ARMY-ANT LIFE AND BEHAVIOR UNDER DRY-SEASON CONDITIONS

3. THE COURSE OF REPRODUCTION AND COLONY BEHAVIOR

T. C. SCHNEIRLA

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 94 : ARTICLE 1 NEW YORK : 1949

ARMY-ANT LIFE AND BEHAVIOR UNDER DRY-SEASON CONDITIONS

ARMY-ANT LIFE AND BEHAVIOR UNDER DRY-SEASON CONDITIONS

•

3. *THE COURSE OF REPRODUCTION AND COLONY BEHAVIOR*

T. C. SCHNEIRLA
Curator, Department of Animal Behavior

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 94 : ARTICLE 1 NEW YORK : 1949

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Volume 94, article 1, pages 1–82, text figures 1–6,
plates 1–2, tables 1–10

Issued September 20, 1949

Price: $1.00 a copy

CONTENTS

INTRODUCTION

THE ENVIRONMENTAL CONDITIONS under which the characteristic behavior pattern of a given animal runs its course with a minimum of disruptive variation and a maximally adaptive outcome are generally considered optimal for that pattern. Presumably, in this sense, the rainy season is optimal for many animals of the tropical forest (cf. Hesse, Allee, and Schmidt, 1937). We have considered the army ants, the tropical American representatives of the ant subfamily Dorylinae, as conforming to this description. For in the rainy season these ants appear to carry out their characteristic activities and life processes with great effectiveness. In a field and laboratory survey conducted in Panama during the rainy seasons of four different years (Schneirla, 1933, 1934, 1938, 1944), among hundreds of colonies studied there was found a highly regular and smoothly organized pattern of colony behavior and concurrent biological processes.

The system of events that is presumably optimal for the ecitons involves regular fluctuations from a condition of extensive and maximally developed daily raids and regular nightly changes of domicile (the nomadic phase) to a condition of much decreased raiding activity and no shifts in nesting site (the statary phase). The nomadic phase is a highly active condition, the statary phase a relatively inactive, sessile condition which persists for some time. Ordinarily the change from one of these phases to the other is a regularly reversible one in any given colony, with nomadic and statary phases alternating throughout the rainy season.

In our previous studies the eciton behavior cycle has been investigated in some detail in relation to the concomitant biological circumstances in the colony. Through these investigations the essential causal basis of the colony behavior cycle has been found in the relation of developing broods to the worker population (Schneirla, 1938).[1] Each brood exerts a major excitatory effect upon the colony as a whole, a trophallactic effect (Wheeler, 1928; Schneirla, 1941) which fluctuates rather precisely according to the developmental condition of the brood, with striking variations appearing concurrently in the predatory forays and nomadic tendency of the given colony. It is critically important for the described correspondence of events in brood condition and colony behavior that in the rainy season the broods appear very regularly, are all very large, and consist entirely of worker individuals, all approximately at the same stage of development. Because broods are produced in this manner during the rainy months, the influence of any given brood is marked at its height and is present or absent almost in an all-or-none fashion. Because the production of successive large broods at regular intervals is attributable to a single queen in each colony, this individual may be considered the effective "pace maker" of the striking rhythm which characterizes behavior in all intact colonies of the species studied.

This systematic interrelationship of reproductive processes and behavior has been found prevalent in the two eciton species that the writer has investigated intensively: *E. burchelli*, prominent among the species that carry out their daily pillaging expeditions in large unitary masses, the "swarm raiders," and *E. hamatum*, representing species that carry out their raids in systems of branching columns, the "column raiders." These two species, both members of the subgenus *Eciton* (*Eciton*), are similarly terrestrial in the sense that they generally establish their temporary nests and carry out their forays on or above the surface of the ground. Although our general investigation has focused upon these two species, our results for various species of *Eciton* (*Eciton*) and of the other two principal eciton subgenera, namely, *Labidus* and *Neivamyrmex* (=*Acamatus*), indicate that a comparable pattern of behavioral and biological events prevails widely among the dorylines in the American tropics.

The nomadic-statary system of events has been established in our investigations for

[1] The term brood is used here in a somewhat special sense appropriate to the unique reproductive situation prevalent in the ecitons, as indicating all developing young present in a colony that are at approximately the same stage of growth. In this sense, a colony may possess either one or two broods at a given time depending on its condition.

doryline species in well-separated parts of Central America. It prevails in the surveyed localities of Panama and southern Mexico (Schneirla, 1938, 1947) where eciton colonies of numerous species are not uncommon in areas of tropical forest. Very relevant here is an early report by W. Müller (1886) on a single colony of *E. burchelli* found by him in his brother's garden at Santa Catharina, Brazil, and kept under periodic observation from February 26 to March 15, 1885. Although Müller's study lasted only 17 days, his description of events suggests a state of affairs clearly conformable with what we have found prevalent in the localities of Central America. In the first few days after the colony was discovered the raids were vigorous, and each night the colony changed its nesting site. Then there occurred, about March 2, a reduction in the vigor of raiding, which, Müller noticed, corresponded to the time when the mature larval brood of the colony had become enclosed in cocoons. The last movement of the short series of nesting changes occurred on March 2. Thereafter, until the study ended on March 15, the colony remained within a hollow tree, moving only with considerable inertia and over short distances, and only when Müller used smoke in attempts to force a change. The raids of the colony were smaller than at first, and on some days no forays were observed. On March 15, about 12 days after the ants had entered the hollow tree, large numbers of eggs were found when smoke forced a shift. Against the background of my own findings for *E. burchelli* (Schneirla, 1945), Müller's colony while under observation may be identified as having passed from the end of a nomadic phase through the principal part of a statary phase.

The evident significance of Müller's results was pointed out by the present writer after he had found evidence for a rhythmic succession of events in eciton colonies under rainy-season conditions (Schneirla, 1933). In the early rainy months of the 1932 season, what was identified as the late part of a statary phase and the first part of a nomadic phase was observed in a colony of *E. hamatum*, and portions of the two phases were observed in other colonies. Further corroboration of cyclic events along these lines was obtained in 1933 (Schneirla, 1934). Numerous studies over a few weeks with each of various colonies representing the two species on which attention had focused, *E. hamatum* and *burchelli*, subsequently indicated the prevalence of a rhythmic alternation of phases during most (if not all) of the rainy season. The first long-term study involving an entire period of two activity phases was carried out in the rainy season of 1936 (Schneirla, 1938), when a colony of *E. hamatum* was studied continually for 42 days. This colony passed from the end of a statary phase through a full nomadic phase of 18 days, then through a full statary phase of 19 days, and had begun a further nomadic phase when the study ended. A similar project involving a colony of *E. burchelli* in the rainy season of 1938 (Schneirla, 1945) corroborated earlier studies of shorter duration with that species in establishing the existence of a behavior-reproduction rhythm. When that study began, the colony was in the course of a nomadic phase, then followed a statary phase of 23 days, next 10 days of nomadism, after which 13 days of a new statary phase had passed when the investigation had to close.

These earlier studies on the activities of individual colonies in the rainy season were limited by an obligatory time schedule. Nevertheless, whether colonies were investigated for a few days or for weeks in sequence, no exceptions were found to the nomad-statary scheme that would weaken the postulation of a causal relationship between brood condition and colony behavior. In the meantime, this relationship was further supported by laboratory observations and tests which indicated the involvement of an excitatory effect exerted upon workers by larval forms, but not by pupal forms except callows. Because the field investigations of different years had been conducted during rainy months from May through September, the conclusion seemed justified that the nomad-statary rhythm must prevail throughout the entire rainy season, or as long as conditions should hold comparable to those of the investigation.

Provisionally, from the standpoint of these studies, it was anticipated that during the dry season, which in the Caribbean tropical forest areas of Central America extends roughly from mid-December to late April (see fig. 1), the eciton rainy-season pattern of events might undergo very considerable changes. It seemed very possible that for these events, dependent as they appeared to be upon the presumably optimal environmental conditions of rainy months, the dry season could prove to be disruptive or even catastrophic in its effect.

Interruptive effects, both direct and indirect in nature, were anticipated. The intervention of directly inhibitory atmospheric effects upon behavior was suggested by the results of many experimental studies indicating a typically depressant effect of high temperatures and low humidities upon insect activities and life processes (Uvarov, 1931; Buxton, 1932; Imms, 1937; Wigglesworth, 1939). This generalization seemed reasonable, although it stemmed largely from laboratory results mainly obtained with Temperate Zone insects, with no satisfactory knowledge available concerning the effects of the tropical dry season on indigenous insects in general and ants in particular. A condition of estivation or summer dormancy, which Uvarov (1931) suggested may be common in the dry months among insects living in tropical areas with clearly marked seasonal differences, would of course affect the ecitons in some manner. If the worker populations of colonies should succumb generally to such a condition, extensive reductions in raiding would be expected with a corresponding reduction in nomadic movements. Any serious falling off in raiding would inevitably bring reductions in the food supply and thereby disrupt production of broods, with further negative consequences for colony behavior. It was thus conceivable that ecitons might operate as do insects of the homodynamic type (Roubaud, 1922) in which reproduction continues unless interrupted by adverse environmental circumstances.

The above suggestions do not exhaust the possible detrimental effects which might arise under dry-season conditions against the eciton cyclic system. In the light of evidence concerning the influence of deficient nutrition and of suboptimal atmospheric conditions upon insect egg production (Uvarov, 1928, 1931; Imms, 1937; Emerson, 1939; Haydak, 1943; Ludwig, 1945), a partial or complete seasonal deficiency might arise in the egg-delivery functions of the eciton queen herself. A general reduction in available colony food might affect the queen's metabolism directly through inanition, or indirectly through possible deficiencies in substances furnished normally in trophallactic relations with brood or workers (Wheeler, 1928). A reduction in the general food supply might be effected either through an actual seasonal decrease in the population of forest insects ordinarily serving as eciton booty, or through a shifting of these insects to more remote locations in which they might be relatively inaccessible.

Numerous references in the earlier literature encouraged the view that the army ants are materially affected in their general activities by seasonal dry conditions. Sumichrast (1868) spoke of the increased activity to be remarked among the "tepeguas" (ecitons) with the first rains, "in relation, it appears to me, with the atmospheric changes," or "more often with a change of season." Von Ihering (1912) noted that in Brazil the ecitons are known as "rain ants" from the fact that they are much more in evidence during the wet months than in the dry season of the year. In discussing his observation of a column of *E. vagans* in which winged males had been found near San José, Costa Rica, late in November of 1911, Wheeler (1912) remarked that " . . . it was not the regular season for forays of these ants, for very few species of the genus were encountered in Panama, Costa Rica, and Guatemala during November, December, and January [i.e., during the first part of the regular dry season]. Only *E. coecum*, which is a subterranean species, appears not to interrupt its forays during these months." Later, after a stay at the Kartabo station in British Guiana, Wheeler (1921) wrote: "The forays seem to be most frequent during the rainy season. At any rate, during the latter part of August 1920, when the rains were becoming somewhat less frequent and copious, fewer armies were encountered in the jungle." From the experience of this seasoned tropical investigator, eciton activities seemed to be at a minimum in the dry season. In the survey made by Allee (1926a, 1926b) of ecological conditions and general animal activities on Barro Colorado Island in the dry season of

1924, ecitons were conspicuous for being almost completely absent from the records.

These suggestions of a considerable reduction and change in activity with dry weather appeared to be supported by the present writer's experience on Barro Colorado Island during May of 1933, when the terrain was unusually dry and the rainfall very light for that time of year, with the first rains of the new season exceptionally delayed. During 10 days of searching, very few colonies of eciton were found. Then, with an increase in daily rainfall, eciton activities became more prominent, and new colonies were found more readily. The striking contrast between these relatively sparse results in dry weather and the more frequent discovery of colonies during the corresponding days of May in 1932, when the wet season definitely had begun, encouraged the impression that dry weather might operate to inhibit eciton activities.

However, such observations are scattered and may well be misleading. It should be noted also that some writers, and Wheeler in particular, may have been influenced by a somewhat more reliable set of facts concerning the off-season adaptations of eciton species in the southern parts of the United States. It was reported by Wheeler (1900) that although *E.* (*Acamatus*) *schmitti* in Texas conducts forays much as do tropical ecitons, during late spring and summer months, "the nomadic habits which have been observed in these forms were not observed in *E. sumichrasti* [=*E. schmitti*]. During the winter and spring months, at least, the Ecitons I have observed occupy the same nest. This they probably continue to do until their young are raised." On the other hand, the suspension of activities which appears to occur seasonally in representatives of the subgenus *Eciton* (*Acamatus*) living in the southern United States may not have any direct relevance to conditions in tropical species of *Eciton*. It may represent a regional adaptation divergent from the tropical pattern and more closely approximate to the seasonal adaptations generally prevalent among Temperate Zone ants.

The question for tropical ecitons is not a simple one. It is of course possible that a normally dominant pattern of activities, which served well during a season when weather and nutriment were optimally adequate for it, might prove to be a serious handicap in the "off season." Selective processes in evolution must have thereby wiped out many species which were ineffectively adapted to seasonal conditions non-optimal for their typical adjustment patterns. Some tropical insects, such as grasshoppers and various other Odonata, appear to thrive in the dry season, when they are the insect types most in evidence in the daytime (Uvarov, 1931). Others, like most of the ants, may adjust to dry weather by minimizing activity in the daytime, with a possible shift to nocturnal activity. For other insects, a general reduction of activity may predominate during the dry months. It is probable that dry-season adaptations range between those that vary only to limited extents from their rainy-season mechanisms and others that may differ in qualitative and basic ways according to season. What happens among the ecitons?

Surprisingly enough, the results of an extensive survey in well-separated parts of southern Mexico during the regular dry season of 1945 (Schneirla, 1947) did not suggest that any fundamental seasonal changes occur. Eciton colonies of five species, including numerous colonies of *E. burchelli* and *hamatum*, were examined as to prevalent behavior and corresponding condition of broods and of queen, with the general finding that all of nearly 25 colonies taken in the survey exhibited the nomadic-statary pattern in very representative ways. However, the method of that investigation was essentially cross-sectional, and no colony was studied for a longer time than four days. It was considered possible that longer studies of given colonies might have revealed variations or interruptions of the regular pattern, or might have brought to light colonies in a persistent condition of dormancy, otherwise overlooked. When our sampling of events in given areas is time limited and open to a possible overemphasis upon the condition of colonies which are discovered through the very fact that they are maintaining the regular activity pattern at the time of search, other possibilities of different character remain. From this study we may say that some at least of the colonies in the investigated areas, although perhaps not all of them, were functioning effectively in terms of the nomad-statary rhythm at the time of survey.

Obviously this objection from the standpoint of sampling can be met only by carrying out a detailed survey of conditions over a considerable time in a given locality, where the activities and biological functions of colonies may be studied longitudinally as well as cross-sectionally. The possibility of such an investigation was opened for the dry season of 1946.

ACKNOWLEDGMENTS

This investigation was carried out while the writer was a Fellow of the John Simon Guggenheim Memorial Foundation. The program of which it is a part has been supported by a grant from the Committee for Research in Problems of Sex, National Research Council.

It is in order here also to acknowledge the many ways in which Mr. James Zetek, resident Custodian of the Canal Zone Biological Area, has aided the arrangements for these investigations on Barro Colorado Island.

To Dr. Harold Hagan of the College of the City of New York and Dr. Roy Whelden of the Haskins Laboratories, Union College, the writer is indebted for valuable histological and cytological studies on the preserved eciton material.

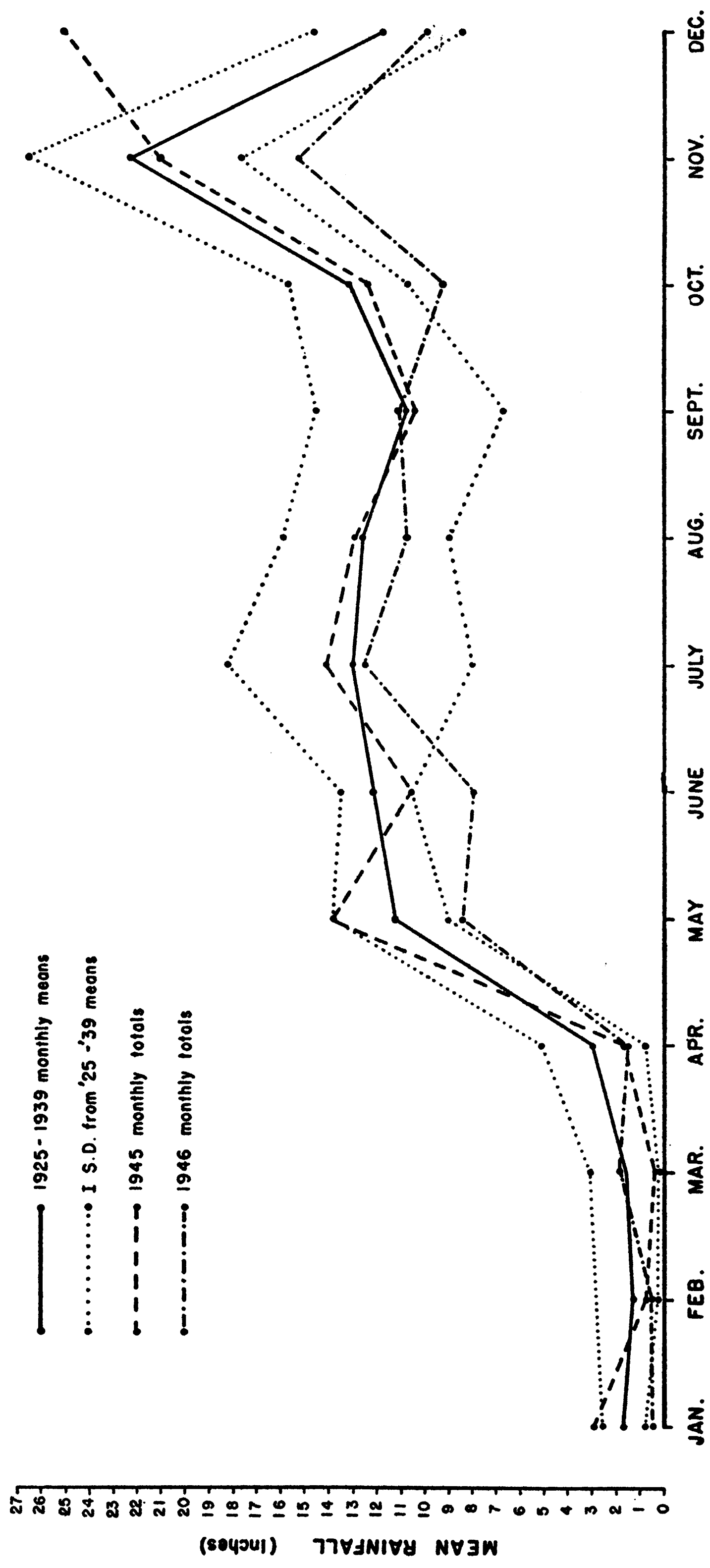

Fig. 1. Rainfall records from Barro Colorado Island, Canal Zone. Precipitation was measured with a United States Weather Bureau rain gauge set in the laboratory clearing. The curves express mean monthly rainfall in inches. Variability in the fifteen-year record is stated in terms of Standard Deviations from the monthly means. The results for the years 1945 and 1946 are given in separate curves. Data from Barro Colorado Island Annual Reports, through the kindness of Mr. James Zetek.

LOCALITY AND CONDITIONS

THIS STUDY extended over a period of four and one-half months in the dry season and early rainy season of 1946, beginning in early February and ending in mid June. The work was done on Barro Colorado Island in the Canal Zone, where investigations of army-ant behavior had been made by the writer during the rainy seasons of four different years from 1932 to 1938.

The insular nature of this biological reservation and its varied terrain and tropical forest cover are features well suited to the purposes of studies such as the present one. In keeping with the general conditions of fauna and flora on the island (Allee, 1926b; Kenoyer, 1929; E. C. Williams, 1941) the insect life is also abundant and typical of the general area (Rau, 1933), ordinarily furnishing an excellent food reserve for the entirely carnivorous ecitons, which abound in a large number of species.

The annual climatic pattern of the island is a fairly regular one, presenting a well-marked distinction between rainy and dry seasons. The summary of rainfall records in figure 1 shows convincingly that the time of the annual rainy season falls rather consistently in the period mid April to mid December, and that of the dry season in the interim. On the basis of this fifteen-year summary of rainfall records, all of which were taken in the laboratory clearing at Barro Colorado, the seasonal difference is indicated to be statistically reliable as concerns rainfall. There are not many forested areas in the tropical belt of the world in which the seasonal differences in rainfall are more clear-cut than these (cf. Clayton and Clayton, 1947).

Because this project was begun early in February of 1946 and continued for somewhat more than four months, it covered most of the dry season except the first five to seven weeks and extended into the early part of the following rainy season.

Two conditions that were somewhat out of the ordinary may be noted from the rainfall records of 1945 and 1946, which are represented in separate curves in figure 1. First, it is of some significance for our present study that the wet season of 1945 was more protracted than usual, with a rather unusually high rainfall indicated for December (more than 3 *S.D.* from the fifteen-year December mean rainfall). In 1945, December was a month of heavy rainfall, although this month ordinarily is dry in its latter half. This fact accounts for the generally good retention of ground moisture well into the early months of 1946, a condition of potential importance for the army-ant situation, both from the standpoint of available insect prey and also the properties of the environment affecting activities such as nesting. The second fact of possible importance is that the period of this study was somewhat scantier as to rain than is ordinarily the case for that time of year, with the rainfall totals of three months below the corresponding averages in the fifteen-year record (see fig. 1), and only that of March close to the average. There were several fairly long sequences of rainless days, and virtually all rains were light ones, up to the crescendo that initiated the rainy season of 1946.

The principal portion of this survey was carried out in the eastern half of the island, especially because of the greater prevalence of second growth and lighter cover which accounts for the fact that in general this part of the island is somewhat drier than the other parts. The forest floor there, with a heavy forest canopy absent in most places, is more open to the sun's rays than is the case elsewhere. Thus the studies were mainly carried out in the sector of the island that ranges farthest towards the dry side in the general condition of its terrain.

GENERAL METHOD AND PROCEDURE

THE GENERAL PLAN of this investigation was to make as thoroughgoing a study as possible of the manner in which eciton colonies pass through the dry season in the given area. The survey was basically longitudinal in that it involved the continued observation of particular colonies throughout the entire four months, but was also cross-sectional in that records were taken on other colonies over shorter periods of time ranging from a few days to weeks or months. The roster of colonies studied may be seen in figures 5 and 6.

Two principal species of the subgenus *Eciton* (*Eciton*) were the focus of investigation, the species *E. hamatum* and *E. burchelli*, which have been featured throughout this entire program. *E. burchelli* is a typical swarm-raiding species and *E. hamatum* a typical column raider. This selection is due to the fact that these species are common and not too difficult to find, as a rule, and also to the fact that both are representatively terrestrial in their activities and nesting and consequently more accessible to study than are partially terrestrial species such as *E. rogeri* in the same subgenus, and predominantly subterranean species in the other subgenera. As before, records were taken on all species of the various subgenera at every good opportunity. Since these two species have been emphasized in the previous work of this program, species comparisons as to seasonal adaptation are thereby facilitated.

The record colony of *E. burchelli* will be referred to as colony '46 B-I; the *E. hamatum* colony as '46 H-B. Other colonies will be referred to by their consecutive symbols in Roman numerals (*E. burchelli*) or in capital and lower-case letters (*E. hamatum*). The first-mentioned colonies of the principal species were kept on record from early February to mid June. A schedule of daily visits was maintained so that records could be kept of the raiding activities and the nightly bivouac-change movements of these colonies. Notes were taken in shorthand of the relevant facts concerning current colony activities and internal colony conditions. In the latter class of evidence were included special behavior conditions in situations such as raiding and bivouac-change movements, condition of the brood (i.e., eggs, larval stage, pupal stage), and condition of the queen. As a rule the last item was checked by sighting the queen at intervals of a few days during the series of nightly bivouac-change treks in a given nomadic period. Neither queen was ever removed during the statary period, when the colonies as a rule were located in rather inaccessible places. This was in keeping with the rule that, for these two colonies, no avoidable disturbance was to be introduced in the bivouacking or other situations of the colonies through the operations of the investigator. The regular taking of brood samples constituted the only exception to this procedure. A periodic inspection of the population of the colony as it passed along in the night-time migration columns enabled a check on the population and condition without interfering with the course of events.

To supplement the general records on the brood or broods, and of course also to get indirect evidence on the condition of the queen at various times, samples of the brood generally ranging between 100 and 200 individuals were taken at three-day intervals when sampling was at all feasible. During certain of the statary phases, however, the brood was not accessible for sampling. Samples were taken in such a way as to avoid undue disturbance of the bivouac or of colony activities.

The procedure was much the same for the investigation of both the longitudinal-study colonies. Each day the situation of the colony was surveyed between 9:00 A.M. and 11:00 A.M. The time was scheduled after mid morning when possible, in order that the raiding system of the day might be prospected and its principal lines sketched at a fairly advanced point in development. (Development of a raid in these species begins at or after dawn; Schneirla, 1938.) Brood samples were taken at this time, on every third day so far as possible. At times when the colony was engaged in nightly bivouac-change movements, the current day's bivouac site was investigated at an opportune time after dusk for the purpose of determining the line of the movement and following it out to the new clustering site. When both of the record colonies were nomadic (i.e., engaged in nightly migrations) at the same time, the regular practice was to visit the *hamatum* colony first and the *burchelli* colony later in the evening, since the bivouac-change process generally was more delayed in the latter. By the use of a measured string laid along the route followed in the change of bivouac, the route could be mapped and its approximate length determined on the following morning.

Additional colonies of both species were on record at all times, for purposes of comparison with the record colonies. As far as possible, the activities of terrestrial *Eciton* colonies in the eastern half of the island were kept under surveillance, and in addition periodic survey trips were made through the other areas. Behavior notes were made from these colonies under secondary study, and periodic brood samples were taken. In all, more than 65 colonies of the two species were studied, over periods ranging for given colonies from two days to two months. A glance at figures 5 and 6 will show that on virtually every day throughout the period of investigation, from two to eight *Eciton* colonies were on current record.

A variety of supplementary tests was carried out in field and laboratory. However, the two record colonies were not disturbed in any way except for the minor intrusion of periodic brood sampling. At the very end of the period of investigation these two colonies were etherized in their respective bivouacs, so that their queens and the bulk of their broods could be removed for fixation and later study. The various tests performed are best described in the sections of the text to which they are relevant. In the field, a few colonies of both species were deprived of their queens, either for a limited time or permanently, and their subsequent activities were noted; other colonies were deprived of the major portion of their brood, and so on. In the laboratory, observations were conducted with small groups of workers with brood taken from the various colonies under study in the field. A circular-column technique (Schneirla, 1944c) was used for testing the responses of males to moving columns of workers from their own and other colonies of the species, the responses of workers to other broods mixed with their own, and the like.

All specimens of the broods, as well as queens, males, and other special material warranting histological and cytological study, were immersed in a modified Bouin's solution for 24 hours, then were placed in 70 per cent alcohol for storage.

RESULTS

STUDIES OF COLONY ACTIVITIES OVER CONSIDERABLE PERIODS OF TIME

COLONY '46 H-A was first taken as the colony representative of *E. hamatum* for long-term study. This colony evidently had just entered the statary condition when it was found on February 7. Until February 22, the colony remained in place within a hollow tree to the west of Shannon 6,[1] with small daily raids; and meanwhile the principal brood passed through the prepupal and the pupal stages. However, it was decided to use colony '46 H-B as the principal representative of *E. hamatum* when that colony was found on February 12, particularly because of the desirability of having at the outset a distinct opposition of activity phases in the record colonies of the two species.

COLONY '46 H-B, *E. hamatum*

When found on February 12, 1946, this colony was engaged in a large nomadic raid, which after dusk passed over into a bivouac-change movement. The bivouac of February 12 was located to the east of station 5, Barbour Trail, in the hollow of a low tree stump. In view of the fact that many thousands of empty worker pupa cases were found beneath the position of the cluster when the site was finally vacated late that night and that a large brood of early callow workers was present, it seemed reasonable to conclude that this colony on February 12 was vacating a statary site which had been occupied for a number of days.

The subsequent activities and changes in condition of colony H-B were observed day after day until June 6, 1946, when the study was terminated.

The important evidence concerning the activities and changes in condition of colony '46 H-B from February 12 to June 6 is summarized in table 1, and in figure 2 the itinerary of the colony is represented to show the spatial relations of the statary and nomadic bivouac places and the general area covered in the raids and movements of the colony. In figure 5 the principal changes in colony activity and in broods are represented, in relation to those of other colonies under study at the respective times. The developmental status of the successive broods produced by this colony through the 115 days of the survey is represented in figure 3.

From table 1 and figure 2 it will be seen that from February 12 to 25, this colony persisted in the nomadic behavior condition, with large daily raids of two or three tree-like systems of columns the rule, and (with only one exception) nightly bivouac changes. The exception occurred on February 15, when the colony was bivouacked somewhere in the lower part of a great mass of brush accumulated in a bend of Lutz Creek. The non-occurrence of a bivouac change on that day cannot be attributed to any lowering of the general colony excitation level, because the raiding was no less vigorous than it had been on the preceding days. Rather, the failure to move seemed attributable to an unusual concurrence of return traffic throughout the late afternoon and early evening, which broke up the exodus into spurts of variable strength and duration. On the following day a typical movement occurred from this site.

