Raiding and Other Outstanding Phenomena in the Behavior of Army Ants

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RAIDING AND OTHER OUTSTANDING PHENOMENA IN THE
BEHAVIOR OF ARMY ANTS

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Ants of the genus Eciton are characterized by their raiding expeditions, and by their temporary colony clusters or "bivouacs." In the matter of raiding, species in which the advance is formed by a large mass of ants may be termed the "swarm raiders," since their behavior is to be broadly distinguished from that of other species, the "column raiders," in which the raiding is marked by relatively small advance groups that head narrow columns.

The behavior of Eicton hamatum, the type species of the genus and a representative column raiding species, has been described. In the raiding of this species a small group of ants, the "pushing party," heads the advance into new territory. The membership of a pushing party constantly changes, due to the fact that each newcomer first meanders excitedly forward, and leaves the group shortly after having made a few hesitant advances. As the ants move forward in this relay manner, the direction of progress is partly determined by the momentum of newcomers and partly by topographical features which (1) furnish guiding tactual stimuli (e.g., a course along the top of a log), or which (2) may split the pushing party, the result being a division of the group (e.g., some of the ants follow the edge of a buttressed root while the others turn to one side of the root).

Behind the advance group, ants move in a narrow column which follows a route first chemically saturated by the excited members of the pushing party. When the ants are very active in raiding, and the advance group is wider than the usual few centimeters, the frequent division of this body gives rise to numerous branching and anastomosing trails. In time, and as the supply of booty is depleted in a given area, the ants desert most of the trails there, and usually they continue to follow one trail that leads into a new raiding zone further on. In this manner the typical fan-shaped complex of moving ant columns is moved forward, and there remains behind a constantly lengthening serpentine route which is closely followed by ants passing up to enter the advanced raiding zone or returning booty-laden toward the bivouac. After a period of active raiding the E. hamatum colony will have formed one system or more of the type sketched in figure 1. The part played by tactual sensitivity in the matter has been suggested, and the chemical factor is of basic importance in the formation, the following and the extinction of trails. For instance, ants passing outward on the principal trail are able to respond to chemical differences that exist
between alternative routes at encountered trail junctions. One observes that newcomers turn onto a branch trail in numbers directly after the first booty-carriers have surged across the junction in passing toward the colony site.

*Eciton vagans* conducts similar raids from the colony bivouac site, which in that species is located beneath the surface of the ground. Although the consolidation columns that connect the raiding front with the bivouac mainly follow a subterranean course, the advanced part of the raid forms on the surface a system of branches and anastomosing columns very similar to that of *E. hamatum*. Also, the behavior of ants in the pushing parties does not differ greatly in the two species. The *E. vagans* raiders emerge upon the surface (e.g., from a crack in the ground or from some insect's tunnel), and if amounts of booty are found the raiding front is extended as in *E. hamatum* forays, with the disappearance of branch trails occurring in much the same manner. If little booty is taken, the ants withdraw along their principal trail into the ground, and may soon emerge at a point some meters removed to repeat the process there.

The Swarm Raiders.—*Eciton burchelli*, although similar in appearance to *E. hamatum*, is a much more excitable and belligerent ant, and its spectacular forays involve masses of raiders that clear insect life rather completely from terrain over which they pass. In early morning the aroused workers spread out over the ground, and as the numbers increase the ants gradually cease to mill about and begin to move away from the colony site. The principal direction of progress is influenced by the manner in which newcomers pass into the body, and also by the general topography. As the forming swarm moves forward it occupies a wider front, and a meter or two in the rear the ants are so reduced in numbers that they form anastomosing columns on which the raiders scurry about erratically at first. The columns of this network (Fig. 2), left behind as the raiding front is advanced, become more distinctly formed in time, and their number is reduced. The result is that a few meters behind the raiding swarm the "consolidation system" dwindles into a single surviving column. The "consolidation trail," which is followed by ants that run between raiding front and bivouac, is a characteristic feature of all *Eciton* raids. Its development from the original raiding complex depends mainly upon the traffic in different parts of the raiding system and especially upon what quantities of booty are carried back through this or that part of the consolidation system, as well as upon the accessibility of alternative routes and the ease with which they may be followed by the ants.

