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A STUDY OF ARMY-ANT LIFE AND BEHAVIOR UNDER DRY-SEASON CONDITIONS WITH SPECIAL REFERENCE TO REPRODUCTIVE FUNCTIONS

1. SOUTHERN MEXICO

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INTRODUCTION

It is probable that the bulk of our literature on the behavior of animals in tropical forests has arisen from observations made during the season of rains, the time when activities tend to be at their peak and most accessible to study. This holds widely for the indigenous insects and particularly the social insects, most of which tend to operate at a depressed level during the dry months in their reproduction as well as in activities such as foraging and construction. Yet the fact seems to be that under the ecological conditions then prevalent, behavior is not simply depressed but may show variations which are significant in comparison with the more effulgent rainy-season patterns. An investigation of the leaf-cutter ants from this angle should prove worth while. For the army ants (American *Eciton* species of the subfamily Dorylinae) the findings of the present study indicate that dry-season observations lend valuable assistance to an understanding of the characteristic behavior pattern.

The writer has outlined what appears to be the fundamental structure of the eciton behavior pattern from a series of investigations carried out with species of *Eciton* (*sensu stricto*) under rainy-season conditions (Schneirla, 1933, 1934, 1938, 1944). Members of this subgenus (at least during the rainy months in which the previous surveys were made) are truly terrestrial in their foraging and nesting, much more accessible for behavior and general biological study than are the more or less subterranean species of other subgenera such as *Labidus* and *Acamatus*[2] (=*Neivamyrmex*). In the time of rains the eciton pattern appears in what may be roughly termed its optimal or most vigorous form, in that the chief activities of organized raiding and nomadic movement then are observable at their maximum. We are concerned here with what variations may occur in this system of activities under dry-weather conditions.

The central feature of the representative eciton behavior pattern in the rainy season is the regular alternation of two distinctive behavior modes in a colony: (1) the *nomadic*, in which large daily raids occur, each terminated by a change of nesting site at the day's end; and (2) the *statary*, in which the daily raids are reduced in vigor (or, as in *Eciton burchelli*, may not occur on certain days), and there is never a change in nesting site. Contrary to the prevalent earlier assumption that eciton nomadic movements are caused by a scarcity of food, the writer has found that control of the highly complex process of shifting reciprocally from one phase to the other of the nomad-statary cycle lies in events internal to the colony rather than external (Schneirla, 1938, 1945). Our evi-

[1] Fellow of the John Simon Guggenheim Memorial Foundation. The American Museum of Natural History and New York University. This investigation was supported by a grant from the Committee for Research in Problems of Sex, National Research Council.

[2] Although Borgmeier (1940) has renamed this subgenus *Neivamyrmex* because of a taxonomic preemption of the name *Acamatus*, no desirable purpose will be served by discarding the familiar name in this paper.

dence shows convincingly that the regular variations in colony behavior do not occur in accordance with external conditions such as food supply—for in the rainy season other insect life, the main source of eciton food, is everywhere abundant in the forest—but according to the internal presence or absence of stimulation from the brood. This, a kind of "drive" factor (roughly comparable to the energizing of an organism through visceral processes), has its principal source in the activities and chemo-stimulative properties of a developing larval brood. A secondary source of similar "social stimulation" centers in a newly emerged brood of callow workers.

The above statement does not reflect a disposition to neglect extrinsic factors in eciton behavior; rather it means that in the rainy season extrinsic factors do not account for the regular nomad-statary fluctuations. The fundamental controller of the colony behavior cycle we have traced to the reproductive cycle of the colony queen, which governs the time at which new broods enter into and pass from effectiveness as sources of "drive," thus indirectly controlling colony behavior (Schneirla, 1944). If there is any extrinsic factor which times or which influences the timing of the regular ovulation processes of the *Eciton* (*sensu stricto*) queen, at present we have no indication of what it may be.[1] However, *a priori* it would seem possible that the cycle may be modified or even interrupted through changes in colony condition under deleterious external conditions such as prevail in the annual time of drought. Under these conditions both the size and the makeup of the brood may be affected, accounting for changes in the "drive" factor influencing the known behavior pattern directly and indirectly. Of the greatest importance are possible changes in the queen's reproductive cycle, a known key factor.

There are, of course, environmental changes which can influence the behavior pattern directly. Two extrinsic effects of diurnal occurrence have been identified as important factors in the regular (i.e., rainy season) eciton behavior schedule. One is the effect of the first daylight in arousing the day's raid of an (internally sensitized) *Eciton* (*sensu stricto*) colony, and, conversely, the effect of dusk in depressing predatory activities.[2] The other is the falling off of raiding activities which characteristically appears during the hours of midday, generally the warmest, driest, and brightest part of the day. Although at present the relative importance of these three atmospheric factors cannot be identified in accounting for the typical noontime lull in eciton activities, the general evidence on insect activities and climatic conditions would encourage taking them all into account. The relative inhibition of army-ant activities under external conditions such as those prevailing at noontime in the rainy season, conditions much more widely prevalent in the dry season, suggests an ecological behavior relationship of importance for our present study.

Numerous questions thus arise concerning what changes may appear in the eciton behavior pattern and its underlying processes under the influence of altered atmospheric circumstances and presumably reduced food supply typically prevailing in the tropical dry season. In addition to possible differences in the raiding and nomadic movements of a colony under dry-season conditions, we are interested in the internal condition of the colony and its reproductive processes in particular. While in the rainy months the nomad-statary rhythm prevails externally, it is traceable internally to the appearance at regular intervals of huge broods numbering tens of thousands of individuals and, as far as our results go, these are all worker forms. What happens to the reproductive func-

[1] Recently Weber (1943) has suggested that lunar cycles may be involved as a control. This seems doubtful for two reasons in particular: first, my records show that new batches of eggs are not ordinarily delivered in a synchronized fashion by queens of different colonies in the same general area; and, second, while a sidereal period is 29.5 days, the eciton queen's cycle is about 36 days in duration. The existence of species and individual variations in the length of this cycle remains to be determined.

[2] This statement holds for the terrestrial species of the subgenus *Eciton* (*sensu stricto*), our subjects in these investigations, which stage daytime raids; its applicability to the subterranean species in the other eciton subgenera is not known. However, contrary to a prevalent impression, no eciton species is "blind" in the sense that its activities are unaffected by a sensitivity to light (Schneirla, 1938).

tions of the eciton colony in the dry season, when and how the sexual forms are produced, how mating occurs and new colonies originate, are all unanswered questions on which light is needed.

GENERAL NATURE AND AREA OF THE INVESTIGATION

Sumichrast (1868), author of the only previous paper dealing with the behavior of ecitons in Mexico, stated, " Thanks to the care with which these insects conceal their nests from view in the most solitary places it is probable that we shall learn only by chance about the winged sexes." ison with conditions prevailing in the season of rains.

For two principal reasons the general area chosen for this investigation was southern Mexico. First of all, it was desirable to survey eciton conditions in localities in which the rainy and dry seasons

