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## A UNIQUE CASE OF CIRCULAR MILLING IN ANTS, CONSIDERED IN RELATION TO TRAIL FOLLOWING AND THE GENERAL PROBLEM OF ORIENTATION<sup>1</sup>

By T. C. SCHNEIRLA<sup>2</sup>

Were insects unable to make and to follow trails, the problems of Victory gardeners, farmers, economic entomologists, and housewives would be considerably reduced. For in almost every insect order from roaches to the social insects there are at least a few species that reach

or return to a food supply, food plants, home quarters, or other places by virtue of their ability to make and to follow trails. It is clear that an understanding of trail making and trail using is desirable for both theoretical and very practical reasons.

### COLLECTIVE FORAGING AND CHEMICAL TRAILS

There are many different forms of trail-ing in insects, from the type of trail that is followed in a relatively rigid, stereotyped manner to routes that are used in a complicated, delicately varying manner, often by a single individual alone. Among the ants, the simplest kind is the collective trail. On such trails the workers of a given ant colony are able to reach a food place in large numbers, with a minimum of delay and difficulty once the "track" is established. In this paper we shall be concerned with collective trails in particular.

One of the least complicated ways in which such a trail may be set up was demonstrated by Eidmann (1927), using a *Myrmica* colony in a laboratory nest. With a new paper floor in place, one individual was permitted to find sugar water in a distant compartment of the nest, and feed upon it. Shortly after the finder had returned to the home compartment, a number of ants was observed to cross the floor of the intervening compartment toward the food place, taking the same route the finder had used in returning, even in its detailed turnings. The simplest

explanation was that the newcomers were following a chemical trail left incidentally by the first ant. Confirmation of this interpretation was found in a further test when a clean floor was substituted for the used one after the finder ant had crossed from the food to the home base. Then other ants came out as before, evidently aroused by the returned food carrier, but this time they were quite unable to follow her path, instead wandering about and reaching the food only by chance.

Other studies throw light on how such trails are made. In work with a *Tapinoma* species, Santschi (1911, 1930) noticed that in returning from the food the first finder rubbed her gaster against the floor, evidently an outcome of her excitement which resulted in a trail of some kind. Inspecting the ground in her wake with a hand lens, Santschi actually saw tiny droplets in the line she had taken, suggesting to him that the products of the ant's anal gland had been deposited when the gaster was rubbed against the floor. Although he thought this was a "deliberate" procedure on the part of the finder, a preferable interpretation is that the lowering of the gaster and opening of the anal-gland orifice occurred merely as incidental

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<sup>1</sup> A contribution of the Department of Animal Behavior, the American Museum of Natural History.

<sup>2</sup> The American Museum of Natural History and New York University.

(i.e., as direct reflex) parts of the ant's general excitement, no more intentional than the release of sweat from the skin glands of an excited human individual. Similarly, v. Frisch and Rösch (1926) have shown that when a honeybee finds a new food place, in her excitement the products of the "scent glands" are released, greatly increasing the chance that other bees will find the place.

The present writer has observed that the findings of Eidmann and Santschi may be applied directly to the case of the small imported ant, the reddish yellow myrmecine *Monomorium pharaonis*, a common kitchen nuisance which displays a singular

ability to establish collective trails to new food places. A *pharaonis* worker, upon leaving a place where she has imbibed or picked up food, generally lowers her gaster so that its tip rubs against the substratum as she moves, thereby leaving chemical traces on the return path which newcomers are observed to follow, usually with relative ease. As a result this tiny ant, wandering individually over relatively large distances around the nest, appears with surprising quickness in considerable numbers at any newly discovered source of food. This characteristic undoubtedly has greatly assisted the almost unmatched distribution of the species.