Each of the bivouac changes of this nomadic period took place over one of the principal trails developed in the given day's raiding, with the exception of the movement on February 16 which occurred over an extension on that day of a route which was begun on the preceding day, when no bivouac change occurred. The movements all were fairly lengthy, ranging over distances between 110 and 240 meters. For the most part, each afternoon exodus underlying a bivouac-change movement (Schneirla, 1938) was well under way by dusk, so that by 8:00 P.M. the movement of the colony uniformly was definitely committed to a given route (among the three principal trails usually available from the bivouac) and generally

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

The nomadic bivouac of colony '46 B-I, *E. burchelli*, on March 3, 1946, flash-photographed at 9:00 P.M. (Approximate width of bivouac, 55 cm.) At the time, the emigration of the evening was well under way. From the bivouac, which was formed beneath the raised end of a moldy log, a wide column may be seen passing around the lower border of the cluster towards the right side (center) of the photograph. At this time the ants were carrying booty objects, and the first carriage of male larvae had yet to occur

The statary bivouac of colony '46 H-D, *E. hamatum*, flash-photographed on March 18, 1946. (Approximate width of bivouac, 78 cm.) The colony was clustered at the time within a niche below some roots near the top of a low stream bank. The position of this bivouac, unusually exposed for a colony in the statary condition, may be attributed to the relatively high general humidity of the surroundings. A few days later this colony shifted to a concealed situation, evidently close to the deserted place (see text)

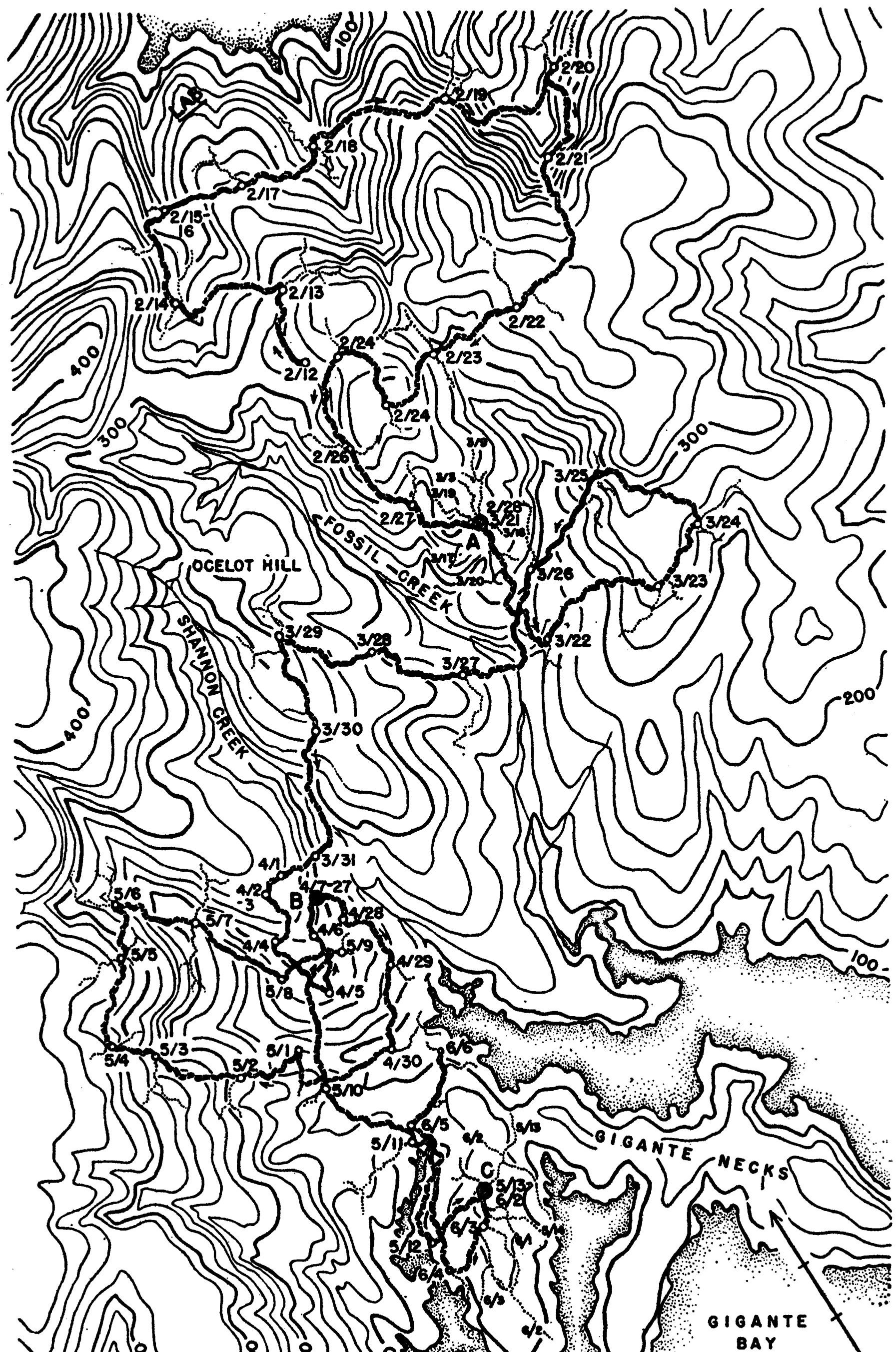

FIG. 2. Eastern portion of Barro Colorado Island, mapped to show the itinerary of colony '46 H-B (*E. hamatum*) during a period of 114 days, February to June, 1946. A, B, C. Double circles indicate successive statary sites; small circles indicate nomadic sites; double broken lines indicate successive routes of emigration; dotted lines indicate the principal routes of some of the daily raiding systems. LAB, laboratory clearing (upper left). Contour interval, 6.1 meters. Scale: Length of the N–S line (lower right corner), 300 meters.

had been completed before 12:00 midnight.

The bivouacs of this period all were single clusters approximating a cylindrical form, located on or close to the ground, depending from surfaces such as the under side of a log or from vines or brush. The clustering places tended to be fairly open situations, with most of the bivouacs exposed on at least one side.

As we have said, on February 12 a very large brood of newly emerged callow workers was found. On the following day a great brood of worker-form individuals in the early larval stage was discovered, in a single mass concentrated near the center of the bivouac. As may be seen from the growth curves in figure 3, the larval development of this brood was completed by February 27, when cocoon spinning on a large scale was observed. The site of that day was the last nomadic bivouacking place of the series, with the colony formed into a regular cylinder beneath a log end on the lower bank of a small ravine.

The queen was observed during the bivouac-change movements of February 14 and February 23, in the contracted condition on both occasions. Although these were the only times she was seen during the series of movements, and no attempt was made to remove her from the bivouac cluster for examination, there is no doubt that she remained contracted throughout the phase.

In this series of 16 days, the colony occupied 15 different bivouac sites, and its movements carried it in a wide, roughly circular course of more than 2500 meters. Since these treks involved much meandering and some major changes in direction and occurred over hilly terrain, this estimate of distance must be considered very inexact. The actual distance covered, beyond doubt, exceeded this estimate.

The last movement of the series, which occurred on the night of February 27, took the colony into the basal hollow of a large broken stump on the southern exposure of a long steep hill about 350 meters to the southwest of Barbour Trail, station 8. Here the ants remained until the night of March 21. Possibly because of the presence of a colony of *E. praedator* bivouacked below the edge of the trunk on the opposite side of the cavity, colony H-B shifted its position about 4 meters on March 2, into the central cavity of the large log of the same broken tree. A regular cylindrical cluster was formed in the cavity about 3 meters from the trunk end of the log. Within this sound hardwood log the colony was so impregnably situated that the regular taking of brood samples was out of the question. Located as it was on the southern exposure of a hill, the general area of this bivouac was quite dry.

After moderately small raids on the first three days of the stay, raiding activity was minimal until March 20. All raids that took place during this period were single-system developments, and on 10 of the 21 days no raids occurred. These raidless days, it should be noted, fell during the central part of the period. A few dozen empty pupa cases were seen on March 17, and the number increased daily until on March 21 brood delivery on a large scale brought out the last of the mature worker pupae. The new brood was large, estimated at more than 20,000 individuals, and was composed entirely of workers. Excluding this new contingent of workers, the adult population of the colony just after this statary period was noticeably very much smaller than at the end of the preceding nomadic phase when the ants entered the log.

There followed a nomadic phase of 17 days, during which large daily raids and regular nightly bivouac-change movements were the rule. The one exception occurred on the morning of March 3, when, following a rather lengthy bivouac change on the preceding evening, the colony shifted just 11 meters from the open position in which it had first clustered under a log, to enter a mass of brush fallen around the standing hulk of a great dead tree. The movement evidently was set off by effects associated with the falling of direct sunlight upon the entire extent of one side of the cluster, and was completed by 11:15 A.M. The raid of that day was a rather irregular one, with numerous short columns which were confined mainly to the area of the brush heap and to the tree hulk from which large quantities of wasp and ant brood were removed. No bivouac change occurred that evening, but virtually all of the ants had returned over the numerous relatively short raiding trails by 7:30 P.M. (The failure of bivouac change arose in a situation which resembled that of February 15, when four rather irregular systems of raiding trails arose from a bivouac housed in a large brush heap.) The bivouacs were somewhat diversified in nature, ranging from fairly regular cylinders under low tree roots (March 22) to an irregular massing near the opening of a mammal burrow (March 29). The bivouacs all were more or less exposed. However, those of the first half of the period tended to be more secluded than later ones, in evident relation to the fact that this part of the itinerary took the colony through a relatively dry area with light cover, in the eastern part of the island. In the first nomadic bivouac on March 21, the colony was found to have a large brood of very young larvae, all worker forms, a brood that developed to larval maturity in the period of nomadic movement and that was enclosed in cocoons on April 5 and 6. On the evening of April 6, at the time this brood was effectively enclosed, the ants carried out their last movement of this series, which took the colony into a complete subterranean cavity beneath a large tree root on the crest of a ravine bank. In contrast to the previous statary location occupied from April 7 to April 26, the general situation of this bivouac was moderately humid. Here the colony remained until April 26, with its bivouac lost to view and inaccessible for the taking of brood samples.

In the ensuing statary phase of 20 days, all raids were single-system forays, and the same bivouac site was retained. On three of the days the colony was not visited, and on 11 of the remaining 17 days raiding developed. In general the raidless days fell during the central part of the period, between the third and the fifteenth days. The one exception occurred on April 23, when no columns were found outside the immediate area near the bivouac when the site was visited at 10:30 A.M. However, the colony became disturbed when I made various fruitless attempts to take brood specimens, and a regular column foray began which presently developed into a fairly definite, although small, raiding system. From this beginning, a raid developed during the day. The raids of this statary period were uniformly small, single-system affairs. When raids occurred on successive days they tended to push out in somewhat different directions, generally with at least a 90° difference in the angle of the chief direction of exodus. Pupa cases were observed in small numbers after April 23, heaped immediately outside the crevice under the root which provided a complete cover for the bivouac. The number of empty cases increased greatly late on April 25 and reached its peak late on April 26. Then, with most of the mature brood out of its cases, the colony staged a vigorous raid in which three principal trail systems developed. Although the bivouac-change movement was well under way by early evening, with great numbers of recently emerged callow workers clogging the lines and tending to cluster at trail junctions, despite the wide extent of the raiding lines the new bivouac lay only 35 meters from the abandoned statary site.

There followed a representative nomadic phase of 16 days, which lasted until May 13. The daily forays, all large, were with only two exceptions three-system developments. Much of the activity of this period took place on the long steep hill to the east of Wheeler Trail between stations 17 and 25, in which the character of the forest offered extensive opportunities to raid insect nests in trees as well as to raid and travel along elevated vine routes. Because of the irregular nature of the terrain in this area, cut by deep arroyos, it happened frequently that an extensive part of a migration route followed a principal raiding trail which ran well above the ground for considerable distances over interlacing vines and tree branches. Mapping the raiding systems and tracking the movement often became a time-consuming process. The bivouac-change movements were generally under way at dusk and were completed during the evening well before 11:00 P.M. as a rule. Frequently the new bivouac cluster was found in a well-formed condition, with a considerable part of the colony already in the new cluster, as early as 8:00 P.M. In fact on two occasions the bivouac of the day had completely disappeared, and the major part of the colony had completed the movement at 7:00 P.M. Such events encouraged the practice of visiting the colony twice daily, with special emphasis upon a thorough morning survey of the raiding system in order to know the possible lines of migration sufficiently well to

TABLE 1

GENERAL RECORD OF BIVOUAC-CHANGE MOVEMENTS OF COLONY '46 H-B, *E. hamatum*

1946	Raiding Systems	Bivouac Change First Observed at	New Bivouac Begun at[a]	Distance of Movement (in Meters)	Special Notes
Feb. 12	2	6:15 P.M.	—	120	Pupa cases at abandoned site
13	3	4:15 P.M.	6:15 P.M.	140	Callow workers; early worker larvae
14	3	6:30 P.M.	—	125	
15	2	—	—	(No movement)	Bivouac in brush heap. Four basal routes
16	3	2:00 P.M.	6:00 P.M.	190	Queen observed in bivouac change (contracted)
17	3	5:45 P.M.	—	225	
18	3	7:50 P.M.	—	210	
19	3	7:50 P.M.	—	160	
20	2	6:30 P.M.	—	125	
21	3	6:20 P.M.	—	260	
22	3	6:55 P.M.	—	200	
23	3	8:00 P.M.	—	150	
24	3	6:45 P.M.	—	165	Bivouac 80 cm. from ground in fallen tree
25	3	8:50 P.M.	—	110	
26	3	6:30 P.M.	7:10 P.M.	165	Bivouac change crossed *E. burchelli*
27	2	6:45 P.M.	—	140	Mature worker larvae, spinning cocoons
28	1 E, NE	None	—		Bivouacked in cavity of large stump
Mar. 1	1 S	None	—		
2	None	None	—		
3	1 N	None	—		
4	None	None	—		
5	None	None	—		Bivouac shifted 2 m. into hollow log
6	None	None	—		
7	None	None	—		
8	(Not visited)	None	—		
9	1 N (weak)	None	—		
10	None	None	—		
11	(Not visited)	None	—		
12	None	None	—		
13	None	None	—		
14	None	None	—		
15	1 E (weak)	None	—		
16	1 SE	None	—		First empty pupa cases outside log
17	1 W	None	—		Fairly vigorous raid
18	None	None	—		
19	1 NW	None	—		
20	1 S	None	—		Vigorous raid

[a] A value is set down in this column only on days when the effective beginning of the bivouac-formation process was observed.

TABLE 1—*Continued*

1946	Raiding Systems	Bivouac Change First Observed at	New Bivouac Begun at	Distance of Movement (in Meters)	Special Notes
21	2	6:35 P.M.	—	110	
22	3	6:40 P.M.	—	320	Broods: callow workers; early worker larvae
23	3	7:00 P.M.	—	160	
24	3	6:00 P.M.	—	155	
25	3	6:35 P.M.	—	200	Bivouacked in mammal burrow
26	2	6:00 P.M.	7:15 P.M.	200	Queen observed in bivouac change (contracted)
27	3	7:00 P.M.	—	150	Two cylinders beside tree Dealate male seen at bivouac
28	3	6:40 P.M.	—	—	
29	3	7:20 P.M.	—	—	
30	3	7:15 P.M.	—	230	
31	3	7:30 P.M.	7:40 P.M.	160	
Apr. 1	3	6:40 P.M.	—	30	Major traffic block in bivouac change
2	3	6:45 P.M.	8:00 P.M.	170	
3	4 (short)	11:00 A.M.	—	15	No evening movement
4	2	7:20 P.M.	7:40 P.M.	180	
5	3	6:30 P.M.	6:55 P.M.	160	Cocoon spinning by mature larvae
6	3	6:40 P.M.	—	60	
7	1 NE	None	—		Bivouac concealed beneath large tree root
8	1 SE	None	—		
9	1 NW	None	—		
10	None	None	—		
11	1 SW, S	None	—		Small raid
12	None	None	—		
13	None	None	—		
14	None	None	—		
15	None	None	—		
16	1 E	None	—		
17	1 SE	None	—		
18	None	None	—		
19	1 NW, N	None	—		
20	None	None	—		
21	1 NE, N	None	—		Fairly vigorous raid
22	1 SW	None	—		
23	None	None	—		Raid started artificially
24	(Not visited)				
25	1 SE	None	—		Numerous empty pupa cases
26	1 SE	None	—		
27	3	6:30 P.M.	6:50 P.M.	30	
28	3	7:00 P.M.	7:15 P.M.	170	Callow workers; early worker larvae
29	3	6:35 P.M.	6:50 P.M.	140	
30	3	7:05 P.M.	7:20 P.M.	170	
May 1	3	6:45 P.M.	—	130	
2	3	7:30 P.M.	7:50 P.M.	150	

TABLE 1—*Continued*

1946	Raiding Systems	Bivouac Change First Observed at	New Bivouac Begun at	Distance of Movement (in Meters)	Special Notes
3	3	6:40 P.M.	7:05 P.M.	125	
4	3	7:00 P.M.	—	175	
5	3	6:30 P.M.	—	190	
6	2	6:40 P.M.	9:00 P.M.	120	Bivouac change interrupted by crossing a *burchelli* movement
7	3	6:30 P.M.	7:00 P.M.	180	
8	3	6:55 P.M.	7:35 P.M.	140	Two-cylinder bivouac under log
9	3	3:00 P.M.	—	190	
10	3	6:20 P.M.	7:25 P.M.	140	
11	3	7:00 P.M.	—	180	Cocoon spinning by mature larvae
12	3	8:30 P.M.	9:20 P.M.	140	
13	1 NE	None	—		Bivouacked well back under low log
14	1 S, SW	None	—		
15	1 S, SW	None	—		May 13, dealated male seen at bivouac 8 P.M.
16	None	None	—		Spinning evidently completed
17	None	None	—		
18	(Not visited)				
19	(Not visited)				
20	None	None	—		
21	(Not visited)				
22	None	None	—		Bivouac cluster more exposed
23	(Not visited)				
24	None	None	—		
25	(Not visited)				
26	None	None	—		
27	(Not visited)	None	—		
28	1 W	None	—		Raid started artificially at 10:40 A.M.
29	(Not visited)	None	—		
30	None	None	—		
31	1 S	None	—		
June 1	1 SW	None	—		Empty pupa cases seen
2	3	6:35 P.M.	—	40	
3	2	7:10 P.M.	8:05 P.M.	110	Callow worker brood. Early worker larvae
4	2	6:35 P.M.	8:30 P.M.	185	Under fallen tree mass
5	3	5:30 P.M.	6:00 P.M.	130	Took queen (contracted) and larval worker brood

hunt down the colony should it "slip away" in the early evening before I could reach the spot. The last movement of the series, that of the night of May 13, was the most complex of all in the sense of frequent traffic disturbances and changes in the direction of principal exodus from the bivouac. It was not until 9:00 P.M. that traffic was clearly directionalized to the east along a considerable part of the route with the other two raiding systems steadily emptying their traffic into the bivouac. The delay and difficulty were partially attributable to the fact that late in the afternoon an *E. rogeri* raid cut for some time the path of the principal raiding system of colony H-B on which an exodus had started. Conditions internal to the colony appeared to be mainly responsible for the irregularities in the exodus.

With the exception of the first movement of the series, the treks were all extensive ones, between 110 and 300 meters in length from the old bivouac to the new site. It is probable that a total distance of more than 2700 meters was covered in this series of movements. In the section of the island covered in this series of moves the forest cover is good for the most part, and there were many humid localities available. The bivouacs formed in places such as beneath large logs were all fairly well in the open, even in two cases when the cluster was established in the entrances to mammal burrows.

The queen, when observed in the course of migration late in the series, was healthy in appearance and in the contracted condition. On the night of May 13 during the first evening in the statary bivouac site on Gigante Hill, a fully dealated *hamatum* male was observed among the workers that were gathered on a flat surface near one end of the bivouac log. In the notes he was described as "just hanging around" among the workers. This male was not seen again, despite frequent visits to the bivouac both by day and night.

The statary bivouac was established under a low moldy log on the north side of Gigante Hill. The cluster was elongated in conformity with the long shallow chamber under the log. In the first few days only a small part of the cluster could be seen, but then it began to be somewhat more exposed all along its front, until in the last third of the period the mass of ants actually bulged outward throughout its exposed width. During the last week of the stay there was a pronounced shifting of the mass towards one end of its chamber. The colony was visited on 13 of the 20 statary days, and on six of these days no raiding was observed. Indicative of the pronounced reduction of raiding even for a statary colony in the dry season, three of the seven raids that were observed took place in the first three days of the period, and two of the remaining ones were started artificially towards the end of the period by my puncturing the bivouac surface to take brood samples. It is possible that on a few occasions, after raidless mornings, a raid may have begun in the afternoon. In any case, it is clear that the central part of the statary period was an interval in which raiding activity was at an ebb.

The mature worker brood evidently began to emerge on May 31, when a few dozen pupa cases were observed at the base of the bivouac. On June 1 and the following day the number had increased greatly, and when the colony moved on the evening of May 2, virtually all of the mature brood of pupal workers had emerged from the cases.

The first bivouac-change movement of the new series was a relatively short one, as is rather typical for that movement. On June 2 and the three following days, until the study was concluded, the daily raids were vigorous ones, involving two or three principal trail systems, all much more vigorous than the best-developed raid of the preceding statary period. The bivouac-change movements were under way relatively early in the evening and after the first day extended over distances greater than 110 meters. The bivouac clusters were all well exposed.

After the movement was nearly completed on the night of June 5, once the queen had been taken as she neared the new bivouac, the mass of the colony was etherized in its position as a regular cylinder beneath a log. While the ants were under ether the population was examined in detail; then the single queen, a large portion of the new brood, and a considerable portion of the adult population, including young callow workers of the brood lately emerged, were taken for appropriate preservation. The young brood was a large one, all very young worker larvae in

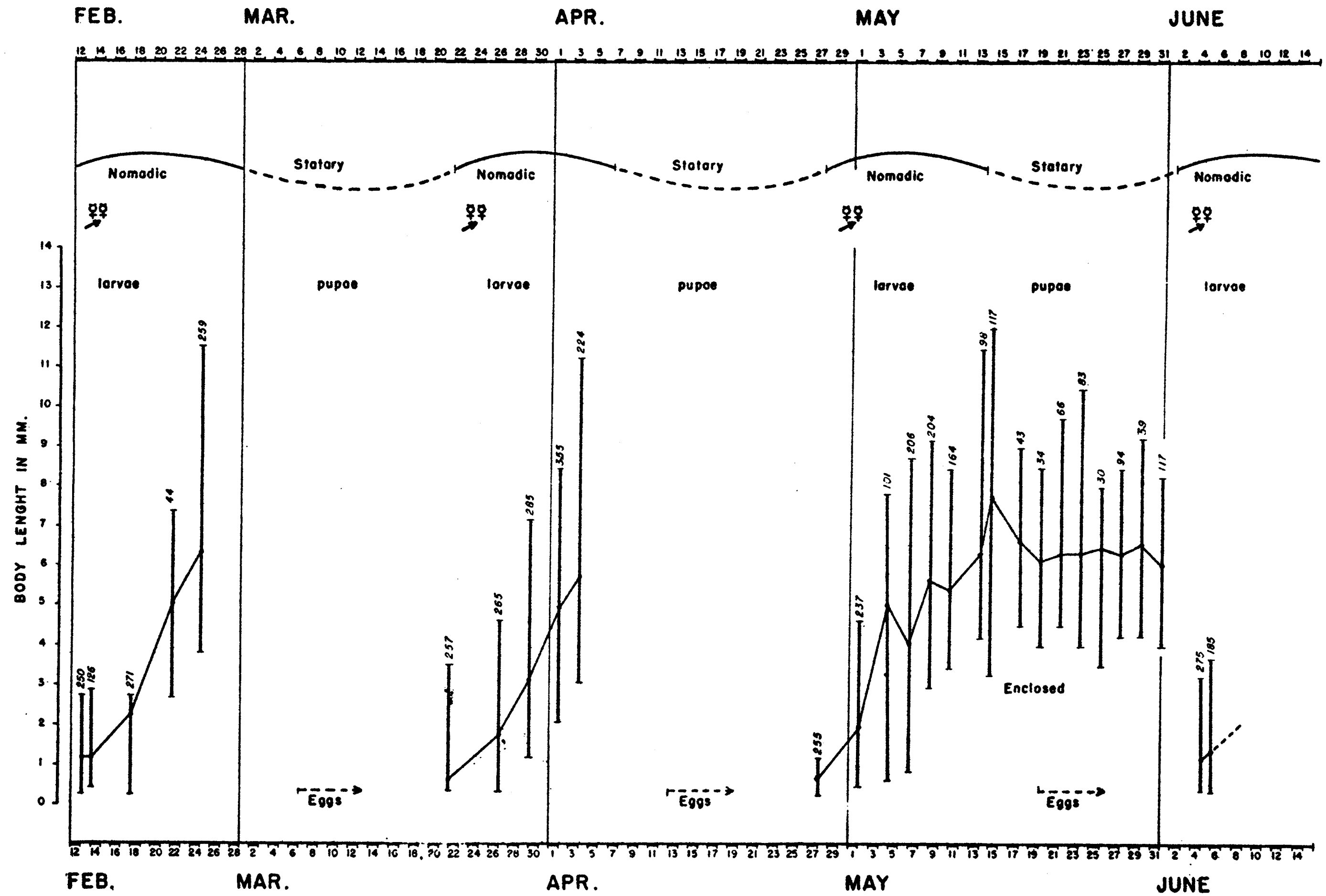

FIG. 3. Record of colony '46 H-B, *E. hamatum*. Behavior changes are indicated (above) as phases of the nomad-statary cycle, and correlated brood changes (below) are expressed in terms of body lengths in samples taken at intervals through the cycles. For each brood sample, a vertical line expresses the range of body lengths (numbers indicate sizes of respective samples); the curve connects the means of successive samples; and the time of appearance of successive worker broods as callows is indicated by appropriate symbols below the nomadic-statary curves.

the characteristic polymorphic distribution. Without much question the colony, if undisturbed, would have completed the nomadic phase in regular fashion, during the larval development of the new brood.

Colony H-B was studied for a continuous sequence of 115 days. During that time it ranged widely over an area comprising nearly one-fourth of the island, following a somewhat rambling course. Its itinerary involved a number of changes in direction as well as actual loops. It is estimated that in its bivouac-change movements from February 12 to June 6, the colony traversed a total linear distance of more than 8500 meters. One consistent feature of its travels was the fact that this colony never raided on its back trail for longer than the early part of a given morning, and that consequently all bivouac-change movements occurred on some other line than the path of the preceding night's approach to the bivouac. In general, each successive movement was likely to diverge by at least 60° from the approach route. The result was that the successive statary bivouac sites, from which the colony raided during a twenty-day stay in each case, were well separated from one another.

During the 115 days of this study only one queen was present, as inspections of the bivouac-change columns at well-separated intervals demonstrated. This queen was regularly functional in a cyclic fashion, a circumstance clearly indicated by the facts of brood production (fig. 3). At the end of the investigation on June 6, as mentioned above, the H-B queen was fixed and preserved for subsequent examination. The specimen was subsequently sectioned and prepared by Dr. Roy Whelden, who is engaged in a study of similar material. With the kindness of Dr. Whelden the following preliminary description of the terminal condition of queen H-B is available for use in the present connection:

"Spermatheca full of tangled sperms. Ovarioles: Lower ends collapsed, often with what remains of disintegrated eggs; upper ends full of small dense cells with many eggs in various early stages of enlargement; no nurse cells present. (Fixation fair.)" The condition of this queen might be characterized as that of a functional individual whose reproductive apparatus is passing through a "resting phase."

The schedule of brood production was as given in table 2, summarized in terms of the respective dates on which pupation and the appearance of each brood as callows were terminated.

TABLE 2

Brood Production Intervals in Colony '46 H-B

Date of Appearance of Successive New Callow Worker Broods	Interval Between Broods (Days)
Feb. 12	—
March 20	37
April 26	37
June 1	36

The first two of the inter-brood intervals were 37 days in duration, and the third was 36 days—an indication of great regularity in the basic brood-production processes of the queen herself. As we have said, the presence of just one queen was established by the inspection of the bivouac-change column at regular intervals, and finally by a thorough search of the colony.

Contrary to the results of studies with numerous other ecition colonies during this period, colony '46 H-B produced only worker broods and no male brood during the entire period of study. All of the four worker broods were large; each of them was estimated to contain a minimum of 20,000 individuals. Thus the colony was increased by a minimum of 80,000 new workers during the 115 days of study, and at the end a fifth brood of similar magnitude was in development. No division of the colony occurred, yet the estimated final size of the population was considerably less than the sum of the estimated population total at the outset plus the estimated total of individuals in the completed broods. Evidently the colony suffered a high mortality rate in its workers during this interval of time.

Dealated males were found in the colony on two separate occasions, and in the light of considerations to be discussed in a later connection, it is possible that a re-insemination of the colony queen may have occurred at some time during the dry season.

The general activity changes of the colony are summarized in table 3.

TABLE 3

DURATION OF SUCCESSIVE PHASES OF THE ACTIVITY CYCLE (COLONY '46 H-B)

Nomadic Phase (Large Daily Raids; Nightly Migrations)	Duration (in Days)	Statary Phase (Small Raids; No Bivouac Changes)	Duration (in Days)
Feb. 12 to Feb. 27	16	Feb. 28 to Mar. 30	21
Mar. 21 to Apr. 6	17	Apr. 7 to Apr. 26	20
Apr. 27 to May 12	16	May 13 to June 1	20
June 2	—		

Thus nomadic and statary phases occurred in regular alternation throughout the period of study—in other words, throughout the greatest part of the dry season. In their durations these phases were strikingly constant, the nomadic phases lasting 16 to 17 days, the statary phases 20 to 21 days.

These facts concerning the synchronization of broods agree in every important respect with the time relations of broods prevalent under rainy-season conditions. Further in agreement with the general pattern of rainy-season conditions, the time relations between the condition of successive broods and major changes in colony behavior were quite regular. From table 1 and figure 3 it will be seen that at the beginning of every nomadic phase in colony behavior a mature brood of callow workers was removed from cocoons, and at the same time a new brood of very young larvae was present. Then during the nomadic phase this new brood ran the course of its larval development to maturity, and a statary condition of the colony set in when the effective enclosure of this brood was completed.[1] It may be seen from tables 1 and 4 that the colony in each of the three statary phases staged raids on the first two and the last two days. In these records we find an indication that the dropping off of raiding is sharp after the first two statary days, and that thereafter raiding is sparse through the intermediate part of the period, with a clear increase in the frequency of forays in the last days before the colony becomes nomadic.