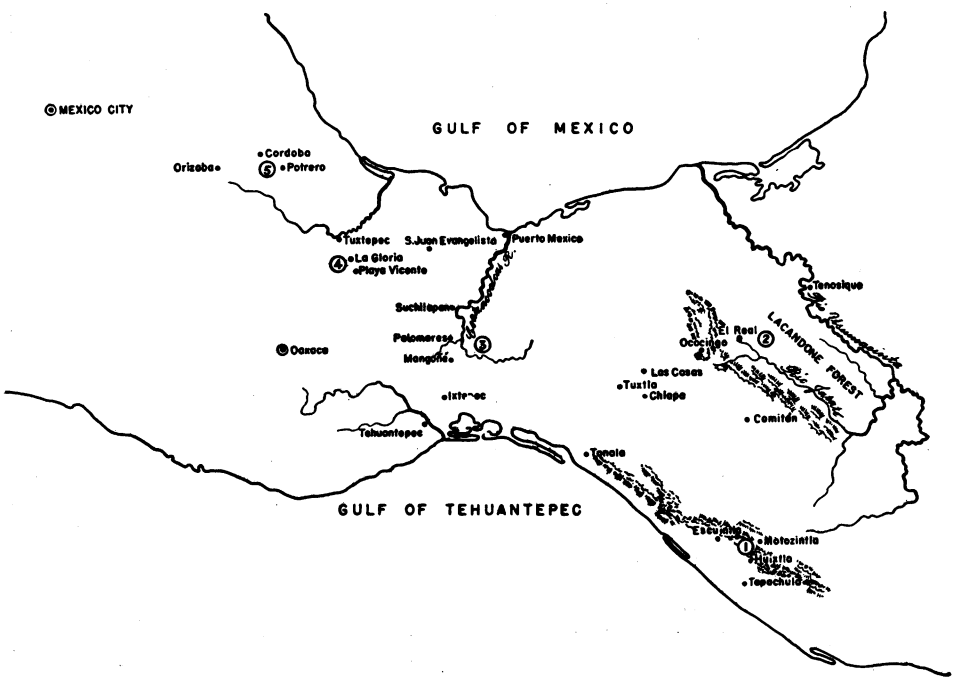

Fig. 1. Map of the isthmus section of southern Mexico, to show the principal localities of the present study. Areas 1 and 2 are in the State of Chiapas, area 3 in the State of Oaxaca, area 4 in Oaxaca near the Vera Cruz border, and area 5 in the State of Vera Cruz.

This complaint is a familiar one to those who have tried to find army-ant bivouacs; they are not easy to locate under any conditions, and, as this study shows, especially in the dry period. The principal aim of this investigation was to find eciton colonies in a variety of localities in the dry season, in order to discover what changes might exist in the form of their activities and in their internal condition in comparare well differentiated (Arias, 1942), and this condition is fulfilled in the portions of the States of Chiapas, Oaxaca, and Vera Cruz in which eciton colonies were examined. Furthermore, in this part of Mexico are located large areas of tropical rain forest, the habitat of the terrestrial *Eciton* (*sensu stricto*) species to be investigated.

The general schedule of the study was as follows: (1) the southern Pacific mountain

slope of the State of Chiapas in the Huixtla-Escuintla area, December 12, 1944, to February 10, 1945, with a resurvey in late March and early April; (2) the Atlantic slope forest of Chiapas in the Jetjá-Lacandone area east of the upper Jatate River, February 26 to March 18, 1945; (3) the Modelo area of the upper Coatzacoalcos River, northeast of Mogoñé in the Tehuantepec Isthmus of the State of Oaxaca, April 17 to 25, 1945; (4) the La Gloria area in the State of Vera Cruz southeast of Tuxtepec, April 29 to May 1, 1945; (5) upper Atoyac River near Potrero, and the upper Metlac River above Fortin, Vera Cruz, May 10 to 15, 1945.[1] The general location of these areas is indicated on the map in figure 1. Eciton colonies were sought out in each place, their current activities (condition of raiding, possible colony movements) investigated, and wherever possible colonies were captured for examination of their contents and preservation of their broods and fertile forms for later study.

[1] It is not possible to express my thanks here to the many good people in Mexico who assisted the investigation in various indispensable ways. Among those to whom I am especially grateful are: Dr. Manuel Martinez Baez, sub-Director of Health in the Mexican government; Dr. L. Figueroa Ortiz, Director of the hospital Centro Médico, Huixtla, and Sra. Figueroa Salano; Sr. and Sra. Enrique Knape; Dr. E. Matuda and family; Sr. Joaquim Escobar; Mr. and Mrs. Dyfrig M. Forbes; Ings. Villas Peres and Humberto Ortega of Departamento Forestal y Caza; Dr. Alfonso Dampf; Dr. Frans Blom; Sr. and Sra. Jose Tarano. In this number should be included one especially zealous assistant, Sr. Carmelino Vargas of Huixtla.

RESULTS AND OBSERVATIONS

Principal Data on Chief Cases Studied

There follows a summary of the data on the principal colonies studied, in chronological order. For each colony are given data on the locality and general conditions, the situation and activities of the colony, general condition of the brood or broods, and the condition of the queen at the time of capture. To the description of each colony is added an estimate of its general activity phase at the time it was observed (see fig. 2). Statements about condition of the broods are based on study of preserved material. Unless otherwise stated, the date given is the day of etherization and capture.

Colony A, *Eciton* (*Eciton*) *burchelli*[2]: Dec. 29, 1944; area I, 25 km. north of Huixtla, Chis., at 1700 meters. On steep rocky slope, moderately dry; light forest cover. Three swarm raids observed, each ending in a short bivouac-change movement, on successive days. When captured, bivouacked under base of small tree next to an overhanging rock, bivouac fairly well hidden. Two distinct broods present: (1) a large brood (i.e., estimated at 30,000 or more) of young worker larvae, a minor part newly hatched eggs; and (2) a large brood of newly emerged callow workers, a small part (2000–3000) still enclosed but mature pupae of workers minor. A single queen present, fully contracted; no other sexual forms. On the basis of its behavior, in relation to the condition of its broods and queen, the colony was judged to be *nomadic*, and to have shifted from the statary condition a few days before, with the emergence of the main part of its pupal brood.

[2] Determinations by Dr. M. R. Smith.

Colony B, *E. burchelli:* Dec. 31, 1944; area I, finca La Victoria, 28 km. north of Huixtla, Chis., 1800 meters. In a moderately humid arroyo between two dry hills, near top of small wooded mountain. Moderate forest cover. Two successive swarm raids observed, without any bivouac-change movements. Bivouacked well back underneath a tree root which formed one undercut bank of a small gully, well covered. Two broods: (1) a very young larval worker brood containing a larger number of recently hatched eggs than the younger brood of colony A; (2) a nearly mature pupal brood, all members pigmented, but with no emerged callows. *Statary.* Estimated very close to entering a new nomadic period. Single queen, fully contracted; no other sexual forms.

Colony C, *E. burchelli:* Jan. 25, 1945; area I (near rancho La Esperanza), 20 km. north of Escuintla, Chis., foothills of Sierra Madre Mts. at 600 meters. On a moderately dry hill, 80 meters from a small running stream. Forest cover fair. Two swarm raids observed on successive days; no bivouac-change movement. Bivouacked in hollow base of large tree which lacked external openings save two small holes used by eciton columns. Two broods: (1) a large brood of early worker larvae, a considerable portion of it newly hatched eggs; (2) a large brood of enclosed, pigmented, nearly mature worker pupae.

Queen contracted; no other sexual forms. *Statary*, but close to new nomadic period.

COLONY D, *E. burchelli:* Jan. 26, 1945; area I, Sierra Madre Mts., 40 km. north of Escuintla, at 1300 meters. On floor of large, well-forested valley, ground and vegetation moderately dry; running stream nearby. Well-developed swarm raid in progress. Bivouac: colony clustered within a mammal burrow (running about 10 cm. below surface) at a point 4 meters from the entrance. One brood only: large brood of mature larvae still engaged in spinning, nearly all members partially enclosed. Queen contracted; no other fertile forms present. Just entering statary period.

COLONY E, *E. burchelli:* Jan. 23, 1945; area I, valley of Huixtla R. near Tuzantan, Chis., at 150 meters. (Found and captured independently by Carmelino Vargas.) On rather dry slope, poor cover, 100 meters from small stream. Bivouac: in mammal burrow about 1 meter from entrance, 15 cm. below surface. Single brood of worker larvae about two-thirds mature. Queen contracted; no other sexual forms. Probably *nomadic.*

COLONY F, *E.* (*Eciton*) *hamatum:* March 3, 1945; area II, hills west of Jetjá, near Santa Cruz R., at 500 meters. On moderately moist hill, 100 meters from running stream. Large trees; fairly good cover. A vigorous column raid with three principal systems (cf. Schneirla, 1938); a bivouac-change movement in progress at 5:00 P.M. Bivouac: an exposed cylinder, hanging from one end of small log to the ground. Two broods: (1) a large brood of young worker larvae, a minor portion of it newly hatched eggs massed in packets; (2) a callow worker brood, with a small part of the worker minor pupae still enclosed. Queen fully contracted; no other sexual forms. *Nomadic.*

