a condition of somewhat variable behavior in which nomadism is irregular, before spinning may have begun to any extent among the male larvae. Occurrences at the bivouac, involving an extensive clustering of workers around a relatively small number of larvae of queen form engaged in spinning, may interrupt nomadism two or three days before a distinctly recognizable statary condition is entered with large-scale spinning by mature male larvae. Indications of such effects may be found in the protocols of colonies '48 H-12, H-19, H-27, and B-XVII.

In *E. hamatum*, three of four nomadic phases when worker larvae were present lasted 17 days, and only one was longer (19 days). As we shall see, the value of 17 days for this species agrees closely with results obtained in previous years.

The statary phases of *hamatum* in the 1948 dry season, for which 12 records were obtained, vary between 17 and 22 days, with

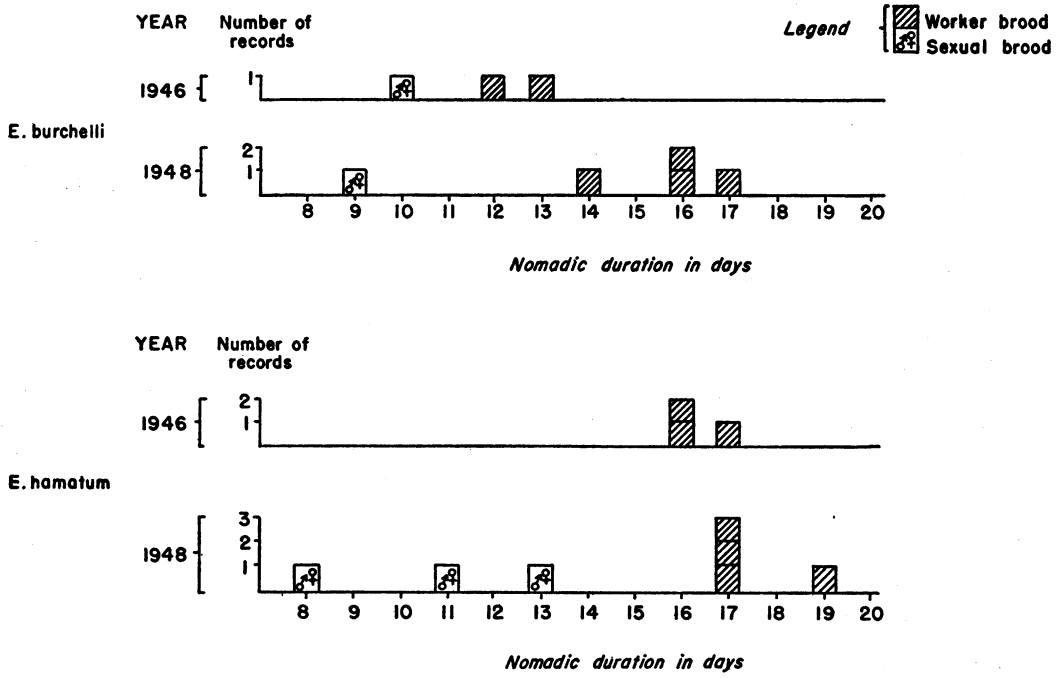


FIG. 6. Duration in days of nomadic phases in colonies of *E. hamatum* and *E. burchelli* studied in the dry seasons of 1946 and 1948.

the mode at 20 days (fig. 7). The most frequent value of 20 days agrees with that obtained in 1946. Thus in *E. hamatum*, with the exception of phases when sexual broods were present, the nomadic and the statary phases appear to have had about the same respective central tendencies in the two years.

Although the nomadic phases evidently were closely similar in this species in the two years, the statary phases show greater variation in 1948 than in 1946 (Schneirla, 1949). As may be seen in figure 7, in 1946 seven cases ranged between 19 and 21 days in duration, whereas in 1948 12 cases ranged between 17 and 22 days. In both years, however, the most frequent nomadic duration is 17 days, the most frequent statary duration 20 days in this species.

In *E. burchelli*, all the nomadic phases recorded with worker broods were longer than the longest nomadic phase of this species recorded in 1946. The four values recorded in 1948 ranged between 14 and 17 days, whereas two phases recorded in 1946 were only 12 and 13 days in duration. The previous records for this species were in 1938, a phase of 11 days, and in 1933, a phase of 13 days, both rainy-season records (Schneirla, 1945). The longest recorded nomadic phases in *E. burchelli* thus were obtained in the dry season of 1948.

On the other hand, with the exception of one record, in 1948 the statary phase in *E. burchelli* appears to have been shorter than in 1946. One exceptionally long record was obtained from colony '48 B-XVII when it had a sexual brood in cocoons, i.e., in post-larval maturation, after a very short nomadic phase of nine days with this sexual brood in larval development. In 1948, six of eight records for this phase were shorter than 21 days (i.e., there were three records of 19 and three records of 20 days), in contrast to 1946, with no statary phases observed in this species shorter than 21 days. In 1946, three of four colonies recorded in this phase had durations of 21 days.

It is interesting to note that for *E. burchelli* in 1948 the nomadic phase usually was somewhat longer than 15 days and thus definitely longer than in 1946, whereas the character-

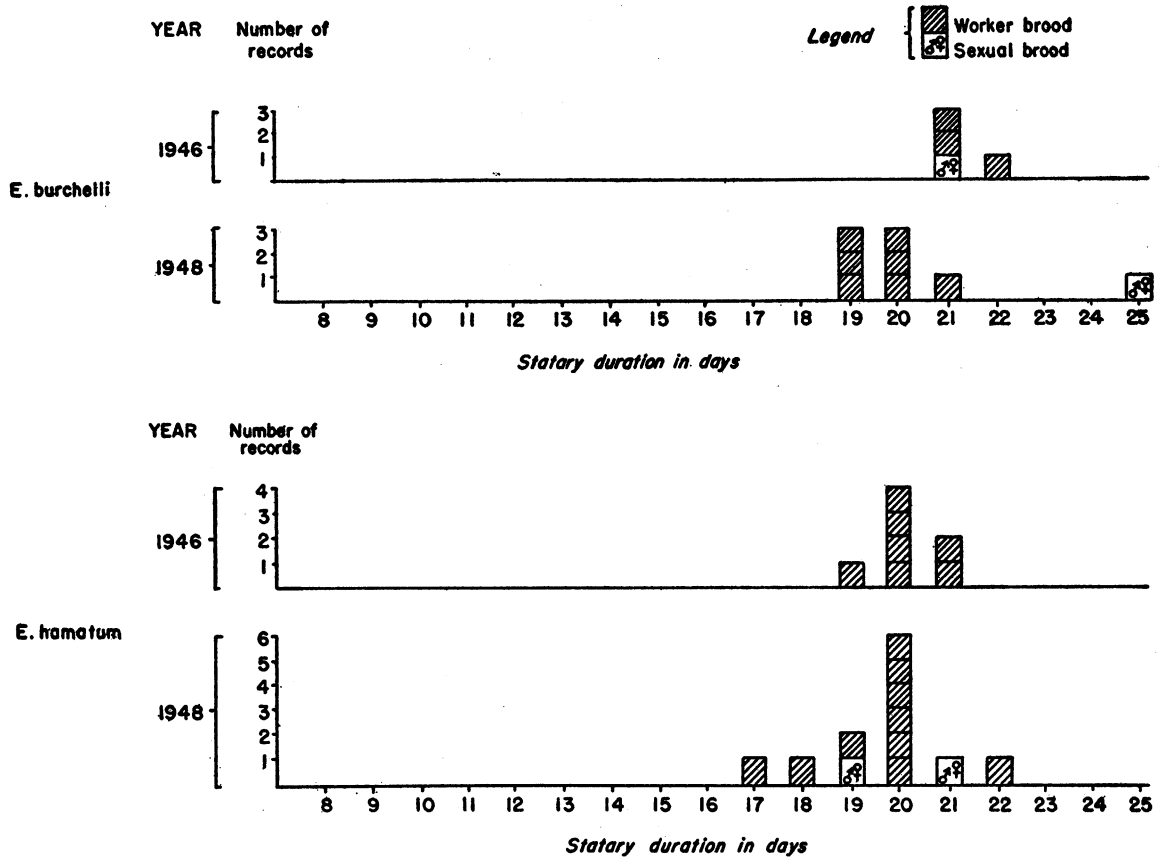


FIG. 7. Duration in days of the statary phases in colonies of *E. hamatum* and *E. burchelli* studied in the dry seasons of 1946 and 1948.

istic duration of the statary phase was 19 or 20 days, slightly shorter than in 1946. Perhaps the longer nomadic and the shorter statary phase values in this species in 1948 as compared with 1946 represented true seasonal differences in which the durations of the two activity phases were related and to some extent reciprocal.

A less pronounced feature of these records is the greater variability of the phase durations in 1948, in both phases for both species, and especially in the statary phase for *E. hamatum*. In this species, there were more cases in 1948 than in 1946 in which a colony tended to move before its pupal brood had entirely emerged. This is a rather unusual occurrence in *E. hamatum*, although it is virtually the rule in *E. burchelli*.

Concerning the relative values of the two phases, it will be seen that in the results both for 1946 and for 1948, the nomadic phase is shorter than the statary phase in both species. In the results for 1948, however, this difference is less marked than in those for 1946, especially in *E. burchelli*, which had a characteristic lengthening of its nomadic phase in 1948.

These records exhibit what appears to be a typical difference between the nomadic and statary phases, with the latter phase the longer in both species. The 1948 records also show what appear to be the characteristic species differences in the phases, with the nomadic phase longer and the statary phase slightly shorter in *E. hamatum* then in *E. burchelli*. However, in 1948 certain new differences appeared, which may have been seasonal, to be considered in a latter connection.

TABLE 2

DATA CONCERNING FUNCTIONAL AND VIRGIN QUEENS OF *E. hamatum* AND *E. burchelli* CAPTURED IN PANAMA IN THE DRY SEASON OF 1947–1948, AND FIXED (BO., MODIFIED BOUIN'S SOLUTION; FORM., FORMALIN) FOR MICROSCOPIC STUDY

Species and Colony Number	Date and Locality	Condition of Colony	Condition of Brood or Broods	Condition of Queen at Time	Disposition
E. hamatum					
'48 PH-1	12/11/47 Area 2	Early nomadic phase; open bivouac, 3-system raid	(1) Early worker larvae; (2) callow workers	Contracted (functional).	Bo.
PH-2	12–11–47 Area 2	Early nomadic phase; open bivouac, 3-system raid	(1) Early worker larvae; (2) callow workers	Contracted (functional)	Bo.
PH-3	12/15/47 Area 2	First statary day; in hollow log; 1-system raid	Mature worker larvae, all spinning cocoons	Slightly physogastric (functional)	Form.
H-19	1/31/48 Area 1	Just ending nomadic phase; hollow log; 2-system raid	Mature male (and queen?) larvae, spinning cocoons	Somewhat physogastric; "sealed off" twice by workers (functional)	Bo.
H-12	1/27/48 Area 1	Nearing end statary phase; 2 small systems; log in thicket	Few maturing virgin queen callows; *ca.* 2000 male callows	Virgin, taken from auxiliary cluster close to bivouac	Bo.
H-12	1/28/48	Same	Same	Virgin, taken from one corner of main bivouac	Alcohol
H-12	1/30/48	Second nomadic day, colony all away	Same	Virgin, "sealed off" at statary site (two)	1 Alcohol; 1 Bo.
DH-1	2/14/48 Area 3, El Real	Early nomadic phase; 3-system raid, semi-open bivouac	Sexual larvae at early stage	Contracted (functional)	Bo.
DH-2	2/16/48 Area 3, Pirre R.	Early nomadic phase; 3-system raid; open bivouac	(1) Early worker larvae; (2) callow workers	Contracted (functional)	Alcohol
DH-3	2/21/48 Area 3, El Real	*Ca.* last day of nomadic phase; 2-system raid; under log in thicket	Brood of sexual larvae (14 queen type, 1317 male type); spinning	Contracted (functional)	Bo.
DH-4	2/27/48 Area 3, Yavisa	Past mid nomadic phase; 3-system raid; open bivouac	Brood of sexual larvae, entering last stage of development	Contracted (functional)	Bo.
H-30	3/ 4/48 Area 1	Last nomadic day; three-system raid; P.M.: to hollow tree	Mature worker larvae; some signs of spinning	Slightly distended, taken from bivouac-change column (functional)	Bo.
H-32	3/ 7/48 Area 1	Last nomadic day; 2-system raid; P.M.: to mammal burrow	Mature worker larvae; spinning seen 3/8/48	Slightly distended, taken from bivouac-change column (functional)	Bo.
H-27	3/11/48 Area 1	Second nomadic day; colony all moved away	Callow males; early worker larvae	Virgin: "sealed off" at statary site (abandoned)	Both Bo.
VH-1	3/ 6/48 Area 4	Late nomadic; very small colony	Mature worker larvae; spinning	Contracted (functional)	Form.
VH-2	3/ 8/48 Area 4	Early nomadic	Callow workers; early worker larvae	Contracted (functional)	Bo.
H-27b	3/19/48 Area 1	Early nomadic; 2-system raid (daughter colony, 2)	Nearly half of H-27 brood: callow males, worker larvae	Contracted (newly fertilized callow)	Bo.
H-27a	3/19/48 Area 1	Early nomadic; 3-system raid (daughter colony, 1)	*Ca.* 60% of H-27 brood: callow males, early worker larvae	Contracted ("old" functional colony queen)	Bo.
E. burchelli					
'48 PB-I	12/18/47 Area 2	Second nomadic day, maximal raid	Immense brood callow workers; early worker larvae	Contracted (functional)	Bo.
DB-II	2/18/48 Area 3, Pirre R.	Early nomadic; medium raid	Callow males; early worker larvae. Less than usual number	Contracted (suspected to be young queen)	Bo.
DB-I	2/23/48 Area 3, El Real	Mid nomadic; hollow stump bivouac	Alate males; medium worker larvae	Contracted (functional)	Bo.
DB-IV	2/27/48 Area 3, Yavisa	End nomadic; pouch 40 cm. up	Mature worker larvae; spinning begun	Contracted (functional)	Bo.
B-XX	3/12/48 Area 1	Early statary; in hollow stump	Early pupal workers; some eggs	Maximally physogastric	Form.
VB-1	3/ 7/48 Area 4	Early statary, small raid	Mature larval workers, mainly enclosed	Somewhat distended	Bo.
B-XIV	3/17/48 Area 1	Mid statary, *ca.* 11 days; hollow tree	Mid pupal workers; eggs	Physogastric	Bo.
B-VIII	4/26/48	Colony taken on last nomadic day, moved alive to New York laboratory	Mature larval worker brood; spinning	Contracted when found dead on 5/28/48, in laboratory nest near workers	Kept as dry specimen
B-XVII	4/27/48 Area 1	Next to last nomadic day	Mature larval brood, sexual forms; males still naked	2 mature queen larvae, both enclosed	1 into Bo. as mature larva; 1 nine days later as pupa