The raiding of *E. burchelli* often involves swarmers more than five meters in width. Larger bodies are likely to divide into two raiding systems; but rarely are more than two systems formed. The ants on the front and flanks of the swarm usually advance rather irregularly, especially when
passing through dense vegetation; and loose wide columns frequently push out from the main body. The ants on such columns advance rapidly and “draw” more raiders after them—a phenomenon based upon tactual sensi-

**Figure 1**

Figure 1. One raiding system of a nomad *Eciton hamatum* colony, two hours after the beginning of the foray. “A,” the beginning of one system of trails; “B,” the bivouac cluster beneath a log; “C,” the point at which the second system of trails begins to branch from its consolidation trail.

**Figure 2**

Figure 2. The raiding system of a statary *Eciton burchelli* colony, three hours after the beginning of the foray. “A” marks the right flank of the raiding swarm, in which the ants are closely concentrated at present; “B” marks the left flank, in the course of a “wheeling” movement; “C,” marks the consolidation column, which connects the raiding front with the bivouac, at “D.”

Typically, the advance of the swarm involves alternate wheeling (“flank-
ing") movements; e.g., as the body swings toward the right, (1) the left flank rapidly spreads forward and is "drawn" inward and somewhat to the right, since (2) the right flank is greatly concentrated at the time and serves as pivot (see Fig. 2). Then the right flank spreads rapidly forward, while the left flank of the swarm slows in its progress and soon becomes concentrated in its turn. This alternate flanking movement of the raiding swarm is mainly responsible for the meandering course that is taken by the eventual consolidation trail. The phenomenon occurs principally as a result of the manner in which contact among individuals limits and directionizes the spreading of a mass of eccentrically running workers over an area; but the process is complicated by other factors as well, and varies greatly at times.4

Eciton praedator likewise is a "swarm raider." Colonies of this species bivouac in subterranean places, but the pattern of raiding behavior is very similar to that of E. burchelli. From the place of emergence a mass of the small ants, often more than three meters in width, advances on the surface in the meandering manner described above, but the advance varies more frequently in its general direction. The swarm of small ants leaves behind it an anastomosis of wide and loosely formed columns which converges into a few consolidation columns in which the ants pass beneath leaves to points in the rear. As in E. burchelli raids, here and there behind the mass there remains a concentration of ants engaged in "mopping up," busily capturing booty that escaped the principal swarm.

The Bivouac-Change.—As is well known, the Eciton colony makes its nest by gathering into a cluster, and the site of this "bivouac" changes from time to time. In E. hamatum and E. burchelli colonies one may ascertain two conditions of general activity, which alternate according to the condition of the brood.5 The colony remains bivouacked in a given place, in the "statary condition," first when the eggs are present and during the period that precedes the development of the eggs into food-consuming larvae, and secondly during the period of about three weeks when the young are enclosed in cocoons. In contrast, the colony removes to a new bivouac site each evening (is in the "nomad condition") during the time the larvae are naked and are consuming food, and again, after the brood has been hatched.

Colonies in the statary condition are less active, and raid much less vigorously than when in the nomad condition. To illustrate the difference, the raiding swarm of a nomad E. burchelli colony usually divides into separate masses, while that of the statary colony rarely does so; the nomad E. hamatum colony usually forms two or three separate raiding systems during its forays, while the statary colony forms but one system (Fig. 1) and on occasional days does not raid at all.

Eciton raids typically show two peaks of activity, one during the morning and the other during the afternoon. These bursts of activity appear to be
related to meteorological changes, as does the first arousal of raiding early in the morning. In nomad *E. hamatum* colonies the second high point in activity precedes a general movement of the colony which begins later in the afternoon and is completed during the first half of the night, as a rule. If three raiding systems have been formed during the day, with three corresponding principal trails leading from the bivouac, the ants respond increasingly to that route on which the most booty is being carried back, and smaller numbers venture forth on the other trails as time goes on. At length, the streaming outward of greater numbers of ants on the eventual bivouac-change route makes difficult the return of booty-carriers on this trail from the advanced raiding front, and these ants are virtually forced to deposit their burdens in piles that form near the places of greatest confusion—i.e., at trail junctions. Consequently, late in the afternoon the raiders are observed mainly returning to the bivouac on the other raiding systems, while on the "popular" system cachés of booty are forming at trail junctions in the advanced raiding area, and few ants succeed in carrying their burdens back to the bivouac. The outward-streaming column of ants at first stimulates raiding by giving it new recruits, but later interferes with it mainly by virtue of the fact that the direction in which ants turn at trail junctions is more and more completely determined by the pressure of the general movement. Usually, in the case of *E. hamatum*, the new bivouac cluster is located between 100–200 meters from the previous site. The *E. burchelli* movement typically gets under way much later in the day, and often follows the principal route of a raiding system established during the afternoon peak of activity.