COLONY G, *E. hamatum:* March 9, 1945; area II, Lacandone forest near upper Jetjá R., at 600 meters. In moderately humid forest, fairly good cover, on slope near running stream. A single long raiding column, unbranched within 60 meters of the bivouac. Bivouac: within hollow buttress of large tree, close to trunk below ground level; completely hidden. Two broods: (1) large masses of eggs in packets, a minority of them recently hatched; (2) a large brood of fairly mature worker pupae, partially pigmented, fully enclosed. Queen contracted; laid no eggs within the two days following capture, evidently having finished the delivery of a mass of eggs a few days before. No other sexual forms. *Statary.*

COLONY H, *E. hamatum:* March 10, 1945; Lacandone forest, near upper Jetjá R., at 750 meters. In moderately humid forest, not more than 150 meters from running stream. A single long raiding column unbranched within 85 meters of the bivouac, used on two successive days. Bivouac: completely enclosed within large decayed log, its major part in a central hollow, with groups of workers and interspersed piles of larvae in numerous cells in the outer portion. A single brood: a large brood of mature worker larvae, engaged in spinning, nearly all members partially enclosed. Queen *physogastric;* her gaster asymmetrically enlarged. *Statary.*

COLONY X3, *E. burchelli*[1]: March 21, 1945; area I, garden of Centro Médico, Huixtla, at 100 meters. Fairly humid part of otherwise dry hill; sparse, variable cover; about 150 meters west of Huixtla R. A small swarm raid, which dwindled away at about 11:15 A.M. Same bivouac site during two days prior to capture. Bivouac: within central hollow and wall cavities of large decayed log (also in ground underneath) in center of sheltered gully. Single large brood of mature larvae, evidently all spinning, with more than two-thirds of them (in general, the larger sizes) well enclosed. No mature queen found, and no other sexual forms. Evidently just entering statary period.

COLONY I, *E. burchelli:* March 27, 1945; area I (finca La Victoria), 29 km. north of Huixtla, Chis., at 1600 meters. Near the top of a moderately dry hill, with fair cover; a running stream in valley 150 meters below. Two heavy swarm raids on successive days, with short bivouac-change movement between. Bivouac: a long curtain, exposed, but far under a large decayed log. A single brood of well-advanced worker larvae, approximately two-thirds mature. Queen contracted. *Nomadic.*

COLONY J, *E.* (*Eciton*) *vagans:* March 27, 1945; area I (finca La Victoria), 28 km. north of Huixtla, Chis., at 1800 meters. Near top of moderately dry hill, in small, fairly humid arroyo under good cover. No raiding observed on March 26; weak column raid March 27. Bivouac: distributed through outer wall of large decayed log, with clusters in bark debris below, all well out of sight. (This colony was first observed on March 26, when a few straggling workers were noted on the bivouac log.) Two broods: (1) packets of newly laid eggs in bivouac; other eggs laid after queen captured; (2) large brood of mature worker larvae in thin envelopes, many of the workers minor still spinning. Queen not physogastric but clearly entering or passing through an egg-laying period. (She continued to lay eggs for three days after capture, almost until her death.) *Statary.*

COLONY K, *E.* (*Eciton*) *rogeri:* April 3, 1945; area I (vicinity of rancho La Esperanza), 20 km. north of Escuintla, at 650 meters. At base of long hill in moderately dry area, under medium cover, only 20 meters from small running stream. Column raids observed on successive days, reduced to a minimum through the midday hours; bivouac-change movement on April 2, another in progress at 5:30 P.M. on April 3 just preceding capture. Bivouac: under a loose roof of matted vines, thin rootlets, and leaf mold, within

[1] This was one of the five colonies whose bivouacs were completely ransacked without my finding any sexual forms. In four of these cases (two *E. burchelli*, one *E. vagans*, and one *E. praedator* colony) it is possible that a mother queen was present but somehow escaped; in one case (*E. praedator*, X4; see below) the presence of a queen seemed doubtful.

the remains of an old tree root, fairly well out of sight. A single large brood of well-advanced worker larvae. Queen contracted. *Nomadic.*

COLONY L, *E. rogeri:* April 4, 1945; area I (vicinity of rancho La Esperanza), at 700 meters. In dense thicket close to small river; a somewhat humid situation. Fairly active column raid, with two well-developed trail systems. Bivouac: mainly in a cluster within the narrow, elongated, central hollow of a massive decayed log. Circumstances indicated previous occupancy of this site for some days. Broods: (1) eggs and very young larvae, in packets in lower part of mass; (2) mature worker pupae, an estimated one-third (mainly workers major and larger intermediates) already emerged as callow workers. Queen contracted. *Statary;* evidently at point of entering a new nomadic phase.

COLONY M, *E. hamatum:* April 23, 1945; area III (10 km. east of Coatzacoalcos R.), at 350 meters. Near bottom of deep, narrow valley between dry hills, a somewhat humid area close to creek bed containing small pools of stagnant water. (General area dry, after weeks without rain.) Extensive raid and bivouac change April 22. Vigorous column raid April 23 with three principal trail systems; at 4:00 P.M. an exodus from the bivouac (incipient bivouac-change movement) dominating one principal trail. Bivouac: curtain mass well back under large log on stream bank. Single large brood of advanced worker larvae close to maturity. Queen contracted. *Nomadic.*

COLONY N, *E. hamatum:* April 23, 1945; area III (close to Coatzacoalcos R.), at 250 meters. On bank of fairly humid arroyo between very dry hills, close to running stream; moderately good cover. Daily column raiding on single trails; on three of six days used route unbranched for 40 meters or more along stream bank. Bivouac: very wide, irregular low cylinder far beneath large fallen tree. Two broods: (1) a few packets of eggs, newly laid; (2) a brood of about 1000–2000 large (*ca.* 19 mm. long) pupae, all males, intermediate in development and enclosed in cocoons, well distributed through walls and interior of bivouac. Queen nearly maximally *physogastric;* laid thousands of eggs before her death two days after capture, and at death contained an estimated 8000 more. *Statary.*

COLONY O, *E. hamatum:* May 1, 1945; area IV, at 200 meters. In dry forest, mainly of palms, poor cover. Light rain fell on May 1, following weeks of drought. Column raid only moderately developed at 10:00 A.M., although with three principal base trails. Raiding dwindled away considerably after 11:00 A.M., when columns became thin and difficult to follow over the brightly lighted floor of the hot and dry forest. Bivouac: mainly hidden; an irregular cylinder, a portion above ground suspended from a low palm leaf which nearly covered it, a smaller part underground in mammal burrow near roots of same palm tree. A large brood of advanced larvae, all worker forms. Queen contracted. A single dealated *E. hamatum* male was found in the subterranean portion of the bivouac. *Nomadic.*

COLONY X5, *E. burchelli:* May 15, 1945; area V, above Fortin, Vera Cruz, near upper Metlac R. at 1100 meters. In moderately humid forest near river's edge, below dry rocky slopes; fair cover. A vigorous swarm raid. Bivouac: a large cylinder in a sizable underground erosion chamber covered by two close-fitting rocks. One brood only, a large brood of well-advanced worker larvae. No queen or other sexual forms found. *Nomadic.*

RECAPITULATION OF PRINCIPAL FINDINGS IN EXAMINING ECITON COLONIES

CONDITION OF THE BROODS

In all, the behavior, situation, and internal contents of 20 eciton colonies were examined, of which 18 were colonies of *Eciton* (*sensu stricto*) and two, *Labidus* species. Of the *Eciton* (*sensu stricto*) species, 15 were found to contain a single fertile queen each. These colonies included six *E. burchelli,* six *E. hamatum,* one *E. vagans,* and two *E. rogeri.* Of the 20 colonies, 19 had one or two relatively immense broods at the time of capture, estimated (in comparison with the bulk of rainy-season broods actually counted in previous studies) at 20,000 or more individuals in each case. The captures described above were made in all parts of the dry season between late December and May, and furthermore all areas sampled were more or less subject to the characteristic seasonal depression of rainfall. It would appear that relatively immense broods can be maintained by the colonies of *Eciton* (*sensu stricto*) [and *E.* (*Labidus*) *praedator*] in a general environment in which atmospheric conditions and food supply (i.e., available insect life) must be far less propitious for general eciton activities and for reproduction than in the rainy season.