#### CHEMICAL TRAILS IN THE RAIDS OF ARMY ANTS

A strikingly different mode of establishing collective routes is found in the *Eciton* species, the army or legionary ants of subtropical and tropical America. Few ants follow their trails in a more slavish and stereotyped manner than do the *Ecitons*. For example, the raiding columns of *E. hamatum*, the golden yellow terrestrial pillager, excel in the rapidity with which new offshot columns are formed over unraided ground (Schneirla, 1938). If the routes which spring up and survive longest during a day of raiding are mapped in detail, the result is a tree-like figure. The trunk line of this trail system leads from the bivouac or home site, with more and more frequent branching as the distance from the bivouac increases. At the very twig end of the system, usually as much as 150-200 meters from headquarters at the end of a given day, the newest trails grow outward into unraided ground from which insect booty is snatched. Each twig column ends in a relatively small group of ants, a few dozen of them in an area usually not more than 25 cm. wide, behaving in a rather peculiar manner as they push onward. Hugging close to the ground with her antennae fitting close to its surface in quick spasms of wasp-like vibratory movement, each newcomer to the group meanders forward hesitantly a few centimeters over fresh terrain, then

quickly turns and rejoins the base column. In this way the trails are extended onward, by a relay process in which no given ant or ants have the "lead" for very long but with many ants participating successively in the trail-blazing process.

*Eciton* trails frequently follow vines, the top edges of tree roots, the worn indentations of peccary trails, and other topographical features along which the ants move readily in antennal contact with a surface. However, a given trail persists and is followed by further ants because it is marked chemically, first of all by the pioneer ants (presumably with their glandular products) as they move excitedly forward, each contributing a limited extension of the track into new terrain. Experience with a given route is not necessary in the *Ecitons*. Any member of the colony can readily follow the trails of each part of the raiding system without having passed over the particular route previously. Thus in special tests, when workers are removed from the bivouac and placed beside any trail of the day, they readily enter and run along the route, whether or not other ants are traveling upon it at the time. Or if *Ecitons* are held captive overnight when the colony moves to a new locality, they are able to follow any fresh trail of the next day when they chance upon it after being released. The chemical traces

evidently remain in existence for some time, despite repeated washing of the ground by heavy rains. This is shown by the fact that when colonies remain in the same bivouac location for as long as three weeks, a periodic occurrence in the terrestrial foragers at least, a long section of trail may drop out of use for two or more days after it is originally formed, then reappear in use as part of a new raiding system.

Evidence for a chemical similarity in the trails of different colonies of the same species is offered by the ability of Ecitons to run a trail of another colony to whose zone they are transferred; however, a certain chemical difference is indicated by a noticeably more hesitant progress than when on trails of their own colony. When a transferred ant encounters foragers of the strange colony she is attacked repeatedly and finally killed unless she flees the trail. Such facts, together with the results of nestmate-recognition

tests in which the distinctive influence of "colony odor" has been demonstrated (Fielde, 1902; Morley, 1942), indicate that ants of different colonies of the same species vary in their immediate effluvia, as well as in the chemical nature of the routes they make. Furthermore, since preliminary tests indicate that an Eciton worker is able to follow the trail of another species (e.g., transported *E. hamatum* workers push hesitantly along a section of *E. burchelli* trail to which they have been transported), a chemical similarity is suggested for the routes of closely related army ant species.<sup>1</sup>

The basis of trail-following thus would appear to rest on the tendency to approach sources of the ant's own colony chemical or similar chemical patterns, and thus to move forward according to the line of this chemical when on trails. What accounts for the ability of the individual worker to respond in this highly adaptive manner?

#### THE ONTOGENETIC BASIS OF TRAIL FOLLOWING IN ARMY ANTS

In the case of the Ecitons it seems improbable that the mere possession of olfactory sensitivity brings with it this capacity for trail following. After hatching, trail following requires a few days to appear, and circumstances do not justify attributing the delay to maturation, i.e., simply to an improved sensitivity based upon further growth of the olfactory tissues themselves. The fact that the callows are able to run long distances when participating in the nightly bivouac-change movements militates against the possibility that it is merely muscular weakness which holds them back in the daytime. The possibility that the irritating effect of light may restrain them at first should be kept in mind; yet circumstances oppose this as the main factor. Normally, *E. hamatum* workers become fairly able trail followers after four or five days from hatching; however, the results of some preliminary tests suggest that being with the colony is essential for the improvement. After *hamatum* pupae had been kept away from the colony for a period of five days following hatching, when placed individually on the raiding trails they seemed helpless and inept in contrast to others of

the same brood that had lived with the colony after hatching.

