PROBLEMS IN THE ENVIRONMENTAL ADAPTATION OF SOME NEW-WORLD SPECIES OF DORYLINE ANTS [1]

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It is a great privilege to join in congratulating the Administration and Staff of the Instituto de Biología on the notable scientific accomplishments represented by the celebration of the twentieth anniversary of that justly famous institution.

The doryline ants of the world are notable for their carnivorous, predatory way of life, and for their characteristic nomadism. Outstanding among general accounts of their activities are those of Bates,[2] Belt,[3] and Wheller.[4 5] A description of numerous Eciton species in Mexico was given by Sumichrast,[6] particularly from observations in the Potrero area when the valley below Córdoba contained a luxuriant tropical forest.

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[1] I welcome this opportunity to acknowledge gratefully the many indispensable ways in which the government and the people of Mexico aided my investigations in southern Mexico in 1945. Among the many friends to whom I owe cordial thanks are the following: Dr. Manuel Martínez Báez, sub-Director of Health in the federal government; Dr. L. Figueroa Ortiz, former Director of the Hospital Centro Médico, Huixtla, and Sra. Figueroa Salano; Sr. and Sra. Enrique Knape of Mogoñé; Dr. E. Matuda and family, Escuintla; Sr. Joaquín Escobar, Motozintla; Mr. and Mrs. Dyfrig M. Forbes, Potrero; Ings. Villas Pérez and Humberto Ortega of Dept. Forestal y Caza; the late Dr. Alfonso Dampf; Dr. Franz Blom; Sr. and Sra. José Tarano. One zealous assistant, Sr. Carmelino Vargas, of Huixtla, Chis., should be mentioned for the outstanding persistence and initiative with which he joined in the project.

[2] Bates, H. W. **The Naturalist on the River Amazons.** 1863, vol. 2.

[3] Belt, T. **The Naturalist in Nicaragua** (pp. 17-27).

[4] Wheeler, W. M. **Ants.** 1910 (Chap. XV).

[5] Wheeler, W. M. Proc. Amer. Acad. Arts Sci., 1921, 56, 291-328.

[6] Sumichrast, F. Trans. Amer. Ent. Soc., 1868, 2, 39-44.

Actually, the nomadic movements of doryline colonies, rather than resulting from the local exhaustion of food as Vosseler [1] thought, are based upon regular biological and behavioral events. The nature of these events became known through studies carried out in Panama during the season of rains. [2 3 4]

The results of these studies may be summarized briefly. Colonies of the terrestrial species **Eciton (E.) hamatum** and **E. (E.) burchelli** exhibit a markedly regular cycle of behavior and reproductive processes, with the alternation of 1) a **nomadic phase** in which the colony develops large daily raids and moves off each night over a raiding trail to a new nesting site, and 2) a **statary phase,** in which raids are minimal or at times absent, and the colony is sessile.

This cycle in colony behavior is paralleled by a rhythm in reproductive events, in that 1) during each nomadic phase a brood develops through its larval stage, and the phase ends exactly with the enclosure of this brood, and 2) during each statary phase a brood passes through pupation and the phase ends exactly when this brood emerges from cocoons. Also, at a time about one-third through each statary phase, a new brood of eggs is laid by the queen—the brood which is in the early larval condition when the colony next changes to nomadism.

Between the cyclic changes in Eciton colony behavior and brood condition there exists a demonstrable causal relationship. In effect, an active larval brood stimulates the worker population of a colony chemotactually, energizing the colony to a high pitch during the interval of principal larval development, and a nomadic behavior condition is maintained. But when this brood becomes enclosed, the daily raids fall off sharply and no major change in nesting site occurs until it emerges as active callow workers, an event which again energizes the colony greatly and sets off nomadism. This system of events is represented in figure 1.

An important difference also exists in the nesting of colonies during the two phases of the activity cycle. Each colony when nomadic changes its location nightly, whereas in the statary condition a given site is occupied for nearly three weeks. In both **E. hamatum** and **E. burchelli** the nomadic nests are all open clusters formed of massed

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1 Vosseler, J. Pflanzer, 1905, 1 (19), 289-302.
2 Schneirla, T. C. Journ. Comp. Psychol., 1933, 15, 267-300.
3 **Ibid.**, 1938, 25, 51-90.
4 Journ. N. Y. Ent. Soc., 1944, 52, 153-192.

workers (see figure 2), but the statary bivouacs in contrast are formed in enclosed places, as within a hollow log or a mammal burrow.