EVIDENCE CONCERNING FUNCTIONAL COLONY QUEENS

Condition of Queen in Relation to Activity Phase of Colony

Altogether, the queens of 67 eciton colonies were observed, 52 on Barro Colorado Island and 15 in the three other areas of investigation. Of these queens, 41 were *E. hamatum* and 26 *E. burchelli*. With the exception of colonies with sexual broods, none of these colonies possessed more than one functional queen (dichthadiigyne). In all instances the condition of the functional queen corresponded to the activity phase of the colony, as the protocols show. That is to say, in every case in which a queen was removed for examination from a colony in the nomadic condition, she proved to be contracted (i.e., non-gravid), and all of the five queens observed in the physogastric condition were in colonies that were nearing the mid point in the statary phase. We may add that two queens of other species, one of *Eciton* (*Eciton*) *vagans* and one of *Eciton* (*Neivamyrmex*) *pilosum*, each removed from an entourage of excited workers in the night-time emigration of her colony, were both in the contracted condition. Thus, in a total of nearly 200 eciton colony queens observed in various investigations during both rainy and dry seasons, gravid queens have been found only during the statary phase of their colonies, and there have been no exceptions to the described general correspondence between condition of queen and colony condition in the activity cycle (Schneirla, 1944a, 1948).

In figure 5 are represented graphically the relationships of colony behavior, brood condition, and condition of queen in the colonies from which queens were captured in areas 2, 3, and 4. Of the 15 queens of *burchelli* and *hamatum* taken in these areas, seven were captured in the first half of the nomadic phase, four in the second half of this phase, three in the first third of the statary phase, and one in the last third. Further data are summarized in the protocols and in table 2. The results for queen's condition are consistent with those for colony behavior and brood condition in all cases. All these queens were contracted, and the only indications of a partial distention occurred in queens taken from colonies (e.g., DH-3, DB-IV) close to the end of the nomadic phase or entering the statary phase. In these special surveys outside area 1, no colonies were found in a condition representing the mid third of the statary phase; accordingly, no physogastric queens were captured in areas 2 and 3. In area 3, however, two weak raiding systems were traced to the inaccessible bivouacs of colonies that were statary at the time.[1]

Because most of the nine queens captured and preserved in area 1 (table 2) were taken systematically to represent critical stages of the cycle in preserved material, their colonies at the time of capture were mainly in the late nomadic and the mid statary conditions. As can be seen from table 2, in each of these cases the condition of behavior and of the brood (or broods) was found to correspond with the queen's condition as in previous descriptions of the cycle (Schneirla, 1944a, 1947). This was also the case with the other 43 colonies of the two species studied in area 1, in which the queen was observed at one or more times during the period of observation but was not captured.

Available knowledge about the physogastric (egg-production) episode of the eciton queen, which evidently is completed during a few days before the mid point in the statary phase, is scanty and largely limited to the capture of a few physogastric queens and to inferences from brood timing (Schneirla, 1944a, 1949). On empirical grounds, the suggestion may be advanced that this episode begins not suddenly but gradually, and even before the nomadic phase has ended.

The above suggestion is supported by data concerning the dimensions of the abdomen in functional queens, considered in relation to the stage of the nomad-statary cycle in which the examination was made. Gaster length (from the median anterior border to the tip of the hypopygium) is used as our expression

[1] One was a colony of *E. hamatum*, the base column of which passed beneath the root mass of a large tree; the other was a colony of *E. burchelli* whose principal column entered a slit in a hollow tree at a point just 30 cm. above the entrance of a nest of stingless bees.

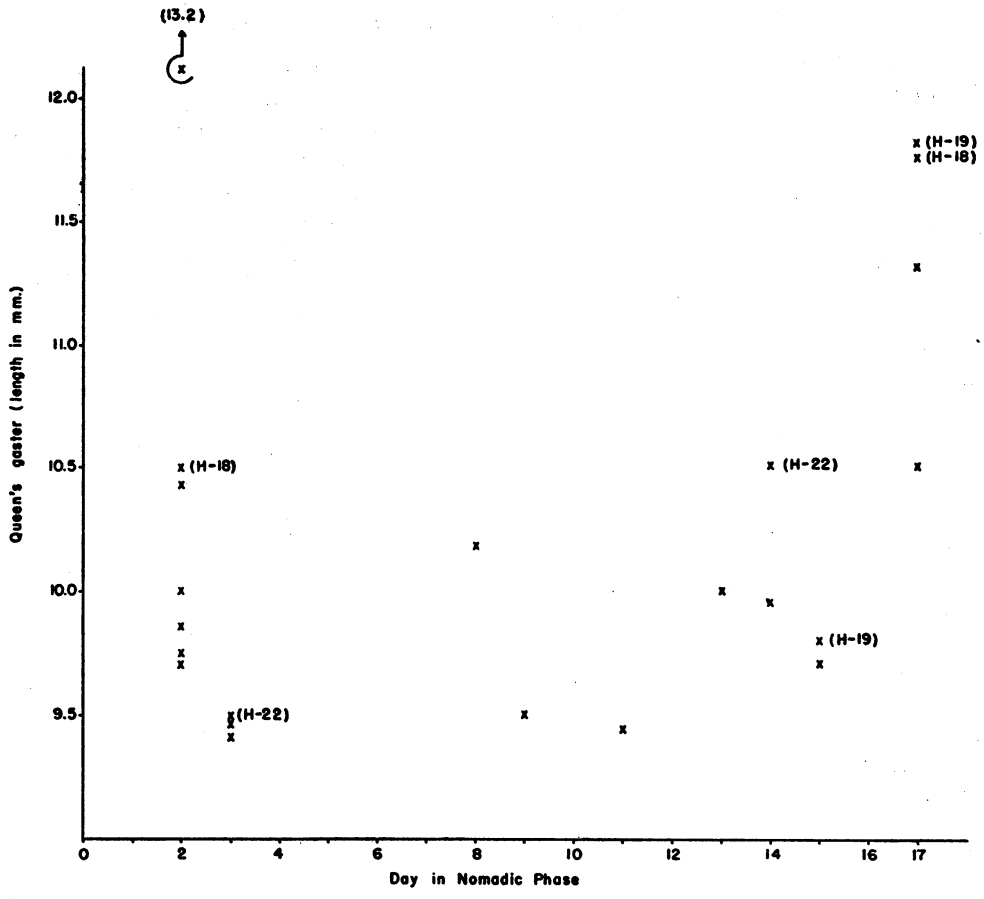
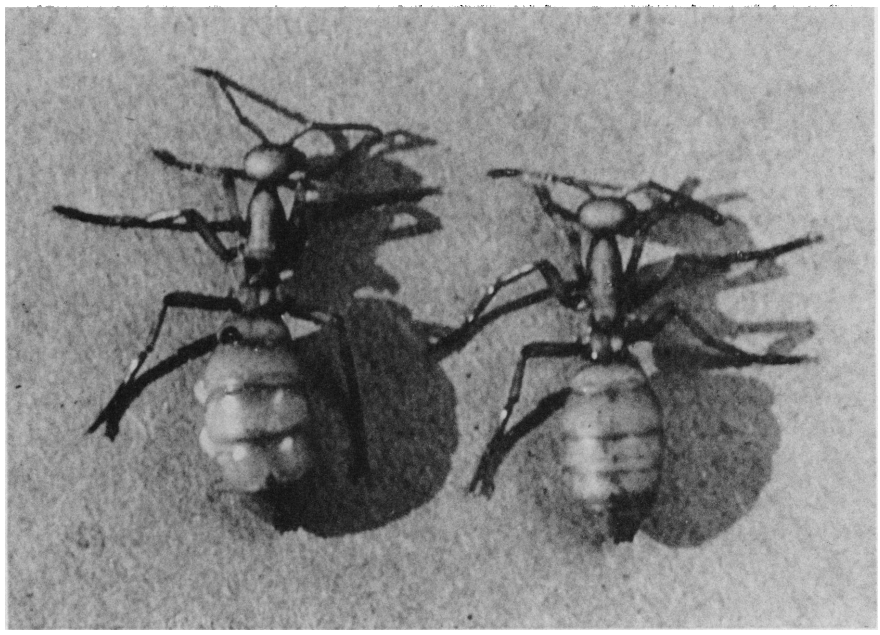


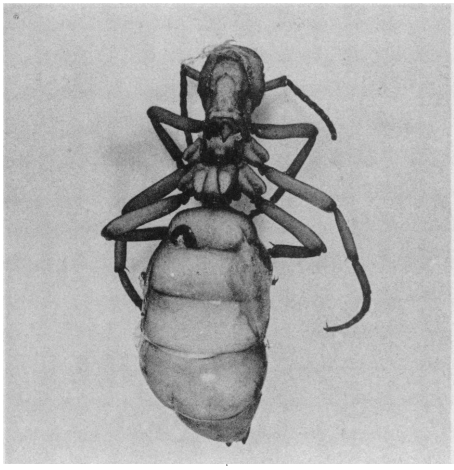
FIG. 8. Length of gaster in the queens of various colonies of *E. hamatum* at different stages in the nomadic phase. Symbols in parentheses represent cases in which measurements were taken at well-separated stages of the phase.

of abdomen bulk, since it was not feasible in all cases to weigh the queens or to take additional measurements.

From the results as represented in figure 8, we note that in six queens of *E. hamatum* measured during the intermediate 10 days of the nomadic phase (i.e., at some time between the third and the twelfth days) only one exceeded 9.5 mm. in abdomen length at the time of measurement, whereas in nine queens measured during the final five days of the phase (i.e., at some time between the thirteenth and the seventeenth days) six fell between 10.0 and 11.8 mm. and the other three measured 9.7 to 10.0 mm. A limited increase in the bulk of the abdomen during the last few days of the nomadic phase is indicated. In three cases, the same queen was measured at two different times in the nomadic phase. These were: queens H-22, which on the third day of the nomadic phase measured 9.5 mm. and on the fourteenth day of the same phase measured 10.5 mm.; H-19, which on the fifteenth nomadic day (December 28) measured 9.8 mm. and on the last day (January 31) of the following nomadic phase measured 11.8 mm.; and H-18, which on the second nomadic day measured 10.5 mm. and on the last day of the same phase measured 11.3 mm. These differences suggest that during the last few days of a nomadic phase the queen's abdomen increases in bulk, a change that may represent the first stages of a further physogastric episode. Comparable



1 2



3 4

1, 2. Photograph from life of two functional queens of *Eciton hamatum* shortly after they had been removed from their colonies. 1. Queen H-19 (over-all length, 21.5 mm.), in the early stages of physogastry, bearing experimental mark clearly visible as a black chevron on left side of first segment of gaster. 2. Queen H-28 (over-all length, 19.6 mm.)

3, 4. Queen H-19 after preservation in Bouin's solution. 3. Dorsal aspect, showing the mark. 4. Ventral aspect. The stretched intersegmental membranes, protruding between adjacent plates of the gaster, indicate the onset of a gravid episode in this queen

differences are found in the queens of E. *burchelli*.[1]

In figure 8 a difference also appears between the queens of *E. hamatum* measured during the intermediate part of the nomadic phase and queens taken at the very beginning of the phase. Of seven *hamatum* queens taken from the first nomadic bivouac (i.e., on the second day of the phase) all were larger abdominally (with a range of gaster lengths from 9.7 to 13.2 mm.) than were three queens taken on the third nomadic day, and all were larger in this respect than five of six queens taken between days 3 to 12. A similar difference was found in queens of *E. burchelli*. In the largest two *burchelli* and the two largest *hamatum* queens taken on the second day of a nomadic phase, white intersegmental membranes could be seen protruding slightly from between the segmental plates of the gaster; however, in neither species was this seen in queens taken thereafter up to the fourth day before the end of the phase. The significance of this fact is discussed below (pp. 344 ff.).

The 15 queens of *E. burchelli* and *E. hamatum* (table 2) taken in the Pequeni River, Darien, and El Valle surveys corresponded in condition to the above descriptions. Nearly all of them were taken at some point in the nomadic phase and all of these were found contracted or nearly fully contracted. Colony PH-3 in the Pequeni area was evidently in its first or second statary day when found, judging from the spinning status of the mature larval brood (a generally reliable sign), and a slight protrusion of intersegmental membranes was observable in its queen. (In a colony of *E. hamatum* examined in its second or third statary day on March 10 during the 1945 study in Mexico, in the Lacandone forest area of eastern Chiapas, marked indications of early distention in the queen were similarly observed.) From the brood signs, colony DH-3 in Darien was terminating a nomadic phase when found, in the last or nearly the last day of the phase, and its queen also was slightly distended when taken from the bivouac. A similar condition was noted in queen VB-I, taken in El Valle in a colony of *E. burchelli* which from reliable signs had just entered a statary phase.