As the detailed report of colony behavior has shown, colony H-B invariably staged a large raid of two or (usually) three identifiable trail systems on each day of the nomadic interval, a raid which had its first beginnings at dawn and which after dusk passed over into a complete exodus of the colony to a new bivouac site. From this new location the foray of the following day was developed. The nightly bivouac-change movement failed in only two cases during the total of 53 days in the nomadic condition, and these were days of separate nomadic phases when somewhat exceptional conditions were involved. With no exceptions the raids that occurred during the respective statary phases were all small affairs typically involving the formation of but one identifiable trail system. There was a surprising total of statary days on which no raids occurred—20 instances in 49 days of observation. Two of the observed raids were set off artificially. Frequently, in the intermediate statary days, there were successions of two or more days without any forays.

With few exceptions the bivouacs of the nomadic phase were located on the surface of the ground, in a more or less exposed position, typically under raised logs, under vines, or against trees. There was a greater tendency towards forming subterranean or more secluded bivouacs when the colony was on the move through the eastern part of the island, which in general presented a drier forest floor because of lighter cover than in other sections. All three of the statary bivouacs were definitely more withdrawn into covered places

[1] By effective enclosure is meant the completion of the thin covering envelopes generally begun on surfaces close to the bivouac, but completed into heavier cocoons within the bivouac during the early days of statary life.

TABLE 4

FREQUENCY OF DAILY RAIDING ON SUCCESSIVE DAYS DURING THE STATARY PHASES OF COLONY '46 H-B (SUM FOR THREE PHASES)

Statary Day	Days on Which Raids Occurred	No Raid	Not Visited	No. of Raids (Length of Each Interval, in Days, in Parentheses[a])	Percentage: Days of Raiding (Two-day Intervals)
1	3				
2	3			6 (6)	100
3	2	1			
4	1	2		3 (6)	50
5	1[b]	2			
6	0	2	1	1 (5)	20
7	0	1	2		
8	0	2	1	0 (3)	0
9	0	1	2		
10	2[c,b]	1		2 (4)	50
11	1	1	1		
12	0	2	1	1 (4)	25
13	1	1	1		
14	0	2	1	1 (4)	25
15	1	1	1		
16	3[c,b,d]			4 (5)	80
17	2[d]		1		
18	1	1	1	3 (4)	75
19	2				
20	3			5 (5)	100

[a] The percentage for each two-day interval is derived from the ratio of number of raids observed to the total of days visited.
[b] Raid exceptionally weak.
[c] Late beginning.
[d] Artificially started.

than were nomadic bivouacs. In the first two statary phases the colony was so effectively withdrawn into completely enclosed cavities that no samples of the brood could be collected.

COLONY '46 B-I, *E. burchelli*

This colony was found on February 7 at 9:15 A.M. near Shannon Trail, station 2. Its bivouac cluster was pouched in the central hollow of a large tree, massed approximately 3 meters from the ground at a point where the lower half of the large bag-like cluster was clearly framed in a vertically extended elliptical knothole. From the fact that an immense brood of mature worker larvae was present, with clear signs that the completion of enclosure in cocoons had just occurred with spinning of cocoons still in evidence, the colony was judged to be in the first or possibly the second day of a new statary phase (see fig. 4). A swarm raid of intermediate proportions was in progress towards the east, and after dusk there was a general return of the raiders into the bivouac. Because indications of a very recent onset of the statary condition were clear, this colony was taken for study to represent the species in a continued survey. The study ended on June 11. The general record of colony B-I is summarized in table 5 and figure 4.

The colony remained in the described statary situation until February 28, with no changes except limited shifts in the height of its bivouac. The raids that occurred were swarm raids of relatively small magnitude from which a general return occurred after dusk as a rule, completed during the evening hours. There were 10 all-day raids ending in evening returns, one raid that ended early in

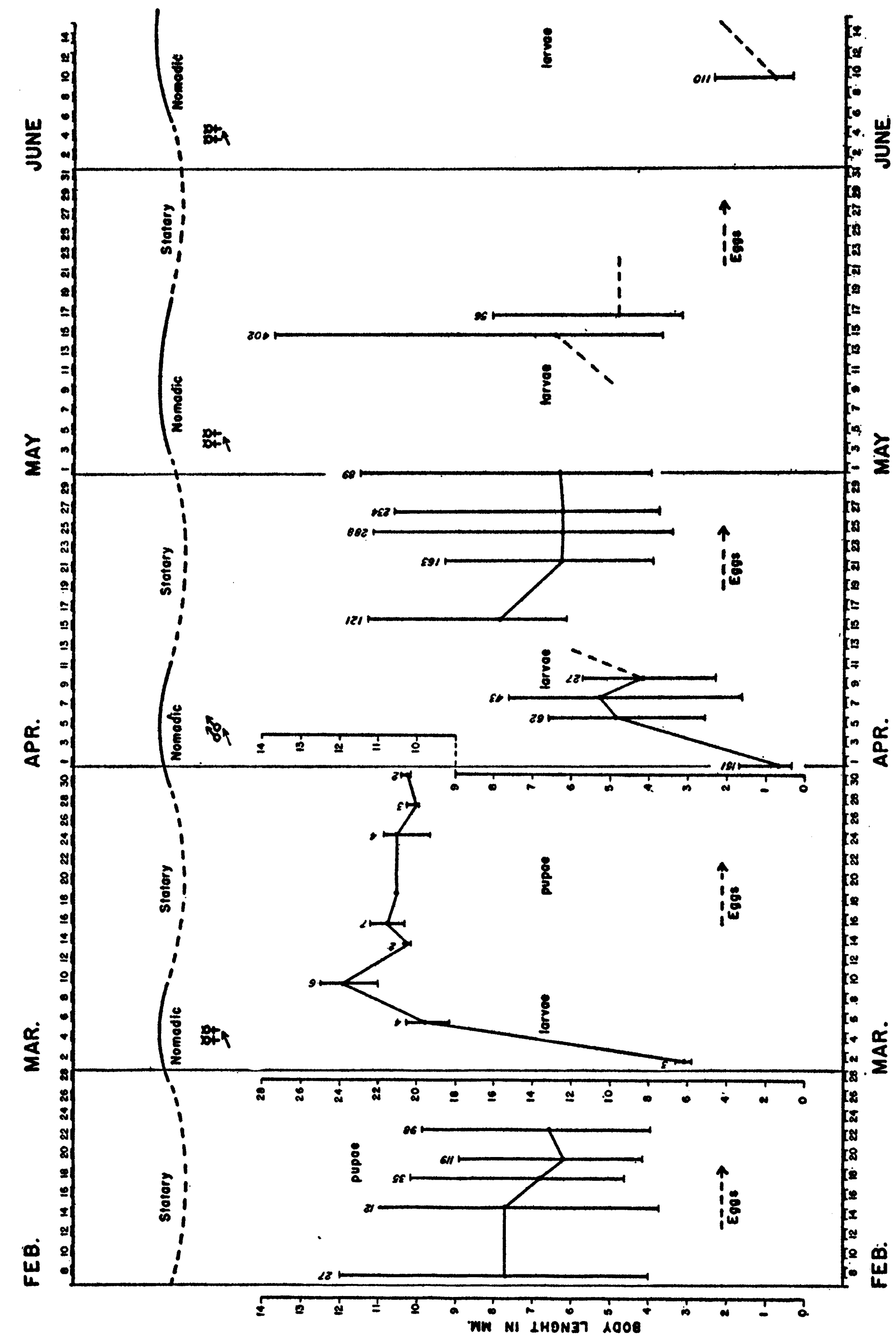

FIG. 4. Record of colony '46 B-I, *E. burchelli*. Behavior changes are indicated (above) as phases of the nomad-statary cycle, and correlated brood condition (below) is expressed in terms of body lengths in samples taken at intervals through the cycles. For each brood sample, a vertical line expresses range of body lengths (numbers indicate sizes of respective samples); the curve connects the means of successive samples; and the time of appearance of successive broods as callows is indicated by appropriate symbols below the nomadic-statary curves. (Note reduction in scale of ordinate for samples of the male brood. Because of sampling difficulties, the last broods are incompletely represented.)

the afternoon and three others that did not begin until early afternoon, one raid set off artificially, and seven raidless days. From table 5 (cf. table 9) it is clear that the days of minimal raiding or of no raiding began after the fourth day of observation and fell largely in the middle of the phase. During the last four days of the stay at this site the daily raids became heavier, as indicated not only by the width of their swarms and the frequency of swarm division as well as ground covered in daily forays, but also by the fact that the night-time returns became noticeably more protracted. The brood passed through its prepupal and pupal development, and on February 24, five days before the phase ended, empty pupa cases began dropping and newly emerged callows were seen in the bivouac walls. This activity neared its peak on February 26, 27, and 28, and on the bivouac-change movement of February 28 that followed a large raid, only a few thousands of cocoons (predominantly of minor worker castes) were seen carried in the procession. These were opened at the first nomadic bivouac during the following day.

The colony was nomadic for just 10 days, until March 10. Surprisingly enough, after the vigorous raids and fairly extensive bivouac-change movements of the first two days, there occurred four days of somewhat depressed general activity. The raids were only moderately extensive during this interval, and on March 2 no bivouac change occurred, while on the following three days the movements were of limited scope. Thereafter an increase to a final high point in the vigor of raiding was noticed, and the nightly bivouac changes were all fairly extensive (pl. 1). The colony, already very large before the new brood of callow workers had been added to its population, now was so large that the bivouac clusters were massive and the nightly movements very time consuming. The bivouacs were all exposed above ground, with the exception of the final nomadic cluster which was formed completely below the surface in a mammal burrow. Typical formations were clusters of roughly cylindrical shape beneath logs, or masses formed against buttressed tree roots.

On March 2 for the first time it was possible to find specimens of the new brood, which was then massed in a few packets in the very center of the large bivouac cluster. At that time the larvae were relatively small, although even then equal in size to mature larvae of major workers, and there appeared to be only a few thousand of them. This brood proved to contain only male larvae, as far as could be ascertained, and probably no more than 3000 individuals finally emerged from it as winged adult males. The larvae, all of approximately the same size, grew very rapidly. In four days after discovery they were fairly well distributed through the bivouac and had become a source of special transport difficulties, accounting for peculiar developments in the bivouac-change movements (Schneirla, 1948). On March 8 the spinning of cocoons among these larvae was observed; partially enclosed larvae were observed on the movement of March 9, and spinning seemed to be at its height on this night and the following day, which was the first at the new statary bivouac site.

In its movement of March 9 the colony entered a large, hollow, lightning-split tree near the bank of Barbour-Lathrop Creek (below Barbour-Lathrop station 3) in which it remained until about March 30. Enclosure of the bulky male larvae seemed to have been completed on March 13, at least so far as activities outside the bivouac were concerned. The bivouac, which was formed in the hollow interior of the "fireplace tree," at first took the form of a large pouch established with its lower curve just opposite the edge of a large triangular opening at the base of the tree. Subsequently its position changed day by day in that it was shifted upward or downward through a distance of less than a meter. These changes evidently occurred in relation to prevalent atmospheric conditions. After March 25 the bivouac formed a large mass which was clustered against the broad rear wall of the tree, at times with its lower edge touching the ground.

On the 17 days visits were paid to the bivouac place, there were nine moderately developed all-day raids, one raid that developed in the afternoon, and seven days on which no raiding occurred beyond a swarming of short duration around the base of the tree early in the morning. It will be noted in table 5 that the raidless days occurred after the fourth

TABLE 5

General Record of Bivouac-change Movements of Colony '46 B-I, *E. burchelli*

1946	Raiding Systems	Bivouac Change First Observed at	Bivouac Begun at	Distance of Movement (in Meters)	Special Notes
Feb. 7	E				2 meters up in open hollow tree
8	S, SE				
9	N				Newly enclosed mature worker larvae
10	W				
11	None				
12	SW				Afternoon beginning of raid
13	NW				Afternoon beginning of raid
14	None				
15	None				
16	SE				Morning only
17	None				
18	None				Raid started artificially in mid morning
19	None				
20	W, NW				
21	W				Afternoon beginning
22	NW				
23	None				
24	N				
25	SW, W				First empty pupa cases seen
26	E				
27	NE				Raiding traffic still returning to bivouac at 9:30 P.M.
28	NW	8:00 P.M.		130	Many unopened cocoons carried
Mar. 1	N			80	Large callow worker brood
2	NW (weaker)	No bivouac-change movement			Brood of early male larvae found
3	N	7:15 P.M.		35	
4	N, NW	9:00 P.M.		20	Took several dealated males in bivouac-change column
5	E	7:45 P.M.		8	
6	W, NW	7:20 P.M.	8:15 P.M.	180	
7	SW (second raid to N)	6:30 P.M.		85	
8	E, NE	6:15 P.M.	10:15 P.M.	138	
9	NE, N	6:15 P.M.		180	Bivouac well inside mammal burrow. Movement lasted until 9:15 A.M., Mar. 10
10	NW				Clustered 1 meter up in open hollow tree
11	NW, N				
12	S, SE				Cocoon spinning by mature male larvae

TABLE 5—*Continued*

1946	Raiding Systems	Bivouac Change First Observed at	Bivouac Begun at	Distance of Movement (in Meters)	Special Notes
13	SE				
14	None				
15	None				
16	None				
17	(Not visited)				
18	(Not visited)				
19	None				
20	(Not visited)				
21	E				Bivouac lower in tree
22	(Not visited)				
23	(Not visited)				
24	(Not visited)				
25	S				Raiding started 8:30 A.M. Cluster much lower
26	(Not visited)				
27	None				Signs of cocoon opening. Cluster near ground
28	S				
29	W, also NE				Cluster forming just outside tree
30	SE, also NE				
31	S, also N	6:00 P.M.		30	Colony division begun
Apr. 1	SE, also NW		6:00 P.M.	40	Colony division blocked. Queen B-I,n taken
2	S, SE, also N		8:15 P.M.	150	
3	N, NE		No bivouac-change movement		
4	NE		9:15 P.M.	150	
5	N (began 1:30 P.M.)		9:00 P.M. (to NE)	85	No raiding in morning
6	N, NE		No bivouac-change movement		
7	SE, S		8:00 P.M.	140	
8	SE		No bivouac-change movement		
9	NE, also SE		7:30 P.M.	80	
10	N, also E		8:15 P.M.	90	Bivouacked in end of hollow log
11	NE		No bivouac-change movement		2 meters up in fig tree
12	E (very large)		8:30 P.M.	105	
13	E				Clustered 1 meter up in open hollow tree
14	W				Large, newly enclosed brood mature worker larvae
15	SE				
16	NW				
17	W, NW				
18	None				

TABLE 5—*Continued*

1946	Raiding Systems	Bivouac Change First Observed at	Bivouac Begun at	Distance of Movement (in Meters)	Special Notes
19	SW (small)				
20	None				
21	None				
22	None				Bivouac bulged outward
23	None				
24	(Not visited)				
25	None				Bivouac extended farther downward
26	(Not visited)				
27	None				Bivouac somewhat expanded
28	(Not visited)				
29	(Not visited)				
30	W				Cluster extended farther downward
May 1	SE, S		8:30 P.M.	50	Movement of colony, but no cocoons open as yet
2	SW				Beneath root mass of large fallen tree
3	S				Cocoon opening extensive
4	N		9:00 P.M.	55	Large part of brood transported, unopened
5	NW		8:00 P.M.	160	
6	SW		9:10 P.M.	170	Callow worker brood nearly all emerged
7	E, later NE		8:20 P.M.	180	
8	NW, W		9:20 P.M.	135	Large brood early worker larvae
9	NW, N		8:30 P.M.	155	Large, elongated cylinder under log
10	W, SW		7:55 P.M.	150	
11	SW			160	
12	W, SW		9:45 P.M.	120	
13	SE		No bivouac-change movement		General return of raiders at 8:00 P.M.
14	E, also NW		9:00 P.M.	60	Bivouac change greatly delayed
15	NE, E		8:00 P.M.	160	Took queen from bivouac-change column
16	SE		No bivouac-change movement		Returned queen after 24 hours in laboratory. Clustered near end of large hollow log
17	N		No bivouac-change movement		
18	E, NE		9:00 P.M.	140	
19	NW (moderate)				Clustered 3 meters up in large hollow tree
20	NE, E				
21	W				
22	(Not visited)				

TABLE 5—*Continued*

1946	Raiding Systems	Bivouac Change First Observed at	Bivouac Begun at	Distance of Movement (in Meters)	Special Notes
23	None				
24	(Not visited)				
25	N (weak)				
26	(Not visited)				
27	S, SE (weak)				
28	(Not visited)				
29	(Not visited)				
30	(Not visited)				
31	SW (weak)				
June 1	(Not visited)				
2	None				
3	S, SW				
4	SW				All raiders returned by 9:00 P.M.
5	N				Empty pupa cases at bivouac tree
6	SE				Bivouac cluster bulged to outside
7	SW		8:15 P.M.	85	Nearly one-third of pupal brood still enclosed
8	NE		No bivouac-change movement		Immense brood of early worker larvae. (In the afternoon captured more than half of it)
9	E		No bivouac-change movement		
10	E		7:30 P.M.	65	
11	NE		6:30 P.M.	105	Removed queen (contracted) from bivouac-change column

day and in general during the intermediate part of the period. Meanwhile the male brood passed through its prepupal and pupal stages, and late on March 25 callow alate males began to emerge. Events then became rather confused, so that the designation of March 30 as the final day of this statary phase is somewhat arbitrary although circumstantially justifiable.

Actually a considerable portion of the colony moved out of the hollow tree on the nights of March 28 and 29, to begin forming a wide cylinder under the overhanging edge of a large log just 3 meters from the statary site (X), the "fireplace tree" itself. On the following night this cylinder grew, although at least three-fifths of the colony remained at site X in the statary bivouac tree. On the night of March 29 there was a further exodus from the large cluster (N) under the large log to a new cylinder (N-1) beneath a smaller log about 5 meters uphill to the northeast. This last movement, together with a continued exodus from the statary bivouac towards the west to the base of a tree under which a concealed bivouac was formed, completely exhausted the cluster N during the night. However, on March 30 a large cluster remained at the statary site in the tree. That evening a movement was under way from N-1 to a new cluster (N-2) about 25 meters from the tree; the movement to the west continued, and a new exodus from the tree cluster had begun to a site (S-1) at which a cylinder was forming, about 6 meters from the bivouac to the south. Male cocoons in considerable numbers, still unopened, were being moved in all three columns from the tree, and in the evening numbers of alate males were observable in the columns N and S in particular. In the morning the statary bivouac site X was completely cleared of *E. burchelli*.

On March 31 large raids occurred to the north from bivouac N-2 and to the southeast from bivouac S-1. These bivouacs were connected by a weak column following the original outgoing raids and hence passing through the abandoned statary bivouac site. From the third (concealed) cluster at W, ants returned to X in a single column, and there they emptied into one of the two available trails in use, going either to N or to S. During the day there was a raid to the north from N-2 and to the southeast from S-2. The evening found a further exodus under way from each of the new bivouacs to new bivouac sites at N-3 and at S-2, respectively. At the same time the withdrawal from W into the base columns moving towards N-3 and S-2 was completed. The segments N-3 and S-2 raided divergently on April 1, and in the evening an exodus took place from each of them. On April 2 it had become clear that the colony had nearly completed a division into a principal segment at S-2 and a smaller segment at N-3; these two segments then were more than 125 meters apart and connected only by a rapidly thinning column of ants on the back trails to the statary bivouac site. Each of the new clusters served as the base of a new raid beginning on the morning of that day.

When the N-3 segment was etherized at midday, it was found to contain in addition to the worker population a few masses of very young (worker) larvae, a single queen, a few hundred alate males, and not more than 100 unopened male cocoons. For reasons that will be reported in a separate connection, this entire series of events may be regarded as a case of true colony division, with N-1-2-3 the minor segment and W a section which for some reason did not break away from the rest of the colony despite a beginning of that process. On the evening of April 2 the N-3 segment, minus the queen and brood which had been removed at midday, began to move back towards the statary bivouac site and thence along the trail leading into S-3, which it joined during the night. Thus on April 3 the colony was reunited at S-3, from which a large foray led to the north.

Subsequent events demonstrated that the S-segment and the queen that remained in it may be considered the basic part of the colony; the N-segment a secondary offshoot centered around a young queen. The study continued with the S-segment, augmented by the N-segment.

Colony '46 B-I may be regarded as having begun a new nomadic phase on March 31, when the evacuation of the statary site was effectively completed. At that time the removal of the major portion of the mature male brood from cocoons had been completed, daily raids were very large, and nightly bivouac changes became the rule. The brood was entirely removed from cocoons by April 3; prior to that the unopened cocoons were dragged along on the nightly movements. After April 2 some nightly flights of males were observed, a process which continued and increased in tempo each night until all males were gone in about three weeks (Schneirla, 1948). On March 31 an immense new brood of worker larvae in the early stages of development was found in the colony. This brood completed its larval development during the nomadic phase of 13 days. Certain irregularities were noticeable in the raiding and bivouac-change activities of the phase. On April 3 the raiding began rather tardily and sluggishly in the morning and developed only moderately during the day; hence it was not surprising that no bivouac-change movement occurred that night. No raid developed during the morning of April 5, although a foray got under way early in the afternoon. On April 6 the raiding developed only moderately, and there was no bivouac-change movement in the evening. Changes of bivouac also failed to occur on April 8 and 11, as well. The possibility was noted that the last two failures of bivouac change may have been due to the complexity of events in the raids of these days, rather than to a deficient development of raiding such as appeared to have been responsible for the failures of bivouac change early in the phase.

In the nearly mature larval worker brood the first spinning was observed on April 10, and on April 12 when the colony moved into its next statary site, the spinning of envelopes was in full progress.

From April 13 to May 3 Colony B-I remained bivouacked in a hollow tree, 100 meters to the south of station 1.5, Barbour-Lathrop Trail. Except for minor shifts in position, the colony did not change from its original situation, in which it formed a large bag about 1 meter from the ground in the open cavity of the lightning-split tree. After April 25 the cluster extended closer to the ground than before, and in the following days its lower edges dropped more and more until it finally touched the floor of the tree. The colony staged forays on each of the first five days of the phase, after which a long interval of relative inactivity set in, marked by smaller raids and many raidless days. Throughout the phase there were eight raids which began before mid morning and lasted until dusk, one raid which was not continued into the afternoon, seven days on which no raiding occurred, and four days on which the situation was not visited. It is important to note that the time of frequent raidless days began after the fifth day and lasted through the intermediate part of the statary phase.

On May 1, at a time when larval reflexes were general throughout the brood, before emergence of callows had begun to any extent, after a fairly vigorous raid, colony B-I moved from its tree to a new position about 45 meters to the east, near "old Pearson" trail station 1.5. There the colony remained bivouacked for two days beneath the root mass of a large fallen tree, and in that time the major part of the new worker brood emerged. The shucking-out of callows had reached its height on the evening of May 4 when the colony entered a nomadic phase, yet thousands of unopened minor worker cocoons were carried along in the column, and the removal process was not completed until about midday of May 6.

There followed a consistent nomadism during the next 12 days, in which the daily raids were large and most of the bivouac-change movements were fairly extensive. One striking characteristic of the migrations was the late time of day at which they started, as a rule. Few of them were definitely under way before 8:00 P.M., and some did not begin recognizably until after 9:30 P.M. Typically, the principal trail would be monopolized by a thick column of returning raiders so that sporadic signs of exodus from the bivouac were opposed by heavy incoming traffic until a relatively late hour. However, the level of excitement in the bivouac would remain visibly rather high. Then, finally, with return traffic running down in numbers and in persistency, a consistent outpouring from the bivouac would commence and gain headway.

The bivouacs of this nomadic phase, like those of preceding periods, were all relatively open clusters, typically formed beneath objects such as vine masses or the ends of raised logs, less frequently against surfaces such as buttressed tree roots. When it was in the open in full view, the huge cluster of this colony was an impressive sight.

Early in the period many packets of a numerous young brood were seen during the bivouac-change movements. However, the taking of brood samples from the bivouac was not attempted at first, to avoid disturbing the bivouac to the extent that would have been necessary. This brood proved to be an exclusively worker brood, which passed through larval development during this nomadic phase. On May 14 and 15 the spinning of cocoons began in this brood, which at that time had reached larval maturity.

On May 15 after a large and vigorous raid the colony moved at night into the interior of a large hollow log, on the hill 200 meters to the east of Barbour-Lathrop Trail, station 7.5. On this night the queen was seen in the movement and was taken to the laboratory for close examination. She was in a mainly contracted condition, vigorously active, and was readily accepted when returned to the bivouac of the colony the following night. At that time the colony was clustered just inside the open end of the same hollow log. Indications of cocoon spinning on an increasing scale were observed on the floor of this log during the following two days, May 16 and 17. In this situation all of the signs of the statary condition were evident, with spinning of cocoons evidently past its peak on May 17. Yet on the night of May 18 the entire colony moved through a distance of nearly 150 meters to a station on the bank of Barbour-Lathrop Creek to the west, southwest of Wheeler Trail, station 2. Here the bivouac was formed about 4 meters up in the hollow interior of a great tree, pouched just above a large triangular opening in the trunk. The rather variable beginning of this statary phase resembled that of the preceding one, in that the colony carried out a bivouac-change movement, after having settled in a fairly well-enclosed bivouacking place when cocoon spinning was nearing its peak. The phase was somewhat exceptional, in the statary series of which it was the fourth, in the frequency with which raids were carried out.[1]

[1] By the first of May the new season of rains had begun, with fairly regular daily downpours of increasing intensity and duration (see fig. 1). This site was located in the ravine of upper Barbour-Lathrop Creek, where the forest cover is excellent, and atmospheric humidity was consistently rather high while colony B-I was present in the district.

There were 12 regular all-day raids, two that started in the afternoon, and only three days on which no raids occurred, in the days on which the colony was visited. As in the other instances, in this case the raidless days that were observed fell during the intermediate days of the statary interval.

On June 5 a considerable number of pupa cases fell from the bivouac; next day the heap was considerably larger. Also, on June 6, the lower edge of the bivouac had dropped for the first time so that it could be seen from outside the tree. The raids of these days were more extensive than before, and that of June 7 was even larger, coming at the end of a day in which pupa cases in great numbers fell from the cluster. That night the colony was engaged in an exodus from the tree. Large numbers of callow workers were to be seen in the column, indicating that considerably more than half of the immense new worker brood had emerged, but on the other hand a few thousands of cocoons were carried along in column. These last were largely of the worker minor type.

Thus on June 7 the colony entered a further nomadic phase. Its first bivouac of this period was an impressive one, and rather exceptional in comparison with previous nomadic bivouacs of colony B-I in that it was formed with its lower edge well above the ground. The raid of June 8 was a notably large one. There was no bivouac-change movement on that evening, despite the fact that until 10:30 P.M. there were sporadic bursts of outgoing traffic competing with a stream of raiders returning to the bivouac. The colony also remained at this same site on the night of June 9, after carrying out a raid of considerable proportions during the day. On the following two days large raids occurred, each followed by a bivouac change of the entire colony to successive new clustering sites.

In the exodus of June 7 a new early larval brood of worker forms was observed, carried in very small packets by ants in the column. On June 8 more than half of this larval brood was removed from the bivouac for preservation. It was found in several large strands gathered close together near the center of the bivouac. At 7:00 P.M. on the following day, after a long heavy rain had settled into a drizzle in the evening, the bivouac was again examined, and most of the remainder of the young larval brood was taken out. Preserved in alcohol and Bouin's fixative, this brood was impressive for its numbers, which (on the basis of previous actual counts of eciton broods) must have exceeded 35,000 individuals.

When the last third of the emigration of this colony on the night of June 11 was observed, the queen was seen making her way along in the forefront of a highly excited mass of workers. She was removed from the procession, in a vigorous condition and fully contracted at the time. Next day she was preserved for eventual histological and cytological study.

Colony '46 B-I was under study through a period of 126 days in all. During that time it moved about within a relatively limited area (compared with colony H-B of *E. hamatum*) of about two-thirds of a mile in diameter in the northeastern part of the island. Sharp changes in direction were not uncommon in the successive movements. The one consistent feature of direction was that no movement ever came within 40° of reversing the direction of the preceding one. After the first nomadic phase there was a noticeable increase in the regularity of direction as well as the distance of movements, emphasized by the fact that the second and fifth statary sites were separated from each other by less than 140 meters, which was about the same as the distance apart of the first and second statary sites. The great size of the colony is believed to have had much to do with the relative cumbersomeness and irregularity in the operations and distances of its nomadic movements.

The circumstances indicated that only one functional queen was present in the colony through the interval of more than four months. A supernumerary queen appeared at the end of the second statary phase and would have become the basis of a colony division, if this section of the colony had not been etherized and the queen and brood removed. Suspicions that she was not the principal colony queen (i.e., responsible for previous broods) were confirmed when the regular cyclic production of broods continued after this queen had been removed. Histological and cytological examination of these two queens has since borne out the conclusion that the supernumerary queen cannot have been involved in the production of broods in colony B-I.

TABLE 6

BROOD-PRODUCTION INTERVALS IN COLONY '46 B-I

Type of Brood	Date New Callow Brood Emerged	Interval Between Broods (in Days)
Worker	Feb. 27	31
Male	March 30	31
Worker	May 3	34
Worker	June 6	34

The schedule of brood production accomplished by colony B-I during the study, in terms of the dates on which emergence of the callow individuals occurred after pupal maturation was completed, is presented in table 6. During the period of study, three worker broods and one male brood were completed, and at the end a new brood of workers was in the early larval stage. It should be noted that in the case of *E. burchelli* the emergence of the brood is a more protracted process than in *E. hamatum*, completed as a rule only after the next nomadic phase has begun. Generally at the time of the first nomadic movement a considerable part (sometimes more than one-third) of the mature pupal brood remains in cocoons, and an additional time of two or even three days is required for the process to be completed. For this reason the actual value of the time interval between broods is not represented in *E. burchelli* by the time elapsing between the start of consecutive nomadic phases. It is probable that the inter-brood times for *E. burchelli* should be a day or two longer than those represented in table 6.