It is evident that during rainy months the colonies of terrestrial Eciton species are adapted very adequately to their environment. Each colony produces a succession of immense broods which appear at regular intervals (roughly each 36 days) throughout the season, and which contain only worker individuals. A correspondingly regular alternation of nomadic and statary phases occurs in colony behavior. The environmental food supply is sufficient for the production of the many successive broods, for maintaining a population level in the colony, and for supporting a rhythmic and maximal reproductive function in the queen. Furthermore, the bivouacs of both phases are adequate as shelters for the colony and as incubators for the succesive broods.

The first investigation of Eciton life under dry-season conditions was undertaken in southern Mexico in 1944-1945. **A priori,** in contrast to the active and regular operations prevalent in the colonies under rainy-season conditions, a passive and irregular adjustment to the dry season was anticipated. It seemed likely that atmospheric conditions must become unfavorable, especially through desiccation, perhaps reducing the nomadic functions of colonies radically, also that food must decrease sharply through a reduction in the numbers and the accessibility of forest arthropods. Under such conditions, it seemed that reproductive functions must be reduced in the colonies, with inevitable interruptions or stoppages in nomad-statary processes. On hypothetical grounds, the production of male and fertile female individuals was expected.

During the dry season of 1944-1945 I carried out field surveys of army-ant conditions in five well-separated forested areas in southern Mexico, including the Pacific and the Atlantic aspects of Chiapas, the upper Coatzacoalcos R. district in the Tehuantepec isthmus, and the area above and below Córdoba in Veracruz.

The results differed strikingly from expectations. Twenty colonies representing four species of **Eciton (Eciton)** were studied, all of which conformed essentially to the cyclic pattern of the rainy season. As figure 1 shows, each colony as found was describable in terms of some stage of the nomadic or statary phase of the cycle, on the basis of raiding, occurrence or non-occurrence of nomadism, brood condition, and condition of the queen. With but one exception, a colony which had a sexual brood, the broods consisted entirely of worker-form in-

dividuals, and, surprisingly enough, were estimated to be substantially as large as those of the rainy months. The detailed results of this investigation have been reported in a separate paper.[1]

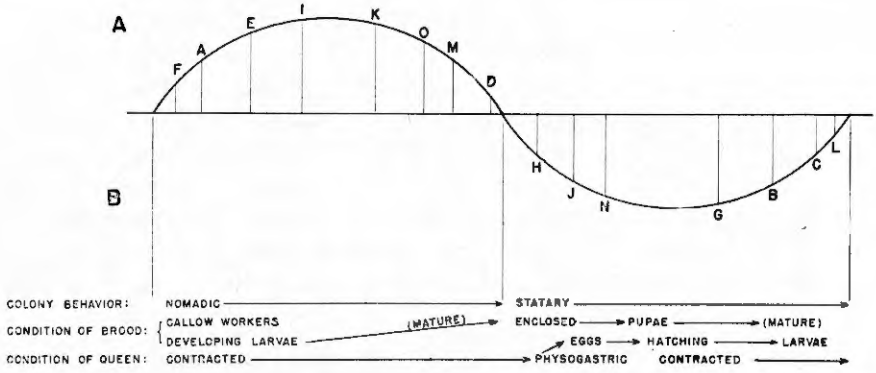

Fig. 1.—Schematic representation of the concurrence of events in the colonies of four Eciton species studied in southern Mexico in 1945. In **A** the crest of the biphasic wave represents the **nomadic phase** of colony activity and the trough represents the **statary phase,** with letters indicating the estimated stage in the cycle reached by each colony at the time of capture. **B** indicates changing aspects in the behavior and biological condition of the colonies at stages of the cycle corresponding to the vertically coincidental points of **A**

That the samples from southern Mexico (figure 1) adequately represent the typical situation of the terrestrial Ecitons was shown by further results from Panama. In the dry season of 1945-1946, on Barro Colorado Island, C. Z., 30 colonies of **E. hamatum** and 20 colonies of **E. burchelli** were studied over varying intervals of time, with all colonies except one [2] conforming to the nomad-statary pattern. One colony of **hamatum** and one of **burchelli** were continually on record for more than four months each, and both exhibited regular nomadic and statary phases throughout. The hamatum colony produced four successive large all-worker broods, the burchelli colony three large all-worker broods and one sexual brood in the series, within the period of study. In that season, 11 cases of colonies with sexual broods were found, with indications that no colony had more than one and that some of the colonies had no such brood. Otherwise,

[1] Schneirla, T. C. Amer. Museum Novitates, 1947, Nº 1336, 1-20.