What is even more surprising, in their detailed makeup the broods of these 19 colonies were all similar in general to those of the many eciton colonies examined under

rainy-season conditions (Schneirla, 1944). All were relatively immense in numbers; furthermore, each brood contained individuals at approximately the same stage of development, and in every one of the 19 colonies the larval and pupal broods contained only worker types of individuals. Although the details of brood population cannot be presented here, it may be said from a survey of fairly large samples that these cases resembled populations of rainy-season broods in the following important respects particularly: each brood formed a continuous series, clearly unimodal large brood samples are arranged on a biphasic curve according to the condition of their broods. Those with single broods of larvae are placed at successive intervals on the crest according to the modal body length of the respective broods, those with enclosed broods (i.e., mature and enclosed larvae, transformed larvae, young pupae, advanced pupae, or nearly mature pigmented pupae) with or without new broods of eggs or young larvae are placed along the trough phase on the same basis. In all respects this arrangement resembles that prepared from the data for 15 eciton (*E.*

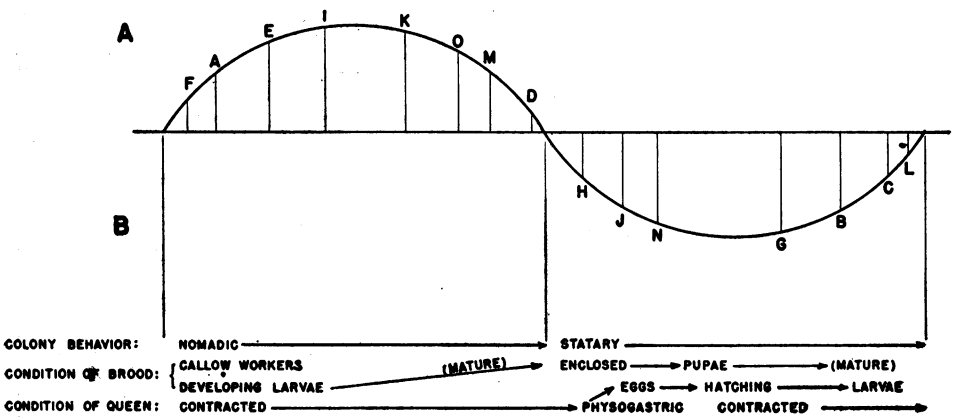

Fig. 2. Schematic diagram to represent the concurrence of events in the eciton colonies studied and captured in southern Mexico in 1945. In A, the crest of the biphasic curve represents the *nomadic* phase of colony activity and the trough represents the *statary* phase, with letters indicating the estimated places in the cycle reached by each given colony at the time of its capture. B indicates changing aspects in the behavior and internal condition of the colonies through parts of the cycle corresponding to the vertically coincidental points of A.

and tapering off to very small numbers at the extremes of maximal (major worker) and minimal (minor worker) sizes. Further similarities to rainy-season broods were noted; for example, in those cases (colonies A and F) in which pupal broods had been largely removed from cocoons as callow workers at the time of capture, the remaining enclosed portion was found to consist of the smallest sizes, workers minor. These facts are of importance not only for colony behavior, but also for questions concerning reproductive function which we shall want to consider.

In figure 2, the 15 colonies taken with their respective fertile queens as well as *hamatum*) colonies studied in the rainy season of 1938 (see Schneirla, 1944, fig. 2). The clearest points are that: (1) colonies with broods of eggs or very young larvae also have enclosed pupal broods whose advancement is separated roughly by the same interval from the general growth stage of the early larval broods of the respective colonies; (2) when callow workers are present, there is also present a larval brood more advanced than that of colonies under point 1; (3) colonies that have broods of larvae beyond the growth point involved in 2 above have no other brood; and (4) colonies with newly enclosed mature larval broods have no other brood. These facts

all may be fitted into a common scheme of a reproductive rhythm (see fig. 2), based (as was that for the rainy season) upon the presumed delivery of new broods at regular intervals of time by a single queen in each colony. Thus, when two broods are present, their growth stages are synchronized, and the growth points of the respective broods fall into place as would be expected from the assumption of a rhythmic egg-delivery process.

There was only one exception to the predominance of worker broods—colony N, taken in the upper Coatzacoalcos area in late April. This colony had one brood exclusively of males (moderately advanced pupae) and a second brood of thousands of eggs just being delivered. The two broods of this colony were found synchronized in their growth stages much as were those of colonies in which only worker forms occurred in the broods.[1]

Condition of the Queens

The condition of the fertile queens in our 15 completely surveyed colonies, as far as the occurrence of contracted or physogastric forms was concerned, also fits the scheme described from rainy-season studies. To emphasize the point, queens in the physogastric or egg-producing condition were found only in the three colonies (H, J, and N) possessing advanced broods in the early pupal condition. The pupal male brood of colony N included about 1000–2000 individuals; however, the queen delivered many thousand eggs prior to her death, and (judging from our previous case, 1944) then contained many thousands of unlaid eggs. The remaining 12 queens all were contracted. From the timing of broods in the latter colonies, as indicated in figure 2, it would appear that the newest brood in each of these cases was delivered (as eggs) about the time when the given colony last possessed a brood entering its pupal development. The correlation of broods described above, and the condition in which the respective queens were found, would hardly seem possible unless these queens had been maintaining regular ovulation rhythms of fairly constant phase duration. As far as our present facts go, they indicate that many, if not all, *Eciton* (*sensu stricto*) queens are able to maintain their characteristic reproductive rhythms throughout the dry period.

[1] It should be noted, however, that the male brood of colony N seemed distinctly more advanced in pupation than have enclosed worker broods taken at the time the colony queen was engaged in egg laying. Although it is possible that the queen's rhythm in this case was somewhat irregular, a more likely explanation is that male broods develop faster than do worker broods.

General Facts Concerning Colony Behavior

In considering colony behavior, first of all it must be remembered that this study was cross sectional in the sense that few of the colonies were under observation for more than two or three days, and some of them for only one day. Furthermore, colony behavior in the dry season is likely to be more irregular, and as we shall find more subject to extrinsic interferences, than in the rainy season, making longer observation periods very desirable. Despite these limitations, the facts check rather well through the series of cases. The colonies that have been termed *nomadic* on the basis of their more vigorous raids and the occurrence of one or more observed bivouac changes just preceding capture are F, A, I, K, and M; the colonies that may be termed *statary* on the basis of limited raiding and the non-occurrence of bivouac changes during one or more days preceding capture are B, C, G, H, J, and N. It will be seen that in each of these instances the observed circumstances of colony behavior coincided with the condition of the brood or broods, essentially as described on the basis of extensive rainy-season studies of *E. hamatum* and *E. burchelli* (Schneirla, 1938, 1945).

The five colonies that were observed and whose bivouacs were ransacked without any fertile forms being found deserve mention here. Two of these were the *E. burchelli* colonies X3 and X5, described above. In these colonies the condition of the brood (X3: mature larvae, mainly enclosed; X5: advanced larvae, not yet mature, unenclosed) and colony behavior (X3: weak raiding, no bivouac change; X5: vigorous raiding, bivouac change probable) corre-

sponds as described above. A correspondence between brood condition and behavior similar to that of colony X3 was observed also in an *E. vagans* colony (X2) that was studied at Jetjá, Chiapas.

This colony (X2) had a mature larval brood (all enclosed but still largely engaged in spinning), and on three successive days staged relatively weak raids leading from the bivouac over the same long base trail. During three days after it was found this colony remained in the same place, tenanting one side of a huge decaying log through an extent of about 2 meters, its workers and brood well distributed among numerous cells in the moist spongy wood. Soon after the investigation of this bivouac began, an *E. praedator* colony (X1) was discovered occupying similarly scattered cells on the other side of this same log (and excavations in the ground beneath), through nearly the same extent of length as the *E. vagans* colony. The *praedator* colony contained a great brood of newly transformed pupae, all workers, and an immense brood of eggs.[1]

It is probable that the fertile queens or dichthadiigynes of the above colonies were present but eluded capture. All of the situations were difficult to search; moreover, judging from the condition of the broods (cf. fig. 2) the queens presumably were contracted in all four cases, and could have escaped with agility and speed.