Within the period of 126 days of study, this colony produced three completed worker broods of 25,000 or more individuals each, a brood of male individuals containing an estimated 3000 individuals, and had a new worker brood in the early larval stage at the end (see fig. 4). The colony was very large at the beginning of the survey, and at a guess included more than 200,000 workers in the end, after a division had been thwarted. The new broods thus noticeably increased the worker population, evidently compensating for heavy worker losses from various causes, presumably raiding casualties and the effects of desiccation in the main. This colony thus survived the dry season as an aggregation of relatively immense size.

The male brood was a transitory part of the population, since all males were gone from the colony within three weeks of the time they emerged as alate callows.

Almost a dozen dealated *burchelli* males were seen in the bivouac-change procession of this colony on the night of March 4, obviously newcomers from another colony of the species in the vicinity (Schneirla, 1948). On the next evening three dealated males were seen in the procession, evidently from the same source. On two later occasions single dealated males were seen in the bivouac-change column.

Colony B-I passed through a series of changes in its pattern of activity, the time limits of which may be summarized roughly as in table 7. During the entire interval of this study there was a regular alternation of nomadic and statary phases in the colony. In other words, this state of affairs prevailed through roughly the entire last three-fourths of the dry season. Interestingly enough, although the duration of the four statary phases as determined by our criteria was relatively constant at 21 days, the nomadic phases varied in duration from 10 to 13 days. It is notable that the nomadic phase of 10 days, definitely the shortest of the three, was the time when male larvae were present.

The typical species pattern of relationships appeared to prevail in the time relations of broods, with the exception that a limited shortening of the nomadic phase may have occurred in connection with the larval development of a male brood. The usual synchronization of broods was in evidence. When a given completed brood emerged as a new callow population of individuals approximately the same age, without exception a further brood was present at the time in the early stage of larval development. All indications pointed to the conclusion that the eggs of each given new brood were laid approximately after the first third of the statary

TABLE 7

DURATION OF SUCCESSIVE PHASES OF THE ACTIVITY CYCLE (COLONY '46 B-I)

Nomadic Phase	Duration (in Days)	Statary Phase	Duration (in Days)
		Feb. 7 to Feb. 27	21
Feb. 28 to Mar. 9	10		
		Mar. 10 to Mar. 30	21
Mar. 31 to Apr. 12	13		
		Apr. 13 to May 3	21
May 4 to May 15	12		
		May 16 to June 6	22

phase. Thus there was always a definite peak in the attainment of a given phase of development in the brood, with a variation of smaller numbers of individuals within not much more than three days earlier or later than this time. Characteristically, the colony tended to begin a new nomadic phase before the entire mature pupal brood had emerged from cocoons and a new statary phase before the spinning had begun in all members of its mature larval brood. The first observation is more secure than the latter, although a variety of records confirms both. On the whole there was a definite coincidence in the conditions of colony behavior and the brood, in that a larval brood passed through its principal development to maturity during each nomadic phase, and a mature brood became enclosed and advanced through pupation during each statary phase.

It was noticeable that the colony tended to vary to a limited extent in the temporal coincidence of brood changes and changes in colony behavior. These variations appeared notably after March 30, that is, beginning with the termination of the second statary phase, when the major behavior changes of the colony in entering both the nomadic and statary phases that followed no longer tended to be clear-cut. In the behavior cycles the colony often would stop for a day or even two without much sign of an evening exodus, somewhat as though it were actually statary. This condition would arise at the beginning of both statary and nomadic phases and seemed to constitute a transitional stage.

There was a relatively marked difference between nomadic and statary phases in the status of general colony behavior. In the nomadic sequences the raids tended to be definitely larger than was the case in the statary phases. When nomadic the colony always staged daily forays of considerable magnitude, but when statary there were frequent raidless days. A general summary of the frequency of raids in the successive statary

TABLE 8

FREQUENCY OF RAIDING DURING THE STATARY PHASES OF *E. burchelli*, COLONY '46 B-I

Statary Phase	Number of All-day Forays	Raids Starting in Afternoon	Raidless Days	Colony not Visited
Feb. 7–Feb. 27[a]	11	3	7	—
Mar. 10–Mar. 30	9	1	7	4
Apr. 13–May 3	9	1	7	4
May 16–June 6	12	2	3	4
	—	—	—	—
Totals	41	7	24	12

[a] Inclusive.

phases is offered in table 8. In the first three statary phases there were no raids on nearly half of the days on which observations were made. In the last statary phase of the study not only were raids observed on more of the days, but these raids were greater in magnitude and in distance from the bivouac. It should be mentioned that the interval of this statary phase fell during the time when an increase in daily rainfall was taking place, with the regular rainy season impending.

Now we may consider the manner in which raids occurred on the successive days of the statary phases in order to contrast the early, the intermediate, and the last sections of the interval as to general colony activity. In table 9 the records of raiding have been massed for the corresponding successive days of the four statary phases.

Table 9 clearly shows the prevalence of forays on the first three and the last days of the statary phases, the dropping off in frequency of raiding that occurred after the first five days, and the increase towards a maximum frequency that took place towards the end of the interval in each case. The results would be even more striking were indices of the vigor and extent of raiding introduced. Clearly, the intermediate part of each statary phase was a time of relatively low activity, as the minimal results for raiding suggest.

Virtually all of the bivouacs in the nomadic intervals were formed on the surface in fairly exposed places, with the exception of an occasional subsurface cluster near the entrance of a mammal burrow or hollow log. The few records of this type were obtained near the end of the nomadic phase. At times near the end of two of the nomadic phases a tendency to form bivouacs in elevated positions (e.g.,

TABLE 9

Number of Raids on Corresponding Days Through Four Consecutive Statary Phases, Colony '46 B-I

Statary Day	Raids	Afternoon Raid Only	No Raid	Colony not Visited	No. of Raids (Length of Each Interval, in Days, in Parentheses[a])	Percentage of Days with Raids (Three-day Intervals)
1	4					
2	3			1		
3	4				11 (11)	100
4	4					
5	2		2			
6	1	1	2		8 (12)	66
7	1	1	1	1		
8			3	1		
9			2	2	2 (8)	25
10	2[b]		2			
11			2	2		
12	2[c]		1	1	4 (9)	44
13			2	2		
14	1		1	2		
15		1	1	2	2 (6)	33
16	3			1		
17			1	3		
18	1	1	2		5 (8)	62
19	4					
20	4					
21	4				12 (12)	100

[a] The percentage for each three-day interval is derived from the ratio of the number of raids observed to the total of days visited.

[b] One raid, morning only; the other, very light.

[c] One raid, very light.

a pouch formed among the columns of a strangler-fig tree) also was noted. All the statary bivouacs were formed in relatively enclosed places, which happened to be hollow trees in all four cases, and at heights of from between 2 and 7 meters from the ground. Three of the four statary bivouacs were formed near openings in the walls of hollow trees.

SUPPLEMENTARY COLONY RECORDS

At any given time during the study two or more colonies of each of the two representative species were on record, in addition to the two colonies that were observed throughout the investigation. These further records are of great importance as a means of determining the extent to which the two "longitudinal" colony records may be representative of conditions peculiar to species and season. In the following chronologically ordered summary of the pertinent facts, records of shorter and longer duration will be presented with a view to reporting the essentials of each colony situation and behavior without duplicating material already given in the principal cases. The order and duration of these studies is shown in figures 5 and 6.

SUPPLEMENTARY *HAMATUM* RECORDS

Colony '46 H-A, *E. hamatum*

A column was crossed at Shannon 3 late on February 7; efforts to find the bivouac were successful on the morning of February 8. The ants were bivouacked within the nearly closed cavity of a small hollow tree on the east face of a small hill west of station 4.5, Shannon Trail. The colony formed a pouch which at the time did not quite reach the ground. Later its height was found to vary within a range of 18 cm. from day to day. On the last two days of the phase the cluster rested on the ground. Until the site was abandoned on the night of February 22, the colony produced only single-system forays at best only moderately developed, the strongest on February 9, 20, and 21, the weakest from February 10 to February 16. In this latter interval there were four days without raids, one day (February 13) on which the foray lasted only through the morning, and another (February 14) with no raid before afternoon. Thus in 14 days of observation this colony staged 10 forays, a record which approaches the maximal performance for this species in the dry season. The colony, when found on February 8, had an immense brood of enclosed worker pupae, and when the bivouac was examined on February 19 with the aid of ether, large packets of newly hatched eggs and young larvae (worker type) were found.

Signs of extensive cocoon opening were seen on February 20, and on February 22, with most of the new brood removed from cocoons, the colony staged a three-system raid which ended in a nocturnal move to a site 180 meters to the northwest. Here a long, open, cylindrical cluster was formed beneath a large log. Next day this cluster was etherized, the single colony queen (contracted) was removed, and more than three-quarters of the young larval brood was also taken out. No movement occurred that night, although at the time of etherization a vigorous three-system raid was in force. There resulted a complex system of events, with a partial shift to the northwest from the first nomadic site late on February 25. During late afternoon on February 26 back trailing still existed through the statary site, and from the first nomadic site near Shannon 3 a long thick column of ants moved off to the northwest on the route used in the partial shift of the preceding day. This column was unbranched for about 400 meters, then led into a system of complex branching columns which extended to within 150 meters of Wheeler Trail, station 15. No central bivouac cluster could be found on the main trail or on any of the advanced branch trails that were investigated. On the following day, February 27, there was no trace of the colony in the vicinity of the former statary and first nomadic bivouac near Shannon Trail, station 4. However, until March 1 columns persisted in the vicinity of Balboa Trail, station 2, and Wheeler Trail, station 15. Efforts to find a central clustering point of the colony were fruitless despite considerable tracing of the trails.

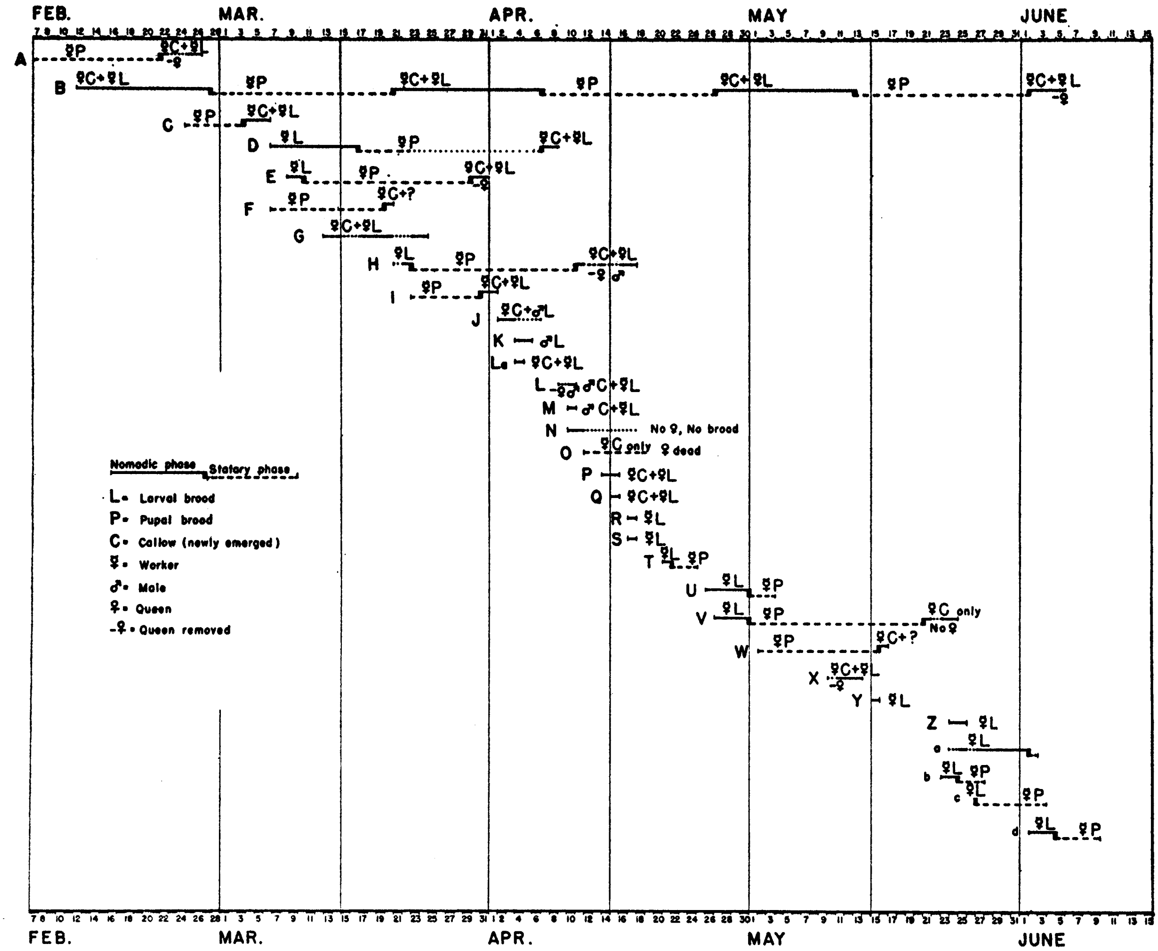

FIG. 5. Sketch of behavior records and correlated brood conditions for colonies of *E. hamatum* studied between February 7 and June 9, 1946. Individual colonies are designated by successive capital and small letters; concurrent colony conditions may be read in the vertical direction. At each differentiated nomadic or statary phase, the correlated brood condition (as well as presence or absence of a queen) is indicated by appropriate symbols (see legend).

This record is regarded as representing the termination of a regular statary phase with the beginning of typical nomadism, a condition which was interrupted by etherization and disturbance of the first bivouac. It is probable that the removal of (nearly all) the young larval brood and the queen variously impeded colony function and made recovery of a "normal" colony behavior pattern impossible.

COLONY '46 H-C, *E. hamatum*

On February 15 and thereafter the activities of an *E. hamatum* colony were noted occasionally on the northwest side of the laboratory clearing and to the east of Fairchild Trail. The bivouac of this colony was found on the evening of March 4, when a bivouac-change column moving from it was discovered to the north of Allee Creek and was first traced to the cluster in formation, then back to the (evidently statary) site being abandoned. A tenancy of some duration here was indicated by signs such as large heaps of empty (worker) pupa cases at the base of a hollow tree beside the moldy log beneath which the colony was completely hidden. At the first nomadic bivouac site on March 5 after a large three-system raid had developed, the bivouac cluster was etherized, and at noon the contents were examined. The queen was found in a nearly contracted condition, and a large, fully emerged brood of callow workers was present, as well as a large brood of very young worker larvae estimated at 20,000. Etherizing the colony interrupted the further development of raiding; consequently there was no movement that night. On March 6 early in the day the queen and the bulk of the young larval brood were returned to the bivouac. The queen was reabsorbed readily with great excitement (cf. '46 H-D and H-H). That evening, after an extensive three-system raid, there occurred a full colony movement to a site 200 meters away to the west.

This colony exhibited the behavioral and brood signs of having just ended a statary phase and begun a nomadic phase, which was interrupted by the effects of etherization upon their day's raid. The interruption was only temporary, and the prompt resumption of nomadic activities appears to have been insured in part at least by the return of their young brood and queen. In this important respect the case of colony H-C may be considered a control upon colony H-A, to which the brood and queen were not returned.

Colony '46 H-D, E, *E. hamatum*

Found on March 7 engaged in a three-system raid in the vicinity of Barbour Trail, station 2, with an open, irregularly cylindrical bivouac under a mass of vines. The bivouac contained a large brood of worker larvae, in the intermediate stage of development, estimated at 25,000 individuals or more. There followed a regular succession of large two- or three-system daily raids and nightly bivouac-change movements of from 120 to 310 meters in extent. The queen was observed towards the end of the lengthy bivouac-change movement that occurred on the night of March 12. In the fully contracted condition, at the time, she was taken to the laboratory for observation. The queen was returned to the new bivouac at 10:30 A.M. on March 13 when a vigorous three-system raid was in progress. The placing of the queen beside a column close to the bivouac soon caused great excitement. There follows a summary of notes taken on the process of her reassimilation:

> The excitement of passing workers rapidly spreads to the bivouac, from which ants come pouring forth in such numbers that the entire surface of the log over which the trail runs into the bivouac is covered with highly aroused workers. Clusters form here and there where the queen stops even briefly in her first random circuitous movements, and a fairly large cluster forms over the piece of cotton on which the queen rested in the air vial in which she was brought from the laboratory. At one time a flat cluster approaching the diameter of a tea saucer forms over and around the queen where she happened to stop; however, in the course of 20 minutes she succeeds in escaping this mass by a process of literally tunneling and burrowing her way out. Wherever the queen hesitates even momentarily in her progress, as at the upturned edge of a leaf she has difficulty in mounting, she is immediately swarmed under by excited workers. At first she moves away from the bivouac, but in the course of time she is redirectionalized mainly by virtue of the press of traffic returning towards the bivouac on the raiding trail, which finally asserts its effect on the workers swarming over the log. In the end the queen disappears into the bivouac, followed closely by a highly agitated crowd of workers, just 95 minutes from the time she was first placed on the log.

In the general character of events this occurrence was quite typical of instances in which a functional eciton queen is returned to her colony under ordinary conditions.

The itinerary of the colony in its movements after March 7 took it through an irregular circular course of more than 800 meters in diameter, ending on March 16 in the crossing of Donato Trail at station 4. On this night a site was reached in a low creek bed far to the east near the shore of Gatun Lake, where the colony formed a large open cluster beneath the undercut bank of a creek (pl. 2). At that time spinning activity was general in the mature larval brood. Virtually complete enclosure of the brood was noted on the evening of March 18. Thereafter no spinning activity occurred outside the bivouac. The open-cylinder formation of the bivouac was retained until sometime after a visit on the morning of March 21, but the colony was gone on the afternoon of March 23 when the vicinity was next visited. Efforts to find it in occasional visits were unsuccessful until the night of April 7, when a *hamatum* bivouac-change column was seen crossing lower Donato Trail and was traced back to this area. Here its origin was found at an enclosed site beneath a tree only 6 meters from the creek bank at which the colony had first settled. It seemed probable that previous hunting had failed through chance coincidence with raidless days of the colony. What caused the colony to move shortly after March 21 can only be surmised. Perhaps the move took place through disturbance from exposure to the occasional rains which occurred through this series of days. Since this colony not only originated from a site to which H-D might well have shifted after March 21, but also exhibited all the signs of a first nomadic movement, and especially possessed great numbers of recently emerged callow workers as well as a large brood of very young larvae, it was very probably H-D. The timing of broods was exactly what would have been expected for colony H-D. The colony was further observed through two days of extensive raiding and night-time bivouac-change movements before the record was discontinued.

This colony was observed during a nomadic series (incomplete) of 10 days, followed by a statary phase lasting 21 days, and the beginning of a new nomadic phase. The coincidence of broods and behavioral conditions through this time corresponded fully to those typical of colony H-B. One rather unusual circumstance was the occupancy of a site in which an open-cylinder type of bivouac was formed during the first days of the statary phase, followed by a shift from this site (evidently to another, more concealed, in the vicinity) later in the interval.

Colony '46 H-E, *E. hamatum*

This colony was found on March 10 near station 11, Van Tyne Trail. A large three-system raid was in progress. Near the bivouac cluster, which was established beneath the roof of a large, partially open, hollow root, there were signs of extensive spinning of cocoons in an immense, evidently mature larval worker brood. That evening the first stages of a bivouac change to the east were observed. However, the colony then was forming a cluster in the open base of a hollow tree, where it was not found on the next day. On March 14 the statary bivouac was found within a mammal burrow about 110 meters east of the site of March 10, and about 20 meters beyond the hollow tree mentioned above. A single-system raid was in progress; the mature larval brood, enclosed, was in the prepupal condition. Specimens of this brood became unobtainable as the colony withdrew in time farther into the recesses of the narrow, winding burrow. Raids were very intermittent; none occurred on more than half the days of visit to the colony. On the evening of March 30, just 20 days from the beginning of the statary phase, the colony staged a large three-system raid and in the evening moved to a site 170 meters to the northwest. There an open cluster was formed under loose matted vines. On the following day at noon, after a large raid of three systems had developed, the bivouac cluster was etherized. In addition to the large brood of newly emerged callow workers, a large new (worker) brood in the early larval condition was present, as well as a contracted queen.

Indications were that this colony passed from the end of one nomadic phase through a full statary phase of 19 days and had begun a new nomadic phase when the study ended. Unfortunately the effects of removing brood and queen could not be determined in satisfactory detail.

Colony '46 H-F, *E. hamatum*

On and after March 6 occasional signs of *hamatum* forays were noticed in the general vicinity of the ravine at Barbour-Lathrop Trail, station 3.5. A column of raiders returning to the statary bivouac of this colony interfered to a considerable extent with the (last nomadic) bivouac-change movement of the *burchelli* colony B-1 on the night of March 9, when the routes of these colonies happened to cross in two places. On the morning of March 10 the statary headquarters of this colony, previously localized through the convergence of successive daily raids, was found to be a regular cylinder far beneath the concave roof of a large, wide, fig-tree root overhanging the creek bed. The bivouac contained a very large, enclosed, prepupal brood of worker individuals; the presence of a possible new brood could not be determined.

Single-system raids were seen on some of the following days; on others no raiding occurred. On March 20 a moderately large raid and cocoon opening were observed; unfortunately the site could not be visited that evening. The colony decamped, for on the following day no ants were on the scene, but the floor of the bivouac cavity and the rocks beneath were strewn with worker-form pupa cases.

The colony evidently passed through a statary phase in this place and produced one brood of mature workers and very probably also a new brood of undetermined nature, before moving away.

Colony '46 H-G, *E. hamatum*

On the evening of March 13 the bivouac-change movement of a *hamatum* colony was followed from the evacuated site to a new open-bivouac situation under a log in a small gully southwest of Barbour Trail, station 8. Great numbers of newly emerged callow workers were seen, and on the following day (with a large three-system raid in progress) a large brood of very young larval workers was found in the bivouac. The movement of that night, to the south, could not be followed out to the new bivouac. What may well have been the same colony was found on March 17, bivouacked on a ravine bank about 200 meters south of Barbour Trail, station 9. Bivouac situation, behavior, and brood condition all indicated that the colony was H-G in all probability. The colony was followed for a few days. Two days later it was located 320 meters to the west of the March 17 bivouac site in an open bivouac cluster, a large raid was in progress, and its larval worker brood was definitely advanced in development. That evening it moved 165 meters to the south; however, the colony could not be followed thereafter. It is possible that a colony that was encountered on March 23 about 300 meters southwest of the large Van Tyne tree was H-G, since location, behavior, and brood condition all answered to what would have been expected in that colony. Two days later this colony passed into the statary condition, in a situation near Fossil Creek which could not be visited after the original observation.

It is probable that the three encounters involved the same colony, which was advancing at the time through the principal part of a distinct nomadic phase, followed by a statary phase which could not be observed.

Colony '46 H-H, *E. hamatum*

This colony was found on March 22 by tracing a long, unbranched, bivouac-change column to the bivouac, a cylinder formed in the central hollow of a large log near station 4 on Wheeler Trail. (A bivouac-change column had been observed crossing Shannon Trail near station 2 on the previous evening, which may well have been that of colony H-H.) The log bivouac settled on March 21 contained a large brood of mature worker larvae, then engaged in cocoon spinning. On the three following days one-system raids occurred, followed by an interval of 10 days in which raids frequently were absent or begun in the afternoon on given days. On March 25 the mass of the bivouac shifted towards the ceiling of the log and approximated a large bag which scarcely touched the floor. On March 26 the entire bivouac was about 30 cm. farther back towards the closed end of the hollow. On March 29 the bivouac formed a large pouch which did not touch the floor of the log, on March 30 it assumed the shape of an inverted cone, the apex of which touched the floor. On April 4, during the night, the entire colony shifted 2 meters from the log to enter a large hollow root close by. On April 10 no raiding was observable at 9:00 A.M.; however, an extensive one-system foray developed in the afternoon. A large two-system raid arose on the morning of April 11, cocoon opening was prominent at the bivouac, and at 7:00 P.M. the colony was engaged in a bivouac-change movement of about 130 meters to the southeast across a deep ravine, on the opposite bank of which a partially exposed cluster had begun to form at one end of a hollow log. On the morning of April 12, the colony formed a long, curtain-type cluster in a deep, overhung recess at one side of the log. A large raid with three distinct trail systems had formed at 10:00 A.M., when the contents of the bivouac were examined. In addition to the sizeable brood of callow workers, just emerged, a large brood of very young worker larvae was found in central clusters. In the bivouac were also found perhaps 2000 still unopened cocoons mainly of mature worker minor and smaller intermediate forms, most of which had been removed before the evening of April 12, the first day after a shift from the statary bivouac. (It is exceptional for *E. hamatum*, although not for *E. burchelli*, to show an incomplete emergence of the mature pupal brood before vacating a statary bivouac site.) The single queen was found in the fully contracted condition, and in addition two dealate males were taken from the bivouac.

The second dealated male was not discovered until 4:30 P.M., on arrival at the laboratory and examination of the contents of the small glass jar into which the queen had been placed with a cluster of workers. This male was then found in copula with the queen, mounted over her with his mandibles holding tightly to one of her large petiolar horns and the tip of his gaster so extensively inserted into her abdomen as to deform her gaster considerably. The pair was still united at 6:00 P.M. when next observed. The male seemed lethargic from the first, and rather unresponsive to stimulation of tarsi or antennal funiculi; the queen, however, reacted very readily, and at intervals even ran about the enclosure carrying the male with her. At 6:30 P.M. the union had been broken; the male, still alive although sluggish in movement, was placed into modified Bouin's solution for eventual study, the queen was placed into an artificial nest with brood and workers. On the evening of April 14, I found queen and workers engaged in an incessant movement in a regular circular column within the nest.

Still alive and apparently in good condition on the morning of April 16, just four days after her capture, the queen was returned to her colony in the field. From the west, where the new bivouac must have been located at some distance, the ants were found backtracking in a thinly followed column to the abandoned bivouac site of April 12 and through it to the former statary site. When set down close to the column, the queen was readily received by the workers, which quickly swarmed over her in numbers on the spot. After 35 minutes in which successive tight clusters formed as the queen moved about and stopped variously on the trail, the queen and her large following of workers moved off towards the west, where the principal part of the colony was located.

This colony entered and passed through a regular statary phase of 20 days during the time of study and was beginning a new nomadic period when observations came to an end.

Colony '46 H-I, *E. hamatum*

On the evening of March 23 a long unbranched column was traced to the bivouac of this colony, established within the completely enclosed central hollow of a large hardwood log to the south of station 9, Shannon Trail. The ants issued from a small crack in one side of the log. Raids occurred intermittently until March 27 and more regularly thereafter. Until March 31 the raids were only moderately developed or relatively small single-system affairs. On March 31, after a vigorous three-system raid the colony moved about 160 meters to a new site where an open half cylinder was formed beside a large log. On the following day, when the contents of the bivouac were examined at a further new site, in addition to the newly emerged brood of callow workers, a large new brood of more than 20,000 very young worker larvae was found.

This colony when found was passing through a statary phase, after which a nomadic phase began in a regular manner.

Colony '46 H-J, *E. hamatum*

When found on April 2 at 11:00 A.M., this colony was engaged in a large, three-system raid. Its bivouac was a half cylinder depending from some vines against the bank of a little gully to the east of station 6 of Shannon Trail. The cluster contained a fully emerged, very large brood of callow workers, and a brood of early male larvae estimated at from 2000 to 3000. That evening this colony moved westward into a new bivouac site, from which another large raid developed on April 4.

This colony was very evidently in the early part of a nomadic phase.

Colony '46 H-K, *E. hamatum*

On the morning of April 4, colony H-K was found by tracking back one of its three highly developed trail systems to the bivouac, a large half cylinder formed beneath a log on the bank of the creek to the east of Wheeler Trail, station 22. In the bivouac was a brood of well-advanced male larvae, estimated at more than 2000 in number.[1] The brood was well distributed through about two-thirds of the bivouac, most of the larvae held by ants in the interior of the cluster, but no larvae were found in one pole of the mass. In the latter section of the bivouac the queen, in the fully contracted condition, was found.

A movement of 220 meters which took the colony towards Drayton 2 that evening involved the extensive development of an "ant roadway" along the route, a clustering of workers on the trail which had its origin in difficulties with the transport of the relatively bulky male larvae (Schneirla, 1948) and which greatly facilitated the carrying of these objects over uneven terrain. Another large foray developed on April 5, followed by a bivouac-change movement to the southwest of Wheeler 24.

This colony was definitely nomadic, at a high point of arousal.

Colony '46 H-Lake, *E. hamatum*

This colony was judged to be considerably below the average in size, yet when discovered on April 4 it supported a fairly vigorous three-system raid. The bivouac was an irregular cylindrical cluster hanging to the ground in an open vine mass, near station 4, Lake Trail. In the bivouac was found a large brood of worker larvae at an early stage of development, as well as large numbers of callow workers, which from the condition of their pigmentation and from the fact that numbers of them were observed on peripheral raiding trails, evidently had emerged four or five days previously. The colony moved away that night.

This colony was judged to be at approximately the first third of the nomadic phase, maintaining a large raid by virtue of the "excitatory magnitude" of its large larval brood.