[2] This colony contained the dried body of its dead queen when found, and without broods was obviously undergoing a degeneration.

regular all-worker broods were the rule. In the dry season of 1947-1948, 32 colonies of **E. hamatum** and 22 of **E. burchelli** were similarly investigated on Barro Colorado, and numerous colonies of these species were studied for short intervals in three other areas of Panama, with substantially equivalent results. [1]

Thus, Eciton colonies meet the conditions of the tropical dry season with essentially the same pattern of activities and processes that prevails for them in the rainy season. With the exception of a possible unique sexual brood, each colony produces great broods of workers in a regular series. The nomad-statary behavior cycles, dependent upon the regular appearance of such broods under rainy-season conditions, continues during the dry season in each surviving colony.

Evidently an adequate food supply for the Ecitons typically is available in the tropical forest in the dry season, notwithstanding seasonal fluctuations in the general population of insects and other arthropods serving as prey. Relatively great quantities of booty are essential for the development of a brood of more than 20,000 worker larvae, yet these must be obtained regularly, for successive worker broods are produced without much evidence of cannibalism. It is significant that the brood populations all have a distribution of polymorphic types approximating that of the rainy season, a series skewed toward the smaller-intermediate worker types. This condition may be understood as a product of daily raids which differ in magnitude according to the condition of the brood, in dependence upon the current brood capacity for chemotactic arousal of workers. A regulative factor is discernible here, in that if more colonies were present in an area than could raise successive broods on the available food, colonies failing in brood-production could not maintain nomad-statary function and would meet extinction.

In the dry season, environmental hazards evidently are at their peak for the year, and especially the chances of exposure to excessive heat and dehydration. Also, large numbers of workers must be lost through routine combat in raiding operations, as when invading the nests of other species of ants. Interestingly enough, few colonies are found with noticeably small worker populations, but populations typically are judged to fall within the characteristic species range,—ca. 60,000-120,000 workers in **E. hamatum.** On the whole, the regular

[1] The basic results of these two investigations are to be published in the Bulletin of the American Museum of Natural History, in 1949 and 1950.

production of worker broods evidently is adequate to compensate ordinary seasonal hazards tending to reduce the worker population.

Observations have shown how these ants meet environmental hazards characteristic of the dry season. For example in their raids, which are essentially daytime functions in the terrestrial species, the columns and masses tend to withdraw from bright and hot zones such as fallen-tree clearings or exposed hillsides, or to reduce their activities in such places, and probe most readily into darker and moister areas. Activities underground and beneath objects are more frequent than in the rainy season. Also, there is a noticeable prolongation of the "siesta" interval during midday hours, when raiding functions are greatly reduced as the workers react to over-stimulative environmental conditions (e.g., bright light, high temperctures) then prevalent by huddling beneath leaves, gathering in moist spots in the shade, or withdrawing into the bivouac. Notwithstanding this temporary reduction of raiding activities, colonies when nomadic evidently accomplish much the same total of raiding as in the rainy months judging from the observable magnitude of predatory activities through the day, and from general booty intake and results accomplished in producing successive broods.

The effectiveness with which colony functions are continued in the dry season is emphasized by the regularity with which nomadic movements (i.e., changes of bivouac) are carried out. Our evidence indicates that for a bivouac-change movement to occur, the raid of the day must reach a describable threshold,—e.g., in **E. hamatum** at least two trail-systems, as compared with the single system of statary-phase raids. In **hamatum** the rarity of a failure to carry out the movement both in the dry season and in the rainy season depends upon the fact that raids are sufficiently large to produce this occurrence in the nomadic phase. The point is essentially the same for **E. burchelli.** Of course, in colonies which had lost the functional queen or a considerable part of the larval brood, nomadism would be interrupted or terminated.

Because the onset of a nomadic phase is attributable to the excitatory effect exerted upon the colony by the emergence of a callow brood, its continuation to the stimulative effect of a further brood in the larval condition, and its termination to the attainment of maturation and enclosure (within cocoons) of this brood, the duration of this phase in different colonies of the species under different seasonal conditions is of great interest from an ecological standpoint. Since the

duration of nomadism depends upon the temporal relationship of two different broods, its constancy or variability must express the relative stability of conditions under which broods are produced and develop. From the available records,[1] in **E. hamatum** the nomadic phase typically is 17 days in duration, less frequently 16 and least often 18 days or longer. In **E. burchelli** this phase is shorter (ca. 13-14 days) and more variable. The existence of definite species norms in nomadic duration indicates that relatively stable conditions govern the production and development of broods in colonies of the species under study.