Few records of queen observations are taken during the statary phase, both because of the typical seclusion or virtual impregnability of the bivouacs and because of the extensive disturbance of the colony necessary to reach the queen under such conditions. The first physogastric queen discovered in any species of *Eciton* (*Eciton*) was queen '38 H-H, *E. hamatum*, removed from the statary bivouac of her colony on the ninth day of the phase, nearly fully physogastric at the time with 17,000+ eggs already laid, by actual count (Schneirla, 1944a). Three records are available of *E. hamatum* queens measured at some time during the statary phase in the 1948 study. Queens H-12 and H-14 were fully distended or approximately so (gaster length *ca.* 20 mm.) when taken from their bivouacs between the sixth and fourteenth days of the phase, whereas queen H-1 was nearly minimal (gaster length 9.5 mm.) when removed and measured on the nineteenth day of a statary phase. The physogastric episode appears to be relatively short, and its peak evidently is passed during a sequence of a few days in the early intermediate part of the statary phase.

Queen '48 H-12 was observed on the third day of each of three successive nomadic phases (on November 23, December 30, and January 31), and on each of these occasions she appeared to be fully contracted. Each time, however, a large new brood had been delivered during the intervening statary phase, with the queen passing through physogastry. On December 21 this queen was temporarily removed from the statary bivouac when physogastric and engaged in egg laying,[2] but when next observed on the third

[1] The queens of both species often exhibit protruding intersegmental membranes (see pl. 16) during the last few days of a nomadic phase, but never during the intermediate part of the phase, even when the gaster is somewhat larger than the species minimum. It is possible that these last cases represent somewhat elderly queens, in which the gaster no longer contracts to the species minimum after each physogastric episode.

[2] This batch of eggs developed into a sexual brood, the only such brood thus far sampled at the egg stage. A few hundred of the eggs, laid by queen H-12 during her detention in the laboratory, were Bouin-fixed and are being studied cytologically by Dr. Roy Whelden.

day of the next nomadic phase she was minimal in gaster size and moved with normal agility during bivouac-change movements.

Similar results were obtained with *E. burchelli*. The queen of colony B-XIV was almost fully contracted (gaster length 10.7 mm.) on January 12, when her colony was passing its fourth or fifth day of a nomadic phase, whereas on March 7, when taken on or about the ninth day of a statary phase, she was physogastric (gaster length 21.8 mm.) and had already laid many thousands of eggs. The queen of colony B-XVI was slightly physogastric (gaster length 14.1 mm.) when taken from her colony on the last day of a nomadic phase; the queen of B-XX was nearly maximally physogastric (gaster length 21.9 mm.) when removed from the hollow-tree bivouac of her colony at a point roughly one-fourth through a statary phase. The queen of colony B-XII was slightly physogastric (gaster length 13.3 mm.) on the evening of the first day of a nomadic phase, as was the queen of B-XI on the second day of the same phase; however, both of these queens were fully contracted when examined during nightly emigrations a few days after the first observations. If *burchelli* queens vary more in the timing and duration of their physogastry then do *hamatum* queens, as the results suggest, further evidence is required to establish the point.

We have found that indications of physogastry frequently appear during the last few days of the nomadic phase, preceding full gravidity and a large-scale production of eggs in the early intermediate days of the statary phase. These reproductive episodes occur roughly at 35-day intervals in the queens of both *E. hamatum* and *burchelli* (Schneirla, 1944a, 1949), with all signs pointing to the prevalence of a condition of complete non-reproductivity in the interim.

The physiology of physogastry is as yet uninvestigated in the doryline queen. Preliminary considerations favor the hypothesis that a recrudescence of the fat bodies beginning late in the nomadic phase may be a prerequisite condition to the processes of large-scale egg maturation which ensue during the first third of the statary phase. The study of preserved material may cast some light on this problem.[1]

Results from the Permanent Marking of Eciton Queens

In virtually all cases the queen was removed from the colony bivouac without the use of ether, to avoid a disruption of normal colony activities (cf. Schneirla, 1948, '46 H-A). To exclude any distortion of afternoon events underlying the eventual bivouac-change movement in nomadic colonies, the removal of queens was confined to the morning hours in most cases. It was by no means possible to remove the queen of a colony from the bivouac whenever desirable for purposes of marking or examination, owing especially to the inaccessibility of given bivouacs and to the hyperexcitability of the worker population at certain times. For such reasons, the queens of some of the colonies periodically observed over considerable intervals of time (e.g., colonies '48 B-I, B-VI, B-XVII, and H-5) were never seen, although the production of broods indicated that a queen was present in each instance.

As the only practicable method of identifying colonies after intervals of time in which their movements could not be followed, a technique for marking the queens was finally adopted, as described in the introductory section of this paper. With the exception of two cases (queens H-1 and B-V, each of which accidentally suffered a slight puncture of an intersegmental membrane during the operation), all operations were performed successfully. All 30 of the marked queens, including even these two, were in a lively and apparently normal condition when returned to their respective bivouacs, and all of them were received by the workers in the typical manner without any sign of attack or other special difficulty impeding the return.

There was never any difficulty in reidenti-

[1] Three queens representing different stages in the activity cycle (early and late parts of the nomadic phase, and the gravid condition of the mid statary phase, respectively) were preserved in 10 per cent formalin, for eventual study of the fatty tissues in this connection. Numerous other queens, Bouin-fixed at representative stages of the cycle, are to be studied by Dr. Roy Whelden with respect to the temporal course of large-scale egg maturation.

fying marked queens, even with the naked eye, once they were recovered from the bivouacs. Although the nicks made in the edges of the tergal plates of the abdomen were very small, in the course of a few weeks a darkening occurred along the cut edges which transformed each nick into a black chevron readily perceptible to the unaided eye (see pl. 16).

Since it is possible that eciton queens remain functional in their colonies for a number of years, in order that other investigators on Barro Colorado Island may be encouraged to check the identifications of eciton colonies when opportunity offers, we have noted in the respective colony protocols the manner in which each of 20 colony queens of *E. hamatum* and 10 queens of *burchelli* was marked in the present investigation.[1]

The first eciton queen (colony H-10) was marked and returned to her colony on November 21, 1947, about three weeks after the investigation began. Of the 30 queens of two species that were marked and returned to their colonies thereafter, eight were recovered and reidentified one or more times before the study ended in March. Notable recoveries in *E. hamatum* were H-12, a colony on record for 76 days; H-18, on record 75 days; and H-22. The last-named colony was found bivouacked close to the same palm tree near Harvard Trail, station 3, both at the beginning and near the end of the same nomadic phase, with an intervening tour of unknown course. Notable reidentifications in *E. burchelli* were colony B-XI, on record for 24 days; B-XIV, on record for 64 days; and B-VIII, on record for 105 days. Between January 12 when colony B-XIV was first discovered in bivouac near Gross Trail, station 3 (and the queen was extracted for marking), until March 1, when it was found in statary bivouac near Lake Trail, station 2, it moved by an unknown course over a distance in a straight line of about 1800 meters from periphery to center of the island (see fig. 4). After colony B-VIII had been "lost" in the vicinity of Balboa Trail, station 6, on January 12, it was not seen again until March 19, on the day before it entered a statary phase in the vicinity of Barbour Trail, station 8, 1100 meters away in a direct line. The itineraries of these and some other reidentified colonies are sketched in figure 4. The circumstances of all rediscoveries are noted in the respective colony protocols.

In view of conditions militating against the recovery of colonies in an investigation such as this, it is not surprising that only 27 per cent of the marked colonies were reidentified. The island is large in effective area, with a highly varied topography and with numerous long peninsulas, so that searching for eciton colonies involves a large element of chance, at best. Only two of the investigators were available for patrolling, and their efforts to find "new" colonies were necessarily intermittent and not too systematic at times, because of other work and because of extended absences from the island after February 20. The colony itineraries sketched in figure 4, together with the results of a previous investigation in which given colonies were tracked for considerable times (Schneirla, 1949), show how relatively mobile these colonies can be in their successive nomadic phases. On the other hand, a consideration of the limited and infrequent nature of raiding during much of the time in the statary phase (i.e., only about half of the time in each colony) suggests another basis for non-discovery (Schneirla, 1949; table 1, this paper).[2] Reidentification records undoubtedly also were reduced by the fact that time did not permit searching down the bivouacs of all colonies whose raiding systems were encountered.

[1] In the code employed, the numbers 1 to 4 refer to the segments of the gaster from front to rear: the letters R, C, or L mean that the nick was made on the right, center, or left side of the given segment, as seen from the rear.

[2] For example, colony H-12, which was found largely by chance when in its second statary bivouac after the original discovery, was located only about 200 meters from the Shannon Trail during this statary phase of nearly three weeks. Yet even if the Shannon Trail had been patrolled several times each day, this colony would have escaped detection at the given site because of the fact that not one of its raids observed during this phase crossed that trail. For various reasons, it frequently happens that the bivouac of a statary colony is passed by even at close distance without being discovered.

The results in hand from rediscovered and reidentified colonies are regarded as a sufficient justification of the rather elaborate procedures required for the marking and recovery of queens in this investigation. It is to be hoped that further efforts to recover these marked queens may be made, so that something may be learned about the longevity of eciton queens and the vicissitudes of their colonies.[1]

Further Evidence on Worker Responses to Functional Queens

The responses of eciton workers to the functional queen of their colony under ordinary conditions are unequivocally favorable to her reacceptance in the colony. When the colony queen is removed from the bivouac, she is almost invariably found in the center of a cluster of tightly clinging workers; in an artificial nest the workers follow her closely and hang to her body and cluster over places where she has rested even briefly. The reaction of workers when a queen is returned to her colony after an absence (Schneirla, 1938; 1944a; 1949, '46 H-D) invariably involves an excited clustering around and upon her so that she is soon covered with a tight and rapidly growing mass of workers of all polymorphic types, including particularly the workers major in proportions greatly exceeding their percentage representation in the colony. The queen makes her way only very slowly into the bivouac when set down near it, because as a rule a variable process arises in which she is usually required literally to burrow her way from beneath a succession of such clusters, which form readily over her whenever she is halted even momentarily as by an irregularity in the path. Such an occurrence is also observed when the queen happens to stop during the nightly emigration. All evidence suggests that the *Eciton* colony queen exudes a powerfully attractive chemical to which the workers of her colony invariably respond positively, as by turning towards, following, or clustering.

In hundreds of cases in which the queen of an *E. hamatum* or *E. burchelli* colony was returned to the colony bivouac after a short period of captivity, including tests both under rainy- and dry-season conditions, only one exception was found to the rule of unanimous reacceptance by the worker population. That exception (in colony '48 H-19, to be discussed presently) occurred during the present investigation.

One normal response of colonies to the absence of the functional queen is of great interest. There are no grounds for accepting Wheeler's (1925) surmise that the removal of the queen immediately causes an "air of apathy or dejection" to settle upon the workers. The sudden change from excitement to quiescent clustering which impressed Wheeler actually occurs whether or not the queen is removed, and follows (with a predictable latency) any stirring up of the colony. However, a reaction always observed in colonies of these species after the queen was removed was a back-tracking of the workers over previously used trails which ordinarily would be abandoned completely, but which in the absence of the queen are likely to be followed by files even for days.

In normal colonies the rule is that during the nomadic phase the bivouac site of the preceding day is vacated completely, and the trails radiating from it are empty of eciton traffic. But after the queen has been removed, not only is the back trail followed to the abandoned bivouac site of the preceding day, but the ants also spread into the abandoned trails radiating from that center, and often also reach and follow the trails of previous days. Thus, when a queen has been kept away from her colony overnight, one has only to follow the correct file (in *E. hamatum*, the correct one of three) of those leading out from the abandoned bivouac site to arrive at the new headquarters. One may ascertain the line by which a newly discovered nomadic colony has approached the bivouac site at which it is found simply

[1] Colony '48 H-23 was rediscovered on August 5, 1949, by Robert and Frances Brown during a short period of work on Barro Colorado Island. More than 18 months from the time the queen was marked on January 15, 1948, she appeared to be in excellent condition, with her mark clearly perceptible and her colony equipped with a large brood of worker larvae and functioning normally. Since this queen must have begun her functional life not later than the 1947 dry season, she would appear to have been functioning in her colony for a minimum of close to three years when last observed.

by removing the queen and observing the lines (other than new raiding trails) which are followed by the ants from the bivouac site of the day.

The described back-trailing in the absence of the queen has been observed in five species of *Eciton* (*Eciton*). This occurrence cannot depend upon whether or not the queen has passed over the bivouac-change route from the abandoned site, for it develops on the following day whether the queen was removed from the old bivouac or from the bivouac-change column at any point up to the very threshold of the new bivouac cluster. It also occurs following the removal of a queen from the new bivouac cluster at the end of a bivouac-change movement.

The explanation is not clear from the available facts. It is conceivable, however, that the back-trailing occurs in the absence of a pervasive chemical effect normally exerted by the queen when present within the bivouac, an effect perhaps necessary for the full stabilization of the cluster. Normally the queen is to be found near the upper center of the cluster once it has been well established, and it may be presumed that the gathering of some thousands of workers minor and others in her vicinity, together with the young broods, furnishes a stimulative basis for bivouac stability. Hypothetically, we may say that in the absence of the pervasive queen chemical, the center becomes unstable, and ants from it are caused to wander peripherally. Why such secondarily disturbed workers are not all taken up in the raid of the day is a complicated matter.

The back-trailing reaction of a queenless colony has one possible adaptive function beyond the fact that if the queen (moving as she often does in an entourage very near the end of the bivouac-change movement) is ever cut off, as by heavy rain, so that the movement is completed without her, the colony can reabsorb her through back-tracking. A second and clearly important adaptive function of such behavior is that, if a queen becomes permanently lost from her colony (through accident, death, or predation), the ants of the colony, by ramifying both forward (in further nomadic movements) and backward (along previous chemical trails), increase the chances that they will cross paths with another colony of their species with which they can fuse. From several cases (e.g., '46 B-IV; '48 H-19 in the present study) we know that queenless colonies are open to the possibility of fusion, whereas it is a clear fact that colonies with queens do not fuse with others.