Colony '46 H-L, *E. hamatum*

When found near station 3, Armour Trail, on April 9 at 10:00 A.M., this colony had developed a moderately large, two-system raid. The bivouac was a half cylinder formed against the overhanging edge of a buttressed tree root, near station 3, Armour Trail. The cluster contained a large number of callow alate males estimated at more than 1000, and a second brood of very young worker larvae judged to be of considerably less than average population size for *E. hamatum*. A single queen was found, in the fully contracted condition, as well as one dealate male. This male was not seen at the time the queen was captured in the field and with a large cluster of workers was placed alive in a container. At the laboratory the male was discovered in full copula with the queen. The coupling persisted for 10 hours, towards the end of which the male (evidently in the first stages of death) began to withdraw from the position of full insertion. The pair was then fixed and preserved. The following preliminary description of the queen's reproductive apparatus is furnished through the kindness of Dr. Roy Whelden, who is engaged in a study of this and similar material:

"There are four or five uniformly rather large discrete ball-like masses of sperms in the spermatheca. There are also present with them many unidentified fragments of tissue apparently introduced with the sperms. The ovarioles contain no mature eggs, but only the very beginnings of enlargment of isolated cells (eggs) surrounded by large numbers of very small cells."

No bivouac-change movement occurred that night; however, after a large raid on April 10, the colony moved away in the evening.

This colony was judged to be in the early part of a nomadic phase.

Colony '46 H-M, *E. hamatum*

When discovered at 10:00 A.M. on the morning of April 10 just 120 meters to the north of colony H-L, this colony was engaged in a rather irregular raid of two recognizable trail systems. The bivouac was a moderately small, somewhat irregular mass clustered under a small log and vines. Unfortunately the situation of the bivouac precluded finding the queen. Hundreds of callow males were found in the cluster, as well as a second

[1] The range in body lengths (10 specimens) of these larvae was 14.5–17.8 mm. The range of mature male larvae in body length has been established roughly as 21–23 mm. from other *hamatum* material. In comparison with growth curves otherwise obtained for the species, it is estimated that the brood of colony H-K was approximately 5.5 days short of maturity.

brood of very young worker larvae gathered together into a few strands near the center of the bivouac. It seemed significant that the two broods of this colony were closely approximate in condition to those of colony H-L, also that the early larval worker broods of both colonies were evidently of a population magnitude distinctly less than the average for *E. hamatum*.

From the layout of raiding trails, the proximity of the bivouacs, and the close similarity of broods, it was considered very likely that these two colonies were the products of a recent division of the same base colony.

COLONY '46 H-N, *E. hamatum*

On April 10 at 10:40 A.M. a column of *hamatum* workers was encountered in the vicinity of Balboa Trail, station 3. This column, which contained limited numbers of booty carriers, was followed to the bivouac, an irregular curtain-type cluster formed in two main sections under the root mass of a fallen tree. In the colony, both in the two raiding systems observed and in the bivouac, were found many thousands of workers just barely lighter in pigmentation than the bulk of the worker population and judged to be callows that had emerged perhaps a week or 10 days before the colony was encountered. A careful examination of the contents of the bivouac disclosed no trace of a further brood, and no queen was found. After the raid of April 10, which seemed to fall somewhat below the degree of development typical of a regular nomadic *hamatum* colony, colony H-N moved that night through a distance of 90 meters to a new bivouac site east of the previous location. Here the colony clustered about 90 cm. from the ground in a niche beneath the overhanging end of a large decayed log. In the foray of April 11, there developed two moderate-sized trail systems. At 6:30 P.M. that evening the colony began to shift over the principal trail of one of these raiding systems to a point 70 meters to the southwest. Here, near the outer limit of that trail system, the new bivouac was established within a long hollow tree root, where the colony was completely enclosed. The bivouac-change movement was inspected at length without any indication of either brood or queen being observed. Only one raiding system was developed on April 12, and no movement of the colony occurred that night.

When the district was next visited on April 15, there was no indication of the colony in the area of the hollow-root bivouac. However, extensive searching brought to light a long, poorly followed *hamatum* column, which was traced to a point only about 40 meters from the place where colony H-N was discovered on April 10. The last portion of trail, in fact, was identifiable as a route in use in the foray of that day. The bivouac could not be found; however, further searching on the morning of April 16 led to the tracking of a thin file of ecitons from this trail section to a bivouac site. The colony formed a long, irregular, curtain-like cluster, located in the posterior part of a deep recess beneath a tree root which had buckled somewhat above the ground. The mass of ants was subjected to a complete inspection without any trace of either brood or queen being disclosed. No change of bivouac occurred that evening; however, the colony could not be found on April 18.

The area was crossed at various times later on. Unfortunately, other work prevented studying this case in detail, so that it is not possible to be sure that the observation of thin *hamatum* files in this district on various days up to April 26 was due to the presence of this colony.

It is possible that H-N actually was colony H-A, which on February 23 had been deprived of its queen and the major part of its young worker brood, then in the early stages of larval development. As an examination of figure 5 indicates, this brood remnant might have been expected to emerge from cocoons as callow workers on or shortly after March 31. It was just 10 days after that time that colony H-N, with a few thousand callow workers evidently more than one week out of cocoons, was discovered. Thus brood conditions, as well as the absence of a queen, suggest that the colonies were the same.

This colony did not clearly exhibit either a nomadic or a statary condition of behavior but an intermediate condition involving moderately small raids and only occasional changes of bivouac, which suggested brood conditions out of the ordinary. The absence of any brood beyond lately emerged callow workers was consistent with this condition and with the fact that no queen was found.

Colony '46 H-O, *E. hamatum*

On April 12 a widely ramifying arrangement of poorly followed trails was found in the general vicinity of Wheeler Trail, stations 25 to 26, extending towards Gigante Point on one side and Drayton Trail on the other. Numerous callow workers were seen variously distributed in the thin columns, and more of them were found in the small clusters at trail junctions. Beyond such junction clusters, which in the afternoon took on the appearance of booty caches, no very large aggregation of ants was found in this arrangement of trails in repeated searching on successive days. In the course of following the thin columns searching for a possible central aggregating place, the dried body of a *hamatum* queen, a headless hulk of thorax and gaster with leg stumps only, was found in one of these small clusters. These remains of what very evidently had been the colony queen were in the midst of a little aggregation of closely clustered workers, with a number of major workers roundabout. Further tracing of the far-flung and irregularly branched set of trails through a distance of more than 500 meters brought forth no sign of any central clustering or bivouac place and no indication of a regular raiding pattern or of migratory activity after the regular species pattern. On April 19 an extent of more than 450 meters of trails was thus fruitlessly followed. In the meantime, up to April 19, the number of ants seemed to decrease, and after April 25, none could be found. The presence of callow workers, together with the remains of a queen, as well as numerous rambling trails rather irregularly related to one another, seems to furnish clues to a recent dissolution of regular colony function.

It is believed that the queen of this colony had died at or before the beginning of the last statary phase, so that without a developing larval brood the colony later became incapable of operating in the typical nomadic manner, with dissolution inevitable.

Colony '46 H-P, *E. hamatum*

When found at 11:00 A.M. on April 15, this colony was bivouacked in a large regular cylinder deep beneath the raised part of a large log to the east of station 21, Wheeler Trail. An extensive three-system raid was in progress. A very large brood of callow workers was present together with a few thousand mature pupae not yet removed from cocoons. Large heaps of empty cases in the tens of thousands were littered about the lower border of the bivouac, and much opening of cocoons was to be seen, suggesting that the colony was about to terminate a statary phase at this site. In several walnut-sized packets thickly swarmed over and permeated by minor workers in large numbers, a second brood of very young worker-type larvae was found near the center of the bivouac cluster. The queen escaped detection among the many clusters of callow workers that formed when the bivouac was examined. That evening, after a day of vigorous raiding, the colony moved off towards the east.

The condition and behavior of '46 H-P were characteristic of a colony in the early part of a nomadic phase.

Colony '46 H-Q, *E. hamatum*

On April 15 this colony was encountered about 200 meters to the east of Fairchild Trail, station 4, engaged in an extensive three-system raid. In the bivouac, which was formed below the low overhanging shell of a hollow log, there were large numbers of callow workers as well as some hundreds of still unopened cocoons containing mature worker minor pupae, with the opening of cocoons actively in progress. Also, a large brood of very young worker larvae was present massed near the enclosed rear portion of the cluster. The queen was not found. Before dusk a broad exodus began over the principal trail to the north. On the following day this colony was gone from the site, leaving large heaps of empty cocoons beneath the former clustering place.

From all indications, like colony H-P this colony was just completing a statary phase when discovered.

Colony '46 H-R, *E. hamatum*

At 10:00 A.M. on April 17 this colony was found to the southeast of station 3.5, Barbour-Lathrop Trail. A well-developed, three-system raid was in progress. The bivouac was a full cylinder formed under a tree root beneath the overhanging bank of a running stream. A large brood of advanced worker larvae was well distributed through the bivouac.

At 3:00 P.M. traffic was variable on the two best-developed routes, which led into separate trail systems to west and north from the bivouac. At this time the afternoon exodus, newly begun, was divided into bursts of traffic intermittently leading from the bivouac first into one and then the other of these principal routes. The variations occurred particularly in relation to the force and persistence of returning traffic on the two lines. This condition continued variably until after 4:00 P.M., when the exodus from the bivouac was judged to be in full swing. At that time the north route appeared to be the potential line of bivouac change, judging by the preponderance of traffic from the bivouac. However, an inspection of peripheral developments on the two systems indicated that the eventual movement very probably would occur through the western system, on which the drift of traffic was more extensively away from the bivouac than on the northern system. A gradual change occurred along these lines in traffic from the bivouac, until at 5:00 P.M. outgoing traffic predominated on the western route, incoming traffic on the northern route. At 5:30 P.M. a consistent westward exodus was observed, and at 6:00 P.M. the transport of larval brood to the west had begun. The outgoing movement on the western line continued without important interruptions until shortly after 8:00 P.M., when the queen appeared from the bivouac and joined the march. Removed from the column for a brief inspection, she proved to be fully contracted and apparently in excellent condition. She ran easily in the column, accompanied by the usual large entourage of excited workers, except for occasional brief stoppages (protracted in most cases by the clustering of workers over her) when obstacles were encountered in the trail. At 9:00 P.M. all ants had left the bivouac site of the day. Incidentally, almost the entire population of the colony passed in review during the observation of this movement, yet no sexual forms other than this single queen were observed.

This colony was judged to be passing through the terminal part of a regular nomadic phase.

Colony '46 H-S, *E. hamatum*

When found at 9:00 A.M. on April 17 to the south of Miller Trail near station 5, this colony was formed in a wide, open cluster against the under side of a large log. An extensive three-system raid was in progress. In the bivouac was found a large brood of nearly mature worker larvae, somewhat more advanced than the brood of colony H-R. The queen was not seen. The bivouac-change movement of that evening was not observed; next day the colony could not be found.

This colony was judged to be very close to the end of a regular nomadic phase.

Colony '46 H-T, *E. hamatum*

When found at 10:30 A.M. on April 21 near station 4 of the Drayton Trail, this colony was engaged in an extensive three-system raid. The bivouac was a large, open cylinder, somewhat irregular in form, under a log. A great brood of virtually mature worker larvae was found, well distributed through the bivouac. Especially noticeable in the walls of the bivouac cluster were small clusters of larvae held amid aggregations of workers with booty, engaged in feeding. Larvae in considerable numbers also had been carried to surfaces on the log near the bivouac, where cocoon spinning in its early stages was in progress. The colony was not disturbed to look for the queen. That night the colony moved 160 meters to take up a position in the deep interior of a large hollow log.

This colony when observed had reached the very end of a nomadic phase and was about to enter a statary phase.

Colony '46 H-U, *E. hamatum*

When this colony was found on April 26 at 10:00 A.M., a large three-system raid was in progress from a bivouac place in the area of Balboa 9. In the open cylindrical bivouac, which depended from the matted branches of a fallen tree, a large brood of moderately advanced worker larvae was found. This brood was fairly well distributed through the cluster, except for the smallest-sized larvae which were massed in strands hanging near the center of the bivouac. That night there was a movement of about 200 meters to the south, to a site from which a large raid developed on the following day. Large raids and nightly movements followed, with the colony shifting in general to the southeast. On April 30 the colony settled within a hollow log (its larval brood then engaged in spinning) at some distance to the southeast of American Museum Trail, station 6. Occasional raids were observed during the following days; however, it was not possible to ascertain the time at which this colony passed from the statary condition.

This record was taken to represent the last days of a regular nomadic phase and the onset of a regular statary phase.

Colony '46 H-V, *E. hamatum*

When this colony was found on April 27, it was located on the hill to the east of Shannon Trail, station 0.5, massed in an irregular cluster beneath a large tree root. A large, three-system raid was under way. In the bivouac, well distributed through the cluster, was found a large brood of well-advanced worker larvae. Large daily raids and nightly bivouac changes occurred regularly until April 30, when the colony moved into a broad cavity beneath the root mass of a fallen tree, to the southeast of Shannon 3.5. At that time the larval brood was fully mature, and cocoon spinning had evidently reached its peak. The colony remained at this site until May 21, with raidless days frequent from May 5 until May 17. On May 18 cocoon opening was well under way, with forays increasing in vigor on this and following days, until on May 21 after a large raid, with cocoon opening completed, the colony moved in the evening to a site 50 meters to the southeast. The new cluster was a regular cylinder formed beneath a large log. After a large, three-system raid had developed next day, the bivouac was etherized towards noon, and its contents were investigated. Large numbers of callow workers were found; however, no young brood could be located in the bivouac, and no queen. Since the search had been interrupted by a torrential rain, another attempt was made that evening at 7:15 P.M., when no definite signs of an exodus had appeared. The result was the same: neither young brood nor queen came to light. No bivouac-change movement occurred, a typical result when the etherization of a colony has seriously disrupted the development of raiding in a nomadic colony. A large raid developed from the same site next day (May 23), and in the evening a regular migration occurred to the northwest. Other work prevented tracing this movement to the new bivouac.

At noon on May 24 ants in a ragged file were observed following the bivouac-change route of the preceding night back to the bivouac site of May 22–23, and through it to the statary site. The ants, unquestionably returned on the back trails from the second nomadic bivouac of colony H-V somewhere to the west, were variously following former raiding trails leading out from both the statary bivouac site and from the first nomadic site. Such behavior is typical in queenless colonies (cf. H-A) and recalls to mind the fact that neither a young larval brood nor a queen could be found in the bivouac of colony H-V, despite careful searching.

It is believed that this record represented the termination of one nomadic phase, followed by a full statary phase of 20 days, then the beginning of a new nomadic phase. It is possible that this colony may have lost its queen before May 1 and consequently was without a young brood, hence without prospects of being able to complete the new nomadic phase in a regular manner.

Colony '46 H-W, *E. hamatum*

This colony was found on May 2, bivouacked within a hollow log 75 meters west of Fairchild Trail, station 1. A large brood of enclosed prepupal worker forms was present. The presumable presence of a second brood in the early larval condition could not be ascertained. The colony was passing through the early intermediate part of a statary phase, judging from the condition of the brood and of raiding, i.e., occasional small raids with intermittent raidless days. Cocoon opening was well under way on May 15, and the bivouac cluster bulged outward from the end of the hollow log, extruded in contrast to its previous situation well back in the hollow. Then on the evening of May 16, after a large raid, the colony moved off southward, leaving a great litter of empty cases. Time did not permit following the raid, hence the new bivouac could not be examined.

However, on May 24 a *hamatum* colony ('46 H-a) was found on the hill to the northwest of station 2, Snyder-Molino Trail, which conformed to the condition to be expected at the time in colony H-W. The colony was staging large daily raids, and in its open cylindrical bivouac cluster was found a large brood of worker larvae intermediate in development. Somewhat exceptional was the fact that no bivouac-change movements occurred after the large raids of May 24 and May 26, although on the intervening days the colony movement was extensive and well under way at dusk. A single queen in the contracted condition was observed.

The exodus of May 25 began before 5:00 P.M., when a steady and crowded column was observed leaving the bivouac of the day; and at 6:00 P.M. the new bivouac was observed under formation at a distance of about 160 meters. The queen did not pass the observation point (selected for flash photography) about midway on this route until 10:20 P.M. and did not reach the new bivouac until 11:00 P.M. The exodus of May 27 was under way at 4:30 P.M., when a steady regular column was observed leaving the bivouac, and at 5:30 P.M. this column had grown to the width (*ca.* 3 cm.) and regular concentration of individuals that are typical in *hamatum* changes of bivouac. Transportation of the larval brood was in full progress at that time. The queen appeared from the bivouac of the day at 7:10 P.M., and with relatively few stoppages completed the passage of 165 meters to the new bivouac site in one hour and 18 minutes. This time the queen was nearly at the end of the movement.

On June 1 this colony settled into a statary condition at a site near the crest of Donato Hill, incidentally just 17 days after the time colony H-W began its nomadic phase (fig. 5).

The record of colony '46 H-W represents passage through a statary phase, with the exception of the first few days, which were unobserved, and entrance into a regular nomadic phase. At this time a young larval brood very probably was present, although it was not possible to check the matter. From the coincidence of time and broods it was considered very likely that colonies H-W and H-a, the latter discovered when completing a regular nomadic phase, were the same.

Colony '46 H-X, *E. hamatum*

This colony was discovered on May 10 about 200 meters to the west of station 20 on the Wheeler Trail. At the time (10:00 A.M.) it was massed in a large open cluster against a log and was engaged in an extensive three-system raid. A large brood of callow workers was present, also a new brood of very young worker larvae, massed in strands at the rear center of the bivouac. Among these strands was found a single queen, fully contracted. It was necessary to use ether in examining the bivouac. The effect was to interfere greatly with raiding activities and evidently to retard the afternoon exodus considerably. That evening no bivouac-change movement occurred. On the following day there developed another large raid, followed in the evening by a regular movement of the colony. Large raids were followed by changes of bivouac both on May 12 and 13.

This colony was judged to be in the early stage of a regular nomadic phase.

Colony '46 H-Y, *E. hamatum*

The colony was found on the morning of May 15, when it was bivouacked about 150 meters to the west of Wheeler station 13 in a regular cylindrical cluster beneath a log. At 10:00 A.M. an extensive three-system raid had developed. The bivouac contained a large brood of nearly mature worker larvae, well distributed through the cluster. Thorough examination was not possible, and no queen was found. That evening the beginning of a regular bivouac-change movement towards the west was observed.

This colony was judged to be passing through the latter part of a nomadic phase.

Colony '46, H-B, *E. hamatum*

This colony was found on May 23, 200 meters to the east of Armour Trail at station 2. A well-developed, three-system raid was in progress at 11:00 A.M. The bivouac was an irregular cylinder beneath vines. When etherized for detailed examination, the cluster was found to contain a large brood of nearly mature worker larvae, among which the first signs of cocoon spinning were observed. The queen, fully contracted, was captured for preservation.

With the kindness of Dr. Roy Whelden, the following preliminary description is offered of the reproductive condition of queen '46 H-b at the time she was captured and fixed in a modified Bouin's solution: "Ovarioles, in part at least, packed with masses of minute cells, but extremely few of these cells show even a slight degree of enlargement." Presumably this represents a condition preliminary to early physogastry. No external signs of physogastry were perceptible in this queen.

The colony movement that evening went unobserved; however, on the following day, although the bivouac site contained no cluster, the ants were still traveling on the trails of May 23. Such back-tracking is a typical reaction to the removal of the queen from a flourishing colony.

This colony was judged to be in the last part of a nomadic phase, about to pass into a statary condition.

Colony '46 H-c, *E. hamatum*

On May 28 a *hamatum* colony was found bivouacked within a hollow log to the south of station 3 on the Balboa Trail. The colony apparently had just entered the site, since its mature larval worker brood was widely engaged in spinning. On June 4 the colony was not raiding, and spinning evidently had been finished.

This colony was judged to be entering a statary phase.

Colony '46 H-d, *E. hamatum*

The raid and bivouac-change movement were observed on June 2, and on June 3 this colony was found bivouacked 250 meters to the east of Wheeler station 24. A vigorous raid was in progress on three systems. That evening the bivouac-change column was followed 160 meters to the southwest. A large raid developed from the new bivouac on the following day, and in the evening another movement occurred to the midst of a mass of vines and rubble in the head of a fallen tree just east of Wheeler Trail, station 25 (only 50 meters from the nomadic bivouac of colony H-B on that date). A large brood of fully mature worker larvae was present, then actively engaged in spinning. The colony was still at this site when I left the island on June 15.

This colony terminated a nomadic phase and entered a statary phase in a regular manner.

SUPPLEMENTARY *BURCHELLI* RECORDS

For convenience of comparison, the results from supplementary colony studies with *E. burchelli* are presented separately in the following pages and are represented graphically in figure 6.

Colony '46 B-II, *E. burchelli*

This colony was found on February 7, bivouacked in the upper interior of a tall tree at a height of about 15 meters from the ground. The site was located 125 meters to the west of the Shannon Trail, at station 6, and was found by following back a principal raiding trail which at 4:30 P.M. on February 7 crossed the Shannon Trail without branching. On the following five days the colony seemed to be relatively inactive. At any rate there was no sign of raiding away from the tree (i.e., raiding in the upper parts of the huge tree may have occurred) with the exception of forays which developed in the afternoon on February 9, 10, and 11. Then on February 13 and 14 there were vigorous raids. Following the morning development of the latter, which involved a rapid swarm advance towards the northeast, activities dropped off markedly until after 3:00 P.M. The colony decamped that night, very probably towards the northeast on its raiding line of the day, for no further sign was seen of its presence in this vicinity.

This colony, which behaved in typical statary manner during the period of observation, may have been encountered later in colony '46 B-II, X.

Colony '46 B-II, X, *E. burchelli*

When encountered at 6:00 P.M. on February 20, this colony was engaged in a bivouac-change movement towards the northeast across Barbour Trail near station 2. The new bivouac was an open cylinder formed beneath the overhanging bank of a "quebrado" on upper Lutz Creek. On the following day a large raid was seen, ending in a change of bivouac to the north, well under

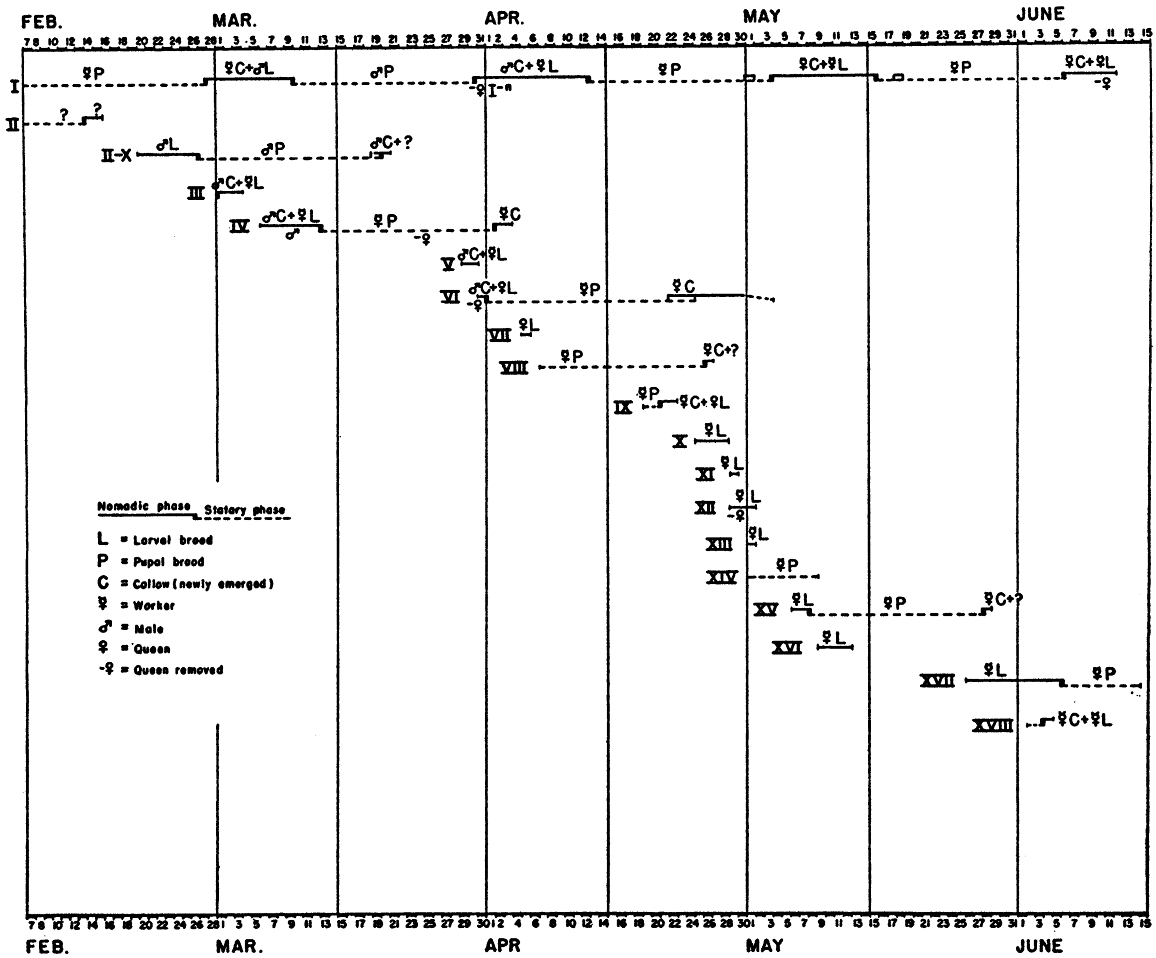

FIG. 6. Sketch of behavior records and correlated brood conditions for colonies of *E. burchelli* studied between February 7 and June 14, 1946. Individual colonies are designated by successive Roman numerals; concurrent colony conditions may be read in the vertical direction. At each differentiated nomadic or statary phase, the correlated brood condition (as well as presence or absence of a queen) is indicated by appropriate symbols (see legend). (Correction: Colony B-VII had a brood of *worker* larvae on Apr. 7.)

way at 4:30 P.M. The bivouac of the following day was 110 meters downstream to the north —a large open cylinder under a log upended on the crest of the high creek bank. This bivouac was found to contain two broods: an immense brood of callow workers and a second brood estimated to number more than 2000 male larvae well advanced in development. The queen was not seen at this time. The examination did not require etherization of the bivouac, and raiding was not interrupted extensively; hence the colony moved after 6:00 P.M. The new bivouac of February 23 was located 140 meters to the northeast, hanging from the upper edge of a broad, undercut, buttressed root to the ground. This structure was exceptionally tall, about 100 cm. high and 35 cm. in diameter, tapered inward to its narrow base on the ground. The raiding was extensive, as on the preceding days, and was terminated in the evening by a bivouac change of 125 meters to the northeast. The raid of February 24 was also a vigorous one, from a bivouac site between the overhanging buttresses of a large tree. The evening movement carried the colony about 60 meters to the north-northeast. The bivouac of February 25 was bagged close to the ground in the open base of a hollow tree, with a large raid to the northwest. That afternoon the first signs of cocoon spinning in the nearly mature male brood were observed. No bivouac-change movement took place in the evening. However, on the following day an extensive raid to the northeast across Donato Trail at station 3 was followed by a night-time move of 160 meters into a large hollow tree on the hill overlooking Gatun Lake. Here, clustered at first 2.5 meters above ground and about 1 meter above the upper rim of a basal opening in the tree, the colony remained for 21 days. Intermittent and never very extensive raids occurred. The raid on March 19 towards the east was an unusually large one, and there was also a fairly well-developed push towards the northwest. When the site was next visited on March 21 the ants were gone; however, a large heap of male pupa cases was collected from the floor of the tree hollow below the former position of the elevated pouch bivouac. By actual count these cases numbered more than 2700. Since the bivouac had been inaccessible during the statary phase, the presence of a new brood could not be checked.

Colony B-II, X when found was terminating a nomadic phase, next passed through a statary phase of 21 days, involving the pupation and maturation of its male brood, and subsequently entered a nomadic phase. Judging from the circumstances of time, position, and brood coincidence, it is possible that this colony was B-II.

Colony '46 B-III, *E. burchelli*

When this colony was found at 8:30 A.M. on March 1, it was evidently engaged in completing a prolonged bivouac-change movement from a site about 300 meters west of station 8, Van Tyne Trail (Schneirla, 1948). At the time only a few hundred ants remained in a small, dwindling cluster beneath the overhanging shell of a hollow log and were emptying into a broad unidirectional column which meandered to a place about 50 meters to the northwest, where an open-cylindrical cluster had formed among vines between the buttressed roots of a tree. The new bivouac was crowded with callow alate males, and alate males by the scores were running in the column connecting the two sites. Evidence that a statary site was being abandoned was found in a single large heap of empty male pupa cases on the ground under the log. (Counted later at the laboratory, these totaled more than 2700.) About 150 unopened or partially opened male cocoons were found in the small log cluster; scores of these cocoons were being dragged along in the column, and many were held in one or another of a few flat clusters formed at intervals beside the moving column that connected the sites. By 9:30 A.M. the movement had been nearly completed, and only a few straggling ants were seen on the trail. At that time a similar straggling column was seen leading from the log towards the southeast; unfortunately, time did not permit following out this file. In the open cylindrical bivouac to the northwest of the log, in addition to the alate males, a large new brood of very young larvae was found, massed in large strands near the center of the cluster. An energetic raid had developed to the south from this site; that evening the colony moved away over the principal trail of this foray. On the following two days the colony staged large raids, terminating in night-time movements over the principal trails.

Evidently the colony had passed through a statary phase at the hollow log, in which its male brood had passed through the prepupal and pupal stages, and a regular nomadic phase had begun at the time of observation.