These conditions involve food supply, brood environment, and regularity of brood production in particular. We have found that throughout the year the tropical forest situation typically furnishes enough booty to maintain many colonies, and that Eciton raiding activities are effective for procuring it. Furthermore, the nomadic movements of the colonies serve to shift them regularly about in the forest, insuring new terrain for exploitation each day at the stage when colony capacity for food consumption is maximal. In an inevitable circular manner, the presence of an active, food-consuming brood insures an increased activity in the worker population, which in turn accounts for an increase in the colony food supply adequate to meet the current needs of the colony. The food supply of a colony thus fluctuates, not unpredictably, but in direct relation to the developmental status of its brood or broods. Some further adaptive consequences of this fact will be considered presently.

In the terrestrial species of Eciton the temporary nests or "bivouacs" of the nomadic phase typically are open masses formed of the clustered bodies of the workers themselves, hanging from some object to the ground (see figure 2). Although temporary, this bivouac is a true nest, since it houses the worker population and since within it the brood (or broods) and the queen are sheltered. In the nomadic phase, no establishment persists more than 24 hours as a rule, and each evening the colony transfers over a raiding trail of the day to a distant location where a new bivouac forms. A colony of **E. hamatum** in one nomadic phase generally establishes 15 different open bivouac clusters, with the successive locations between 150 and 350 meters distant from one another.

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[1] Schneirla, T. C. Bull. Amer. Mus. Nat. Hist. (in press), 1949.

Although the brood "incubator" is changed thus frequently, it must afford a very effective environment for the brood, from the consistent temporal relationships found for broods of many different colonies within a species. With the exception of the evening interval during which the larval brood is carried by workers over the route to

Fig. 2.—A nomadic bivouac cluster of a colony of **Eciton hamatum**, forming a cylinder approximately 40 cm. in D. (Vegetation has been cleared away for capture of the colony)

a new place, this brood remains within the bivouac mass. Once established, each new bivouac remains in place throughout the night, and during the following day when its walls and basic structure are maintained despite the absence of a large part of the worker population engaged in raiding. The bivouac is not a static, fixed structure, for two significant types of change occur during the day. First, during the morning as workers leave for the raid, the bivouac walls become increasingly porous and its bottom edge (next the ground) more or less undercut. Such changes may facilitate the ventilation of brood and queen in the bivouac interior, thereby making the bivouac wall

a variable insulator adjustable to outer conditions. Second, there occurs a limited shifting of the bivouac wall away from places in which excitatory conditions such as bright light or excessively high temperature may strike it persistently. Such disturbing conditions literally cause the bivouac wall to "melt away" as workers disengage themselves and shift position, and conditions remain in flux until the affected section of the bivouac has reassembled in a less disturbing situation. Through such plastic processes based upon the responses of workers to environmental conditions, the bivouac of the terrestrial army ant species becomes an exceedingly stable environment for colony, queen, and brood.

The most stable shelter of all is effective in the statary phase, when the same site is occupied for many days,—typically 20 days in **E. hamatum** and 21 in **burchelli.** Since this phase begins with the enclosure of a mature larval brood and ends with the emergence of the same brood from cocoons, it follows that the development of the enclosed brood must run a highly regular course from colony to colony within the species. The statary site into which colonies shift when their larval broods are mature and spinning cocoons almost always is **enclosed,** as contrasted with the **open** nomadic site in which the bivouac wall is the principal insulator. Within its physical "shell" (e.g., the hollow tree) in the statary phase, the colony —as our records show—has an environment in which both temperature and humidity fluctuate within much narrower limits than in the open nomadic bivouac situation.

What causes the abrupt shift into the sheltered statary bivouac site, after successive open sites have been occupied, is not clear, although the adaptive gains for the colony are evident. Since statary bivouac sites are found somewhat lower in temperature than the last sites of the nomadic phase, the shift may depend upon a changed thermotactic reactivity of the worker population to its environment. This change might appear rather quickly late in the nomadic phase, as a product of intra-bivouac temperatures elevated through the metabolism and activities of the nearly mature larvae. More definite is the fact that the enclosure of the mature larval brood is responsible for the colony **remaining** at the sheltered site. The stimulative effect of the brood upon workers falls greatly when the larvae become covered; then the vigor of daily raids drops sharply, below the threshold essential for nomadic movement, and remains relatively low for a considerable time until a further climactic brood change occurs.