The case of colony '48 H-19 presents some new and perplexing questions. This colony operated regularly as a unit up to the time its queen was removed from what very probably would have been the statary site for the pupal maturation of a sexual brood. Within 30 hours after the queen's removal the colony began to move away, not in an ordinary bivouac-change process, but in a long movement which resulted in complete fusion with another colony of its species. Plainly the absence of the queen somehow unstabilized this colony so that it could not remain within the log in which it had settled. Colony H-19 constitutes our first case in which a colony did not receive its queen (but actually "sealed her off") when she was returned after an absence. Presumably, the "mixed" reaction of this colony to its returned queen was due somehow to the fact that a brood of mature larvae of the sexual forms was present and had been developing in the colony during the preceding weeks. A consideration of the differences in colony responses to worker and sexual broods may throw light upon the problems of normal and abnormal reactions to colony queens.

RESULTS CONCERNING BROOD PRODUCTION

Production of Worker Broods

All the colonies of *Eciton* investigated during 1947–1948 possessed developing broods. In 32 colonies of *E. hamatum* studied then on Barro Colorado Island, 43 broods were recorded (40 of these worker broods), and in 20 colonies of *E. burchelli*, 23 broods were found (22 of these worker broods). In 10 colonies of *E. hamatum* found in areas 2, 3, and 4, 10 broods were found (seven of these worker broods), and in six colonies of *E.*

burchelli found in these areas, nine broods were found (six of these worker broods). Thus in 68 colonies of the two species investigated, 94 broods were found in all, of which 10 were broods of sexual forms and 84 all-worker broods.

Thus, the eciton colonies under investigation from the latter part of the 1947 rainy season through most of the 1948 dry season all were found to be regular and prolific in their production of broods. No identifiable differences in brood productivity were found between the last five weeks of the rainy season and the first three months of the regular dry season. Without exception, the worker broods found in colonies of the two species were closely comparable in population magnitude to the worker broods of these species in the rainy months (Schneirla, 1944). That is to say, a worker brood of *E. hamatum* was estimated to number roughly 20,000 individuals at a minimum, and a brood of *E. burchelli* roughly 25,000 individuals. The broods appeared to be close to the typical species magnitude even in cases (e.g., '48 H-4 and VH-1) in which the adult populations appeared to be exceptionally small for functional colonies. The fact that worker broods of *E. burchelli* usually have a population magnitude about 15 per cent or more above those of *E. hamatum* also is typical under rainy-season conditions.[1]

The graphic summary of colony records in figures 2 and 3 indicates that all colonies were regularly functional in brood production while under study, much as in various rainy seasons (Schneirla, 1938, 1944a) and in the dry seasons of 1945 and 1946 (Schneirla, 1947, 1949). As noted above, the broods approximated the characteristic species magnitude; also, the population frequency of the respective polymorphic types was much the same as in the rainy months. In the absence of exact population surveys, these statements should be held as tentative.

Our results summarized in tables 2 and 3 and in figures 2, 3, and 8 indicate that the queens of all colonies discovered in this study were involved in egg production at a time about one-third through each statary phase of the colony. This follows not only from direct evidence concerning the queen, discussed previously in this paper, but also from evidence represented in figures 2 and 3 concerning the synchronization of broods. In all essential respects, this evidence conforms to the previously described pattern (Schneirla, 1938, 1944a) of eciton brood production. Specifically, when only one brood is present this brood has a developmental status somewhere between the early larval condition and the early pre-pupal condition, whereas if two broods are present, these are in distinctively different developmental conditions rather exactly synchronized. Our results concerning the durations of nomadic and statary phases in the two species, considered above, indicate that (except when sexual broods were involved) colonies of *E. hamatum* delivered new worker broods roughly at 37-day intervals, and *E. burchelli* roughly at 34-day intervals. Thus in colonies that were rediscovered and identified after given intervals of time (e.g., H-12, H-18, B-XII, B-XIV), brood conditions at rediscovery conformed to this expectation. Perhaps the most striking case was that of colony B-VIII (see fig. 3).

Production of Sexual Broods

Sexual broods are those containing reproductive individuals, males and fertile females. No such broods, but only all-worker broods, were found in previous studies in the rainy season (Schneirla, 1938). The sexual broods apparently are unique to the dry season in the eciton species investigated (Schneirla, 1948, 1949).

In the present investigation, although worker broods were produced with regularity in both species during both rainy and dry months, sexual broods were discovered only after the dry season was well under way. Only worker broods were found at first on Barro Colorado Island and in the Pequeni River area during early December. However, on the island on December 21, after roughly 10 days of consistently dry weather, in a statary colony of *E. hamatum* ('48 H-12) the queen was found engaged in laying eggs which eventually developed into reproductive individuals. Three more colonies with sexual broods were found later on the island, and

[1] These estimates of brood population are based upon actual census counts of eciton broods taken under rainy-season conditions (Schneirla, 1938, 1944a).

six in Darien during the last two weeks of February. The last sexual brood observed was matured on the island during early March, and none were found on the island (or in the El Valle area) thereafter. In 1948, in the areas studied, the production of sexual broods apparently began only after the dry season was well under way and ended before its termination.

It is interesting to note that sexual broods were discovered in only four cases in a total of 52 colonies of the two species studied on Barro Colorado Island. On the other hand, in eight colonies of the two species from which detailed records were obtained in Darien during the latter part of February, six colonies were found with sexual broods. In view of the extent to which patrolling was carried out on the island, and the limited time during which a one-man search was conducted in Darien, this difference would not seem attributable to chance. It would appear that only a part (and probably less than half) of the colonies of these species on Barro Colorado Island can have produced sexual broods during the 1948 season.

Our investigation brought to light an important new fact concerning the composition of the eciton sexual brood. These broods contain no individuals of the worker castes but only males and functional females (dichthadiigynes) in great disproportion, with relatively few of the latter. In *E. burchelli* the number of males appears to range between 2500 and 3000, whereas in *E. hamatum* the number is probably not much greater than 1500 to 2000 as a rule. Our evidence suggests that the number of developing queens is reduced (through cannibalism and possibly other causes) during larval and pupal development. Records of various types (including one thorough census in colony '48 HD-3) indicate that at larval maturity the number of developing queens probably does not exceed two dozen in either species, and that at pupal maturity and emergence as callows the number of queens is only about six.

It was established in this study that the developing queens are about two or three days more advanced in development than most of the males. In colony B-XVII, *E. burchelli*, and in colonies H-12, H-27, and DH-3, *E. hamatum*, the mature queen larvae were observed spinning cocoons or already enclosed about two days before spinning activity became general in male larvae. In colony DH-3, more than one dozen mature larvae of the queen form were found already encased in envelopes, among more than 1300 mature male larvae, all of which were still devoid of silken enclosures. Because of the relatively small number of females in proportion to males in the sexual broods, the developing queens were not discovered in 1946. Their discovery became possible in the present investigation once the hypothesis of distinctive queen-and-worker broods appeared to have been excluded, when the probability became reasonable that young queens regularly appear as precocious forms in the (otherwise) male broods.

Our preserved material includes both serial samples and large single samples of the sexual broods of both species. The serial samples, taken on Barro Colorado Island, range from the early larval condition, and from the egg in one case, to the mature pupal condition. Queen forms have been obtained mainly as mature larvae and as callows; however, in one case (colony DH-1) queen types have been identified in an early larval brood, and in another (colony B-XVII) a queen pupa was obtained by raising a mature larva to the pupal stage in the laboratory. This material is Bouin-fixed and available for histological study.

In this connection we present only a résumé of the principal facts concerning the production of sexual broods. Further evidence will be reported in a forthcoming paper dealing specifically with the problem of sexual broods and their significance for colony function.

RESULTS CONCERNING GENERAL COLONY BEHAVIOR

Behavior Associated with Sexual Broods

In detailed observations of colonies H-12, H-19, and H-27, and briefer examinations of other colonies including six colonies of the two species studied for short times in Darien, the relation of sexual-brood production to colony behavior was investigated. There are

significant differences between the reactions of the worker population to the reproductive type of brood and to worker broods, centering particularly around the superior attractiveness of the sexual type of brood for the workers. Simple tests show that this greater attractiveness has a chemotactic basis.

There are numerous indications that sexual broods exert a different chemotactic effect upon the adult worker population of a colony than do worker broods. The sexual brood has a location in the bivouac which is distinctly separate from that of the regular or functional colony queen. The close and heavy clustering of workers about the young queens, even when these are still in the larval stage, indicates that they begin to be established as centers of aggregation (i. e., as sub-nuclei) in the bivouac considerably earlier than the time of their emergence as callows. Thus, the bivouac appears to become effectively polarized. This process, never observed with worker broods, may have its beginning at some time during early larval development of the sexual brood.

We had suspected from observations of colony H-12 that a colony with sexual brood may be considered unstable with respect to its functional queen. Also, from occasional observations of empty cocoons in taking brood samples during the pupal stage, it was considered likely that a brood cannibalism centered about the borderline between the pole of the bivouac occupied by the functional queen (and her new brood of eggs or early worker larvae) and the area of the sexual brood. However, the extent of such instability in the colony was not appreciated until the queen of colony '48 H-19 was taken from her colony at the time when the sexual brood had reached larval maturity. When this queen was removed, there were signs that spinning by mature female larvae had begun and that the colony would settle into a statary bivouac without further major emigrations. As may be seen from the protocol for colony H-19 and from the discussion of results concerning queens, the H-19 queen was not reaccepted when she was returned to the colony about 28 hours after her removal but was twice "sealed off" by workers. In more than 200 cases, no queen taken from a colony with only worker broods has been thus rejected upon her return to the bivouac.

The evidence from colonies H-12 and H-27 in particular indicates that the process of colony division is a specific outcome of the appearance of sexual broods. Because of experimental intervention, colonies H-12 and H-19 did not divide, although a recognizable beginning of the process occurred in the former case. It is probable that interference with the situation in taking brood samples also blocked colony division in the case of '48 B-XVII. In colony H-27, in which events proceeded without interference (as by the taking of brood samples), a clear-cut fission occurred through which two daughter colonies arose, with the old functional colony queen in one of them and in the other new colony one of the callow queens of the current brood.

Our evidence indicates that at larval maturity a chemical polarization of the bivouac exists, based upon the presence of the sexual brood, whereby the functional queen is seated in the bivouac well apart from the larvae of the sexual forms, and a considerable part of the worker population appears to be rather unstable in its reactivity to her. The "sealing-off" response of workers to the queen, under conditions such as were introduced in colony '48 H-19, involves reactions somewhat like those ordinarily given only to strange queens from other colonies of the species, involving nipping and pulling at legs and antennae and holding in place. This reaction, described in the protocols of colonies H-12, H-19, and H-27, characteristically appears in the discarding of supernumerary young queens at the time (a few days after the first queens appear) when the emergence from cocoons of the few thousand mature males in the sexual brood furnishes the adequate stimulus for a great rise in extra-bivouac activity and a colony division.

Characteristic reactions of the worker population to the predominantly male portion of the sexual brood have been described: for the period of larval development (when the impressive "eciton roadway" appears during bivouac-change movement), for the spinning of cocoons by mature larvae, and for the postemergence time when the alate males remain in the bivouac in the daytime

and run the bivouac-change route at night (Schneirla, 1948). The reactivity of workers to alate males, although it indicates a lower degree of attractiveness than do responses to the functional colony queen or to callow queens, is nevertheless pronounced. In the bivouac, the workers form a tight little cluster about each male, and during the bivouac-change movement each male typically is followed closely by a fairly large entourage of workers running beside him or closely after him, many of them touching him with mouth parts or grasping him with mandibles.

Colony Mobility and Regularity of Nomadic Movement

In a total of 136 nomadic days involving 10 colonies of *E. hamatum* observed in 1948, there were only five failures to move. It is significant that four of these non-movement days in the nomadic phase occurred in just two colonies, H-27a and H-27b, within days 2 to 4 of the phase (table 3). In a total of 83 nomadic days involving eight colonies of *E. burchelli* observed in 1948, there were 10 failures to move on given days, and four of these cases of non-movement occurred on days 2 and 3 of the nomadic phase. The apparent significance of these facts is discussed below (pp. 341 ff.).

It is evident that even in the dry season failures to move during a regular nomadic phase are relatively rare in *E. hamatum* as compared with *E. burchelli*. The species difference is emphasized when it is recognized that all but one of the failures to move in *E. hamatum* occurred in the two daughter colonies of H-27, under conditions which (as we shall demonstrate) were exceptional. Our results also indicate that failures to move are less frequent in *E. burchelli* during rainy months than in the dry season. (See table 3.) From the results, it is clear that in the 1948 dry season the colonies of both investigated species of eciton, when nomadic

TABLE 3

Failure to Emigrate in Nomadic Colonies of *E. hamatum* and *burchelli* During Rainy and Dry Seasons

Season and Year	Species	Number of Colonies Represented	Aggregate of Nomadic Days	Number of Failures to Move	Nomadic Day of Failure (*E. hamatum*, 1–17; *E. burchelli*, 1–*ca.* 14)
Rainy '33, '38, '48	*E. burchelli*	3	43	5[a]	3, 4, 6, 9, 10
Rainy '32, '36, '48	*E. hamatum*	4	71	1	
Dry '46, '48	*E. burchelli*	7	96	16	2 (2 cases), 3 (4 cases), 4, 5, 6 (2 cases), 7, 8, 9, 10, 12, 13
Dry '46, '48	*E. hamatum*	8	134	2	4, 14
	E. hamatum (H-27a)	1	9	3	2, 3, 4
	E. hamatum (H-27b)	1	9	1	3

[a] Four of these failures occurred in a single colony, '33 B-I, subjected to an experimental reduction of the larval brood (see text, p. 241).

by virtue of brood condition, emerged rather consistently in nightly bivouac-change movements.