Normally, for some time after a new brood of mature pupae is removed from its cocoons by adult workers, these callows (light-colored and readily distinguished from regular workers) remain in the bivouac without venturing upon the raiding trails to any extent. Then, after a day or two, they begin to appear on trails in the daytime, and are observed in progressively increasing numbers at points farther from the bivouac. There is also a noticeable change in their behavior during this period. Upon the trails they move slowly and hesitantly at first, unable to move rapidly or to go very far in a given direction without stopping. Repeatedly bumped and shunted about by the regulars, they generally pass along at the sides of the column for limited distances, readily drifting into groups at trail-division points. Gradually their deficiency seems to decrease, until after a few days when

<sup>1</sup> Almost a virgin field awaits investigation in the biochemistry of trail secretions in insects, and particularly ants. To the writer's knowledge, the only study of Eciton chemical is the work of Melander and Brues (1906). These investigators found no traces of formic acid in whole body distillates of various *Eciton* (*Acamatus* = *Neiomyrmex*) species of the southern United States. However, the outcome of further tests suggested that the basic substance probably is leucin.

deepening pigmentation has made their external appearance difficult to distinguish from that of regular workers, their trail running likewise is close to the general standard.

In view of this evidence suggesting the importance of experience, the preferable hypothesis seems to be one centering around the postulation of a rudimentary learning process of the "habituation" type in which there develops an increased readiness to approach the colony chemical. In the colony, this chemical dominates environmental stimulation from the time of hatching; whether resting or feeding in the bivouac the callow is stimulated by it, as indeed she was stimulated during her active larval period. Thus it is very possible that through a simple conditioning process, perhaps begun during the larval period, the callow moves about readily in the presence of this chemical and, more important, turns toward increases in its concentration.<sup>1</sup> Gradually, as she moves about more freely, the new worker drifts into the trails in responding to the Eciton chemical and to the movements of departing foragers. Early bivouac life thus may lead directly into trail running, with the initial hesitancy of the callow decreasing as she becomes better trained to run freely forward in the presence of the colony chemical. This hypothesis is consistent with a theory for social insects in general which takes into account not only the original equipment and physiological maturation of the individual, but also the importance of early environment and early activities for the development of social reaction patterns (e.g., Wheeler, 1928a; Maier and Schneirla, 1935, chap. 7).

One feature of early life which must hasten the *Eciton* trail-habituation process considerably is participation in the bivouac-change movement of the colony. Regularly, when a new brood hatches, the *E. hamatum* colony shifts to a new bivouac site at the end of each day (Schneirla, 1938). At first the callows do not readily

join the drift of workers from the cluster; rather they leave the interior of the bivouac passively when shunted along with outgoing groups of workers, and huddle near the exit until incidentally absorbed into the exodus. Much confusion results from the tendency of callows to hesitate, waver, and turn around when brushed or bumped by foragers returning to the bivouac. By degrees the callows are absorbed into the outgoing movement, until after a few hours they drain from the bivouac in a steady stream, moving along in a thick column with few interruptions. During the early post-hatching period callows are seen in numbers outside the bivouac only when they join bivouac-change movements; then they are able to progress in a regular manner only when conditions in the column afford an environment of uniform chemo-tactual stimulation promoting continuous movement in one direction. Running the trail under these "hand-fed" conditions would seem to contribute fundamentally to an ability to make progress in the daytime, developing as foragers under shifting tactual conditions by responding to the chemical trail itself.

The Eciton bivouac-change movement sharpens our view of army-ant progress in columns as a routine stereotyped following of chemical lines. The view is quite defensible, since under any conditions the ants are oriented mainly by the chemical path, and only secondarily by other factors. Through visual stimulation, for example, they are aroused in the morning (Schneirla, 1940) and are caused to shift their bivouacs away from bright light, yet appropriate tests on their foraging and other column activities give no evidence that visual factors are involved in orientation. On the other hand, the prevalent importance of an olfactory basis is readily demonstrated by simple tests of the "Finger-versuch" type (see Brun, 1914). Rubbing a finger across a trail causes a serious interruption, with the ants assembling on each side of the violated zone, unable to cross until the gap has been passed by some of them in a manner resembling the pioneer process of trail mak-