Colony '46 B-IV, *E. burchelli*

When it was found on March 6 at 10:15 A.M., this colony formed a large, irregular bivouac cluster beneath some vines to the southeast of station 3, Barbour Trail. A large raid had developed towards the north. The colony was clustered in a large open mass among some fallen palm branches. In the bivouac were found a large post-callow brood of many hundreds of alate males and a great brood of approximately half-mature worker larvae. When the bivouac-change movement got under way after 6:00 P.M. that evening, the colony shifted about 125 meters to the westward along the principal trail of a second raiding system which had developed during the afternoon. On the two following days this pattern of events was repeated with secondary variations. In the movement of March 8 a dealate male was seen in the column, and another was seen in the column on the night of March 11. The bivouacs of successive days all tended to be clusters formed more or less in the open, with the exception of March 9 when the ants massed within the basal cavity of a hollow fig tree to the north of station 5, Snyder-Molino Trail. The principal raids and consequently the nightly movements tended to shift the colony in general towards the north. Meanwhile, the departure flights of numerous males occurred nightly (Schneirla, 1948). On March 12 after a large raid the colony moved in the evening about 60 meters into a small hollow tree close to station 2, Wheeler Trail, where it formed a pouch about 80 cm. above ground. This pouch bivouac was situated just above the top of a triangular opening in the base of the tree. At that time the larval worker brood was mature, and through this opening signs of cocoon-spinning activity could be seen amid workers clustered on the floor of the cavity and walls of the tree. It is probable that the major part of the spinning activity occurred on the crumbling inner walls of the tree above the bivouac. On successive days after March 13 relatively small raids occurred in different directions, but after March 16 and until March 29 forays were irregular and always relatively weak in development.

On March 22, the tenth day in this situation and approximately midway through the statary phase, the colony was etherized in an attempt to take the queen during the presumed time of egg laying. The plan was successful, in that after the principal part of the bivouac had been brought down with its mass of worker cocoons, a few large packets of eggs and finally the physogastric queen were secured from the upper part of the tree cavity by means of brushing with a long-handled, improvised broom. Circumstances indicated that the queen, with her large entourage of minor workers, had been located in an upper section of the bivouac distinctly separated from the lower part of the cluster in which the great brood of enclosed worker pupae was held. The fully gravid condition in which the queen was found, despite the masses of eggs present, indicated that she had not yet passed the peak of her relatively brief egg-laying period.[1] This queen was kept alive in the laboratory for 16 hours, during which occasional observations were made of her prolific egg production while more than 2000 eggs were laid (cf. Schneirla, 1944a); then she was fixed and preserved. Although at 2:30 P.M. the bivouac had been rather thoroughly disrupted, with masses of etherized ants and pupal brood spread around at the base of the tree, when next observed at 9:30 P.M. the bivouac cluster had been re-formed into a pouch and all of the pupal brood had been gathered into the bivouac.

After March 29 the daily raids increased progressively in vigor and extent of development with successive days. On March 31 there were some signs of cocoon opening. This activity had become general on April 2, judging by the "snow" of pupa cases which fell from the bivouac bag. The raid of April 2 was much more extensive than the raids of just preceding days, and after dusk a general bivouac-change movement of the colony got under way to the east. When the movement occurred, an estimated one-fifth of the mature pupal brood (nearly all minor worker forms) remained in cocoons. Although the movement was not followed out, the B-IV ants evidently emptied in large part or entirely into the trails of colony B-VI, since later on evidence of a more or less complete fusion of these (queenless) colonies was obtained.

Colony B-IV was under study through seven nomadic days, followed by a regular statary phase of 21 days and the beginning of a new nomadic phase. Circumstances to be described indicate that the removal of the B-IV queen and most of the new brood led to basic and unusual differences in colony behavior at the end of the statary phase.

COLONY '46 B-V, *E. burchelli*

On March 29 this colony was found at a site approximately 350 meters to the southeast of station 8, Shannon Trail. The bivouac was an irregular cluster formed about a tree and clump of lianas, with its base about 1 meter from the ground. Distributed through the cluster were several hundreds of alate males, as well as a second brood of nearly mature worker larvae. An energetic raid was in progress towards the northeast. About 6:30 P.M. the colony began to move over the principal trail to a tall, standing, hollow stump about 150 meters away, where it

[1] A queen of *E. hamatum* taken when physogastric, with a distended gaster of even smaller proportions than that of the B-IV queen, was found on examination to contain more than 18,000 eggs in various stages approaching maturation (Schneirla, 1944a).

clustered within the upper part about 2 meters from the ground. On the following day a vigorous swarm raid to the northeast was followed by a movement over the principal trail which began shortly after dusk. Time permitted observation of only the first part of this bivouac change. In both of these colony movements, the flight escapes of numerous alate males were observed.

The colony was judged to be in the last stage of a nomadic phase. From the fact that late on March 30 some cocoon spinning was observed in the larval worker brood, then mature, it is probable that the colony became statary on or shortly after March 30.

COLONY '46 B-VI, *E. burchelli*

This colony was found at 4:30 P.M. on March 31, clustered under some tumbled branches between two logs in the lower part of Lutz Creek. A highly developed raid was in progress to the southwest, and at about 5:00 P.M. the beginning was observed of a persistent outward exodus upon the principal trail. In the bivouac were found an estimated 500 alate males and a second very large brood of nearly mature worker larvae, the latter extensively engaged in cocoon spinning. When the bivouac-change movement was more than four-fifths completed, at about 10:00 P.M., the queen was observed leaving the old bivouac, followed by the typical fan of highly excited workers. The queen was in the contracted condition and ran easily in the column. Just before she and her entourage reached the terminus, the queen was removed from the column for behavior study and preservation. After a trek of about 200 meters, the ants mounted the trunk of a large fig tree in a column which could be seen for a distance of fully 15 meters from the ground. They then passed from view, evidently to a clustering site in the upper trunk recesses of the tall tree. The colony staged forays to the north and east on the two following days.

When the site was next visited on April 4, a complex and very special process of movement was observed on an extensive circular trail which had connections both with the B-VI fig-tree site and the hollow tree at Wheeler 2 formerly occupied by colony B-IV. A junction and a partial fusion of the two colonies were suspected, not only because of the existence of trails connecting the two bivouac places around the two arcs of a circle approaching 300 meters in diameter, but also because there were running in the far-flung circular column large numbers of callow workers (from colony B-IV), and the ants were also carrying thousands of newly enclosed mature larvae (from colony B-VI). This circuit remained in fairly consistent use up to the afternoon of April 9. (Ants were again observed following the wide circular route on the morning of April 19.) Further proceedings could not be followed closely. Hence the transfer of the B-VI bivouac to a mammal burrow about 40 meters to the southeast of the original fig-tree site, which occurred some time between April 4 and 11, was not seen. The continuation of scattered daily traffic on the connecting trails previously described, including the wide circular route, and the occurrence of occasional daily raids from the new base alone, left small doubt that the bivouac of colony B-VI had shifted. Only occasional thin files were seen on the (evidently abandoned) fig tree.

After April 18 raids occurred daily with increasing vigor. On April 21 the emergence of callow workers from cocoons was first observed, a process which continued for some days, apparently reaching its peak about April 25. What may be described as a gradual and very irregular beginning of nomadism started on the evening of April 22, with the formation on this and following evenings of new, open, cylindrical clusters. The cluster of April 22 was close to the burrow, and that of April 23 was at a distance of 80 meters to the east. Both of these were reabsorbed into the mass in the mammal burrow. The complex process reached a peak on the evening of April 25, when the mass of the colony moved to form a large cluster in a capacious recess below the overhanging bank of Lutz Creek, 180 meters from the abandoned burrow site. Great numbers of recently emerged callow workers were observed in the column, but also a considerable number (estimated at a few thousand) of unopened cocoons was carried along. The occupants of these cocoons, mainly workers minor and smaller intermediates, were largely removed within the following two days.

On the morning of April 29, interspersed along the bivouac-change route of the previous night were numerous small clusters formed beside the trail at intervals, evidently clusters set up in the confusion of the movement, from which the ants were slow in disengaging themselves. The tendency to straggle along the routes of preceding bivouac-change movements became even more noticeable on the following days, when the large colony changed its main base with increasing sluggishness and irregularity. The colony was last observed as a recognizable unit on the morning of May 3 when a loose irregular column of ants was seen on the back trail from Lutz Creek to the south, moving towards a junction with a far-flung circular complex of interconnected trails in the area immediately to the northwest of station 5, Barbour Trail. One-half of the large circle consisted of a thick column of unidirectional traffic (of bivouac-change appearance) including large numbers of callow workers. This thick column ended on a steep gully bank where ants numbering tens of thousands were clustered loosely in a more or less continuous layer, a thick, carpet-like mass spread over an area of about 1.5 by 3 meters. (In addition to the main aggregation, this carpet-like cluster, the colony at the time had much smaller groups of clusters at two other places in the circular trail complex.) The other half of the wide circular column led into an area from which a fairly large swarm raid had developed in the direction of Donato Trail, station 5. Booty carriers returning from this raid were found wandering in both directions around the circular trail, depositing their burdens rather promiscuously at a number of clustering places. In comparison with the routine of activities to be observed in a regularly functioning *burchelli* colony, all was confusion. Subsequently it became impossible to keep in touch with events in the time available for a daily inspection. On the following days, until April 10, ragged *burchelli* columns were encountered from time to time in the general vicinity of Donato Trail, station 6. The B-VI ants seemed to be shifting in general to the eastward. Attempts to follow out the trails were unsuccessful as far as discovery of a central clustering site was concerned. Nothing beyond ball-sized clusters and plate-sized masses at trail junctions were found, studding an increasingly spread complex of columns on trails which seemed to grow more and more irregular in pattern.

It is believed that colony '46 B-VI, after the final movement of a nomadic phase, settled into a more or less regular statary condition, interrupted by a short movement of unknown cause (perhaps occasioned by the excitement of a fusion with a part or all of colony B-IV with its great brood of callow workers) to a subterranean clustering site in the vicinity. The emergence after April 22 of a huge brood of callow workers attributable to the B-VI queen led to the resumption of nomadic behavior in a somewhat irregular way. In the days after April 30 the nomadic behavior became noticeably and increasingly irregular until by May 3 clear signs of disorganization had appeared.

Efforts were made at various times throughout the series of observations to establish the presence of a brood of young worker larvae, the later stages developed from eggs laid by the B-IV queen before her capture. (The B-VI queen had been removed before her further batch of eggs was delivered.) Although circumstances indicated that a considerable part or all of the B-IV colony had fused with colony B-VI, no such brood was ever discovered. It is probable that the young worker larvae of colony B-IV were consumed at an early phase of the colony junction, an outcome which later findings have indicated is to be anticipated in connection with a colony union.

The large broodless and queenless colony seemed to fall off rapidly in its capacity for organized and unitary action, a few days following the appearance of nomadism, when its callows were becoming more effectively incorporated into the population of adult workers. Subsequent observations indicated an increasingly ramifying and irregular behavior pattern in raiding and movement, a cessation of central "bivouac" aggregation, and an eventual loss of adequate unity.

COLONY '46 B-VII, *E. burchelli*

On the morning of April 5, this colony was found bivouacked at a point to the east of station 13 on the Wheeler Trail. The colony formed a long elliptical mass beneath a log, from which a large raid had developed to the southwest at 10:00 A.M. In the bivouac was found a large brood of nearly mature worker larvae. On the following morning this bivouac was gone, but ants were crossing Wheeler Trail at station 13.5 towards the southwest upon a line which had been used by this colony on the preceding day, and across Wheeler Trail at station 15 a large swarm raid operated towards the east.

From the coincidence of locality of operation and of brood condition, it is possible that colonies B-VII and B-VIII were the same. The behavior pattern was that of a colony in the late part of a nomadic phase.

COLONY '46 B-VIII, *E. burchelli*

On April 7 during an intensive search for colony B-VII in the area of its presumed location, colony B-VIII was discovered at 9:30 A.M., bivouacked within the almost completely sealed basal hollow of a large tree near station 3 on the Armour Trail and raiding southward. There were various signs that a large brood of mature worker larvae was present, especially the fact that spinning of cases was observed in a small triangular niche containing crumbling wood at the base of the tree. Daily visits to the site during the next 20 days gave general evidence on the frequency of raiding and condition of the brood. After the first four to five days, during which raids occurred daily, there was a long succession of days in which virtually no raiding occurred. Of course on some of the days, afternoon raids may have been staged, unobserved because morning visits were the rule. This section of the record is similar to that already noted for colony B-I; the difference is the non-occurrence of raids on the mornings (and perhaps also the afternoons) throughout the latter part of the stay. Thus after April 15, on the last 12 days of the stay, colony B-VIII had morning raids under way on two days only, April 21 and 26. (The site was not visited on April 20 and 24.) The colony therefore seemed to be unusually sluggish during the last days of the statary phase (cf. table 8).

In the final series of five days, only on the last day was a morning raid observed, and even that raid was slow in getting under way. Limited samples of the brood were taken at intervals, when the pouch of the bivouac reached sufficiently close to the ground to permit puncturing the sack through the small basal opening in the tree. A large worker brood was present which passed from larval maturity to pupal maturity during the 20 or more days in the tree. A large segment of this brood had been removed from cocoons within the two or three days before the colony moved away on the night of April 26. It was not possible to check for the presence of a further brood.

Although the beginning of this statary phase was not precisely established, it is probable that the colony (perhaps B-VII) was discovered within a day or two of its initial tenancy in the hollow tree.

COLONY '46 B-IX, *E. burchelli*

At 10:15 A.M. on April 19 this colony was found bivouacked in a pouch 2 meters from the ground within the basal hollow of a large tree on the bank of Fossil Creek near station 13, Shannon Trail. A moderately large swarm raid to the east was developing. On the following three days extensive raids were staged to the northeast, north, and south, respectively. A large brood of nearly mature worker pupae was found, with a few hundred individuals (mainly workers major) removed from cocoons on April 19, and rapidly increasing numbers removed on the following two days. The greater part of this brood had emerged as callow workers when the colony moved from the tree on the evening of April 21. The bivouac of the following day was a large open cluster massed against a buttressed tree root. Within it were found some hundreds of still unopened worker minor cocoons, as well as a large new brood of worker larvae in the early stage of development, assembled into a single long cluster located centrally in the bivouac. The raid of the day was a very large one, towards the northwest, which furnished the bivouac-change route followed that night.

The colony terminated a statary phase in a regular manner and began a nomadic phase.

COLONY '46 B-X, *E. burchelli*

At 7:20 P.M. on April 25 the bivouac-change column of this colony was encountered on the move into a cluster which had begun to form beneath a large ancient log in the bed of lower Shannon Stream near Shannon Trail, station 13. On the following morning at 9:30 A.M. an extensive raid had developed southward from the large open cylinder of the new bivouac; later a second smaller foray developed to the northwest. The colony had a very large brood of larval workers, then approaching full maturation. That evening at 7:20 P.M. a bivouac change was well under way to the southwest and east, through a distance of 160 meters. On the following two days similar large raids developed from the respective new bivouac sites, and on both evenings the bivouac-change movement was well under way before 8:00 P.M. In these successive movements the colony passed clockwise through a large elliptical path of about 300 meters in diameter, so that on April 28 its bivouac site was barely 50 meters downstream on the bank of Shannon Creek from the site occupied on April 25. After a large raid had developed to the east on April 28, the bivouac-change movement was slow in getting under way, and had not definitely begun at 7:30 P.M. when the colony was last seen.

This period was judged to have involved successive days of nomadic activity, in a colony that was evidently close to the point of entering a statary phase.

Colony '46, B-XII, *E. burchelli*

On April 29 at 11:30 A.M. this colony was found about 100 meters to the east of Wheeler Trail, station 25. Its changes of location and daily raids had been under general observation during the two preceding days. The bivouac of the day was massed in a large open cylinder beneath a log. The colony was raiding vigorously to the southwest in a foray divided at 11:30 A.M. into two swarm systems. A large brood of worker larvae at approximately the mid-point of development was found in the bivouac. Among the strands of minor-worker larvae accumulated near the center of the cluster was found the queen, in the fully contracted condition and surrounded by large numbers of workers minor. The queen was removed for preservation. That night the colony moved to the southwest, along a line which was not traced out to the new bivouac. At 1:40 P.M. on the following day columns were discovered on the trails which led through the April 29 site, although the foray of the new day was directed towards the south. At 10:45 A.M. on the following day a moderately large cluster of *E. burchelli* was found, with numerous thousands of worker larvae, formed exactly at the junction of trails close to the April 29 bivouac site. A considerable part of the colony had back-tracked, and from this cluster a raid had developed towards the north. In the evening these ants evacuated the site, moving off on the trail to the southeast. On the following morning the cluster was gone, yet thin files of *E. burchelli* continued in evidence on the various trails which had been in use on April 29 and 30. These ants were gone at 6:15 P.M. on May 2, and no further signs of the colony were observed on following days.

This colony was judged to be in the intermediate stages of a nomadic phase when regular activities were disrupted by etherization of the bivouac and removal of the queen. In all probability the eventual outcome was dissolution of the colony.

Colony '46 B-XIII, *E. burchelli*

This colony was found at 9:40 A.M. on May 1, engaged in a well-developed raid towards the west, from a bivouac site near Shannon Trail, station 4. The bivouac was a large cluster between two buttressed tree roots. In the cluster was found a very large brood of worker larvae about two-thirds developed, as well as a single queen in the fully contracted condition. This queen was replaced after examination. That evening at 7:45 P.M. a bivouac-change movement was well under way along the route of the day's principal raiding trail to the west-southwest. On the following day there was no trace of *burchelli* in the vicinity.

This colony was estimated to be in the late stages of a nomadic phase. Its raiding and bivouac-change activities were not interrupted noticeably by a temporary removal of the queen without ether and by the taking of approximately 10 per cent of the larval worker brood for preservation.

Colony '46 B-XIV, *E. burchelli*

When found at 11:30 A.M. on May 1 this colony was bivouacked within a hollow log about 200 meters to the east of Wheeler Trail, station 20. An enclosed brood of worker forms in the early stages of pupation was present; a moderately developed raid was in progress towards the east. When next visited on May 5 the colony was raiding towards the southeast. No raid was in progress at 10:30 A.M. on May 7; however, a raid developed when the ants were excited by my attempts to take specimens of the brood. The termination of this statary phase was not observed.

COLONY '46 B-XV, *E. burchelli*

This colony was found on May 6, bivouacked in an open mass beneath overhanging tree roots on a stream bank to the east of Wheeler Trail, station 22. A large brood of mature worker larvae was present. An extensive raid to the southeast was followed in the evening by a bivouac change over the principal raiding trail. From the new bivouac downstream another large raid developed on May 7, with an evening movement into the upper part of a tall hollow tree some distance to the southeast of Wheeler Trail, station 24. Here the colony remained, raiding intermittently, until May 28.

This case represents the termination of a nomadic phase, followed by the beginning of a statary phase.

COLONY '46 B-XVI, *E. burchelli*

The colony was found at 10:00 A.M. on May 9, when it was carrying out a large raid to the northwest from its open bivouac south of Wheeler Trail, station 11. A bivouac-change movement occurred that evening along the principal raiding trail of the day. A large brood of worker larvae was present, about two-thirds grown. During the next three days large daily raids and nightly shifts of bivouac occurred regularly.

These observations represent a portion of a regular nomadic activity phase, evidently about midway through the interval.

COLONY '46 B-XVII, *E. burchelli*

This colony was first encountered on May 26, when it was raiding extensively to the northwest from its open bivouac under a large log near station 3, Barbour Trail. The bivouac change of that night took it to a site about 110 meters to the northwest. There were large daily raids during the following five days, each followed by a nightly movement. On June 3 the colony reached a bivouac site near station 3, Wheeler Trail. During this time, the presence of a large brood of worker larvae nearing maturity was ascertained. This was a colony of large size, approaching the population magnitude of colony '46 B-I which was very large even for *E. burchelli*. Signs of cocoon spinning were observed on the night of June 4; then on the night of June 5 the colony moved into a large fig tree in the ravine south of station 5, Snyder-Molino Trail. Here it remained, well concealed within the convoluted columns of the trunk, when I left the island on June 14.

This case involved the regular ending of a nomadic phase, followed by a statary condition.

COLONY '46 B-XVIII, *E. burchelli*

On June 2 this colony was found massed in a large cylinder deep in the hollow of a log near station 1, Drayton Trail. A large brood of mature worker pupae was present, with indications that the emergence of callows was beginning. At 8:15 P.M. raiders were still returning in column from the raid of the day to the southeast. The raid of June 4 was a large one to the southwest. In the movement of the colony, which took place that night over the principal raiding trail, great numbers of callow workers were in evidence; however, a large part of the brood was carried along still enclosed in cocoons.

This observation involved the termination of a statary phase and the regular beginning of a nomadic phase.

SUMMARY AND DISCUSSION

YEAR-AROUND CONTINUANCE OF THE ECITON PATTERN

THE PRIMARY OBJECTIVE of this investigation was to discover what differences might exist between the strikingly regular nomadic-statary pattern of army-ant species in the rainy season, and conditions in the dry season. In the rainy season, the system of behavioral and biological events designated by the term "nomadic-statary pattern" runs a course which is remarkable for its adaptive precision and its regularity in each colony. These circumstances may be considered optimal for tropical ecitons, in the sense that in the rainy months no maladaptive variations or disruptions ordinarily intrude themselves in the smoothly running system of events dependent upon queen, brood, and workers in each colony.

The present project involved a continuous study of colonies in both of the test species, *E. burchelli* and *E. hamatum*, during more than four months of the 1946 dry season. Shorter surveys ranging in time from two days to two months were carried out with numerous other colonies of both species. In all, 18 colonies of *E. burchelli* and 31 of *E. hamatum* were studied. My investigation of 1946 thereby improved upon the survey of 1945 carried out in southern Mexico in that it was both longitudinal and cross-sectional in nature, with prospects of obtaining a better-rounded and more respresentative picture of the situation under given seasonal conditions throughout the army-ant population of a given area.

The results indicate the prevalence of the representative nomadic-statary pattern through the dry season in the tropical ecitons studied. The pattern continues effectively in the colonies, despite radical differences in the conditions of the general environment. This outcome lends emphasis to the versatility of behavioral and biological properties in the given organism and the extent of its adaptive resourcefulness under more taxing environmental conditions. Scattered but numerous notes on tropical species of the subgenera *Labidus* and *Neivamyrmex* indicate that a comparable system of events may hold widely among tropical dorylines.

This not altogether anticipated finding raises a number of questions concerning the essential mechanism of environmental adaptation in the eciton colony and its possible seasonal variations. A further question of importance concerns the nature of the effective environmental limits beyond which the eciton nomad-statary pattern might cease to be adaptive.

SEASONAL PHASE DURATIONS OF THE NOMAD-STATARY CYLE

As a means of comparing seasonal adjustments it is desirable to know the phase durations in the nomadic-statary pattern and their range of variation in the two principal seasons of the year. The cases represented in table 10 involved colonies for which one or more complete phases of the cycle were recorded. Unfortunately, collecting such data was not the main point of earlier studies in rainy-season months (Schneirla, 1938, 1944b); hence less evidence exists on the cycles in that season than would be desirable. However, because of the great uniformity as to prevalent cyclic conditions among the many colonies then investigated, the reliability of the available results should not be held lightly.

From these data there would appear to be no great difference in the duration of corresponding phases in the eciton cycle in the two seasons of year. For *E. hamatum* the nomadic phase runs from 16 to 18 days in length, the statary phase from 19 to 21 days; for *E. burchelli*, the nomadic phase runs from 10 to 13 days, the statary phase from 20 to 23 days. It will be noticed in table 10, as concerns *E. hamatum*, that in the rainy-season records from 1936 the nomadic phase is somewhat longer and the statary phase somewhat shorter than is typical in the 1946 dry-season records. In the case of *E. burchelli*, matters are reversed, with the rainy-season nomadic record shorter and the statary record longer

TABLE 10

DURATION (IN DAYS) OF PHASES IN THE ECITON CYCLE DURING THE PRINCIPAL SEASONS

(Only records of at least one complete phase are included; incomplete phases are indicated by a dash. Data for successive phases are arranged consecutively for each colony represented. The dry-season data (1946) are arranged in vertical columns roughly based upon correspondence in time.)

Rainy season

Colony	Nomadic	Statary	Nomadic	Statary	Nomadic
E. hamatum '36		—	18	19	—
E. burchelli '38	—	23	11	—	

Dry season

Colony	Statary	Nomadic	Statary	Nomadic	Statary	Nomadic	Statary	Nomadic
E. hamatum								
'46 H-B		16	21	17	20	16	20	—
'46 H-D				—	21	—		
'46 H-E				—	19	—		
'46 H-H				—	20	—		
'46 H-V						—	20	—
E. burchelli								
'46 B-I	21	10[a]	21	13	21	12	22	—
'46 B-II, X		—	21[a]					
'46 B-IV		—	20					

[a] Male brood. Others are worker broods.

than the corresponding dry-season records. From evidence reported on cyclic changes in the two seasons of the year it would appear that if characteristic seasonal differences exist in phase duration they are likely to be relatively small.

What I have found concerning phase durations in the two seasons suggests that a relatively stable set of processes underlies the typical eciton behavior pattern throughout the year. Examination of the values in table 10 shows that in both seasons the complete cycle (i.e., of nomadic and statary phases together) lasts 36 or 37 days in *E. hamatum* and 32 or 33 days in *E. burchelli*. In view of the close relationship that has been found between brood processes and colony behavior in the rainy season, and just recently in the dry season, the approximate values for cycle duration in the two seasons indicate the probability that common factors are involved in developmental processes at all times of year.

In this paper, evidence has been offered for the dry season concerning the dependence of major changes in the behavior cycle upon trophallactic stimulative effects from the brood (cf. Schneirla, 1941). The present results (see figs. 3 and 4) abundantly show that in the dry season the two phases of the cycle begin and end in conjunction with the respective climactic brood changes that have been described for them under rainy-season conditions. Especially notable as a special point here are variations in colony raiding activities during the statary phase in relation to changes in brood condition. The statary phase begins with an abrupt decline in raiding and a cessation of nomadism on the day the mature larval brood is effectively enclosed through spinning (figs. 3 and 4). Spinning by larvae continues within their envelopes, thickening the cocoon walls, during the next few days. Tables 4 and 8 show that after the first few statary days, once such brood activity has ceased, there is a notable falling off in the frequency and vigor of raiding. This low point persists in extra-bivouac activities until brood maturation brings in the factor of reflex activities in the nearly mature pupae, excitatory to workers. Then, in both species as in the rainy season, there is a sharp crescendo in daily raiding. A few days later, when the effective emergence of this mature brood releases some tens of thousands of highly active callow workers (or a few thousand males) into the bivouac, colony activity abruptly attains nomadic status.

The described concurrence between major changes in the colony behavior cycle and in brood condition is corroborated fully in the foregoing case reports, which are summarized in figures 3, 4, 5, and 6. As far as the major points of change in the cycle are concerned, these relationships differ in no important respect from occurrences under rainy-season conditions. However, certain secondary differences appear which merit discussion.

SPECIES DIFFERENCES IN PHASE DURATION

Species differences in the duration and precision of behavior-reproductive rhythms may be a useful source of information about the basis of the rhythms. From table 10 we see that the representative value for the nomadic phase in *E. hamatum* is 17 days with relatively little variation, whereas that for *E. burchelli* is shorter by three or four days and is more variable. The species are considerably more alike in the statary phase, the duration of which ranges close to 20 days in *E. hamatum*, whereas in *E. burchelli* it is most frequently 21 days.

It is interesting to note that the pronounced species difference occurs in the nomadic phase of the behavior cycle, which basically depends upon the duration of larval development and the temporal synchronization of two broods (Schneirla, 1938, 1944a, 1944b), rather than in the statary phase, the limits of which are dependent upon processes within a single brood then passing through pupation. We may consider certain indications that the described species difference is attributable both to features of brood development and of adult responsiveness.

Nomadism often begins in *burchelli* colonies when the pupal brood, although mature, is still enclosed to the extent of as much as one-third of the brood population. The excess cocoons which are carried along and are opened during the first few nomadic days are predominantly those of smaller intermediate and minor-type workers. In contrast, the nomadic phase in *E. hamatum* typically begins rather precisely on the day when the last and greatest part of the callow brood has been removed from cocoons.

A greater variability on the part of *E. burchelli* in beginning and apparently also in ending the nomadic phase is evidenced, particularly in the dry season, by the proneness of colonies of that species to relapse into a statary form of behavior for a day or two after a nomadic phase apparently has begun, or to return to a nomadic behavior after the ostensible beginning of a statary phase. It will be noted that instances of this kind appear on various occasions in the record of colony '46 B-I (table 5) but are absent from the record of colony '46 H-B (table 1).

There are indications that the greater variability of *E. burchelli*, especially in beginning nomadism, is dependent upon somewhat more complex and apparently less precise relationships between adult behavior and brood developmental processes than are effective in *E. hamatum*. A variety of observational evidence indicates that *burchelli* workers have a lower excitation threshold than *hamatum* workers, represented by the fact that the former are typically much the easier to disturb by minor interference with their bivouacs or raiding activities.

Certain characteristics of brood development also appear important for nomadic variability. From the sampling of innumerable broods and the capture of some of them entire, the impression is gained not only that *burchelli* broods are often much larger than the maximum for *E. hamatum*, but also that a wider range of developmental time often characterizes the former. Thus spinning in a brood of mature larvae tends to persist over a longer time in *E. burchelli*, and there is usually a longer interval than in *E. hamatum* between the emergence of the first callows (major and larger intermediate workers, mainly) and the last ones (smaller intermediates and minor workers, mainly) from cocoons. Consistent with these features in the brood, indications appear in taking queens that the *burchelli* queen is physogastric and engaged in egg laying for a somewhat longer time than the *hamatum* queen, suggesting that the former generally requires a somewhat longer time to lay a larger brood than the latter can produce.

Hence there are several indications that in *E. burchelli* the relationships between processes of brood development and adult behavior are more complex and variable than in *hamatum*. As for the species difference existing in duration of the nomadic phase, its basis may possibly lie in a different synchronization of successive broods, one setting off the phase with its pupal maturation, the next terminating the phase with its larval maturation. The reasons for the shorter interval between broods in *E. burchelli* are not clear at present.