A conception of the area of movement and the approximate itinerary of representative colonies of both *E. hamatum* and *E. burchelli* can be gained from figure 4. The bivouac-change movements of *burchelli* tended to be about 90 to 130 meters in length, and those of *E. hamatum* from 120 to 220 meters, with much variation (greater in *burchelli*) and a few longer and shorter movements beyond the given ranges in both cases.

Representative colony itineraries are sketched in figure 4, in which can be seen some typical courses of nomadic colonies in both species. For example, colony H-1 in a single nomadic phase made a circuit of the large Donato Hill in an elliptical course roughly 700 meters in its long diameter. An even more impressive journey was made by colony H-11, which in 17 nomadic moves covered both lateral faces of the long Fairchild Peninsula, first moving from the base along the western slopes in a meandering course, then turning back from near the tip to range the eastern slope. In a comparable manner, colony H-17 shifted around the hillside overlooking the cove below the end of Van Tyne Trail, meandering from the hills through the tangle of vegetation along the shore.

A glimpse of colony mobility during successive nomadic phases, comparable to the case of colony '46 H-B (Schneirla, 1949), was obtained in the case of colony '48 H-12. Colony H-12 was first followed for a few days at the beginning of a nomadic phase, and the record ended when the colony was operating in the vicinity of Wheeler 18, on November 23, 1947. On December 12 it was next found in a statary bivouac to the east of Shannon 3. In the ensuing nomadic phase the colony moved across Ocelot Hill to the general area of Barbour Hill, where a further statary phase occurred. When nomadic movement was resumed, after a few shifts the colony was last seen on February 3 in the vicinity of the Van Tyne tree. In two successive nomadic phases this colony moved to a locality roughly 1800 meters in a straight line from the initial site, but actually much farther in its meandering course over rough terrain. A comparable record was obtained from colony H-18, which was under observation in successive movements on Fairchild Hill until January 17, and was next observed on February 3 in the vicinity of Wheeler 5, at a distance of about 1200 meters in a straight line from the area of previous observation. An irregularity of general path typical of the species, resembling that already described for colony '46 H-B, can be seen in the course of colony H-19, from the time the colony was discovered on December 28 until its fusion with colony H-28 was completed on February 4.

Representative itineraries of *E. burchelli* are also sketched in figure 4. Colony B-VIII was followed through a circuit that took it from the vicinity of Shannon 3, first into the general area of the laboratory and across Wheeler 3, thence in a series of longer moves to the vicinity of Balboa 6, where it was last seen on January 12. When next encountered on March 20, this colony was terminating a nomadic phase, the last stop of which was in the area of Barbour 9, at a distance of roughly 1200 meters in a straight line from the scene of the preceding observation 68 days before. As another example, colony B-XII was found in statary bivouac at the cascades in Fossil Creek and moved off to the eastward on the night of January 19, beginning a nomadic phase. It was next seen on January 28 about 550 meters directly to the west from the cascades site, in the vicinity of American Museum Trail, station 3. After that time, in completing the given nomadic phase and in the early movements of a further nomadic phase, this colony moved an additional distance of more than 1200 meters. It was last seen on March 2, in the vicinity of Armour 7, at a point about 1300 meters from the area of the initial observation on January 3.

A rather interesting case is represented by colony B-XIV. On January 12 this colony was discovered in the area of Gross Trail, station 2, in the early nomadic condition. After the queen had been marked and the brood sampled, the record of this colony was discontinued on the following day. The colony was not see again until February 25, when it was rediscovered in statary condition near Lake Trail, station 2, at a point roughly

1800 meters from the Gross 2 site. The exact route by which this colony traveled to the latter location is a matter of conjecture.

The distances given above are rough approximations, which without much doubt fall considerably below the distances actually covered by the various colonies. No colony of either species ever moves far in a direct line, as may be seen from the general courses taken by colonies which were continuously on record for some time (e.g., colonies H-1, H-19, and B-VIII in the 1948 series; and colony H-B in the 1946 series, Schneirla, 1949). A precise statement of distances traveled is out of the question here, in view of the typical irregularity of the courses, the many vertical displacements occasioned by rugged terrain, and the frequent use of elevated pathways. It is probable that to represent the actual distances more closely an increment of at least 40 per cent should be added to the estimates.

Thus we find that in the dry season the colonies of both *E. hamatum* and *E. burchelli* are highly mobile and that each colony successfully shifts its base of operations over considerable distances during successive nomadic phases. Beyond the cases represented in figure 4 and discussed above, many others can be found in the protocols to illustrate this point. From our present results it seems probable that in general the colonies are able to move about with a freedom approaching that of the rainy season. This finding is of interest both from the standpoint of an adequate colony food supply, as facilitated by a nomadic existence, and also with respect to an effective cross-breeding of colonies based upon the appearance of sexual broods in the dry season.

Trail Making and Trail Following

Our observations indicate that in the dry season eciton chemical trails are reëmployed with greater readiness and frequency, and after considerably longer intervals of time, than in the rainy season. Several instances were noted in the present investigation after the dry season began, in which a colony would follow a section of trail formed on a previous day by a colony of its own species, or even of another species (i.e., a following of *burchelli* trail sections by *hamatum*, and vice versa). A notable example is furnished by the ants of colony H-27, which after an interval of 31 days chanced upon and followed the identical path taken by the same colony in its nomadic movements of February 10 and 11.

Although cases have been observed in which the abandoned trail of another colony is followed for a considerable distance, the secondary use of trails made by other colonies ordinarily seems mainly limited to relatively short sections. Trails in use tend to be avoided through repulsion by ants of the strange colony encountered en route; abandoned trails recently made may be avoided through reversal of traffic when no booty is encountered (Schneirla, 1938). Even so, the second-hand use of trails made by other colonies of the species seems to be a frequent occurrence. The extent to which trails may be used secondarily under appropriate conditions is shown by the behavior of colony H-19 in following a section of H-28 trail more than 450 meters long which had been developed by the latter colony during the preceding week.

In our notes there are some cases in which a colony used sections of chemical trail originated by colonies of another species. Thus a trail segment approaching 40 meters in length made by colony H-15, *E. hamatum*, was employed by colony B-VIII, *E. burchelli*, after an interval of more than three weeks. The chemical traces of the other species can be followed, despite indications of disturbance in the initial encounters of pioneering workers with the track. A chemotactic effect may be the principal deterring factor in this case, rather than booty depletion, since these two species overlap only partially in their types of prey.

The probability that the inter-colony and even the inter-species transfer of trails occurs more frequently and over longer intervals in the dry season than in the rainy season is supported by the fact that secondary use of trails was observed more frequently and prominently during the dry season studies of 1946 and 1948 than in previous investigations in the rainy season. Such a seasonal difference might be based upon a more rapid disappearance (e.g., through volatilization or

chemical "decay") of trails repeatedly subjected to washing or wetting in rainy months.

The network of chemical trails which seems to persist in the forest in the dry season is a matter of great potential significance for the dissemination of males through their post-flight interval of terrestrial wandering (Schneirla, 1948). Males run freely on the trails of their own species, and this is presumably the principal means whereby some of them are able to get into the bivouacs of strange colonies. It is even possible that at times they may thereby reach colonies of species other than their own, an event of doubtful significance. On one occasion in this study, a dead dealated male of *E. vagans* was found close to the lower border of a bivouac of *E. hamatum* (colony H-19 on January 13 in statary phase). Although minus his wings, this male was an intact specimen. It is possible that he had wandered to the statary site along one of the various chemical trails leading radially from this bivouac and had been killed by the H-19 workers.[1] This, however, is our only record of the kind.

Behavior Dependent upon Brood Condition

This investigation confirmed previous findings (Schneirla, 1938, 1944a, 1944b, 1948, 1949) concerning the dependence of critical changes in colony behavior upon the condition of the brood population of the eciton colony. In this connection some supplementary results bearing upon these relationships may be mentioned.

Evidence has been presented for the existence of a heightened "siesta effect" in the dry season, an effect that may represent an accentuated inhibition of extra-bivouac activity during midday hours through repressive environmental factors reaching their peak at that time (Schneirla, 1949). On Barro Colorado Island this effect was more impressive in 1948 than in 1946, when ground moisture was somewhat better retained. Raiding activities were noticeably curbed at midday in all instances; however, the reduction was sharpest for colonies in the statary condition and particularly during the intermediate part of the phase. At that time, it frequently happened that no traffic whatever would be seen on the principal trail of the day within a considerable distance (sometimes more than 50 meters) from the bivouac. Thus on three successive days a search for the bivouac of colony H-21 was unsuccessful, through the fact that trails near the bivouac were deserted during early afternoon hours. On the last day of the given statary phase, with a more vigorous raid in progress, the base-trail column was tracked readily to the secluded bivouac. The accentuation of the "siesta effect" in the intermediate section of the statary phase would appear attributable to a minimum of brood stimulation prevalent at the time.

A striking expression of the brood-colony excitatory relationship prevails in the latter half of the nomadic phase. Then the larval brood already is rather widely distributed through the bivouac in the daytime and is very noticeable in the evening movement. Although the steady exodus of workers from the bivouac may be well under way by late afternoon, the brood generally is not carried extensively into the movement until early evening. There are inevitable traffic interruptions, both in starting out from the old bivouac and at trail junction points along the route, which underlie the following significant occurrences. In the early stages of brood transportation one typically finds the eciton larvae dumped upon booty not only in booty caches which have persisted at former trail junctions but also on the ground close to both the bivouac site which is being abandoned and the new bivouac site, frequently itself a former cache or trail junction point. For example, at 7:50 P.M. on December 6, during the bivouac-change movement of colony H-11 on its fifteenth nomadic day, it was noted that "At each of three former trail junctions, at distances of 75, 90 and 125 meters from the old bivouac, there is a soup-plate sized heap composed of larvae mingled with booty, with hundreds of workers standing around, occasionally shifting the larvae and hauling them about. Both larvae and workers are engaged in feeding. Through

[1] Von Ihering (1912), who found the male of another *Labidus* species in an *Eciton* (*Labidus*) *coecum* nest, considered it likely that eciton males "not infrequently fly" to nests of other species. However, a direct flight by males to other bivouacs even of their own species would seem highly exceptional.

these clusters the thick procession of the bivouac-change column moves, and is joined by workers carrying larvae from the gatherings. . . . At about 9:00 P.M. when the queen has moved through this area with her entourage of workers, these gatherings are dissipating rapidly as workers carry away both larvae and booty. . . . At this time, close beside the new bivouac, there is a large and growing cluster of workers, larvae, and booty." Observations show that such gatherings form through the piling of larvae upon cache heaps of booty which have accumulated mainly in the afternoon (Schneirla, 1933, 1938).

Thus brood feeding goes on very extensively during the interval of the bivouac-change movement. Then the characteristic eciton method of feeding larval brood, by dumping the larvae upon booty or the reverse, is to be seen at intervals along the way in former booty caches of the raiding period. Similar aggregations, in which callow workers are gathered and feeding occurs, are characteristic of the bivouac-change movements of the first two or three days of a nomadic phase.

Such occurrences express the high degree to which workers are stimulated by the larval brood during the advancing nomadic phase. An intimate excitatory relationship between larvae and workers through chemotactic stimulation is indicated, providing the basis for an extensive feeding of the larval brood and for augmented extra-bivouac activities on the part of workers. It is important to note that the rather prolonged exposure of the brood to general atmospheric conditions occurs at a time of day when outer conditions are seemingly very equable, since the larvae then are exposed in dim light or darkness and the air is moderately cool and more humid than before dusk. It is even possible that this period of exposure may play an essential part in the development of the larvae. Its significance for brood nutrition and for colony trophallaxis is evident.

SUMMARY AND DISCUSSION

THE PRESENT INVESTIGATION has brought to light facts that reëmphasize the remarkable success of the ecitons in meeting the conditions of the tropical dry season, with further evidence on the adaptive processes involved. In the four areas of study in Panama, 41 colonies of *E. hamatum* and 26 colonies of *E. burchelli* were investigated, and all were found in essential conformity with the nomad-statary cycle as previously described (Schneirla, 1938, 1944a), both in colony behavior and in brood condition. This is clear from figures 2, 3, and 5. All phases of the cycle were represented in the various colonies, without any indication of a significant synchronization of their rhythms, a matter in agreement with previous results (Schneirla, 1949).

As far as eciton functions are concerned, no sharp seasonal differences have been found. Through the last weeks of the 1947 rainy season, through the transition period from rainy to dry weather, and through a considerable part of the 1948 dry season, the described cyclic pattern of events held in all the eciton colonies investigated. There remains no question that the nomad-statary pattern of events is maintained throughout the year as the basis on which colonies of *Eciton* (*Eciton*) in Central America adjust to their environment.

For colonies with worker broods, no important differences seem to exist in the duration of the nomadic and statary phases, respectively, in the rainy and dry seasons (Schneirla, 1949). The results concerning phase durations in the rainy season are insufficient to permit more than a tentative statement on that point. In the dry season of 1946 as compared with 1948 there were limited differences in the duration of nomadic phases in both of the eciton species studied. As can be seen from figures 6 and 7, the difference is more pronounced for *E. burchelli* than for *E. hamatum*. The durations of the statary phases appear to have been more alike in the dry seasons of the two years, except for a suggestion that this value was somewhat more variable in the 1948 season than in 1946.

In view of the demonstrated relationship between brood condition and colony behavior in these species (Schneirla, 1938, 1944a, 1944b, 1949) it is an impressive fact that the respective phases of the activity cycle in both species vary about a mode or characteristic duration value in the dry seasons of different years. It is notable that the length of the statary phase is much the same for both species (*ca.* 20 days), whereas that of the nomadic phase shows a greater difference between the species (*ca.* 17 days in *hamatum;* 13 to 15 for *burchelli*), as well as a limited seasonal difference.