<sup>1</sup> Thorpe's researches (1939) with the ichneumon fly in particular have led him to adopt a theory based upon the postulation of a chemically dominated conditioning process governing the response of predatory adults to given prey upon which the individual has fed as a larva.

ing. When a portion of trail on a leaf is moved laterally so that each end is a few inches from its former position, there is an interruption which eventuates in activities similar to initial trail making, with the difference that the displaced section may become part of the trail bridge if the pioneers chance to reach it. Such tests show that a chemical trail is an indispensable basis for the route. However, considerable liberties may be taken with sections of trail on movable objects, as long as the ends join the main trail somehow. In one frequently repeated test, a trail section on a

long slender limb was quickly turned end for end, so that the east end touched the place formerly occupied by the west end, and vice versa. After a brief commotion caused by the lifting itself, traffic soon resumed without much difficulty. Since relatively long sections of trail may be thus reversed without blocking the ants, the Eciton path appears to be a simple homogeneous chemical track, not polarized chemically as are the trails of many other collective foragers under given conditions (e.g., *Lasius* species, Brun, 1914).

## CIRCULAR COLUMNS AND STEREOTYPY IN TRAIL FOLLOWING

### CIRCULAR TRAILS IN PROCESSIONARY CATERPILLARS

The psychological limitations of insects engaging in this type of trail orientation are suggested strikingly when the insects form and continue to follow circular trails. In volume 6 of his "Souvenirs entomologiques," Fabre reported an interesting case of this type observed in 1896, perhaps the first scientific record of the phenomenon for any animal.<sup>1</sup> Some processionary caterpillars (*Cnethocampa pityocampa*) he had hatched were seen to form a column around the upper rim of a large vase in a circular path 1.35 meters in circumference. Fabre hastened to assist the retention of this column by brushing away all threads remaining on the sides of the vase after the larvae had mounted, and by removing all excess late comers which might have swollen the column beyond the limits of space on the rim. Once started on the endless trail, the caterpillars circled in this path for seven days, moving more or less continuously except for halts caused by low temperatures during the nights. These

and many other lepidopterous larvae of similar behavior ordinarily follow one another in winding columns by virtue of contact with a thread or threads spun by those first to pass over the ground. In the processions formed by the caterpillars of the American buck moth *Hemilenca maia*, Marshall (1904) found that removing the leading individual usually served to halt the whole line in place for some time, until the "leader" was returned or until some other larvae chanced to proceed. This suggests that in this species only the first individual or the first few to pass along are actively involved in spinning, while the others merely follow the trail. Contact with the thread is not the sole factor in following the path, since when Marshall removed a portion of thread between neighboring caterpillars in the body of the procession those behind were not stopped. However, rubbing across the path with a moistened finger in addition to removing the thread brought those following to a halt, with a delay of a few minutes before the gap could be crossed. Evidently, in the buck moth at least, the trail is followed chemically as well as tactually.

<sup>1</sup> A similar case of persistent circling in a *Cnethocampa* species was reported by Dubois in 1899, with a brief discussion of the track itself. There is no evidence to indicate that Dubois did not discover the phenomenon independently.

WHEELER'S LABORATORY CASE IN *Eciton schmitti*

That Ecitons may form circular processions of a kind very similar to that observed by Fabre in lepidopterous larvae was first reported by Wheeler (1910), with the following description of the behavior.

In captivity Ecitons are remarkably restless, at least at certain times during the day. Part of a fine colony of *E. schmitti* which I kept some years ago, exhibited this restlessness in a striking and ludicrous manner. The colony was at first confined in a tall glass jar on a square board surrounded by a water moat. The ants kept going up and down the inside of the jar in files for many hours. Finally I removed the lid. The file at once advanced over the rim and descended on the outer surface till it reached the circular base of the jar where it turned to the left at a right angle and proceeded completely around the base till it met the column at the turning point. To my surprise it kept right on over the same circumference which