In only one instance, an *E. praedator* colony in Vera Cruz State (area IV), did the circumstances suggest that no queen may have been present at the time of capture. This colony was established in the deep and extensive subterranean excavations of a *Solenopsis geminata* nest from which it had evidently driven the original owners some time before. The eciton workers were in abundance in this nest, but only one evening raid was staged during three days of observation. An immense pupal brood was present, pigmented and well advanced, all members at nearly the same stage of development. However, no eggs were present, as might have been expected from the case of the *E. praedator* colony X1, which had two well-spaced broods when taken.

[1] It is unusual to find two eciton colonies bivouacked as close together as these were, with cells along their upper borders actually intermingled (i.e., some *vagans*-occupied cells in *praedator* territory, and vice versa). Despite a careful demolition and search of the entire log and the extensive *praedator* excavations beneath, no queens or other fertile forms were found.

To What Extent Do These Results Typify Eciton Dry-season Conditions?

In view of the fact that the survey involved numerous well-separated areas and sampled a variety of ecological situations ranging from fairly humid to very dry, from low to high altitudes, and extended through almost all of the dry period, it is probable that in general the results portray fairly well how eciton colonies pass through the dry season. The predominance among our cases of huge broods entirely of workers, spaced in their time relations much as was found in Panama under rainy-season conditions, indicates that eciton queens can maintain their reproductive functions on much the same rhythmic basis during both the rainy and dry times of year. Correspondingly, our findings show that in the dry months colony behavior may fluctuate between nomadic and statary phases much as it does in the time of rains (Schneirla, 1938, 1945). This picture very probably represents the basic trend of events, yet we must consider the possibility that important variations characteristic of the season may well be passed over in a cross sectional survey such as the present one.

For example, although there are numerous reasons for believing that the fertile forms develop at some time during the dry period, we cannot add much here to the meager evidence on that score. Despite the fact that winged males of various eciton species were taken at lights from late February onward, male developmental forms were found in only one of 20 colonies whose bivouacs were throughly inspected, and only one bivouac was found with a dealate male. Furthermore, no young queens were

brought to light in the bivouacs, only individuals that were clearly functioning as the single reproductive dichthadiigynes of the respective colonies.

Circumstances such as these suggest that the development of sexual forms and their presence in eciton colonies as mature individuals must constitute a relatively brief episode in the course of dry-season events. It may be suggested also that broods containing the sexual forms must be very limited in number in any given colony, and that some colonies may fail to produce any broods of such individuals. Only a study of events in given colonies over considerable periods of time can readily clarify these matters.

Army Ants in General Relation to Dry-season Conditions

That sustained dry weather exerts profound effects upon insect life is a well-known fact (Uvarov, 1931), although the rise and scope of such effects are still understood only in a preliminary way. With the exception of a few forms such as some orthopterans and, of course, ticks, insects in general are greatly reduced in their activity, particularly in the daytime. Most of the ants are held to a relatively low level, as compared with rainy-season functions. The army ants are no exception, as previous writers have noted. Smith (1858) quoted Bates on an observation of *E. drepanophorum* (= *E. hamatum*) traveling in a column he considered not a predatory but a true migratory movement. Bates' reasons for so thinking are of interest: "The procession was not a predatory affair, because all of the small-headed individuals conveyed in their mandibles a little cluster of white maggots, probably larvae of their own species. I have no doubt of its being a migration, as at the time of observation a change of season was taking place, the river retreating from the beach, and the open places above, about to be burnt up by the hot sun of the dry season."

Although the circumstances support Bates' identification of this movement as a change of bivouac, the season of occurrence is not at all a useful clue, for we have found that bivouac-change movements occur during the dry season much as in the time of rains. However, certain behavior differences are notable.

Our survey shows that while there is apparent no radical qualitative change in eciton colony behavior with the coming of the dry season, the activities of colonies may undergo a considerable general reduction in vigor with limited qualitative changes resulting. However, the literature contains certain misconceptions concerning the nature and degree of such changes. A frequent one is that raiding and other movements are suspended almost altogether during the dry season. For example, in Sumichrast's (1868) discussion of Mexican army-ant behavior, based especially on notes from the Potrero area below Cordoba when a flourishing tropical forest existed there, it is stated that: "Beside the changes of domicile, which are so generally in relation with the atmospheric variation as to serve as a rule to the inhabitants of the country, the *Eciton* devotes itself every season to excursions for pillage ...invading the habitations of the country. These visits ordinarily take place at the beginning and the end of the rainy season, and almost always during the night." Without interpretation, such statements readily give rise to misconceptions. Observations of this kind, typical as they are, depend mainly upon eciton raids noticed near inhabited places, and are influenced by the swarm-raiding activities of *E.* (*Labidus*) *praedator* in particular. It is a fact that colonies of this species, commonest of the subterranean ecitons (in the subgenera *Labidus* and *Acamatus*) to be seen, are far more likely to range outside rain forest areas and in clearings than are the colonies of terrestrial *Eciton* (*sensu stricto*) species. Our own notes show that, although *praedator* raids invade settled places much less frequently during the dry months than in rainy times, such raids do occur, especially in early morning or in evening or after a

general increase in humidity. Their raids are seldom witnessed in dry times, not because conditions render the ants altogether inactive, but because eciton swarms do not readily cross the open, dry, and generally dusty areas (with scanty subterranean routes) commonly encountered around villages and haciendas.

On numerous occasions in different localities variations in the prominence of *praedator* activities according to atmospheric conditions were noted. For instance, during a seven-hour hike up the Huixtla River Valley on April 10 in the morning and early afternoon, no eciton raids were encountered. Throughout the day the atmosphere was dry, the trail dusty and exposed to bright sunlight except in occasional patches of forest. When I returned next day over the same route, the air was humid and the sky overcast after a light but prolonged rain on the previous evening. Then the well-thronged columns or swarms of five different *E. praedator* colonies were seen, and in one forested ravine an *E. burchelli* raid was observed. As another example, for two days in early February I hunted ecitons in the fairly well-forested but dry valley of La Esperanza (area I) without success; yet on the third day, after a light rain during the night, four raids (of *Labidus* and *Acamatus* species) were encountered during the morning, and two others in late afternoon.

It is interesting to note that natives in different areas commonly accept eciton raids as an omen of rain. According to von Ihering (1894) *E. praedator* is known in Brazil as the "rain ant," because of the frequency with which its raids are noticed shortly before heavy rains. The basis of this fact is readily understandable, for we should expect that (in addition to atmospheric changes) the darkening which commonly precedes rain would account for increased *praedator* activities in open areas where the ants would be noticed. However, in the present writer's experience with eciton activities, such spurts in raiding are better indicators of rain-just-past than of rain-to-come. In any case, a distorted picture of eciton activities is certain to result if we rely upon impressions obtained from encounters with species such as *E. praedator* outside the forest.

The Dry-season Activities of Terrestrial Eciton Species

For the terrestrial ecitons, our major interest in this paper, we have activity records representing the greatest part of the dry season, taken from a variety of localities and ecological situations in the forests of southern Mexico. In the first place, it may be said in general that colonies of the *Eciton* (*sensu stricto*) species are able to continue both their daytime raids and their bivouac-change movements throughout the dry months. Our evidence shows that the vigor of the diurnal raids and the occurrence or non-occurrence of bivouac-change movements then fluctuates much as in the rainy season (Schneirla, 1938, 1945) according to internal changes dependent upon condition of the brood.

However, extrinsic conditions exert a much greater influence in the dry season in accounting for behavior irregularities in given colonies. The raids tend to be smaller in dry situations, even in colonies identifiable as nomadic (i.e., maximally excitable). In the wet season, colonies of *E. hamatum* may be depended upon to stage definite daily raids (even when statary), with their columns generally in full view on the surface; however, under dry-season conditions statary *hamatum* colonies sometimes go raidless on given days, and nomadic colonies often stage rather small raids. Furthermore, in dry situations or under sparse forest cover *hamatum* columns frequently slip beneath leaves and other objects even for considerable distances, as *E. rogeri* and *vagans* columns do far more frequently. The midday lull in raiding, a regular feature of the daily routine in rainy months (and an important factor in the development of a colony removal at the end of a raid), is much more pronounced and lasts longer in the dry period, sometimes to the extent that raiding is suspended altogether through the noonday hours.