Another fact that emphasizes the dependence of phase durations upon brood condition is that in both seasons when a sexual brood is present the nomadic phase is always shorter in both species than when worker broods are involved. The difference clearly depends upon the fact that the larval stage of sexual broods in eciton is completed in distinctly less time than is that of worker broods (Schneirla, 1949). On the other hand, the fact that no distinctive difference appears in the statary phase, whether sexual or worker broods are present, suggests that the duration of development within the cocoon (i.e., of pre-pupal and pupal stages) is more closely similar for the two types of broods.

In view of the dependence of colony behavior upon the timing of brood development, facts concerning the duration of the two activity phases have interesting implications for the adjustment of colonies to their environments. Because the development of insect larvae depends very intimately upon properties of the environment such as food supply, temperature, and humidity (Chapman, 1927; Uvarov, 1928, 1931; Wigglesworth, 1939), large seasonal and intra-seasonal differences might be anticipated in the eciton phase durations, unless the brood were effectively insulated against environmental vicissitudes. However, the relative constancy of the phase durations indicates that the processes of worker behavior involved with colony food supply and bivouac-formation (i.e., the brood "incubator") must be very adequate throughout the year.

On the whole, the forest floor of Barro Colorado was considerably drier in the 1948 dry season than in 1946, yet judging from the colony activity phases as indicators, the eciton brood production processes do not appear to have been greatly affected by such variations.

The fact that the statary phase is relatively constant in both species may be attributed to a highly regular pupal development under standard environmental conditions in the statary bivouacs. Matters were very different for the transferred brood of colony '48 B-VIII. On March 21, when the mature worker larvae of this colony were spinning cocoons, approximately half of the brood, many thousands of workers, and the queen were captured and placed in a cylindrical wire nest. On the same day in the evening, the uncaptured section of the colony moved with its mainly enclosed brood into a hollow tree, beginning a statary phase. The captive section was soon moved by plane to New York, where it was housed thereafter in the Museum laboratory. It is highly probable that the section of B-VIII remaining in the forest left its hollow tree when its pupal brood emerged after about 20 days, a result typical for the species and the season. However, the unconsumed portion of the enclosed brood in the captive section was not removed from cocoons as mature callow workers until April 30, when large numbers of callows were in evidence and when a circular column of workers developed in an area adjoining the nest.[1] There is little question that the exceptionally long pupal development of this brood was attributable to unavoidable disturbances and abnormally variable environmental conditions incident to the period of captivity.

We have found that eciton colonies in the nomadic condition are able to shift their nesting sites with considerable regularity throughout the year. The principal records on the consistency of nomadism are summarized in table 3 (p. 335). This table shows that colonies of *E. hamatum* seldom fail to move nightly when in the nomadic condition, even in the dry season. For example, in the 1946 dry season, in a total of 53 nomadic days in colony '46 H-B, there were only two failures to move (Schneirla, 1949). If the daughter colonies of '48 H-27 are excepted as special cases, a quite justifiable procedure (as will be seen presently), our record for *hamatum* colonies in both seasons is only three failures to move in a total of 205 nomadic days involving 12 colonies. Clearly the bivouac-change mechanism functions well under all seasonal conditions in this species.

In colonies of *E burchelli*, a seasonal difference may be effective in the consistency of bivouac changes. This process appears to be fairly regular in the rainy season, for in a total of 43 nomadic days involving three colonies, four of five failures to move occurred in a colony ('33 B-I) that had been deprived of a large part of its brood. With this colony excepted, our records show only one failure to move in a total of 31 nomadic days involving two *burchelli* colonies. In contrast, in a total of 96 nomadic days involving seven colonies of *E. burchelli* in the dry season, there were 16 failures to move, and only one of these colonies ('48 B-XVIII, with seven observed nomadic days) was free of such occurrences. Occasional lapses of bivouac-change movements would appear to be characteristic of *burchelli* in the dry season, but not in the rainy season. *E. hamatum*, in contrast, when nomadic appears to operate very consistently in both seasons.

From our theory of eciton cyclic behavior and underlying brood processes (Schneirla, 1938, 1944a), the failure of bivouac change would be expected to occur as a consequence of (1) exceptional extra-bivouac conditions distorting the normal pattern of raiding developments or the early stages of bivouac change (e.g., two instances in colony '46 H-B; Schneirla, 1949), (2) extrinsic factors such as inhibitive atmospheric conditions which might serve to reduce the development of raiding, or (3) conditions operating to lower the ordinary level of brood stimulation in the colony. The fact that failures to move appear occasionally in *burchelli* although not in *hamatum* during the dry season may be due to a greater susceptibility of *burchelli* to the first two factors. The difference would

[1] This activity expresses a high degree of excitation among workers. No circling had appeared in this partial colony during the entire previous time following its capture. This circular column persisted for about 24 hours.

appear to lie particularly in their pattern of raiding and especially in the fact that *burchelli* generally has but one principal trail from the bivouac in contrast to three main trails (less frequently, two) in *hamatum*. Analysis of events in the development of a bivouac-change movement from the raid of a given day (Schneirla, 1945) indicates that with the single-system basis in *burchelli* interferences such as the following are likely to block the emigration. We have observed that larval spinning activities generally disrupt the beginning of a bivouac-change movement on the principal trail so that the movement is either delayed, or, because return traffic thereby becomes dominant all of the way to the bivouac, is prevented altogether. Bivouac-change movements are delayed in *hamatum* colonies on a similar basis late in the nomadic phase, but a complete failure of colony movement is opposed by the availability of two or three main routes from the bivouac. A contributive factor in both species in the dry season is an inhibitory effect of midday atmospheric conditions (factor 2) which delays the beginning of the afternoon resurgence from the bivouac and thereby renders subsequent events somewhat more variable than in the rainy season.

As we have pointed out (Schneirla 1938, 1944a, 1949) brood-stimulation influences (factor 3) have a variable and progressive rather than a constant effect through the nomadic phase. We have postulated two brood-stimulation factors: (a) an excitatory effect from the emergence of the callow (i.e., mature pupal) brood which is responsible for arousing a departure from the statary site, but which drops to a minimum within a very few days, and (b) an excitatory effect from the young larval brood, minimal at first but increasing throughout the phase to reach a maximum when the larvae are nearly mature. Thus, after colony '33 B-I (*E. burchelli*) had been deprived of about one-third of its pupal brood and more than half of its young larval worker brood during the late days of a statary phase, raids of subnormal strength were frequent during the early days of the ensuing nomadic phase, and no changes of bivouac occurred on the third, fifth, sixth, and tenth days of the 13-day phase. The fact that in a total of 16 failures to move on the part of seven *burchelli* colonies studied in the dry season, six occurred on the second and third nomadic days (i.e., during the first one-sixth of the phase) indicates that the brood excitation factor must be weakest at that time. We have suggested (Schneirla, 1948, 1949) that, at the corresponding time when a sexual brood in the larval stage is present, the factor is similarly weak because such broods (much smaller in numbers than worker broods) may then be still insufficiently developed and not widely enough distributed in the bivouac to exercise a very appreciable excitatory effect upon the colony. On this basis we have interpreted the failure of colony '46 B-I to move on its second day of the nomadic phase (March 1, 1946), also its subnormal raids and short emigrations on the two following days, when a sexual brood was present in the early larval stages.[1]

Cases in which bivouac-change processes fail in nomadic *hamatum* colonies are significant for this discussion, because of their exceptional nature. In the 1948 dry season there were only four failures to move in 96 recorded nomadic days involving eight colonies of *hamatum*. All of these instances occurred in the two daughter colonies arising from the division of colony H-27 after its sexual brood had emerged and within the first four days after the daughter colonies had moved away from the statary site (cf. table 3, p. 335). As can be seen from the colony protocols, after a vigorous divergent movement on the first nomadic day, the new colony 27a exhibited subnormal raiding and did not undergo any bivouac-change movements on days 2, 3, and 4, but thereafter approximated the normal pattern of raiding and nightly emigration. The new colony 27b after the first day dropped noticeably in the vigor of its raiding, and failed to move on the evening of the third nomadic day, but thereafter recovered as had 27a. The initially deficient nomadic behavior of these new colonies is understandable as a result of a temporarily sub-threshold brood stimulation effect.

[1] A comparable behavior in colony '48 B-XVI may have been due likewise to the presence of a young sexual brood (concentrated locally) or to the complete absence of a young larval brood because of the possible death of the queen in the preceding statary phase.

Further analysis of this case will be enlightening. The callow male brood and the early larval worker brood of colony H-27 were divided between the daughter colonies when they moved divergently from the statary site. In this bilateral division of the two H-27 broods, daughter colony H-27a received a smaller part of each brood (an estimated 40 per cent or less of the whole) than 27b. When the stimulative effect of the callow male complement decreased sharply, as is typical after the first nomadic day, the excitatory influence of the halved larval brood was insufficient to bring extra-bivouac activities to the level essential for nightly emigration, and both daughter colonies faltered for a few days. The lapse was somewhat more pronounced in colony 27a, which had the smaller part of both broods. With further development of the young worker larvae and also when the alate males began their nightly escapes (Schneirla, 1948), the brood excitation factor regained the level essential for regular nomadic behavior, and both colonies thereafter approximated the nomadic pattern typical of the species.

Evidence from specific observations also supports our postulation of an excitatory effect from the young larval brood which is very weak initially in the nomadic phase but quickly becomes a factor of importance as the callow brood factor wanes. On the second nomadic day the young larval brood is always gathered into a single bolus in the very center of the bivouac, where it is surrounded by workers minor and is seemingly sequestered from the main population. This was the condition of the young brood of colony '48 H-2 on the day of capture (November 8, 1947), very probably nomadic day 2. When a sample of this brood numbering about 2000 larvae was placed in a laboratory nest with about 1000 workers of the colony, the workers were not very active even in moderately bright light, and accordingly no circular column formed until 48 hours had passed. In a comparable nest assemblage taken on November 7 from colony '48 H-1, then estimated to be in the third or fourth nomadic day, worker activity was considerably more vigorous from the start, and a circular column began within a few hours. Although the H-2 larvae were kept in a single cluster for more than one day after having been installed in the nest, from the start the H-1 larvae were divided into many small packets, and the larger individuals were held more or less separately by workers. The activity of larvae was clearly evident in the H-1 nest. In their case, it was noted that "The entire anterior end oscillates vigorously as the workers touch the larva, and often when they do not," whereas "Most of the H-2 larvae (and even the largest) seem to be incapable of movement." After about 30 hours, larval activity became more apparent in the H-2 nest, and soon a circular column of workers carrying larvae had formed. Our results, typified by these observations, suggest that within the first few days of the nomadic phase there is a notable increase in the excitatory effect of the young larval brood from an initial low value. The difference in this effect upon the general adult population is suggested by the position of the young brood in the bivouac, at first gathered into a single compact mass and centrally located but later distributed more widely throughout the interior of the cluster.

It is apparent from the above considerations that the division of a parent colony into three or more parts might risk a loss of daughter colonies if the broods were divided more or less evenly among the sections. Even a two-way division, as our findings suggest, entails the possibility that at least one of the parts may not be able to function nomadically in a fully adequate way through a series of days which might be critical for survival of the unit. This problem will be considered in a forthcoming paper.

The results of this investigation confirm previous conclusions that colonies of the two investigated species continue their regular production of broods without any break in the dry season. From the results concerning phase durations we see that the typical interbrood interval (except when sexual broods are involved) is 34 days in *E. burchelli* and 37 days in *hamatum*. This means that although worker mortality must be greater in the dry season than during the rains (Schneirla, 1949) regular reinforcements to the worker population are available throughout the season. Among 52 colonies of the two species studied in 1948 on Barro Colorado Island, only two

distinctly undersized colonies were found, both of *E. hamatum*. One ('48 H-4) was found in November before the rainy season had ended; the other (H-28), midway in the dry season. Both colonies, despite their small populations of adult workers, had broods of normal size and were operating in the manner characteristic of the species.

The infrequency with which very small colonies are encountered in the dry season would suggest that one or more factors must oppose depopulation. One, obviously, is the regular replenishment of population losses by new broods. Also there are behavioral factors such as the withdrawal responses of workers to overstimulation (as from bright light and desiccation) which operate to keep the colonies under forest cover and reduce extra-bivouac activities to a minimum during the midday hours. However, it is conceivable (Schneirla, 1947) that colonies of these typically sylvan species of *Eciton* (*Eciton*) are frequently trapped in exposed areas, as in cleared ground which breaks the forest, and become irreparably depleted before their own activities might lead them back to the forest. Examples of colonies so endangered might be VH-2 and VB-1, found in the El Valle area bivouacked in dry deforested ground outside the border of the forest proper, and both noticeably small for their species.

A factor tending to preserve queenless worker groups is a fusion of such populations with others when their trails happen to cross. Ordinarily, the worker populations of different colonies repel each other when they chance to meet; however, our evidence suggests that the workers of a queenless colony somehow change, either in their reactions to the chemotactic effects of foreign colonies or in their own chemotactic effect upon foreign populations, or in both.

Because of these and other possible agencies operating against any extreme depletion of an eciton colony population even in the dry season, it is possible that in fairly well-forested areas ecitons seldom perish as whole colony populations, but may be saved even when their queens happen to die. (Thus colony '48 H-19 was saved as a worker population, at the expense of its sexual brood, through a fusion with colony '48 H-28, itself a somewhat undersized colony.) Otherwise, it would seem that queenless and degenerating colonies would be found more frequently in the course of intensive surveys such as were conducted in this program during 1946 and 1948. Colony '46 H-O was the only clear natural case of the kind encountered in 1946, and no such cases were found in the 1948 investigation. Even so, the need for caution on this point should be emphasized, in view of the fact that queenless and essentially non-functional colonies, through a chronic inability to stage regular forays and bivouac-change movements, ordinarily would not be found as readily as would normally functioning colonies (cf. table 1). Our results from the study of colony '46 B-IV+VI would indicate that dissolution must set in rapidly once regular brood processes have ceased to influence colony behavior.