was long enough to accommodate all the individuals. They continued going round and round the circular base of the jar, following one another like so many sheep, without the slightest inkling that they were perpetually traversing the same path. They behaved exactly as they do on one of their predatory expeditions. They kept up this gyration for forty-six hours before the column broke and spread over the board to the water's edge and clustered in the manner so characteristic of this and the allied species (*E. opacithorax*, *sumichrasti*, etc.). I have never seen a more astonishing exhibition of the limitations of instinct. For nearly two whole days these blind creatures, so dependent on the contact-odor sense of their antennae, kept palpating their uniformly smooth, odoriferous trail and the advancing bodies of the ants immediately preceding them, without perceiving that they were making no progress but only wasting their energies, till the spell was finally broken by some more venturesome members of the colony (Wheeler, 1910, p. 265).

## A CASE OF ECITON MILLING IN THE OPEN

Although I had observed in detail many raids of the Central American species of *Eciton* and had frequently set up circular-trail formations with these ants in the laboratory, under natural conditions nothing but short-lived or ambiguous instances of circular-column behavior appeared until September 4, 1936, when a striking case was discovered in the laboratory clearing at Barro Colorado Island, Canal Zone. On the preceding day a swarm of the small black *E. praedator* had worked its way from the north up the laboratory hill, crossed the grounds near the cookhouse, and after passing near the west corner of Haskins Memorial Library finally dwindled out toward dusk in the general vicinity of the Chapman cottage. At 7:30 A.M. on September 4, Rosa, the laboratory cook, excitedly called my attention to an occurrence which beyond doubt was a sequel to the foregoing raid. There follows a summary of my notes.

At about 7:30 A.M. a singular milling group of *Eciton praedator* workers is discovered on the cement walk in front of the Haskins Library (fig. 1). There are several hundred of them, mainly intermediates and large minor workers, the size classes most frequent in raids. Most of them are running in a circular column which moves counterclockwise, rotating about a small

circular cluster of ants huddled in the center. Although at this time the ring varies in width around its circumference and at intervals moves rather eccentrically, these measurements are fairly consistent for the period 7:30 A.M. to 8:15 A.M.: outside diameter of the ring, 10–11.5 cm.; width of the ring, 4–5 cm.; diameter of central cluster, 1–2 cm. The outer margin of the ring is somewhat irregular, due to the frequent straying of a few ants or a ragged file of them tangentially in the direction of rotation. Usually such deviates continue moving with the column, though more slowly, and soon rejoin the principal throng. Less frequently some of them lose contact with the column, then rest in place or move about hesitantly for a time, at length blundering back where they are swept into the main activity once more. If an ant chances to set off in the clockwise direction when she reenters the rotation, her movement is soon reversed in the course of a series of contacts and head-on collisions in the throng.

The column does not move strictly as a unit, but at times it behaves as though two or more individual rings of ants were moving more or less independently around a common center. Although ants in files near the periphery are moving faster than those near the center, the first impression that the inner files usually complete their revolution sooner than the outermost ones is readily confirmed. Apparently as a consequence of this difference in speed, there are observable indications of friction between adjacent parts of the procession, with here and there a file in the column deviating somewhat from its concentric course as contact with ants

moving beside it at a different rate causes some of the ants to stray. Jagged irregular gaps appear intermittently between bands in the circular column when one concentric part draws briefly away from a neighboring section. Such behavior, occurring at intervals in the general movement, may contribute to a general eccentric wobbling that characterizes the movement. The deviations of sub-groups are sel-

rival to the main action. At 8:15 when I must leave for forest observations (at the time considered more important) the central cluster of huddled ants, at first piled two or three deep, is visibly dissolving into the movement. The size of the cluster plainly decreases as more and more of the quiescent ants are stirred into action through repeated brushing of the hurrying throng against them.