That the relative constancy of the statary phase in both species is attributable to the fact that its initiation and termination depend upon successive crucial developmental changes in the same brood has been mentioned. It suggests that a relatively stable ecological situation is effective as a rule, in which only minimal fluctuations can occur from the standard of brood growth. In this phase especially, the variable conditions of the general dry-season environment evidently are effectively buffered through eciton nesting procedures.

A PERSISTENT MAXIMAL FUNCTION IN THE QUEEN

From the facts concerning continuous cyclic processes in the colonies, it is clear that a prolific and regular function must prevail in the colony queen throughout the year. It is difficult to think of any other animal in which the reproductive contribution of the female even remotely approaches that of the eciton queen in quantity, regularity, and persistence. These qualities are approached most closely by some termite queens, with the important difference that egg laying in these insects lacks the precisely synchronized periodicity of broods which is effective in the ecitons.

At present data are lacking concerning reproduction in the tropical species of myrmecines and dolichoderines which are probably the most prolific reproducers among all ants. However, even with the additional adaptive asset of polygyny common in their colonies, it is doubtful that many of them exceed the common eciton performance in volume per year. Almost certainly they do not approach it in regularity and periodicity.

As an illustration of the typical eciton production level, in the case of colony '46 H-B (fig. 3) there were produced during the interval of study five successive worker broods emerging at intervals of almost exactly 36 days, with a probable minimum of 20,000 individuals in each brood. The supply of new worker individuals commonly made available in the intact eciton colony through a single reproductive female is truly phenomenal in its extent and regularity.

With a minority of explicable exceptions, to be discussed below, among more than 50 intact eciton colonies investigated in the dry months of 1946, all possessed queens that were maintaining a prodigious egg production approaching the rainy-season level in brood size. The condition of the queen (contracted or physogastric) regularly bore the relationship to the status of developing broods which is familiar from rainy-season studies (Schneirla, 1944a), and a periodic reproductive function was indicated by the synchronization of broods (see figs. 5 and 6). When queens were present, circumstances indicated a function near maximum in all cases; in other words, I have found no evidence that declines or interruptions occur in this process during the dry months.

The exceptions were few and understandable. One *hamatum* colony ('46 H-N) of irregular behavior was found in which repeated examination disclosed no brood, but neither was a queen brought to light in this case. From the circumstances of time and place, it is possible that this colony may have been '46 H-A, from which the queen had been taken a few weeks before, entering a stage of degeneration after its developing brood had matured to worker status. In another exceptional case, colony '46 H-O, evidence was found that the queen had died some time before the colony was encountered. This colony when found had no clustering center, was scattered over an irregular set of ramifying trails, and was evidently approaching an eventual dissolution.

The case of colonies '46 B-IV and B-VI at first took a different course after their respective queens had been removed. When the trails of these two colonies happened to cross, a large part or all of colony B-IV fused with B-VI while the latter was still in a statary phase. Consequently, when the pupal worker brood of colony B-VI emerged, the new aggregate B-IV+VI exhibited a nomadic behavior for a few days. This was its last behavior of a systematic character, for the loss of the queens early in the preceding statary phase had of course precluded any further broods. Had the queen remained, a brood delivered in the early part of the statary phase by now would have been well under way in larval development (cf. fig. 4) and capable of sustaining nomadic activity in the colony for a predictable time. With both queens gone, the inevitable result in this case was inertia and disintegration. It would appear that the process of colony fusion must serve as an important adaptive mechanism promoting the survival of queenless colonies.

From the above considerations it is evident that the relative species constancy found in nomad-statary phases is the result of given characteristics of timing and quantitative capacity in the queen's function. What sets the queen into the great labors of her comparatively brief egg-laying episode? Whatever their nature, the responsible factors operate periodically, with a regularity indicated by the fairly constant inter-brood periods found in colonies '46 H-B (about 36 days) and B-I (about 33 days) in a study lasting somewhat longer than four months (tables 2 and 6). The reproductive response of the queen is also a prolific one, evidenced by the fact that the worker broods regularly approach the magnitude of such broods in rainy months. From the evidence it is probable that ordinarily a colony queen produces about 10 of these great broods each year. There is no reason to doubt that the generative performance of a given eciton reproductive can last more than one year at the characteristic high level. Certainly a maximal function persisted in the queens of colonies '46 H-B and B-I during about one-third of a year, with the last broods of these queens, prior to capture, closely similar to early ones in that period. Finally, the queen's periodic response is a transitory one, temporally limited to a relatively short interval of a few days, as in the rainy season.

The one event of major importance which from all indications is specific to the dry season is the production of male broods (Schneirla, 1948). From the fact that evidently only one such brood may be produced by any one colony in a given season, and because such broods come within a limited time well after dry weather has begun, these departures from the consistent production of worker broods would seem to represent a special reaction in the queen to the impact of dry conditions. If the Dzierzon rule applies to the ecitons, this lot of males is the only brood in the year arising from unfertilized eggs. What the nature of this exceptional reaction may be can only be conjectured at present (Schneirla, 1948). Although the sterilization seems to be a completely effective one at the given time, it evidently represents a temporary condition from which the queen recovers quite adequately. From the evidence, in each case the singular all-male brood is preceded and followed in the series by broods consisting entirely of workers. The case of colony '46 B-I is representative.

The year-around consistency of the eciton queen's periodic reproductive feat is all the more striking when certain potential environmental hazards are considered. As numerous investigators have demonstrated, detrimental effects and often a stoppage of insect fertility may be produced by environmental conditions such as atmospheric dryness, high temperatures, and deficiency in available food (Uvarov, 1928, 1931; Buxton, 1932; Himmer, 1932; Anderson, 1935; Haydak, 1943; Ludwig, 1945). Although the evidence comes mainly from laboratory investigations on Temperate Zone insects, one would expect it to apply at least in part to the dry-season life of tropical forest insects. The present study deals with terrestrial eciton species, which might be expected to suffer most of all in continued dry weather, yet it is apparent from the findings that successful adaptations are typical in the colonies.

POSSIBLE EXTRINSIC EFFECTS UPON ECITON RHYTHM

It is not known at the present time what factors are responsible for setting the eciton queen into her remarkably periodic egg-laying episodes. The controllers may be extrinsic or intrinsic to the queen (Schneirla, 1944a), or a combination of these. At present, with the internal processes of the dichthadiigyne a matter of guesswork, at least a beginning may be made on the problem by examining the possibility that external factors may be involved.

This project involved the detailed and continuous study of two colonies in different species, with numerous other colonies under investigation for shorter periods. Thus at any one time, two or more colonies in each of two species were on record as to their status with reference to the nomad-statary rhythm. The results are presented schematically in figures 5 and 6, so that by reading vertically at any given date mark the possibility of a general concurrence of colony rhythms may be examined. An effective coincidence of colony rhythms would of course suggest a synchronization of underlying processes under some periodic external regulation. Such an effect if present might be more or less comparable to the known influence of decreasing or increasing day length upon reproductive changes in many birds and mammals (Rowan, 1931; Marshall, 1936; Bissonnette, 1936). For instance, Weber (1943) has suggested that doryline activities may have some important relation to lunar cycles.

However, a study of the conditions of various colonies surveyed concurrently in this project shows rather convincingly, as do previous results for both dry- and rainy-season conditions (Schneirla, 1938, 1947), that no real correspondence beyond chance exists in the rhythms of the various colonies. For example, to consider the condition of the *hamatum* colonies on record March 21 (fig. 5): colony H-B was in its second day of nomadism and H-F in its third day, whereas H-H was entering a statary phase, H-D was in its eighth statary day, and H-E in its twelfth. Or at a much later date, on May 21 colony H-B was in the early part of a statary phase, colony H-V was beginning a nomadic phase, and H-X was about to end a nomadic phase. Similarly in *E. burchelli* (fig. 6), on April 5 when colonies B-I and B-IV were entering a nomadic phase, B-VIII was ending that phase, while B-V and B-VI were beginning a statary phase. Such comparisons are typical in their outcome, in that no synchronization of colony rhythms in the same species is indicated. Likewise there is no evidence of an interspecies correspondence in rhythms. For instance, when the study opened colonies '46 H-B and B-I were in opposite phases—B-I was statary while H-B was entering a nomadic phase. During the following four months these two colonies, as did other colonies of the two species, exhibited all possible differences in phase, one from another. The results hardly support the postulation of a common extrinsic regulation of colony rhythms.

This does not mean that the regulation of rhythmic processes in any given colony necessarily proceeds without the intervention of extrinsic influences. It is true that at an earlier time in the general investigation (Schneirla, 1944a) the concept of a basic pacemaking process intrinsic to the queen seemed consistent with available evidence. The variability exhibited by both species in the duration of the nomadic phase does not necessarily oppose the hypothesis of intrinsic control, since absolute precision is not an essential criterion of rhythmic organic processes. On the other hand, certain new considerations appear to favor the alternative.

In four cases where queens were taken from colonies nearing the end of the nomadic phase or just becoming statary, attempts have failed to bring them into physogastry under laboratory conditions. Two of these queens remained in their colonies housed in laboratory nests with their mature larval worker broods; the other two were placed in artificial nests, each with about 200 workers and a comparable quantity of brood. The most obvious reason for non-physogastry at the time when egg production would ordinarily occur is insufficiency of food. The food that could be given these colonies and part colonies fell short of requirements, with the result that broods were consumed and queens remained contracted in all cases.

Thus we have the fact that under the conditions of these laboratory tests it was not possible to furnish the queens, of necessity through the workers, sufficient food to permit the production of a great quantity of eggs. Evidently no eggs at all were produced. This outcome suggests that feeding of the queen, perhaps together with other external factors, ordinarily may be responsible alone for initiating physogastry, without the involvement of an intrinsic "trigger mechanism."

A consideration of normal occurrences favors the view that a synchronized change in feeding of the queen may occur in the course of a nomadic phase. The colony then has a great larval brood which, as it nears maturity, exerts a trophallactic effect of steadily increasing magnitude upon the workers. Consequently, through the last nomadic days, the daily predatory forays increase markedly in their scope, with a corresponding marked increase in return of booty. Although the brood now is capable of consuming greater quantities of food than before, the "bonanza" must also afford a considerable surplus for the queen over what she received in earlier nomadic days. Such an overfeeding of the queen thus would come at a regular point in the cycle, representing the possible basis of a change in her metabolism which could lead to physogastry and the delivery of a further brood.[1]

It is thus a possibility worth testing that the initiation of physogastry in the eciton queen depends primarily upon circumstances initiated through the progress towards maturity of a large larval brood more than upon causes intrinsic to the queen herself. If this hypothesis is correct, we should expect that in a colony subjected to a continual resubstitution of young larval broods, the queen would lose her rhythmic reproductive function until one of these broods was permitted to reach maturity.

TROPHIC CONDITIONS UNDERLYING REGULAR BROOD PRODUCTION

If, in the dry season, eciton colonies were not generally successful in producing populous broods with regularity, the typical behavior rhythms could not prevail as widely as I have found them. As in the case of colony '46 H-A and others, a sufficient reduction of the brood of larvae impairs nomadic behavior correspondingly, and removal of the queen results in a complete disappearance of the nomad-statary rhythm as soon as the supply of broods has run out. The effectiveness of an active brood as a stimulogenous factor is illustrated by occurrences in a queenless colony (such as '46 B-VI) which starts out nomadically after a statary phase but maintains the condition only as long as the maximal trophallactic effect of its callow brood continues. After a few days, when the callows behave much like adult workers and their special excitatory function has waned, the colony begins to behave irregularly and its eventual ruination is assured. Colony '46 H-O represents a case of this kind that occurred naturally. It is probable that such casualties of whole colonies are not infrequent in the dry season.

The eciton pattern is thus a complex circular system, in which the periodic appearance of a further brood in the larval condition maintains a routine of very productive daily raids, as well as regular changes in nest site which insure newer territory to plunder, and this routine in turn insures the production of further large broods.

Because it is doubtful that eciton colonies could survive long on any basis other than the typical pattern, which requires large broods in a regular series, the fact that dry-season broods approach those of rainy months in their timing and population is highly important for species adaptation. A qualitative difference, the production of one male brood in the dry season, does not alter the picture (Schneirla, 1948). This suggests a year-around similarity in the effective ecological and trophic conditions of brood development, in view of numerous studies which have demonstrated the critical influence of factors such as temperature, low humidity, and feeding in insect growth (Bodine, 1925; Chapman, 1927; Himmer, 1932; Hoskins and Craig, 1935; Richards and Miller, 1937; Wigglesworth, 1939; Ludwig and Anderson, 1942; and Ludwig, 1945). Maintenance of a given food maximum is unquestionably of great impor-

[1] In queens captured during the terminal part of a nomadic phase, one often notices a partial distention of the gaster, with the intersegmental membranes visible, which is never found in queens taken earlier in the nomadic phase.

tance for eciton development. Quantity of food has been found an important developmental factor in many insects (Kopéc, 1924; Northrup, 1930; Imms, 1937; Richards and Miller, 1937; Wigglesworth, 1939). It is well known that variations in amount of food may cause larval insects to be advanced or retarded in time of pupation. With deficient food, a polymorphic ant such as eciton would be expected to produce larger numbers of intermediate and minor-type workers in the castes. Any appreciable decrease in food supply almost certainly would be reflected in brood development and thereby in colony behavior. The fact that such effects do not appear prominently will bear further examination.

With respect to food, a variety of direct and indirect effects of dry-season conditions upon eciton life might be expected. Because the army ants depend mainly upon insects and forest arthropods for their booty, a change in their own level of activity or in the activity or abundance of other insects might be materially important from their standpoint. There is much evidence from laboratory studies indicating that arthropod activity is in fact depressed by conditions such as high temperature and low relative humidity in particular (Herter, 1924; Kennedy, 1927; Buxton, 1924a, 1924b, 1932; Chapman, 1927, 1928; Bodenheimer and Klein, 1930; Uvarov, 1931; Eidmann, 1936; Gösswald, 1938, 1941; and Wigglesworth, 1939). Field results show that in times of drought many insects are far less active and far less in evidence than otherwise (Dogel, 1924; Larrimer *et al.*, 1931; and Weber, 1941). Dammerman (1925, 1927) reported that the population of soil insects during the dry season was considerably less than in the rainy season. Others have reported local population decreases dependent upon climate (Janisch, 1930; Buxton, 1933).

From such evidence, the eciton food supply might be expected to drop radically both in accessibility and in amount during the dry months. However, in the absence of adequate studies in tropical rain forest, the possibility remains that (except in partially deforested areas) the general effect of the dry season may be a rearrangement and shifting of local insect populations rather than any material reduction in general numbers (Buxton, 1923, 1933; Kennedy, 1928; Bodenheimer, 1928, 1937; Hesse, Allee, and Schmidt, 1937; Emerson, 1939; King, 1939; Goetsch, 1940; Pickles, 1940). It is of course conceivable that local decreases may occur through seasonal effects. But against such possible decreases may be set the rises typical of arthropods such as many orthopterans, common booty of the swarm-raiding ecitons, which appear more numerously in dry weather. Furthermore, among the wasps, ants, and other common insect victims (either as adults, as brood, or both) of army-ant predation, many species are fairly prolific, in the production of sexual forms in particular. Thus possible species difference in the abundance of eciton booty may be effectively balanced off against one another. Because of the typical diurnal seclusion of most insects and the tendency to concentrate locally, it is probable that eciton booty is subject to local variations in its accessibility in the dry months. An over-all reduction in the available quantity is more problematic.

That there is a substantial reduction in the quantity of booty actually taken is very doubtful. From earlier considerations, it would appear that the effective food intake of any army-ant colony could not undergo a very great reduction without affecting the rhythmic course of events very materially. There is good reason to believe that consumption of the brood would occur were the bivouac food supply to fall below a given minimum, yet my notes contain no definite indications of brood cannibalism even at the height of the dry season. For a colony of intermediate population size (*ca.* 80,000 workers) the necessary quantity of food, from daily estimates, rises to an amount approaching 2 quarts daily when the larval brood nears maturity. Yet under the conditions of this study most of the eciton colonies in the area managed to "corral" enough booty to raise successive large worker broods to maturity—broods not only close in population magnitude to those of rainy months but also with much the same distribution of polymorphic types.[1]

It is now clear that the representative pat-

[1] As for male broods, although their population size is only about 10 per cent that of worker broods (Schneirla, 1948), their tissue bulk at maturity approaches or exceeds that of worker broods.

terns of predatory activities are continued in both *E. hamatum* and *burchelli* through the dry months, with secondary differences only. In the nomadic phase the raid of *E. hamatum* is describable as three tree-like systems of branching trails which build up during the daytime; that of *E. burchelli* as a swarm advance with a fan-shaped mass of consolidation columns in its rear from which a single column connects with the bivouac, the swarm undergoing multiple division in vigorous raids. The statary-phase raid of *E. hamatum* is reduced to a single trail system; that of *burchelli* to a considerably smaller swarm and fan.

In the dry season the raids of both species tend to deviate relatively more from their typical "column-raiding" and "swarm-raiding" patterns than under rainy-season conditions. There is a greater variability in the course of the *burchelli* swarms and the *hamatum* "pushing parties" in the van, which paves the way for a noticeably greater irregularity in the base trails. These differences are attributable in part to the distribution of booty, now definitely more subject to concentration in "islands" such as brush heaps and local nesting places than in rainy weather, and partly to environmental effects in occasional areas which appear to be hot, bright, or dry enough to divert the advance somewhat. In the dry season, *E. hamatum* tends, far more than in rainy months, to run beneath objects such as leaves, often for considerable distances. Such behavioral differences, attributable on the whole to more disturbing local variations in environmental conditions, not only serve to reduce the exposure of foragers in numbers to potentially hazardous conditions but also to operate adaptively to increase the chances of finding booty.

Thus the behavior mechanisms involved in the two main patterns of eciton raiding appear to be sufficiently plastic to surmount the variety of environmental risks encountered and to gather in sufficient food to meet dry-season conditions. Through an aggregate of relatively simple mechanisms (Schneirla, 1938, 1941)—mass responses based upon individual behavior processes—the ants in their swarms (e.g., *E. burchelli*) or system of branching columns (*E. hamatum*) are capable of spreading in variable numbers forward or laterally, according to conditions affecting the responses of workers in a given center of activity. From the nature of the booty brought forth and from glimpses of the columns, it is evident that the raiders are successful in reaching very diversified places from epiphytes high in trees to subterranean niches or nest excavations where potential prey may be secluded. On the ground, the pseudopodic columns either pass rapidly through vacant zones or withdraw, thereby increasing their chances of hitting upon booty concentrations in the vicinity. The result is that, although the ecitons work somewhat differently in the dry season against greater difficulties and presumably also work harder with greater casualties than in the rainy season, a nutritive setting in the colony is produced which is adequate for their typical system of reproductive processes.

PERSEVERANCE OF NOMADISM

The dry-season maintenance of nomadism is manifestly important for successful colony adaptation in the ecitons, through insuring a steady and large supply of food in the tapping of numerous areas. We may refer for an example to the record of colony '46 H-B, all essential details of which were duplicated in shorter records from other colonies of the species. In the period of 114 days it was under study, this colony passed through three complete nomad-statary cycles, in which altogether 79+ daily raids were carried out from a total of 53 different nomadic bivouac sites and three statary sites. From the itinerary plotted in figure 2 it will be seen that the travels of this colony in the time of study covered a considerable portion of the eastern zone of the island. The function of nomadism in opening fresh ground is emphasized by the fact that these successive bivouac places generally lay more than 150 meters apart. It is desirable to bear in mind that the raiding zones of different colonies of *E. hamatum* seldom overlap even partially on successive days.

In the two species studied, bivouac-change movements of the dry season bear much the same general relationship to raiding that has been described for the rainy months (Schneirla, 1933, 1938, 1945). That is, the raids are built up from dawn through the day and furnish the excitatory basis and the principal route for the colony movement, which occurs mainly after dark. The findings seem to indicate that the basic process of eciton nomadism is much the same throughout the year. As in the rainy season, superadded trophallactic effects from an active brood bring colony raiding to the magnitude essential for setting off a change of bivouac. Large daily raids are definitely prerequisite to nomadism.

The impression of Sumichrast (1868) and other authors that eciton migrations hinge in some manner upon atmospheric conditions and therefore undergo a virtual suspension in the tropical dry season is not supported by the facts at hand. It is understandable how such an inference might be made from changes in the activities of *E.* (*Labidus*) *praedator*, a species frequently observed near clearings and settlements (Schneirla, 1947). But my general notes show that even *E. praedator* is capable of nomadism in the dry season, in dependence upon brood conditions rather than upon the weather. An important point is that certain differences typical of dry-season bivouac-change movements, in comparison with those of the wet season, increase the probability that they will escape general notice. It is true that occasionally in the dry season nomadic movement will not occur on a given day, even when colony condition is adequate. However, from my long-term records, such lapses occur not quite one-fifth of the time in *E. burchelli* (table 5), and much less frequently in *E. hamatum* (table 1). More frequently the process lags considerably in getting under way definitely, so that many of the movements are altogether nocturnal in the dry season. The basis of these secondary differences will be considered later in the present discussion.

It is well to mention here that the foregoing discussion of trophic factors in their relation to the eciton pattern should not be taken as supporting in any way the "food exhaustion" hypothesis advanced by various writers (Lund, 1831; Vosseler, 1905; *et al.*) to account for doryline nomadism. The verdict of both Heape (1931) and Fraenkel (1932) that the movements of doryline colonies are to be considered "emigrations" and not cases of "migration" was not well founded, mainly dependent as it was upon Vosseler's (1905) and Carpenter's (1925) really unsupported appraisal of colony movement as a response to a local depletion of booty. This conception of colony nomadism is not valid either for the American dorylines or, very probably, for Old World forms (Schneirla, 1938, 1944).

For convenience, the bivouac-change movement of a given day may be termed an "emigration" because in Heape's sense it is a mass movement without a return, in contradistinction to which the nightly movements constituting a regular nomadic series are properly regarded as a "migration." These series of movements are not essentially attributable to factors concerning alimentary, climatic, or over-population conditions, as Heape concludes is the case for emigrations. Rather, they meet the criteria which Williams (1930; see also Williams, Cockbill, and Gibbs, 1942) judges most essential to animal migration, that is, the eciton movements are periodic and essentially unidirectional, they are carried out actively by the animals themselves, their direction depends essentially upon the behavior of the animals themselves, and their outcome is a passing from one to another of a series of daily fields of operations.

Accordingly, for eciton behavior, an "emigration" as the term is used by Heape may be considered one part or phase of a "migration." The basis of army-ant migration actually rests in a regular and recurrent set of reproductive processes, involving in its outcome a return at regular intervals to the same kind of behavioral and ecological situation, although not to an identical locality of previous operations (Schneirla, 1944b). This means that a "return" is made periodically to statary bivouac conditions, which represent a distinctively different kind of environment from the conditions of nomadic bivouacs.

MAJOR ADAPTATIONS TO SEASONAL CONDITIONS

Without question the dry season presents the greatest range of atmospheric conditions and the greatest heterogeneity of such conditions in the tropical forest environment, when for most of the animals non-optimal circumstances are more common than at other times of year. There is little doubt that the dry season is the most arduous time of year for the terrestrial species of army ants.

Presumably the processes of eciton brood development are as delicately affected by environmental conditions, and as adversely affected by low humidity and high temperature in particular, as are such processes in numerous other insects that have been investigated (Chapman, 1927; Uvarov, 1931; Imms, 1937; Wigglesworth, 1939). However, from the relative constancy of the nomad-statary phases which must be referred to a very regular brood development, it is apparent that the ecitons achieve comparatively stable environmental conditions for their broods even under dry-season conditions.

Because the eciton colony cluster furnishes the effective environment of the brood (Schneirla, 1933), evidences of a relatively uniform brood development under somewhat strenuous conditions speak for a rather close approximation of an optimal brood environment in the location, formation, and behavior of the bivouacs.

All bivouacs may be considered "shelters" for the colony and its brood; but, more than that, bivouacs are housing structures with resilient and reactive properties. The "shelter" feature is accentuated throughout the year in the statary phase, when the colony typically is housed within an enclosure such as a hollow log or tree. Although colony bivouacs in the nomadic phase tend to be relatively exposed and seldom housed thus in physical shells, they are nonetheless to be considered shelters. In the dry season the tendency towards occupancy of cavities is more pronounced than in rainy months, and the ordinarily terrestrial species of eciton may go into well-enclosed sites even in the nomadic phase. The dependence of this seasonal difference upon atmospheric conditions is indicated by a more frequent occupancy of underground sites in very dry areas, as were certain localities surveyed in southern Mexico in the spring of 1945 (Schneirla, 1947) and in the eastern section of Barro Colorado Island in 1946, where a relatively light second-growth cover exposed the ground to marked desiccation. On the other hand after a somewhat protracted rainy season in 1945, in many areas on the island the forest floor remained fairly moist well into the dry months. In such areas the bivouacs of the terrestrial ecitons exhibited much less frequently the shift into subterranean places, tree cavities, and the like than was observed in the drier eastern section.

Thus in their bivouacking the ecitons appear to be very responsive to atmospheric conditions in the general environment. Because of the causal nexus demonstrated between changes in brood development and the phases of the colony behavior cycle and in view of the crucial influence of environmental conditions upon insect growth processes, it follows that the effective ecological conditions within dry-season bivouacs cannot be very different from those of the rainy season. Because the "selection" of bivouac arises in a variety of ways through responses to diversified environmental conditions, and because the relative fluctuation or constancy of micro-environmental conditions within the bivouac must depend upon the behavior of workers making up the living structure, the desirability of a thoroughgoing study of bivouac formation from the ecological standpoint is indicated. In this space only a beginning may be sketched.

The outlines of the problem may be suggested by pointing out some behavior processes among workers that contribute towards the attainment of a new bivouac site. All raiding activities contribute more or less to that outcome (however indirect the relationship may be), in particular because the eventual new bivouac site attained in the evening or night generally lies on or close to a route or trail junction developed in the daytime. The responses of workers in the pushing parties or protrusions of swarms probing into new terrain are of course basic in this respect (Schneirla, 1933, 1938, 1944b). The advance of such groups of variably moving workers ordinarily is influenced in demonstrable ways not only by a readiness to enter humid ground and to turn back from bright, dry areas, but also by a typical quickening of movement into places in which booty is discovered in quantities, thus into places likely to be more equable in an ecological sense. Also it is not uncommon during the raids to see concentrations of workers in damp spots on leaves, logs, or similar places, indicating a direct responsiveness to moisture. At such places traffic interferences may arise that often result in major column divisions, affording possible sites for cache formations of booty around which workers cluster later in the day and (particularly if in the outskirts of the raiding zone) the possibility of an eventual bivouac site there or near by. It is apparent that responses to differences in temperature and humidity (and light as well) are basic to such occurrences, approximating the "tropistic" reaction modes common among insects (Kennedy, 1927; Chapman, 1928; Bodenheimer, 1931; Fraenkel and Gunn, 1940).

Further "selective" behavioral processes are involved after dusk when raiding ceases, whereupon local assemblages grow at places such as those mentioned above, with an increasing tendency to cluster in the absence of light. In the rather complex events of the following hours (Schneirla, 1938) the persistence of one incipient cluster and the "melting away" of others along the line of movement appears to involve a complex set of reactions which may very well depend in part upon local differences in humidity and temperature. In view of certain year-around similarities in the kinds of sites taken, for example, spaces beneath logs, ecological conditions facilitating the local clustering of workers must be fairly similar in rainy and dry seasons. However, the fact that the bivouac-change processes often are more protracted and more variable in the dry months, with a greater lag in hitting upon the final bivouac site, indicates a greater scarcity than in rainy times of feasible clustering spots approximating the species optimum. A more complete analysis than this would be needed to indicate satisfactorily the complex serial behavior processes, under heterogeneous environmental conditions, actually involved in the "selection" of bivouac sites.

Once a colony has formed its cluster in a given place, limited shifts may occur in advance of the next major emigration, if adequately stimulative disturbances arise. Although a complete exodus of the colony over a considerable distance can occur only as the outcome of a major raid, short movements of the bivouac in part or even as a whole may come about through the local action of light (e.g., sun flecks), high temperature, or drying. Such post-formation shifts are not infrequent. However, as a rule they do not involve a displacement greater than the diameter of the bivouac and seldom more than a few meters. Within about four months, colony '46 H-B made only one exceptional movement of more than 1 meter (i.e., other than nightly emigrations), when in the morning of April 3 a broad exposure of its bivouac to full sunlight after 9:00 A.M. forced a movement of the entire colony through a distance of 10 meters into a brush heap. Although eciton colonies are constitutionally incapable of any great amount of emigration when in the statary condition, limited displacements are commonly effective in meeting whatever adverse environmental changes may occur, once a statary bivouac is settled. This was the situation in Müller's (1886) colony of *E. burchelli*, which moved only very short distances when treated with smoke. In most cases it is probable that the action of heat, bright light, and other dry-season emergencies will disturb the ants sufficiently to produce an effective relocation of the colony. It is, however, conceivable that colonies are sometimes extinguished when deleterious conditions such as extreme dryness arise in a general locality after the statary phase is well under way, when no reasonably adequate spot is available in the vicinity.

It is apparent that the ecitons have a variety of ways in which dry-season hazards may be counteracted. With their bivouac, they accomplish an adaptation to possible seasonal risks to insect fertility and reproduction, through housing queen and brood securely in the daytime when environmental conditions are most hazardous. Also, as we shall see, in this season there are characteristic diurnal occurrences which account for a lagging of the main bivouac-change trek further into the evening and night than in rainy weather, as a rule. Thus when the queen travels and the brood is moved from one specialized environment to a new one, outer conditions are far less likely to affect them adversely than at any time of day.