This investigation has furnished further evidence that eciton queens are not ordinarily affected by dry-season conditions to the extent that their prolific and regular reproductive capacity is noticeably impaired. In fact, with the exception of the sexual brood, no important difference appears in the function of the single colony queens from one season to the other during the year. Present evidence suggests that consideration should be given to the effect of extrinsic factors as the principal if not exclusive initiators of the periodically recurrent gravid condition in the army ant queen. In view of the fact that a partial physogastry is frequently apparent a few days before the end of a nomadic phase, it is conceivable that this condition first involves a recrudescence of the fatty tissues of the abdomen under the influence of overfeeding. Such an overfeeding might begin by virtue of a considerable increase in the colony food supply when forays reach a crescendo in the late nomadic phase. Previously, we may assume, reproductive processes have been held in abeyance (i.e., with resorption of all oöcytes) in an underfed queen. But once the threshold of the physiological changes (e.g., recrudescence of fatty tissues) leading to gravidity is reached, the essential organic processes are maintained and accelerated through overfeeding even after the colony has become statary with the enclosure of the mature larval brood. Although raiding then drops sharply from the nomadic level, con-

ditions prevail which permit overfeeding of the queen to continue. Every colony continues to carry out daily raids during the first three or four days of the statary phase, by virtue of the excitatory effect of continued spinning activities in the mature larval brood (Schneirla, 1938, 1949). However, this brood has been enclosed and has not consumed any food from the first statary day. Consequently, during the initial part of the statary phase one finds a surplus of booty in all colonies, with quantities of food heaped near the queen. It is evident that the queen then may be plied with food to an extent possible at no other time during the nomad-statary cycle. In both *E. hamatum* and *burchelli*, each relatively brief interval of physogastry and egg production sets in about one week after the beginning of the statary phase (Schneirla, 1938, 1944a).

It is of interest to note that in both of the investigated species, queens observed on the second nomadic day (i.e., the first day in an exposed bivouac) are often somewhat physogastric, although on the following day and thereafter the fully contracted condition is the rule (fig. 8). This condition might represent the last stages of a physogastry which has persisted through the statary phase after egg production ends, to disappear abruptly when the colony becomes nomadic. On the other hand, a temporary and partial physogastry may be involved, initiated by a time-limited overfeeding of the queen during the terminal days of the statary phase and cut short at the beginning of nomadism. Circumstances favor the second view. Although the food supply is minimal in the bivouac during the intermediate part of the statary phase when forays are few and small, it rises sharply during the final days, when daily raids become regular and are larger (Schneirla, 1949). At that time the nearly mature pupal brood, which through its reflex activities accounts for the rise in colony excitement, is still enclosed and is not feeding; hence during these few days the queen may receive abnormally large quantities of food. However, this condition is of short duration and must end promptly when the callow brood emerges and begins its voracious feeding. Soon thereafter feeding evidently becomes general in the young larval brood, prolonging the interval of a reduced food supply for the queen until the latter part of the nomadic phase.

There is no evidence that the last described episode of limited physogastry, if it actually occurs on a wide scale among army-ant colonies, has any direct significance for reproduction.[1] Its main function may concern the metabolic recovery of the queen from the depletions of the preceding gravid episode.

The investigations of 1946 and 1948 both show clearly that in some of the eciton colonies of a given area sexual broods may be produced in the dry season, breaking the routine production of worker broods which otherwise continues through the year. It is probable that no more than one such brood is produced annually by a given colony. On Barro Colorado Island, during a four-month survey in the dry season of 1946, 11 such broods were discovered in different colonies of the two species, whereas only four such cases were found on the island in a survey of equal duration in 1948, in a total of about 50 colonies of the two species studied in each of these surveys. In the particular locality and during the periods of study, not all of the colonies can have produced sexual broods. In comparison with these results, the fact that in Darien, within a survey of only two weeks, six of eight colonies studied in the two species had sexual broods is not readily understood. Either the difference is attributable to a considerably greater production of sexual broods throughout the eciton population of Darien than at Barro Colorado in 1948, or the search in Darien happened to come during a sharp peak of sexual-brood production. Both of these possibilities may deserve consideration.

Little that is definite can be said at the present time about the biological conditions underlying the production of sexual broods in ecitons. Evidently the queens of particular colonies are influenced in some manner by the initial impact of effective dry-season conditions to produce a single brood which consists mainly of (unfertilized?) eggs producing

[1] Although small numbers of unhatched eggs have been found in some of the early larval broods sampled on the second and third nomadic days, these evidently soon disappear from the broods; whether through some insufficiency in the eggs themselves or through cannibalism by larval brood or workers, cannot be said.

males (Schneirla, 1947, 1949) but which (as we know from the present investigation) also contains a considerably smaller number of (fertilized?) eggs producing females.[1] The number of eggs originally laid may be much smaller than that in the average worker brood; we do not know definitely. There are signs of a cannibalism by workers, effective both during the larval and the post-larval development of the sexual brood, which reduces the brood from an unknown initial magnitude to about 2000 individuals in *E. hamatum* and 3000 in *burchelli*. From our present evidence, somewhat fewer than 20 individuals of the queen type are present at the stage of mature larvae and only about six upon their emergence as callows. The first statement depends mainly upon a complete census made of colony DH-3 in Darien, the second upon counts of callow queens in colonies H-12 and H-27 on Barro Colorado. Our findings indicate that throughout the life of a sexual brood, factors are in operation that tend to reduce the number of eventually functional females and males (i.e., those that actually mate) to a characteristic minimum (Schneirla, 1947). One factor effective for a selection among the developing queens is worker cannibalism, a second is the "sealing off" process which operates in connection with colony division. There may be others.

From general considerations alone, the adaptive aspects of sexual-brood production in the ecitons are impressive in their adequacy and precision. First of all are the factors that operate to reduce this brood to only about one-tenth the size of the typical worker brood. This condition may be due to limitations upon egg production by the queen, as well as to worker cannibalism during development. In any case, the queen's contribution is a determinative one: a "mixed" batch of queen-producing and male-producing eggs, the former type of eggs probably much fewer in number than the latter and almost certainly laid at the beginning of the series. The reduced population of this brood seems crucial, for with the number of individuals considerably fewer than in a worker brood, an overfeeding of all members can occur which greatly exceeds that maximally possible in the populous setting of a worker brood. What we have said is based on the reasonable assumption that the Dzierzon rule applies in the case of the doryline ants as it does widely among other social insects (Wheeler, 1928; Berland, 1948; Pasteels, 1949), and on the corollary postulate that the queen type and worker type of individuals develop from eggs that are genetically equivalent but differentiated through trophic factors promoting different growth patterns. It is possible that the different trophic setting begins with a superior metabolic background in the queen oöcytes; it is reasonable to consider an overfeeding by workers as an important factor in the differentiation of queen type from worker type of young (Haydak, 1943; Flanders, 1946; Kuwabara, 1948).

The process of colony division in tropical ecitons occurs as a direct outcome of the appearance of a sexual brood and is thus an event peculiar to the dry season. From our results, the specific mechanisms of fission evidently center around the presence of developing queens in the brood. An exceptionally compelling trophallactic process seems to be involved basically in the important events preceding the final splitting of the mother colony. Both developing males and queens have a strong attractiveness for the workers which clearly exceeds that exerted by developing worker forms. Observations and tests show that this sexual brood effect has a chemotactic basis, and there are indications that it is operative even from the time the sexual brood is entering the intermediate stage of larval development, if not before. Hence a study of colony division must begin early in the life of the sexual brood.

In all probability, it is the unique chemotactic properties of the sexual brood in their effect upon workers that leads to a polarization in the structure of nomadic bivouacs

[1] From the evidence now available,, there is no doubt that the brood which Wheeler (1921) discovered in a colony of *E. burchelli* at Kartabo, British Guiana, in August of 1920 was a regular sexual brood as described here. The reported circumstances indicate that the colony was about to complete a statary phase which had been spent in a hollow tree, that the two "fresh-looking" queens discovered had emerged very recently after having developed in the current mature brood, and that the impending emergence of the "several hundred" mature males still enclosed in cocoons might have furnished the basis for a division of the colony.

during the larval stage of the sexual brood. In the distinctive pattern that arises, the functional queen of the colony is located in a brood-free zone opposite the section of the bivouac in which a part of the colony is clustered with the larvae of sexual form. Worker cannibalism at the expense of the brood appears to center particularly around the border zone between these two main sections of the bivouac. Also we find that during the course of larval development of the sexual brood, a considerable portion of the worker population becomes unstable with respect to the "old" functional queen of the colony. It is reasonable to conjecture that this condition depends upon the extent to which a segment of the worker population may affiliate itself chemotactically with the sexual brood, or perhaps more particularly with the queen larvae. In contrast to hundreds of instances in which functional queens have been removed from the bivouacs of their colonies when worker broods were present and returned at intervals of a few hours to one or two days later without any question of their complete chemotactic acceptability to the worker population, very different results were obtained in the case of colony '48 H-19 in the present investigation. In this instance, the removal of the queen and her detention from the bivouac containing a brood of mature larvae of sexual forms resulted in conflicting responses by workers and two clear-cut, sealing-off episodes as specific reactions involved in rejection of the returned queen.

Another factor of crucial importance for colony division is the precocious development of the young queens with respect to the males. From the outcome, it is not unreasonable to believe that the presumably fertilized eggs from which these queens develop are laid in advance of the presumably unfertilized eggs producing males. The fact is that the queen larvae mature and spin their cocoons in advance of the males by two or three days, a circumstance through which we were able to capture these individuals notwithstanding their small representation in the brood population. Cocoon spinning by queen larvae creates a great commotion at the bivouac, with a strong cluster of workers forming about each queen larva engaged in the activity. Apparently these occurrences frequently interfere with the forays and bivouac-change movements to the extent that the colony may become statary before many of the male larvae have begun to spin. It is conceivable that such a premature cessation of bivouac-change movements may facilitate the persistence of colony sub-centers established about queen larvae during the spinning.

Furthermore, we have ascertained that the young queens emerge from their cocoons as callow adults within two or three days before a large-scale emergence of the males begins. Our observations of worker responses to these queens indicate that their presence in the colony as active individuals may both facilitate a sub-sectioning of the worker population, already under way, and sharpen worker responses in the direction of "acceptance" or "non-acceptance." The small clusters formed about the first one or two queens to emerge soon separate from the main bivouac but remain stationed near by; these aggregations are based on unequivocal "acceptance" by workers in the respective groups. In contrast, worker reactions to the callow queens which emerge somewhat later involve a combination of attraction-and-clustering with disturbance-and-nipping. A gradation thus exists among the young queens of the small series in the extent to which they attract or repel workers, clearly a selective process of considerable adaptive significance. Beyond doubt, the one or two young queens that receive the unequivocal clustering reaction of workers have the best chance of becoming established in daughter colonies; the others are sequestered and finally abandoned through a characteristic sealing-off reaction, as described in the protocols for colonies H-12 and H-27. It is apparent that the old colony queen also is involved in these complex intramural selective processes, with the possibility that under appropriate conditions she herself may be sealed off and abandoned along with the unsuccessful young queens. We lack specific evidence of such an outcome.

The synchronization of events in the delivery of a sexual brood is very precise. First the young queens emerge and sub-centers are established in the colony through cumulative worker reactions. Then in two or three days the emergence of alate males in large numbers

stirs up the colony and leads to an emigration on the day of maximal arousal. Evidently the principal sub-sections of the population then form the basis for a divergent movement and eventual fission of the colony, in strong contrast to the unidirectional movement which ordinarily occurs at the end of a statary phase in colonies possessing mature worker broods. Presumably, workers affiliated chemotactically with a given sub-section of the colony become predominant in one of the radial lines of emigration, and tend to exclude those of another sub-section.

We have suggested the possibility that a multilateral division of a colony might entail the extinction of one or more of the new daughter colonies. Although utilizable chemical trails radiate from the statary bivouac site in various directions as a result of previous raids, there appear to exist definite behavioral and biological restrictions upon the occurrence of more than two divergent movements involving different queens with their respective worker contingents. Perhaps most important of all these factors is the gradient which we have postulated in chemotactic responses by workers to the young queens. The problem will be considered in a later paper.

From the apparent fact that sexual broods are not produced by all the colonies of a given species during a particular dry season, it would follow that the colony division process must be restricted correspondingly. There is reason to believe that a division is inevitable when a sexual brood is produced, notwithstanding the fact that in our investigation only one definite process of complete division was observed in four cases studied in detail. The division occurred in colony H-27, which was the only one of these colonies not subjected to experimental changes. In the case of colony H-12 some of the young queens, including what were very probably the two best established ones in the series, were removed for specific investigative reasons. In the case of colony H-19, following the removal of the old queen and her rejection by workers, a fusion with colony H-28 occurred which had the consumption of the H-19 sexual brood in the combined colony as its sequel. In colony B-XVII a division may have been forestalled through the effects of successive artificial interventions for the purpose of sampling the brood and the removal of the only two young queen individuals (as mature larvae) that were observed. In view of the characteristically stereotyped pattern and species uniformity of essential eciton events, we are inclined to believe that our present evidence affords a reliable outline of the main processes in colony division. It is conceivable that the process of sexual brood production and colony division may afford a mechanism for the replacement of superannuated queens. Although in all our cases of a blocked or complete colony division (except H-19) the former functional queen survived the division, the condition of the queen may govern her chances of surviving the colony division process. The strong indication of our evidence that the impact of dry-season conditions somehow initiates the production of sexual broods may mean that all queens are susceptible when a propitious seasonally conditioned extrinsic situation is effective. Our finding that some colonies produce sexual broods before others, and that some colonies seem to produce no sexual broods at all in a given season, may be simply a matter of how dry-season conditions affect different colonies depending on variables determined by the location of their (statary) bivouacs. The evident importance of ecological factors for sexual brood production certainly does not exclude age-conditioned factors such as sperm exhaustion in the queen.