Thus the colony is very effectively sheltered while the queen passes through physogastry and the critical process of egg-delivery..

In the terrestrial species of Eciton, a single queen in each colony produces the successive large broods which appear at regular intervals. Each mass of eggs is laid within a few days, always before the midpoint of a statary phase. The factors causing the queen to become gravid at this point in the cycle obviously are responsible for the regularity of brood-production, and also (indirectly) for the rhythmic changes in colony behavior. These factors may be 1) intrinsic to the queen, 2) basically extrinsic to the queen, and 3) both of these.

Because nothing is known at present of hormonal or other intraorganic processes underlying egg-production in the Eciton queen, the validity of factors '1' and '3' cannot be evaluated here. As for factor '2', at present there is no reason to believe that Eciton cycles are governed by periodic external events such as lunar cycles. Not only are the periods of lunar cycles and those of known Eciton cycles very different, but also the phases of different colonies show no significant coincidence, as though a general external control were involved.

There is, however, a possibility that certain events extrinsic to the queen but which arise in a regular and recurrent manner within the biological functions of a particular colony, may insure its rhythm. The nature of the causal pattern is suggested by the fact that although Eciton queens are found with fully contracted abdomens during most of the nomadic phase, indicating a resting condition in reproductive processes, queens are frequently found with somewhat enlarged gasters a few days before the phase ends. This is the time when, as various evidence shows, the nearly mature larval brood exerts its maximal stimulative effect on the colony and the daily raids consequently reach their peak. An unusual excess of food then is seen in the bivouacs, presumably leading to an increased feeding of the queen, thereby causing a recrudescence of her fat bodies and large-scale egg-production.

Such an over-feeding of the queen can be maintained even after the colony becomes statary, for although the larval brood is then considerably less stimulative to workers than before, it nevertheless continues to exert an appreciable excitatory effect (although at lower intensity) for a few days while spinning continues within cocoons. The brood is sufficiently active to stimulate the workers appreciably and increase the intensity of raiding somewhat, although

brood feeding has stopped; hence sufficient food remains available to support a continued over-feeding of the queen and maintain her progress toward full physogastry. If this theory is correct, the initiation of each further Eciton brood may be regarded as a circular (or "feed-back") process in that each large-scale maturation of eggs in the queen is set off by a nutritive condition arising indirectly through the maturation of the preceding brood. [1]

Our evidence shows that only all-worker broods are produced by Eciton colonies in the rainy season, also that the regular production of such broods continues throughout the year, with one exception in the dry months. Then, during the first half of the season, some but not all of the colonies produce one brood composed mainly of males but also containing a very few queen-form females. It is an interesting fact, and an important one, that the young queens are precocious with respect to the males, since they reach larval maturity, and later emerge from their cocoons, two or three days in advance of the males. No colony evidently has more than one sexual brood in a particular dry season, preceded and followed by all-worker broods. Evidently the sexual broods are produced somehow through the initial effective impact of dry-season conditions upon the Eciton colony queens, but each queen recovers from this effect after one exceptional brood has been delivered, for then only worker broods appear. Consistent with this view, seasonal and local differences are found in the frequency and timing of sexual broods, apparently in relation to the degree and the variability of dry weather once the dry season has begun.

A selective process evidently operates among the young queens as well as the males of a sexual brood. For example, signs of brood mortality (empty cocoons, suggesting cannibalism by workers) are found, particularly in the part of the bivouac in which the sexual brood is concentrated and the brood-free section in which the "old" colony queen is located. Although the colony remains unitary until the males emerge, indications of latent divisions of the worker popula-

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[1] The possibility that extrinsic factors initiate each regular brood-production episode in the Eciton queen is favored by evidence for the occurrence of an abortive physogastry during the last days of the statary phase and the first day or two in the following nomadic phase. This condition may result from the stimulation of colony raiding through reflex activities of the nearly mature pupal brood, accounting for a temporary food surplus and possible over-feeding of the queen. This situation evidently disappears when the callow brood appears and promptly makes great inroads on the colony food supply.

tion appear, evidently resulting from differential chemotactic attraction of workers to the sexual brood and to the "old" queen. For example, when a worker brood is present, the functional queen **invariably** is reaccepted very readily when she is returned to the bivouac after a test removal; however, a functional queen removed when her colony had a sexual brood nearing the mature larval stage was rejected, with conflict among workers, when she was returned. Evidences of conflicting affiliations among the workers of a colony when a sexual brood is present are valid clues to events underlying an eventual colony division. Brood cannibalism by workers evidently occurs upon this basis.