Another species on which extensive notes are available is *E. burchelli*. While in the rainy season colonies of this species pass numerous raidless days in the central part

of the statary period (Schneirla, 1945), daily raids occur regularly when a colony is nomadic. In the dry season the reduction is much greater, and raidless days sometimes occur even in *burchelli* colonies whose internal (brood) conditions fit the picture of nomadism. Of interest is the fact, to be expected from this, that under such conditions *burchelli* colonies which ostensibly are nomadic do not always stage bivouac-change movements. That is, a return to the same bivouac ensues, rather than a removal over raiding trials, towards the end of a given day on which the raids are notably underdeveloped.

The failure of bivouac-change movements when raids are small is a result to be expected from our theory of the relationship between raiding and bivouac change (Schneirla, 1938), accounting for the latter occurrence as an outcome of large raids in a maximally (internally) excited colony. Our evidence tends to suggest that in the dry season the inhibiting effect of external conditions frequently counterbalances the stimulative effect of internal "drive," so that a colony internally fitted for nomadism may fail to move. This may well be a matter of considerable importance for colony survival.

Most of the record colonies described in the preceding section were studied and captured when in more humid situations under fairly good cover; few of them in very dry, exposed areas.

In the driest forests (e.g., area III, area IV) eciton colonies were most difficult to find, not only because their raids were encountered much less frequently than in more humid areas (e.g., area II), but also because the bivouacs when discovered were likely to be unassailably secluded below great rocks or tree bases, or in the recesses of dry, hard ground.

For three days during April of 1946 the writer hunted ecitons in the Potrero area, in which Sumichrast (1868) worked. Both the valley, which is now almost completely denuded of forest except for narrow strips along the Atoyac River, and the low bordering mountains, which are losing their sparse forests through progressive clearing, were at the time sweltering in the heat of a protracted drought. No traces of army ants were discovered, although when the search shifted to the far more humid vicinity of the Metlac River above Cordoba, a colony of *E. burchelli* was found on the first day.

One evident reason why searches for eciton colonies in dry areas often are fruitless is that raids tend to be smaller or less frequent, and the columns thin and partially concealed in such localities. Under such conditions the colonies are likely to be missed unless a rain or an occasional dark misty period accounts for a spurt in extra-colony activities. Because we lack evidence on the internal conditions and behavior of colonies which happen to pass considerable periods in very dry localities, nothing can be said here concerning possible interruptions or distortions of the regular eciton rhythm in reproduction and behavior in such cases. It should be noted that certain behavioral factors which operate in normal raiding serve to keep colonies out of very non-optimal situations in a diversified environment. In general, the pushing parties of column-raiding species and the large bodies of swarm-raiding species advance more readily into humid places affording a fair supply of booty than into spots which are dry, brightly illuminated, and sparse in booty. Such matters have been touched upon in a previous connection (Schneirla, 1938). Since bivouac-change movements follow main routes developed in raiding, army-ant colonies evidently adjust fairly well to dry-season conditions by operating and settling more frequently in fairly optimal zones such as ravines than in drier and more exposed parts of their environment. Even so, the latter possibility should not be overlooked as an ever-present hazard.

There is one way in which eciton colonies conceivably are "caught" for considerable periods of time in non-optimal situations where they may lose heavily in numbers. This possibility arises through the fact that normally a colony is not mobile or nomadic unless adequate intrinsic (i.e., brood) excitation exists. Let us say that a colony with a brood of mature larvae bivouacs in a fairly humid arroyo in the last move of a

given nomadic period. With this brood enclosed the colony becomes statary or sessile, and presently the general area dries out. On the basis of its current internal condition the colony cannot escape. From our evidence, only local shifts through short distances might occur in response to the irritating effects of bright light or high temperature, taking the bivouac cluster deeper into subterranean cavities or farther beneath objects such as large rocks or logs but not out of the given area. Under such conditions raids would diminish in scope and frequency, further reducing the supply of moisture available through food. Since laboratory tests of a preliminary nature indicate that the desiccation tolerance of eciton workers is fairly low, it is possible that through circumstances such as those outlined above many colonies suffer drastic reductions in personnel or even extermination.

Although on the whole eciton colonies seem to operate fairly effectively in the dry season, notwithstanding hazards such as that just discussed, in the general literature there has been a tendency to regard doryline nomadic movements as subject to complete suspension during the dry months (Brauns, 1901; Santschi, 1908). To be sure, certain records do suggest that a halt in activities may occur in groups living outside the tropics. For instance, Wheeler (1900) reported for the *Acamatus* species of Texas a tendency to suspend the "ancestral nomadic condition" during winter and early spring, when the same nest site is occupied during an extended period. As evidence for a spring re-arousal, he observed an *E.* (*A.*) *schmitti* colony on the march May 1, and at other times saw colonies moving in files at about that time, indicating to him that in spring these species leave their winter quarters to resume their marauding expeditions. Less definitely, Santschi (1908) stated that although *Dorylus* migrations are of general occurrence they are not obligatory, and under certain conditions these ants may inhabit the same nest for long periods of time.

If such observations hold for species which have adjusted to conditions outside tropical zones, our evidence on the other hand indicates that colonies of the tropic dwelling ecitons, i.e., *Eciton* (*sensu stricto*) in particular and probably the others as well, do not conform. We have found that colonies of the terrestrial army ants become mobile or nomadic at given times in the dry season, under the influence of much the same factors which arouse their nomadic movements during the season of rains. In the areas surveyed in this study, no evidence was found for a dry-season suspension of eciton nomadism, although, as we have mentioned, an occasional daily failure of bivouac change may occur in an otherwise nomadic colony. The possibility nevertheless remains that longer suspensions may come about in exceptionally nonoptimal situations or under special reproductive conditions as yet unknown.

A Horizontal Shift in the Level of Nesting

The bivouacking of tropical ecitons is affected strikingly by dry-season conditions in what may be termed the horizontal level of the sites, if not in duration of occupancy. Under the conditions generally prevalent in southern Mexico during the period of this study, colonies of the ordinarily terrestrial eciton species tend to form their clusters in subterranean places rather than on or above the surface, as in the rainy season (Schneirla, 1938). Their rainy-season bivouacs are found almost invariably above ground: those of nomadic colonies ordinarily exposed (e.g., clustered between the buttressed roots of a tree), those of statary colonies concealed as a rule and in elevated situations (e.g., the upper interior of a hollow tree). In the dry season even nomadic colonies may go below ground, to form their clusters in cavities such as mammal burrows or spaces beneath rocks or vegetation. Atmospheric conditions apparently have much to do with the change, for surface bivouacs are found with greater frequency in more humid localities (e.g., our area II). Colonies entering the statary condition tend to move into more secluded, better covered niches than do nomadic colonies. In moister places they are found well ensconced in the recesses of large, decaying logs; in drier places the

bivouacs frequently are in relatively inaccessible subterranean cavities.

The fact that our present evidence concerning colony behavior almost altogether concerns colonies with large worker broods raises the question of when and how the sexual forms are produced, and how their occurrence influences colony behavior.

The Problem of Fertile Eciton Individuals

The Production of Males

Among ants it is generally true that the sexual forms are produced seasonally at times characteristic of given species. In the temperate zone, the males and females of certain species such as *Prenolepis imparis* appear in the spring, those of others such as *Formica incerta* during the summer (Talbot, 1945). For the dorylines, one may gather from the fragmentary evidence available that males and young queens are produced at some time during the dry season. The present writer found no fertile forms in eciton broods during four annual periods of rainy-season investigation in Panama (Schneirla, 1938).

The evasiveness of this problem is expressible by the fact that the wasp-like males of both Old and New World dorylines were taken independently at lights and were given separate taxonomic standing long before their affinity with corresponding worker forms had been established (Wheeler, 1921). Since the time when Savage (1849) found dealated males marching in a column of *Anomma nigricans* workers, both by inference and by direct observation the species affiliations of a long series of doryline males have been identified (Sumichrast, 1868; Müller, 1886; Mayr, 1886; Emery, 1896; Wheeler, 1921; and Smith, 1942). However, the conditions under which males are produced are still virtually unknown.