From the probability that eciton chemical trails are more persistent under dry-season conditions than in the rainy season, as our evidence suggests, certain important adaptive consequences may arise. For one thing, the distribution of eciton males would be facilitated thereby, as well as the survival of a minimal number of them in the post-flight intervals against inevitable hazards after the wings are dropped (Schneirla, 1948). The persistance of chemical trails as a virtual network in the forest would operate to decrease the random wandering of dealate males and to increase the chances that some of them may find their way into bivouacs of the species. The system of trails radiating from a statary bivouac must be an important asset to such males, through both the manner in which the long routes converge upon the

bivouac center and the fact that statary worker populations are relatively quiescent and presumably more receptive to somewhat strange individuals than are nomadic colonies.

It is also conceivable that the greater dry-season persistence of chemical trails assists colony operations involving the gathering of booty from well-separated concentrations and also facilitates colony mobility. In the statary phase particularly, one frequently notices in the dry season that routes unused for several days may be rapidly extended early in the day, with the result that soon a long unbranched base column extends far from the bivouac (sometimes more than 400 meters) to tap remote terrain. Although this feature of statary raiding is also observable in the rainy months (Schneirla, 1933), in the dry period it seems to be accentuated, enabling colonies better to adapt to the latter season.

Another significance of more persistent chemical trails has to do with the total economy of a species population. We have observed that within a few days after the removal of its queen, a colony may fuse with another of its species if the trails happen to cross (Schneirla, 1949). After their queen has been gone for some time, workers become more receptive to (and perhaps more tolerated by) those of foreign colonies, presumably on the basis of a chemotactic change. Thus populations may fuse that would ordinarily repel each other. Although such events presumably may occur at any time of year, in the dry season the chances that colonies will cross paths must be considerably increased through the trail persistence factor. Worker populations that would otherwise perish (e.g., the population of colony '46 H-O; Schneirla, 1949) may thereby be salvaged. Thus the fusion of colony '48 H-19 with H-28 brought the (initially undersized) H-28 colony to the population norm of the species and also saved many thousands of otherwise doomed workers, although at the expense of the H-19 sexual brood.

A mechanism of obvious adaptive importance is the back-tracking of eciton workers on ordinarily abandoned trails when the colony queen is absent. Normally a nomadic colony advances into new terrain without more than a limited retracing of yesterday's route of approach to the current bivouac (Schneirla, 1933, 1938, 1944b). However, within a few hours after the queen had been removed from the bivouac, we find workers spreading back to ramify through the forest over old trails. No specific explanation is suggested by our present evidence, except the negative fact that the occurrence or non-occurrence of such retracing cannot depend upon any property of the back trails themselves. Rather, it may be due to the absence of some effect (conceivably a pervasive chemotactic effect) ordinarily exerted by the queen upon the bivouac. However this may be, the back-tracking represents an increase in the chances that the colony may regain contact with the queen and reabsorb her if she has happened to get cut off from the previous bivouac-change movement. In view of the fact that the queen with her entourage frequently travels near the very end of the column in the emigration, such an occurrence may not be out of the question.

From the fact that queenless colonies may continue such trailing for days, with an indefinite termination unless they can fuse with another colony of the species, a further adaptive significance of this behavior is evident. The fusion process inevitably is facilitated by the extended survival time of chemical trails in the dry season.

It is unlikely that such eciton behavior processes, highly adaptive as they seem to be in various ways, should be regarded as aberrant or unusual parts of the eciton pattern. Rather, they stem directly from the characteristics of that pattern itself, when certain features of the ordinary life situation are changed. In a somewhat less prominent but very effective way, variations in the typical species raiding pattern serve as adequate adjustments to emergencies arising in the dry season. These considerations further demonstrate the adequacy with which the eciton system of behavioral and biological functions can operate through the year to meet even the extreme seasonal hazards of the tropical forest environment.

PRINCIPAL RESULTS AND CONCLUSIONS

FROM THE LAST WEEKS of the 1947 rainy season in Panama through the greater part of the 1948 dry season, no outstanding differences were found in the activities and condition of eciton colonies. At Barro Colorado Island and in three other areas in Panama, a total of 41 colonies of *E. hamatum* and 26 of *E. burchelli* was investigated, together with colonies of other species, without the discovery of any significant departures from the previously described nomad-statary pattern in colony behavior and biological processes.

With the exception that the nomadic phases of *burchelli* colonies tended to be somewhat longer and more variable, only minor differences were found in the phase durations for the two species in 1948 as compared with those for the 1946 dry season. The evidence seems conclusive that, barring serious environmental disturbances, colonies of these species continue their regular production of broods throughout the year, with corresponding shifts in colony behavior depending on the alternate presence and absence of maximal trophallactic stimulation from developing broods.

By marking the queens of numerous colonies in a permanent way, we obtained extended records of colony functions and mobility without a schedule of continued observations. With 18 marked queens of *E. hamatum* and eight of *burchelli* remaining on Barro Colorado Island in their respective colonies at the end of this investigation, subsequent recaptures may throw light on the duration of function in these queens.

Our evidence coincides with that from the 1946 dry-season study in showing that the colonies of these and other species of eciton are not significantly less mobile and extensive in their operations than in the rainy season. Colonies of *E. hamatum* when in the nomadic condition carry out bivouac-change movements with full consistency during the two seasons. Nomadic *burchelli* colonies, however, are occasionally subject to a failure of emigration in the dry season, in contrast to a nearly maximal consistency in this respect in the rainy season. An environmental inhibition of extra-bivouac activities during midday in the dry season at times indirectly hampers nomadism in *burchelli* (but not *hamatum*, because of species differences in the pattern of raiding).

In this investigation further evidence was obtained that eciton sexual broods are unique to the dry season and arise somehow through the initial impact of dry-season conditions upon the queen. It is probable that no colony produces more than one sexual brood and that some of the colonies produce only worker broods in a particular dry season. In the dry season of 1948, the production of eciton sexual broods was either more frequent or more concentrated in time among the colonies of Darien than among those of Barro Colorado Island. This may indicate that sexual broods are produced among colonies in a given area in dependence on dry-season characteristics such as the abruptness of its onset, and the degree and persistence of the seasonal conditions. Somehow eciton queens must become readjusted to the seasonal change so that evidently no more than one sexual brood is produced in any one colony, in a succession of worker broods.

Young queens are produced in the same brood with the males, in the two species of *Eciton* investigated. Only a very few young queens are present upon emergence as callow individuals, with some 2000 males in *E. hamatum* and 3000 in *burchelli*. The small size of the sexual brood as compared with worker broods may be due to the queen's laying an extraordinarily small batch of eggs; but also, the number of both queen and male individuals may be subject to reduction through worker cannibalism effective during the developmental period.

The production of a sexual brood introduces the conditions adequate for a division of the eciton colony. The basis is provided by a marked chemotactic affinity of workers for the developing sexual brood, which accounts for an exceptional instability in the reactions of a part of the colony to the "old" queen, and introduces a nascent (behavioral) subdivision of the colony even while the brood is developing and the colony is still a unit. It is probable that distinctive aggregations of

workers have become affiliated with the various young queens by the time of larval maturity. There is evidence for individual differences in the chemotactic attractiveness of the young queens for workers, effective at the time the queens emerge as callows. This gradient, ranging from a prevalent attractiveness to a disturbing effect, underlies a complex process in colony behavior whereby just one (or, at times, perhaps two) of the young queens survives as the functional queen of a daughter colony, with the others sealed off by workers and eventually abandoned. Under appropriate conditions the old colony queen may not survive this competitive procedure. Numerous potent selective factors are involved in reducing to a decided minimum the number of both males and females finally involved in functional reproductive processes in the ecitons.

It is important for effective eciton colony division that the queens are somewhat precocious in development and appear as callows a few days in advance of the males. In particular, this fact insures that the advanced stages underlying colony partition, involving a greatly sharpened (although indirect) competition among queens, have been attained by the time the males emerge. The appearance of the males then arouses the worker population to the high level of raiding at which nomadism ensues. In sharp contrast to the unilateral nomadic movement when a worker brood emerges, the colony here moves off divergently in two daughter sections by virtue of a preëxisting chemotactically based split in the population. Both through factors arising from the development of the sexual brood and from the processes of its emergence, the division of the colony is held to a bilateral rather than a multilateral occurrence. We have advanced reasons for believing that if an eciton colony were to divide into more than two daughter colonies, the survival of one or more of these would be endangered.

Eciton chemical trails appear to be more persistent in the dry season than during the rains. Old trails of other colonies are often used (and at times even of other species), a fact that facilitates the development of mass forays under the most arduous conditions of the year. The persistence of trails facilitates a back-tracking which occurs when a colony has lost its queen and thereby increases the chances of fusion with a functional colony of the species. It also increases the likelihood that post-flight eciton males will reach foreign colonies of their species.

Queenless eciton colonies are capable of fusing with other colonies of the species, presumably through changes in the normal pattern of chemotactic condition and reactivity. Such occurrences are facilitated by the described back-tracking process, as well as by the persistence of chemical trails.

REFERENCES[1]

BERLAND, L.
1948. La reproduction chez les insectes hyménoptères. L'Année Biol., ser. 3, vol. 24, pp. 105–115.

BREDER, C. M., JR.
1946. Amphibians and reptiles of the Rio Chucunaque drainage, Darien, Panama, with notes on their life histories and habits. Bull. Amer. Mus. Nat. Hist., vol. 86, pp. 381–435.

CHAPMAN, R. N.
1931. Animal ecology with especial reference to insects. New York.

COHIC, F.
1947. Observations morphologiques et écologiques sur *Dorylus* (*Anomma*) *nigricans* Illiger. Rev. Française Ent., vol. 14, suppl., pp. 229–276, figs. 1–50.

FLANDERS, S. E.
1946. Haploidy as a factor in the polymorphic differentiation of the Hymenoptera. Science, vol. 103, pp. 555–556.

GOLDMAN, E. A.
1920. Mammals of Panama. Smithsonian Misc. Coll., vol. 49, pp. 1–309.

HAYDAK, M.
1943. Larval food and determination of castes in the honeybee. Jour. Econ. Ent., vol. 36, pp. 778–792.

HESSE, R., W. C. ALLEE, AND K. P. SCHMIDT
1937. Ecological animal geography. New York and London.

IHERING, H. VON
1912. Biologie und Verbreitung der brasilianischen Arten von Eciton. Entom. Mitt., vol. 1, pp. 226–235.

KUWABARA, M.
1948. Ueber die Regulation im weisellosen Volke der Honigbiene (*Apis mellifica*) besonders die Bestimmung des neuen Weisels. Jour. Fac. Sci. Hokkaido Univ., ser. 6, vol. 9, pp. 359–381.

SCHNEIRLA, T. C.
1933. Studies on army ants in Panama. Jour. Comp. Psychol., vol. 15, pp. 267–299.
1934. Raiding and other outstanding phenomena in the behavior of army ants. Proc. Natl. Acad. Sci., vol. 20, pp. 316–321.
1938. A theory of army-ant behavior based upon the analysis of activities in a representative species. Jour. Comp. Psychol., vol. 25, pp. 51–90.
1944a. The reproduction functions of the army-ant queen as pace-makers of the group behavior pattern. Jour. New York Ent. Soc., vol. 52, pp. 153–192.
1944b. Studies on the army-ant behavior pattern.—Nomadism in the swarm-raider *Eciton burchelli*. Proc. Amer. Phil. Soc., vol. 87, pp. 438–457.
1944c. A unique case of circular milling in ants, considered in relation to trail following and the general problem of orientation. Amer. Mus. Novitates, no. 1253, pp. 1–26.
1945. The army-ant behavior pattern: Nomad-statary relations in the swarmers and the problem of migration. Biol. Bull., vol. 88, pp. 166–193.
1947. A study of army-ant life and behavior under dry-season conditions with special reference to reproductive functions. 1. Southern Mexico. Amer. Mus. Novitates, no. 1336, pp. 1–20.
1948. Army-ant life and behavior under dry-season conditions with special reference to reproductive functions. 2. The appearance and fate of the males. Zoologica, vol. 33, pp. 89–112.
1949. Army-ant life and behavior under dry-season conditions. 3. The course of reproduction and colony behavior. Bull. Amer. Mus. Nat. Hist., vol. 94, pp. 1–82, figs. 1–6, pls. 1–2, tables 1–10.

UVAROV, B. P.
1928. Insect nutrition and metabolism—a summary of the literature. Trans. Ent. Soc. London, 1928, pt. 2, pp. 255–343.
1931. Insects and climate. *Ibid.*, vol. 79, pp. 1–247.

VERLAINE, L.
1926. Les reines fécondées des hyménoptères sociaux peuvent-elles engendrer des mâles. Ann. Bull. Soc. Ent. Belgique, vol. 66, pp. 287–318.

VOSSELER, J.
1905. Die ostafrikanische Treiberameise (Siafu). Pflanzer, year 1, no. 19, pp. 289–302.

WEBER, N. A.
1949. A new Panama *Eciton* (Hymenoptera, Formicidae). Amer. Mus. Novitates, no. 1441, pp. 1–8.

[1] A more extensive list of references on this subject will be found in the preceding paper of this series (Schneirla, 1949).

WHEELER, W. M.
1912. The male of *Eciton vagans* Olivier. Psyche, vol. 19, pp. 206–207.
1921. Observations on army ants in British Guiana. Proc. Amer. Acad. Arts and Sci., vol. 56, pp. 291–328.
1925. The finding of the queen of the army ant *Eciton hamatum* Fabricius. Biol. Bull., vol. 49, pp. 139–149.
WIGGLESWORTH, V. B.
1939. The principles of insect physiology. New York.