Other Colony Activities.—The social life of the ants in and about the relatively thin-walled bivouac cluster presents an intriguing problem. Beebe, for instance, has described the manner in which the *E. burchelli* colony behaves at the time the larvae spin their cocoons.6 An equally interesting event is the opening of cocoons when the pupae are mature. Judging from experiments, it is rarely that an *E. burchelli* or *E. hamatum* callow escapes unassisted from its case. Rather, the adults respond to the movements of the enclosed individual, pick it up from among the cocoons heaped within wall pockets of the cluster, and carry this cocoon to the outside of the wall. At first ants catch hold of the ends of the cocoon, but as other workers are excited by the stir and join the group a tear is started sooner or later in the middle of the case by some worker's mandibles (and possibly by the tarsal hooks of the enclosed moving callow), and the case is eventually ripped open as this tear is enlarged. The enclosed individual struggles out as the workers lick and tug upon her body, and is soon carried into the interior of the cluster, while the empty case falls to the ground.

The opening of cocoons usually requires from two to four days, since the pupae differ somewhat in the time at which they attain maturity. The
larger workers and majors stir before the smaller workers do, in these two species at least, and are therefore removed from their cases before many of the minors begin to darken and to move within their cocoons.

The number of individuals in the Eciton brood is large. In a captured *E. hamatum* colony of about 30,000 workers, there were counted 32,479 cocoons. However, *Eciton* colonies cannot increase indefinitely in size, since at cocoon-opening time, after many new individuals have emerged, a portion of the colony moves from the statary site along a raiding route and forms an independent colony. This would suggest a rapid increase in the number of colonies, and indeed army ant colonies are plentiful; but prolific reproduction is probably compensated by decimation of numbers and possibly by extinction of entire colonies during the dry season.

1 The National Research Council, through its Committee on Grants-in-Aid, has supported an investigation of *Eciton* behavior, carried out during the summers of 1932 and 1933 on Barro Colorado Island in the Canal Zone. The first portion of the work has been reported in the *Jour. Comp. Psychol.*, April (1933).


3 These raids have been described by different writers, notably by Bates (Bates, H., 1863, *The Naturalist on the River Amazons*) and by Belt (Belt, T., 1874, *The Naturalist in Nicaragua*). Any ground or lower tree animal life that is accessible or that cannot escape is torn into pieces and carried back to the colony bivouac. Scorpions and tarantulas are frequently captured, but the only vertebrate that I have seen killed was a small Coral snake that happened to be resting in a cul-de-sac under a tree root. Not infrequently, lizards dart in and out among the masses of ants, snatching up insects flushed out by the Ecitons, as do the Ant Birds from their perches near the ground. The Ant Birds attend the swarm raids almost exclusively, since the manner in which the column raiders cover territory limits their booty largely to the larvae and pupae of insects. To capture such an object from the ant holding it would necessitate swallowing both morsel and *Eciton* carrier, and these birds seldom eat army ants.

4 A detailed report on this and related matters in the behavior of representative *Eciton* species is to be published during the latter part of the present year.

5 W. Müller (Kosmos, 1886), from his study of an *Eciton burchelli* colony, was first to suggest the possibility of a relationship between the food-consuming ability of the *Eciton* colony, as affected by the presence of active larvae, and the general activity of the group.


7 Wheeler (op. cit., note 2) found two "...evidently recently emerged females" in an *E. burchelli* colony he examined during the latter part of the rainy season in British Guiana, and suggested that new *Eciton* colonies may be formed through the fission of older colonies. The division which I have observed to take place in *E. hamatum* and *E. burchelli* colonies on a number of occasions during the first two months of the Panama rainy season indicates that such is the case. These instances of fission must have been based upon females of the previous season, since it is a notable fact that no queen or male forms were found among the brood of several colonies examined during the months of June and July.