In a number of scattered instances, males have been discovered in doryline nests as immature forms or as mature winged adults. In Paraná, Brazil, Hetschko (Mayr, 1886) found a colony of *E.* (*Acamatus*) *hetschkoi* occupying subterranean galleries in which a number of winged males were found amid the workers. On April 12, 1914, Gallardo (1915) discovered a nest of *E.* (*A.*) *spegazzinii* established beneath the patio tiles of his home at Bella Vista in the Argentine, and in digging it out a compact group of about 50 males was discovered in one section of the subterranean chambers. On October 23, 1916, Luederwaldt (1918) investigated a large colony of *E.* (*L.*) *praedator* established in an old termitarium in a garden at São Paulo, Brazil, finding enclosed worker pupae as well as numerous open cases 20 mm. in length from which males evidently had emerged. (Incidentally, the queen was physogastric and masses of newly laid eggs were found, a state of affairs which fits our scheme of the eciton reproductive rhythm.) Hubrich, as reported by Bruch (1924), took numerous male pupae in cocoons from a nest of *E.* (*A.*) *hetschkoi* found in the Alta Gracia Mountains of Argentina.[1]

All of the above cases involved species of the subgenera *Labidus* and *Acamatus* (= *Neivamyrmex*), which frequently emerge from the forest into clearings. The terrestrial species of *Eciton* (*sensu stricto*), virtually never found outside the bounds of rain forest, have been discovered with male broods only twice, to the writer's knowledge. At the Kartabo station in British Guiana on July 18, 1920, near the end of the rather irregular rainy season of that locality, Wheeler (1921) and Emerson found a colony of *E. burchelli* which contained a brood of more than 100 nearly full-grown male pupae in cocoons. The lot of male pupae represented a distinct brood, which evidently contained no worker forms.[2]

The second instance is our *E. hamatum* colony N, taken on April 23 near the upper Coatzacoalcos River, in which was found the only male brood present in any of the 20 colonies captured in the present study. This was an all-male brood of somewhat

[1] Date of capture not given in original.

[2] Dr. Emerson has assured me that no worker pupae were found with this brood.

more than 1000 pupae, enclosed and well advanced in pupation. The single queen was physogastric with many thousands of eggs already laid towards a further brood.

From these scattered facts certain conclusions may be drawn very tentatively. First, although we shall not use space here to check local seasonal changes with the dates given above, from fragmentary evidence we may conclude that eciton males probably develop at some time during the dry season. The evidence at hand further suggests that the males develop in distinctive and relatively small broods of this one sex alone. And although exceptional conditions must be required to produce a male brood, a few facts intimate that these broods may well appear at regular points in the eciton reproductive cycle when worker broods might otherwise come. At any rate, in the *E. praedator* colony of Luederwaldt and the *E. hamatum* colony N of the present study, the presence of masses of eggs in addition to the brood of advanced male pupae seems to represent a coincidence of broods which agrees closely with the synchronization holding for the reproductive cycle under rainy-season conditions (Schneirla, 1944).

The Problem of Doryline Queen Production

To our previous evidence that one queen only is present in the established eciton colony (Schneirla, 1944), 15 new cases may be added from the present study, making a total of 34 *Eciton* (*sensu stricto*) colonies of five different species from which single dichthadiigyne individuals have been taken by the present writer. Furthermore, among the 15 colonies of this subgenus from which queens have been captured by others, with but a single exception only one queen was found in each instance, and single queens have been found in nearly all colonies of other eciton subgenera from which captures have been made. From these results it would appear that in the event more than one individual of this caste is found in an eciton bivouac, we are dealing with a relatively temporary condition involving one or more new queens.

It should be emphasized that finding a queen in the contracted condition cannot be accepted as evidence that she is a "young," newly emerged, and not yet gravid individual. We have made it clear why dichthadiigynes have been discovered in the contracted condition in most instances. Our evidence (Schneirla, 1938, 1944) establishes the existence of a reproductive cycle in the *Eciton* (*sensu stricto*) queen, in which she becomes gravid at recurrent but relatively brief intervals, but otherwise remains contracted. Circumstances indicate that the condition holds more or less in the other subgenera as well. Cases are very rare in which eciton queens have been captured under conditions definitely establishing their recent emergence.

To the writer's knowledge, in only one instance on record has an *Eciton* (*sensu stricto*) colony been found with at least one evidently "new" queen. This was at the Kartabo station in British Guiana, on July 19, 1920, when, as mentioned above, Wheeler (1921) and Emerson found a colony of *E. burchelli* with a brood of nearly mature male pupae. When the colony was being smoked out of its hollow tree bivouacking place, ". . .Mr. Emerson observed a large halting mass of workers in the column and on thrusting his tweezers into it drew forth a young queen which was being very slowly piloted along by a dense cloud of attendants. At 3:00 P.M. a second queen, precisely like the first, was discovered in one of the masses of ants resting on leaves a few yards from the tree." Wheeler (1921) reasoned that, "the two females had evidently recently emerged for their colors were very brilliant and the delicate golden pile on their bodies was intact. Moreover, their ovaries were undeveloped as shown by the relatively small size of the gaster."

Unfortunately, we cannot be sure about the youth of either queen in this instance. The mother queen may well have escaped in the melée, or may have died previously as Wheeler thought, leaving two new queens; or, one of the supposedly "young" individuals actually may have been the older dichthadiigyne in a contracted state. In *Eciton* (*sensu stricto*) queens, a "fresh" appearance may be a deceptive clue to age.

According to the present writer's theory the mother queen would be anticipated in the contracted state under the brood conditions described in Wheeler's Kartabo colony, i.e., in an eciton colony with a nearly mature pupal brood the fertile queen would not ordinarily enter a new egg-delivery phase for a least three additional weeks (Schneirla, 1938). Yet, since the monogynic condition seems to hold in eciton, it is probable that at least one of these queens was new.

Two instances are on record for the other eciton subgenera. In late March and early April, of 1899, near Austin, Texas, Wheeler (1900) discovered two different colonies of *E.* (*Acamatus*) *schmitti*, each with one queen. One of these queens was physogastric and died on April 18, a week after capture, having laid nearly all of her eggs; the other (more nearly contracted) continued to lay eggs from time to time in the artificial nest, but altogether laid very few. Then, in the midst of the mass of workers with which the two queens had been placed, on April 20 a new queen was found, intermediate between the first two in size and appearance. Wheeler (1900) thought this individual could not have been overlooked in the first examination of the colony, and hence "must have developed within the nest during less than a month from an insect closely resembling a worker in size and appearance. The workers must have been feeding her abundantly." It is a reasonable inference that the queen last found was a young individual. However, she may have been in the colony when it was captured, since it is not at all impossible to overlook a contracted queen in the midst of active or clustered workers.

The engineer Ogloblin sent to Carlos Bruch (1934) two queens of *E.* (*N.*) *hetschkoi ogloblini* found in the Argentine on October 20, 1932, in the same nest beneath a stone. Both queens were contracted; however, eggs were present in the nest, and when the captures were placed in an observation nest one of the queens was observed depositing eggs. The other queen laid no eggs, and "appeared to be virgin," although "neither of the two presented the characteristic signs of gestation."

From none of these three instances is it clear how the supernumerary queens were produced. The meager evidence carries the suggestion that whether queens appear in worker broods, with males, or in special broods exclusively containing queens, only a few of them are produced at one time. Since they are wingless, and very attractive to the workers, it is probable that they do not leave the colony readily; hence if their number were very large, they would be taken in the bivouacs more frequently and in greater numbers. In the present study 20 colonies were examined in the dry season, without one being found with queens other than its single fertile individual. It is possible that the production of dichthadiigynes in a given colony occurs under conditions even more exceptional than does the production of males. The specific conditions of queen production and their season of maturation remain to be discovered.

SUMMARY AND DISCUSSION

The dry season appears to bring no very radical changes in the life of army ants, perhaps fewer important changes than with most other insects. Atmospheric conditions commonly inhibit their raiding to some extent, particularly through midday, when the typical slack period is generally more pronounced than in the rainy season and sometimes approaches a stoppage. However, the ecitons do not appear to enter a resting or dormant condition as a regular response to dry weather. The colonies encountered in southern Mexico in the course of the present study approximated rainy-season conditions more closely in their internal condition and behavior than the present writer had expected. In fact colonies of terrestrial eciton species have been found capable of staging daily raids and carrying out nomadic movements even in rather dry forest areas.