By the time the young queens are mature, their number has dropped (from more than two dozen as mature larvae) to about six, as against some 2000 males in the brood in **E. hamatum** and 3000 in **burchelli.** The selective process previously in evidence reaches a climax when the queens emerge from cocoons. They appear within two or three days before the males. This affords time for a virtual completion of the queen-selection process (through differential responses of workers to the callow queens) before emergence of the males enforces nomadism and fission of the colony. Worker reactions to the young queens vary from an uncomplicated attraction to and clustering about some of them (those first to appear?) to a partial acceptance combined with nipping and holding in place, a more or less "inimical" response, to others. Worker aggregations formed about the leading queens in this gradient are first to separate from the parent bivouac (although before actual division they remain in small clusters close to and connected with it),—whereas for the other young queens this process is incomplete and variously complicated by "negative" worker reactions.

The eventual colony division is a separation into two sections which move divergently from the statary bivouac site on different raiding trails,— one daughter colony containing the "leading" member of the hierarchy of callow queens, the other the "old" functional queen of the parent colony.[1] Through the "negative" reactions of workers, the other young queens are "sealed off" from the movement and are finally abandoned.

Two highly adaptive features may be discerned in this process of queen selection. In addition to an inevitable gametic selection, the

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[1] Although it is probable that under appropriate conditions the functional queen of the parent colony (e. g., when elderly) is superseded by a callow queen at colony division, this event has yet to be observed.

process operates against a division of the colony into more than two parts. Were this not effective, one or more of the daughter colonies would risk extinction. For although the emergence of the males initiates a divergent movement of colony sections and sets off nomadism, the continued energizing of nomadic function depends upon a stimulative effect from the new brood of worker larvae. This further brood, produced as eggs by the "old" queen during the previous statary phase, is divided between the daughter colonies at the time of colony fission. Ordinarily, even with no more than a two-way division of colony and brood, a "nomadic weakness" may persist in the daughter colonies until the half-brood of each has reached a fairly advanced stage of development and exerts a greater stimulative effect. If a multilateral division were to occur, from the writer's theory a failure of nomadism might be expected, preventing further brood production in the queen (or its beginning in the young queen), and the colony would degenerate in the absence of a capacity for nomad-statary function.

Many other highly adaptive processes are discernible in Eciton life. For example, while hundreds of alate males are flying off nightly from the daughter Eciton colonies after division has occurred, these colonies are operating nomadically, thereby insuring a maximal distribution of their stocks of males. Circumstances indicate that cross-breeding is predominant among the Ecitons, and that for mating to occur the male must make his way, first by a flight and then (when dealate) by following Eciton ground trails, to a strange bivouac. Because of the many hazards involved, few males survive for eventual mating with the apterous females of other colonies. Thus, although males are greatly preponderant in the Eciton sexual broods, selectivity may be relatively higher among them than among the young queens.

Finally, we may mention a process which promotes the conservation of workers. Ordinarily, functional colonies do not mix, but repel one another when their paths happen to cross. However, after a colony has lost its queen, its worker population may fuse with that of another colony of the species provided their trails intersect. This interesting occurrence, based upon the intricacies of Eciton chemotactic processes, conserves worker populations which, lacking a queen, would otherwise perish through failure of nomad-statary operations.

To summarize, we have discussed some of the chief aspects of the behavior and biology of the terrestrial Eciton species from the standpoint of species survival. The events are precisely adaptive in

that they meet effectively the typical situations and hazards of the tropical-forest environment, in both seasons of year. The main processes in the system are: forming the "bivouacs" or temporary nests, the prolific and regular reproductive functioning of the queen, the routine production of successive great all-worker broods throughout the year and the production of the unique sexual brood in the dry season, the execution of booty-capturing raids in dependence upon the condition of developing broods, and the periodic resumption of regular nomadic movements.

These events form a system in which they are closely interrelated. The system, which is adequately described in terms of the "nomad-statary cycle," is circular and self-maintaining in the sense that a given process in it (e.g., production of a new brood by the queen) leads inevitably to further processes (e.g., presence of a larval brood, excitatory to the worker population) insuring its recurrence. In the tropical forest setting we find the Eciton pattern highly successful both in its self-regulatory properties and in its adequate interrelationship with the conditions of the environment.