It is probable that desiccation and other deleterious consequences of non-optimal atmospheric conditions may be offset by a variety of adaptive mechanisms in the ecitons. For one thing, there is a maximal exploitation of available atmospheric moisture not only through the special placement of bivouacs but also through a tendency in the workers to cluster in local damp spots in the course of their raiding. Also, the eciton adaptations presumably include physiological readjustments comparable to the known capacities of many insects to resist desiccation through organic mechanisms operating against loss of water (Uvarov, 1931; Buxton, 1932; Mellanby, 1935; Ludwig, 1945). Such processes may underlie the inhibition of external activities in the ecitons under pronounced dry-weather conditions, particularly when such atmospheric conditions are at their peak during midday hours. At such times, in *E. hamatum* particularly, the workers are not much in evidence on more exposed sections of trail, having scurried about until a sheltered clustering place or the bivouac was encountered. At such times the columns of this species tend to approximate the covert aspect which is characteristic in more hypogaeic members of its subgenus such as *E. rogeri* and *E. vagans* even in the rainy season.[1]

Inhibitory effects upon insect activity might well be expected under tropical dry-season conditions (Chapman, 1928; Hesse, Allee, and Schmidt, 1937). Any marked overall seasonal inhibition of eciton predatory activity in particular would constitute a fact of considerable significance for tropical forest economy, in view of the inroads made by the army ants into the populations of countless forest arthropods. From the standpoint of eciton welfare, a depression of activity through seasonal effects might well constitute a hazard to species survival if it were to hold the development of daily raids below the threshold essential for nomadism.

Such effects might be introduced not only through high temperatures and low humidity but also through increased light intensity after many of the trees had shed their leaves. The sensitive manner in which the foraging activities of many ants are affected by temperature changes has been demonstrated by Shapley (1920), Pratt (1925), and Sturdza (1935). Kennedy (1927) and others have pointed out that strong light may have the effect of inducing a condition of torpor in the insect, through steady overstimulation. Buxton (1924b) reported an inhibition of activity in *Messor barbarus* during midday hours, and comparable results were obtained by Bodenheimer and Klein (1930) with the same species. Occurrences of this kind are explained by Buxton as attributable to an overstimulation by light.[2]

An almost invariable feature of the daily routine is the "siesta effect," a falling off in activity through midday hours, observable in army-ant activities even in the rainy season (Schneirla, 1938). [A comparable effect has been reported for certain Temperate Zone ants by Kennedy and Talbot (1940) and for desert ants by Pickles (1946).] This phenomenon is much more pronounced in the dry season, sometimes to the extent that most of the ants away from the bivouac may be huddled in gatherings beneath leaves and other objects, and that frequently the foray as an organized mass function remains at an ebb until mid-afternoon. The question whether or not this occurrence is maladaptive to any serious extent requires us to consider more widely the relation of extra-bivouac activities to diurnal atmospheric conditions.

Beyond a deepening of the characteristic

[1] Species such as *E. (Labidus) crassicorne*, which during rainy months regularly carry out daytime raids in the forest, in dry weather tend to raid nocturnally and are infrequently seen by daylight. The existence of a hierarchy of species reaction patterns is indicated, presumably related to the differential effect of environmental factors such as atmospheric conditions and light upon various dorylines.

[2] From the fact that activity continues at midday provided the relative humidity remains above 45° C., however bright the light, Buxton believes that the inhibition otherwise effective may be attributed to the effect of infrared rays in the solar spectrum. Presumably these rays are cut off by water vapor when relative humidity is sufficiently high.

midday "siesta," dry-season activities are marked by a frequent tendency of forays to begin sluggishly in the morning. Further indications of a dry-season retardation in extra-bivouac functions are especially noticeable in the statary phase. For example, colony '46 H-B when in that condition staged raids only 51 per cent of the time (on 26 days in a total of 51 observed statary days), in contrast to colony '36 H-A in the rainy season, with raids every day in 23 observed statary days. A similar difference appears in the case of *E. burchelli*, although less strikingly. Colony '46 B-I in the dry season raided 63 per cent of the time when in the statary phase (on 33 days in a total of 52 observed statary days), whereas in the rainy season three colonies of *burchelli* raided on 77 per cent of the observed days (41 days in a total of 53). The difference would be accentuated if weakly developed raids, much more common in the dry season, were also taken into account.

The extent of retardation in activity evidently depends upon conditions which differ according to time of day. This is noticed especially in the central part of the statary phase, when days without any raiding are frequent, and also when there are days on which no forays break out until after midday (tables 4 and 8). Hence a depression of activity, although often evidenced in the morning and afternoon, appears then to be less effective than through midday. This is indicated by the fact that on days when no extra-bivouac activity begins in ordinary ways, forays may be set off artificially in the early hours of morning or in late afternoon, but not through the noontime period.

These results seem explicable on the assumption that in the dry months a statary colony is subject not only to the absence of a major internal excitatory factor based on an active brood, but also to a seasonal extrinsic inhibitory effect, probably attributable to atmospheric conditions.

Although nomadic forays even in the dry season are evidently not subject to major depressions of activity as a rule, moderate effects of this kind are noticed. It is frequently observed that the raids of both *E. hamatum* and *burchelli* tend to lag somewhat in getting under way in the first part of the morning, and also that the noontime siesta period tends to be somewhat deeper and longer than in the rainy season. Contrary to results for the statary phase, nomadic-phase lapses of this sort are more frequent in *burchelli*. Thus colony '46 B-I, in a total of 43 observed nomadic days, failed on 10 occasions to develop forays of sufficient strength to reach the threshold of a bivouac-change process, whereas in colony '46 H-B this occurred only twice in a total of 53 nomadic days. In contrast, during rainy months a change of bivouac is virtually certain to occur in both species after each daily raid in the nomadic phase.

These findings indicate the importance of the excitatory effect introduced by an active brood, which evidently is powerful enough to cancel out a seasonal extrinsic inhibitory effect, with a sufficient remainder in population arousal to insure effective colony operations in the nomadic phase. Most of the time the magnitude of the raids that are elicited suffices to insure a daily movement of the colony and also to bring in a haul of booty on which the large larval brood may be raised to maturity. Under the conditions, these results are essential for an effective continuance of the nomadic-statary cycle and for colony survival.[1]

It is probable that on the whole the accentuated reduction of raiding when colonies are statary in the dry season is not seriously detrimental to colony welfare. A possible adaptive function is even recognizable, in that remaining under cover or in the bivouac serves to reduce the chances of over-exposure to environmental conditions which may quickly become hazardous when near their peaks. In all probability, unavoidable exposure to extreme atmospheric conditions when outside the bivouac in the dry season, and especially the risk of desiccation, is a far greater source of casualties in eciton worker populations than is any lack of food. This view is encouraged by the frequency with which colonies bring large broods successfully through pupation without much indica-

[1] The possibility must be kept in mind that subnormal activity appearing occasionally in nomadic colonies in the dry season may be attributable not only to a lethargizing of workers through atmospheric effects exerted directly but also to indirect effects through an inhibition of brood activity which in turn reduces trophallactic excitation of workers.

tion of cannibalism, despite a curtailment of raiding and a consequent reduction of food in the colony.

Because a large brood population can be maintained through the time of quasi-dormancy in eciton colonies, when the emergence time of the callows arrives there is introduced a trophallactic excitatory effect of sufficient intensity to arouse nomadism in the colony. Here also, the result is maintenance of a critical point of change in the eciton cycle despite seasonal interferences with its basis in the colony.

Although, contrary to what might be expected, there is no great reduction in the frequency of nomadic movements in the dry season, at times the regularity of this process is impaired somewhat, particularly in *burchelli.* Also there are secondary differences from the rainy-season condition of nomadism in both species. Often in the dry months the afternoon exodus lags in getting under way, and occasionally, as we have seen, a colony may not change its bivouac on given days. The relation of such occurrences to a depressing effect of atmospheric conditions on raiding activities is suggested by various signs, notably deficiencies in the development of foraging, or a particularly extensive siesta, on days when no change of bivouac ensues. When conditions at the forest floor are noticeably hot, bright, and dry over a considerable area, activity on the trunk routes drops to a minimum, and most of the foragers are likely to be huddled in sheltered places with only a minority in action. At such times the afternoon exodus is likely to be not only exceptionally slow in developing but also lacking in strength and persistence. This feature, together with an apparent lassitude in raiding during the few hours before dusk, constitutes shortcomings through which extra-bivouac developments may fall somewhat below the effective threshold of colony movement. The outcome is somewhat comparable to the effect typically produced by etherizing a nomadic colony, illustrated by the reduction of raiding and consequent inhibition of bivouac-change processes in colony '46 H-Y on May 22. It would appear that in the dry season the occurrence of an emigration is opposed by environmental effects exerted both upon raiding activities and upon processes whereby an afternoon exodus develops in the bivouac.

FACTORS IN SPECIES ADAPTATION

Because *E. hamatum* as against *E. burchelli* (and *E. praedator*) is the principal species to be reckoned with as surface raiders, it should be emphasized that its spheres of activity are rather different, although a given amount of competition evidently does exist among them. The point is that although on the whole these species work over much the same ground, they exploit it rather differently. *E. hamatum* with its extensively branched columns and small terminal raiding groups covers a wide area loosely, whereas the swarms of *burchelli* (and *praedator*) cover less ground but pillage it more thoroughly. Typically a nomadic colony raid of *E. hamatum* ranges over somewhat more than 180° of arc to a distance of 150–225 meters from the bivouac, whereas a nomadic *burchelli* swarm raid usually covers less than 45° of arc within a distance of less than 150 meters from the bivouac. The small predatory terminal groups of *hamatum* capture mainly the soft-bodied young of other insects, whereas the large sweeping masses of *E. burchelli* take in all types of arthropods at all stages, and occasionally other animals also, as their booty.[1] The swarm protrusions of *burchelli* tend to work somewhat more in the higher vegetation than the columns of *hamatum*, whereas *hamatum* operates more below ground, as in the galleries of insect nests. These and other differences of comparable nature would appear to act as limiting factors on species competition.

At present there is no satisfactory basis for evaluating interspecies territorial conflict, except for a general description of typical results in direct encounters. When colonies of the two species cross paths, there ensues a

[1] *Eciton praedator* is similar to *burchelli* in the generalized nature of its prey but ranges more widely towards the smaller organisms and also goes more extensively underground and less frequently into the upper vegetation than *burchelli.*

regular series of behavioral adjustments involving little carnage, and at length the two bodies of ecitons either diverge or continue to work common ground, usually to a limited extent of overlapping, through a by-passing of their columns (as on vines) at collision points. Casualties are few, as a rule, owing to the prompt formation of mutually opposed lines of workers, both intermediates and majors, stretched in place motionless except for rapidly vibrating antennae directed at the source of disturbance, while behind these "picket lines" ordinary activities are resumed. I have observed adequate readjustments to occur along these lines, even in the extreme case in which the central part of a raid of one species (e.g., a *burchelli* swarm) heads directly through the bivouac ground and across the base trails of a colony of the other species. The raiding bodies divide and rejoin according to circumstances, often crossing each other through hitting upon bridges over vines and the like at junction points. The principal loss appears to be in raiding time; however, as a rule this loss is not great because of the effectiveness with which "picket lines" set up by peripheral groups lead to mutual avoiding responses.[1]

In addition to a limited species competition for food as well as for territory, an indirect competition based upon the biological resources of the general area rather than upon food species alone must be viewed as a possibility. For example, the welfare of a given species might depend upon the inroads of another species into arthropod reproductivity broadly, rather than simply, into populations of given mutual food species. Competition in regard to adequate nest sites must also be considered as a factor limiting the number of colonies. There is every probability that such relations between species and among colonies of a given species are intensified in the dry season, when on the whole the booty supply would appear to be more variable and adequate nesting sites less numerous than in rainy times.

Although taking a seasonal census of army-ant colonies on Barro Colorado Island has not been feasible thus far, the impression gained from numerous attempts at sampling is that annual fluctuations are not great in the number of colonies of a given species. Despite the probability that an undetermined number of eciton colonies divides during the dry season of each year, the species total of colonies evidently remains fairly well within given bounds. At a very rough estimate, the maximum may lie near 45 colonies for each of the principal species found on the island, which approaches 7 square miles in map area. The production of new colonies through a fission process may account for replacements which counterbalance the seasonal loss of whole colonies. After an unusually difficult season has reduced the species total of colonies to an extreme low, it is conceivable that this replacement process would operate in an accelerated way through the effect of a temporary relaxation of intraspecies competition.

How many colonies are lost through dry-season hazards cannot be said at present, because, as mentioned, one's chances of finding colonies undergoing dissolution are relatively small. How great the losses may be in the worker personnel of functional colonies through ordinary operations in the dry season is suggested by the case of colony '46 H-B. This colony retained its unity without any division during a period of 114 days from February to June, in which a minimal increment of 100,000 workers in five broods was produced. At the end of the first statary phase the colony appeared distinctly smaller than before, and, when the study ended early in June, it did not seem to be much larger than in early February when its population was estimated at 80,000 individuals. The probability is that, notwithstanding a prolific and regular reproduction of new worker increments, natural factors are effective which impose definite limits upon the eciton colony populations. Climatic hazards incurred in extra-bivouac activities may be given priority in this respect.

At present we have no reliable information concerning the relative worker mortality in various species during the dry season, although such differences may exist depending upon differences in environmental exposure

[1] A chance meeting of two colonies of the same species results in a comparable process of mutual avoidance, except in the rare event that one of the colonies (or both of them, as in colonies '46 B-IV and B-VI), lacks a queen, when fusion may be the outcome.

involved in the swarm-raiding and column-raiding patterns. From the standpoint of adaptive significance, there is accordingly no way of evaluating the fact that the colonies of *E. burchelli* typically range well above those of *hamatum* in population size, and also have larger broods which issue with slightly greater frequency (i.e., about every 32 days instead of 36). The colonies of *burchelli* at times are sufficiently large to appear enormous and unwieldy, both in their principal activities and in their bivouac formations. Beyond the factor of a regular functional worker mortality and losses through exposure, as well as a possible mortality of unknown magnitude due to parisitism, the occurrence of colony division, which may well be an event peculiar to the dry season, would appear to be of importance for imposing an upper limit on colony size. No evidence is available that blocks of workers are separated from the raids and lost, under ordinary forest conditions (cf. Schneirla, 1944c), although this may happen occasionally through irregularities in the organization of forays in very large colonies particularly. Although colony '46 B-I was relatively great in size, particularly when further worker broods accrued after a division had been prevented, it continued to function passably well as a unit to the end of the study. A large colony size evidently need not endanger nomad-statary function seriously, as long as a queen is present and broods continue to appear regularly.

Although it is possible that the upper limit of population size may be high without jeopardizing colony survival, there must exist a minimal size below which a colony cannot function effectively in the typical eciton cyclic manner. It is questionable whether a very small worker population could maintain daily raids of sufficient magnitude to carry a larval brood through its development in a regular nomadic interval and bring the queen into a further egg-laying phase. It is possible furthermore that an undersized colony could not both conduct daily raids of sufficient scope to feed the population and lead into bivouac-change movements, and at the same time maintain a bivouac shelter adequate for the regular development of its brood. Whether or not a substandard colony could survive despite the expected irregularities in its behavior pattern is difficult to say. The fact is that functioning colonies of either test species falling below an estimated population of 40,000 workers have not been encountered in the forest up to the present.

In this paper numerous ways have been described whereby the arduous conditions of the dry-season environment are met by virtue of the adaptive resources of the eciton pattern. Ordinarily a sufficient supply of booty is procured to keep the reproductive processes of the queen near their maximum and to raise the resulting series of large broods, which provides the basis for maintaining a cyclic pattern of colony behavior. There are indications of various secondary modifications in raiding and emigration, an adaptive placement of bivouacs, and a limited shifting of these resilient structures under disturbing conditions, all of which promote an effective adjustment of colonies to maladaptive circumstances incident to the season.

Yet, as has been suggested, the costs of such adaptation must be large, almost certainly in individuals and perhaps also in colonies. It is important not to overstress the positive aspects of eciton adjustment to dry-season conditions, impressive as they appear to be, in view of the imminent possibility that (especially through the constitutional immobility of failing colonies) the negative aspects may have come incompletely to attention. On the whole it is likely that the conditions of the dry season may constitute a levelling factor of major importance in the regulation of army-ant populations.

CONCLUSIONS

1. THE SYSTEM of behavioral and biological processes that constitutes the nomad-statary pattern in the tropical army ants persists throughout the year in the species of *Eciton* (*Eciton*) studied. Differences that have been identified in the pattern under dry-season conditions are secondary in nature and do not fundamentally impair the effective continuance of the described cyclic system of events.

2. The two investigated eciton species present much the same differences in the duration of their characteristic nomadic and statary phases in the two seasons. In *E. burchelli* the nomadic phase is somewhat more variable and is shorter than in *hamatum*, whereas the statary phase is closely similar in the two species. These facts concerning behavior are referable mainly to species differences in brood production and development.

3. The similar phase durations in the eciton cycle in the two seasons indicate a fairly close equivalence in the bivouac conditions under which broods develop. It is significant that phase variability is greater in the nomadic phase of the cycle, when different open bivouac sites are occupied daily, than it is in the statary phase when the same enclosed site is held throughout the interval.

4. The regular booty haul in the dry season evidently is comparable to that in the rainy season, especially from the fact that most of the colonies bring to maturity successive, large, all-worker broods close to those of the rainy season in population and in polymorphic range (and a single all-male brood in some cases). Through trophallactic relationships between brood and workers, maintenance of brood-production processes near the maximum insures the continuance of a representative nomadic-statary cycle.

5. The queen's cyclic function holds substantially as in the rainy season, except that one male brood may appear in the dry season, presumably from unfertilized eggs. It is suggested that each new gravid phase in the queen may arise through an accelerated feeding indirectly synchronized with the maturation of a larval brood rather than primarily through intrinsic causes in the queen.

6. The principal difference in dry-season predatory forays as against those of the rainy season is that in the former the midday lull or "siesta" interval is more pronounced, especially during the statary phase. This fact, together with a reduction in the frequency of statary raids and occasional interferences in raids and emigrations in the nomadic phase, suggests that extra-colony activities are subject to a special inhibitory influence, presumably exerted by seasonal atmospheric conditions.

7. The behavior mechanisms involved in eciton raiding are sufficiently plastic to absorb a variety of environmental interferences and hazards which arise in the dry season. As a consequence, colony food intake is about the same, and the frequency of bivouac-change movements is not much lower than in the rainy season.

8. An adaptation of importance for seasonal adjustment is the capacity to form bivouacs in optimal ecological situations. Once a bivouac is established, limited readjustments may occur under disturbing environmental conditions.

9. Although most eciton colonies operate fairly well through the dry season, heavy losses in worker personnel may be incurred, and some colonies may be wiped out. Colonies would appear especially vulnerable to seasonal hazards such as mass desiccation, when the locality of a statary bivouac dries out once the ants become immobilized. Loss of the queen leads to extinction of the colony, unless it can fuse with an intact colony through a chance crossing of trails.

BIBLIOGRAPHY

ALLEE, W. C.
1926a. Measurement of environmental factors in the tropical rain-forest of Panama. Ecology, vol. 7, pp. 273–302.
1926b. Distribution of animals in a tropical rain-forest with relation to environmental factors. *Ibid.*, vol. 7, pp. 455–468.

ANDERSEN, K. T.
1935. Experimentelle Untersuchungen über den Einfluss der Temperatur auf die Eierzeugung von Insekten. Biol. Zentralbl., vol. 55, no. 11/12, pp. 571–590.

Bissonnette, T. H.
1936. Sexual photoperiodicity. Quart. Rev. Biol., vol. 11, pp. 371–386.

BODENHEIMER, F. S.
1928. Welche Faktoren regulieren die Individuenzahl einer Insektenart in der Natur? Biol. Zentralbl., vol. 48, pp. 714–739.
1931. Über die Temperaturabhängigkeiten von Insekten III. Die Beziehungen der Vorzugstemperatur zur Luftfeuchtigkeit der Umgebung. Zeitschr. Vergleich. Physiol., vol. 13, no. 4, pp. 740–747.
1937. Population problems of social insects. Biol. Rev., vol. 12, pp. 393–430.

BODENHEIMER, F. S., AND H. KLEIN
1930. Über die Temperaturabhängigkeit von Insekten. II. Die Abhängigkeit der Aktivität bei der Ernteameise Messor semirufus, E. André, von Temperatur und anderen Faktoren. Zeitschr. Vergleich. Physiol., vol. 11, pp. 345–385.

BODINE, J.
1925. Effect of temperature on the rate of embryonic development of certain Orthoptera. Jour. Exp. Zool., vol. 42, pp. 91–109.

BUXTON, P.
1923. Animal life in deserts. London, 176 pp.
1942a. Heat, moisture and animal life in deserts. Proc. Roy. Soc. London, vol. 96, ser. B, pp. 123–131.
1924b. Physical factors controlling harvesting in an ant. Trans. Ent. Soc. London, 1924, pp. 538–543.
1932. Terrestrial insects and the humidity of the environment. Biol. Rev., vol. 7, pp. 275–320.
1933. The effect of climatic conditions upon populations of insects. Trans. Roy. Soc. Trop. Med. and Hyg., vol. 26, no. 4, pp. 325–364.

CARPENTER, G.
1925. A naturalist in East Africa. Oxford.

CHAPMAN, R. N.
1927. Animal ecology with especial reference to insects. Minneapolis.
1928. Temperature as an ecological factor in animals. Amer. Nat., vol. 62, pp. 289–310.

CLAYTON, H. H., AND FRANCES L. CLAYTON
1947. World weather records 1931–1940. Smithsonian Misc. Publ., vol. 156, 646 pp.

DAMMERMAN, K.
1925. First contribution to a study of the tropical soil and surface fauna. Treubia, vol. 6, pp. 107–139.
1937. Second contribution to a study of the tropical soil and surface fauna. *Ibid.*, vol. 16, pp. 127–147.

DOGEL, V.
1924. Quantitative studies on terrestrial fauna. Rev. Zool. Russe, vol. 4, pp. 148–154. (*Ibid.*, Russian text, pp. 117–147.)

DORMAN, S. C., W. HALE, AND W. M. HOSKINS
1938. The laboratory rearing of flesh flies and the relations between temperature, diet, and egg production. Jour. Econ. Ent., vol. 31, pp. 44–51.

EIDMANN, H.
1936. Zur Kenntnis des Blattschneiderameise *Atta sexdens* L. insbesondere ihrer Ökologie. Zeitschr. ang. Ent., vol. 22, pp. 185–241, 385–436.

EMERSON, A. E.
1939. Populations of social insects. Ecol. Monogr., vol. 9, pp. 287–300.

FRAENKEL, G.
1932. Die Wanderungen der Insekten. Ergeb. Biol., vol. 9, pp. 1–238.

FRAENKEL, G., AND D. L. GUNN
1940. The orientation of animals. Oxford.

GÖSSWALD, K.
1938. Über den Einfluss von verschiedener Temperatur und Luftfeuchtigkeit auf die Lebensäusserungen der Ameisen. I. Die Lebensdauer ökologisch verschiedener Ameisenarten unter dem Einfluss bestimmter Luftfeuchtigkeit und Temperatur. Zeitschr. wiss. Zool., vol. 151, pp. 337–381.
1941. II. Über den Feuchtigkeitssinn ökologisch verschiedener Ameisenarten und seine Beziehung zu Biotop, Wohn- und Lebens-weise. *Ibid.*, vol. 154, pp. 247–344.

GOETSCH, W.
1940. Vergleichende Biologie der Insektenstaaten. Leipzig.

HAYDAK, M.
1943. Larval food and development of castes in the honeybee. Jour. Econ. Ent., vol. 36, no. 5, pp. 778–792.
HEAPE, W.
1931. Emigration, migration, and nomadism. Cambridge.
HERTER, K.
1924. Untersuchungen über den Temperatursinn einiger Insekten. Zeitschr. vergleich. Physiol., vol. 1, pp. 220–288.
HESSE, R., W. C. ALLEE, AND K. P. SCHMIDT
1937. Ecological animal geography. New York and London.
HIMMER, A.
1932. Die Temperaturverhältnisse bei den sozialen Hymenopteren. Biol. Rev., vol. 7, pp. 224–253.
HOSKINS, W. M., AND R. CRAIG
1935. Recent progress in insect physiology. Physiol. Rev., vol. 15, pp. 525–596.
IHERING, H. VON
1912. Biologie und Verbreitung der brasilianischen Arten von Eciton. Ent. Mitt., vol. 1, no. 8, pp. 226–235.
IMMS, A. D.
1937. Recent advances in entomology. Philadelphia.
JANISCH, E.
1930. Experimentelle Untersuchungen über die Wirkung der Unweltfaktoren auf Insekten. I. Die Massenvermehrung der Baumwolleule *Prodenia littoralis* in Ägypten. Zeitschr. Morph. Ökol. Tiere, vol. 17, pp. 339–416, 2 figs.
KENNEDY, C. N.
1927. Some non-nervous factors that condition the sensitivity of insects to moisture, temperature, light and odors. Ann. Ent. Soc. Amer., vol. 20, pp. 87–106.
1928. Evolutionary level in relation to geographic, seasonal and diurnal distribution of insects. Ecology, vol. 9, pp. 367–379.
KENOYER, L. A.
1929. General and successional ecology of the lower tropical rain-forest at Barro Colorado Island, Panama. Ecology, vol. 10, pp. 201–222.
KING, K. M.
1939. Population studies of soil insects. Ecology, vol. 9, pp. 270–286.
KOPÉC, S.
1923. Studies on the influence of inanition on the development and the duration of life in insects. Biol. Bull., vol. 46, pp. 1–34.
LARRIMER, W. H., ET AL.
1931. Symposium: The effect of the 1930 drought upon insect population. Jour. Econ. Ent., vol. 24, no. 3, pp. 651–662.
LUDWIG, D.
1945. The effects of atmospheric humidity on animal life. Physiol. Zool., vol. 18, pp. 103–135.
LUDWIG, D., AND J. ANDERSON
1942. Effects of different humidities, at various temperatures, on the early development of four saturniid moths (*Platysamia cecropia* Linnaeus, *Telea polyphemus* Cramer, *Samia walkeri* Felder and Felder, and *Callosamia promethea* Drury), and on the weights and water content of their larvae. Ecology, vol. 23, pp. 259–274.
LUND, M.
1831. Lettre sur les habitudes de quelques fourmis du Brésil, adressée à M. Audouin. Ann. Sci. Nat. Zool., ser. 1, vol. 23, pp. 113–138.
MARSHALL, F.
1936. Sexual periodicity and the causes which determine it. Phil. Trans. Roy. Soc. London, ser. B, vol. 226, pp. 423–456.
MELLANBY, K.
1935. The evaporation of water from insects. Biol. Rev., vol. 10, pp. 317–333.
MÜLLER, W.
1886. Beobachtungen an Wanderameisen (*Eciton hamatum* Fabr.). Kosmos, Jahrg. 10, vol. 18, pp. 81–93.
PICKLES, W.
1940. Fluctuations in the populations, weights, and biomasses of ants at Thornhill, Yorkshire, from 1935 to 1939. Trans. Roy. Ent. Soc. London, vol. 90, pt. 17, pp. 467–485.
1946. The "siesta" in ants of the genus Messor Hym. Formicidae. Ent. Rec., vol. 58, pp. 110–111.
PRATT, K.
1925. Thermokinetrics of Crematogaster lineolata (Say). Jour. Comp. Psychol., vol. 5, pp. 265–269.
RAU, P.
1933. The jungle bees and wasps of Barro Colorado Island. Kirkwood, Missouri.
RICHARDS, A., AND A. MILLER
1937. Insect development analyzed by experimental methods: a review. Jour. New York Ent. Soc., vol. 45, pp. 1–60, 149–210.
ROUBAUD, E.
1922. Études sur le sommeil d'hiver préimaginal des muscides. Bull. Biol. France et Belgique, vol. 56, pp. 455–544.

ROWAN, W.
1931. The riddle of migration. Baltimore.
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 reproductive 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. II. The appearance and fate of the males. Zoologica, vol. 33, pp. 89–112.
SHAPLEY, H.
1920. Thermokinetics of *Liometopum apiculatum* Mayr. Proc. Natl. Acad. Sci., vol. 6, pp.. 204–211.
STURDZA, S. A.
1935. Quelques observations relatives à l'action de la température sur l'activité motrice de la fourmi rousse (*Formica rufa pratensis* Retz.) Notationes Biol., vol. 3, no. 1, pp. 1–10.
SUMICHRAST, F.
1868. Notes on the habits of certain species of Mexican Hymenoptera. Trans. Amer. Ent. Soc., vol. 2, pp. 39–44.
TALBOT, MARY
1934. Distribution of ant species in the Chicago region with reference to ecological factors and physical toleration. Ecology, vol. 15, pp. 416–439.
TALBOT, MARY, AND C. H. KENNEDY
1940. The slave-making ant, *Formica sanguinea subintegra* Emery, its raids, nuptual flights and nest structure. Ann. Ent. Soc. Amer., vol. 33, pp. 560–577.
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.
VOSSELER, J.
1905. Die ostafrikanische Treiberameise (Siafu). Pflanzer, Jahrg. 1, no. 19, pp. 289–302.
WEBER, N.
1941. Notes on the effect of drouth upon the nesting habits of ants. Canadian Ent., vol. 73, pp. 140–141.
1943. The ants of the Imatong Mountains. Bull. Mus. Comp. Zool., vol. 93, pp. 265–389.
WHEELER, W. M.
1900. The female of *Eciton sumichrasti* Norton, with some notes on the habits of Texas ecitons. Amer. Nat., vol. 34, pp. 563–574.
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 Sci., vol. 56, pp. 291–328.
1928. The social insects. New York.
WIGGLESWORTH, V. B.
1939. The principles of insect physiology. New York.
WILLIAMS, C. B.
1930. The migration of butterflies. Biol. Monogr. and Man., no. 9, pp. 473.
WILLIAMS, C. B., G. F. COCKBILL, AND M. E. GIBBS
1942. Studies in the migration of Lepidoptera. Trans. Roy Ent. Soc. London, vol. 92, pt. 1, pp. 1–283.
WILLIAMS, E. C.
1941. An ecological study of the floor fauna of the Panama rain forest. Bull. Chicago Acad. Sci., vol. 6, pp. 63–124.