The apparent success with which army-

ant colonies adapt to adverse dry-season conditions evidently depends upon two mechanisms in particular. First, by virtue of their typical responses in raiding and in the subsequent bivouac-change movements colonies generally manage to remain in the vicinity of more optimal zones such as ravines. The basis is a crude selective process arising through the tendency of advance raiders to be influenced somewhat in their movements by variations in illumination, humidity, and booty supply — obviously a major factor influencing the path of territorial change since the eventual bivouac-change movements of a colony follow the main lines of its raiding. A second important mechanism of adaptation to dry weather in ordinarily terrestrial species is the tendency to withdraw into moist and dark recesses, and underground places in particular, when the surface terrain is dry. This variation in bivouacking clearly depends upon atmospheric conditions, since in humid places with fairly good forest cover one is likely to find the terrestrial ecitons occupying surface bivouacs as in the rainy season. As a rule, however, it is notable that in the statary phase of their activity cycle colonies in dry areas tend to go down into subterranean retreats instead of going up (e.g., into hollow standing trees) as colonies do with great frequency in the time of rains. This may be considered a special phase of the typical eciton *altitudinal migration* upon which we have commented (Schneirla, 1945).

Beyond differences such as these, what we have found in this survey indicates that the fundamental pattern of eciton activities in the dry season is substantially that of the rainy season. Among more than 50 colonies encountered, 20 colonies of *Eciton* (*sensu stricto*) (representing four different species) were thoroughly investigated both in behavior and in internal condition, with the finding that each of them at the time of study coincided in all particulars with some definite stage of the previously described nomad-statary cycle. None but secondary variations were discovered. For instance, colonies in their nomadic phase occasionally stage definitely smaller raids than those of the rainy season, and at times no bivouac-change movement occurs after such underdeveloped forays—a result to be expected from our general theory (Schneirla, 1938). When colonies are in the statary condition the dry-season inhibition of raiding is correspondingly more pronounced than in nomadic circumstances. Statary colonies typically exhibit more raidless days than under rainy-season conditions, the more so when in very dry and exposed situations. However, we return to the fact that in widely separated parts of southern Mexico and at very different times in the dry season the described nomad-statary cycle of events appeared to prevail among the various species of terrestrial ecitons encountered.

It is possible that this survey has not sampled adequately the entire range of eciton reactions to dry-season conditions. In certain of our areas it was difficult or impossible to find army-ant colonies, although the reports of residents indicated that the "soldadas" put in an appearance in the time of rains. It might be expected that in dry or poorly covered areas furnishing a sparse supply of booty, eciton colonies become so inhibited in their external activities that even repeated searching of the same terrain fails to disclose their presence. In the absence of direct evidence, we have suggested that under given conditions colonies may undergo prolonged desiccation and starvation even to the point of extermination. A time of particular vulnerability would seem to be the statary period, if the last nomadic moves happen to carry a colony into an area which subsequently dries out during the time when the possession of an enclosed and inactive pupal brood does not promote effective bivouac-change movements. Laboratory tests indicate that a colony in such straits could be expected to consume its brood, and although no instances of extreme brood cannibalism have been observed in the field, the possibility exists as one buffer against extermination. Another is the manner in which ecitons can shift the position of their bivouac through limited distances when subjected to non-optimal extremes of bright light or atmospheric dryness. Despite such incidental safeguards, it is quite possible that the dry

season makes fairly heavy inroads among the population of eciton colonies.

From our evidence certain new inferences may be drawn concerning the reproductive capacities of the army-ant queen. Evidently the functional eciton queen is able to continue her reproductive rhythm under dry-season conditions, producing her new broods at well-separated intervals in a manner resembling her rainy-season performance. Whether her rhythmic function is maintained throughout the dry season, as it is during the rainy season, cannot be said here. However, granting the deficiencies of cross-sectional evidence, it should be emphasized that our records strongly support the possibility. Judging from the brood circumstances of their colonies, all of our queens taken at various times in the dry season were at a definite stage of the reproductive cycle when captured. Circumstantially, our findings also suggest that in the dry season the duration of the inter-ovulation periods must be fairly constant for the queens of different colonies. Were this not so, we should not expect to find the regular coincidence of broods and queen's condition which held without exception in colonies taken randomly as and where they were found.

Even more surprising is the fact that eciton queens are very prolific under seemingly adverse dry-season conditions. The broods are predominantly large, typically approaching the magnitude of rainy-season broods, and with but one exception in our cases each brood represented a graduated series of developing workers. The ability of the queens to produce broods of such proportions, and of the colonies to carry them through the period of larval development when they consume relatively great quantities of food, shows that even in dry weather the rain forest environment furnishes the very considerable quantities of booty which are essential. Were the supply of other insects and in particular their developing forms to drop greatly in the dry season, the tropical ecitons obviously could not continue to exist on the typically high metabolic and activity level of their nomad-statary pattern, since the phases of that pattern are closely (although indirectly) balanced against food supply.

This study has added relatively little evidence on one of the most baffling questions of eciton life: the problem of when and under what circumstances the sexual forms appear. Concerning the fertile females we have only the conclusion from previous investigations that new queens do not appear during the principal part of the regular rainy season. When this study began the writer held the notion that these critically important individuals might well appear during the latter part of the dry season. The principal basis of this expectation was that after a long period of relative inanition, increased temperature, and other special dry-season conditions, certain special changes in brood production might arise provided the queen's fertility continued. In particular, very small broods might be expected, either because of the queen's lowered metabolic resources or because of brood cannibalism by starved workers, or both of these causes. If all or most of the eggs in such a reduced brood were fertilized (diploid?), on the basis of Dzierzon's theory[1] they could give rise to female individuals, either workers or queens according to conditions. The assumption is warranted at this stage that the critical determining condition is an overfeeding during larval development which would carry some individuals beyond the threshold of the worker pattern and produce queens or dichthadiigyne forms. Such overfeeding would not be expected with broods of immense size as in the regular rainy season, since under such conditions even with plentiful food all of the larvae in the bivouac are fed equivalently and on substantially the same chance basis which holds all below the queen development threshold. This hypothesis for the queen production process is based upon the premise that quantitative differences in feeding influence the development of larvae arising from genetically equivalent fertilized eggs.[2]

[1] Supported for bees by recent work such as Haydak's (1943) and for ants by Wesson (1940).

[2] The possibility of qualitatively differentiated feeding, not satisfactorily demonstrated in other social insects (Haydak, 1943), seems even more doubtful for the ecitons with their relatively crude food delivery processes.

Although no colonies with supernumerary queens were found at any time during the present study, the possibility remains that such colonies (if broods were small and extra-bivouac activities minimal) were unavoidably passed over in the search or were among those whose bivouacs eluded study. It seems probable, in any event, that queen production is a relatively brief episode in the annual life of the ecitons.

Fortunately more evidence is available for the males. From the scattered records of eciton male captures in Central and South America, it seems probable that the males appear in distinct broods of a few thousand or less individuals, and that their development characteristically occurs in the dry season. On the grounds of admittedly scanty evidence, it may be suggested further that the male brood or broods of a given colony are limited seasonal events regularly synchronized with the queen's reproductive cycle but occurring under exceptional conditions. Synchronization of these broods in the cycle is a reasonable inference, although the cases are few, but nothing definite can be offered concerning the specific conditions of their appearance. It seems possible that somehow the fertilization of eggs is blocked altogether during a given ovulation episode. Whether this is a matter of seasonal depletion of sperm, or a temporary inhibition of the insemination process owing to special ecological circumstances (e.g., high temperature, dryness), or a reduced metabolic condition of the queen (owing, for example, to starvation; Wheeler, 1928), only further investigation can reveal. The apparent seasonal regularity and temporary nature of the unknown sterile condition evidently involved suggests that it is not simply a matter of exhausting the sperm supply but must involve a special change of more complex nature in the queen.

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