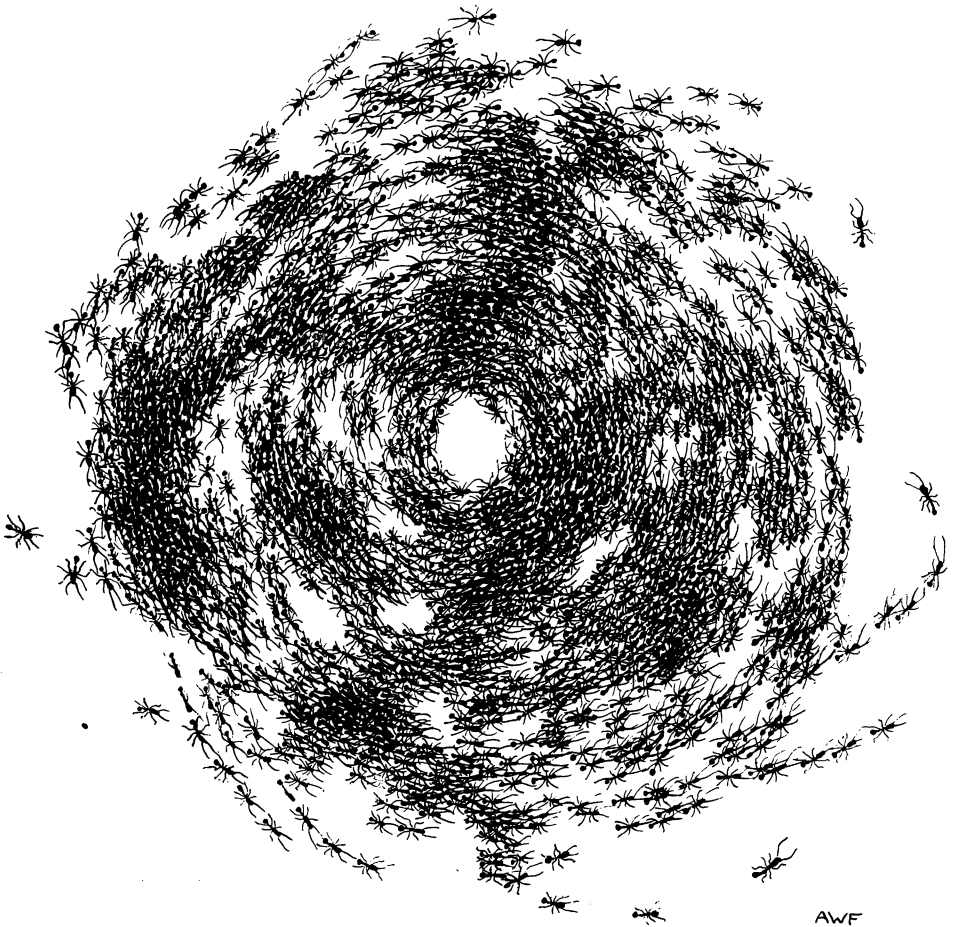


Fig. 1. The circular column of *Eciton praedator*, as drawn from a photograph taken shortly before 12:00 P.M. At that time the ring was approximately 14 cm. in diameter.

dom marked or lasting, yet occasionally there arises an eddy that may nearly circle upon itself, causing confusion until broken down by the persistent force of the general rotatory motion. A sub-rotation of this kind was observed at one time near the margin of the ring, a completed circling within the general movement which threatened for a time to become a persistent

12:00 P.M.: The circular column is moving more rapidly as a whole than in the early morning, rotating as before in the counterclockwise direction. The ring has expanded, now approaching 14-15 cm. in diameter. In general there are wider intervals between its individual members, and more obvious gaps appear intermittently between concentric sub-groups. The

central cluster has disappeared altogether, and there is now a bare central space about 1–2.5 cm. wide, entered only by an occasional ant which has momentarily turned too sharply to keep in touch with the innermost file. Since 8:15 A.M. the entire ring has shifted its position so that the center is now about 12 cm. from its former place, closer to the wall of the building. At 12:10 the ring is mainly exposed to direct sunlight, with only about 60° of arc on the side toward the library falling within the shade.

At 12:15 P.M. rain sets in. Ants in the mill are of course disturbed by the drops, particularly on the side away from the building. This side of the mill, although mainly protected from the direct downpour by the wide eave of the building, is still reached by a spattering of droplets which strikes the ants and dampens the substratum. Ecitons entering the exposed area soon hesitate, then are forced to move onward as others push up behind. Forced to run through the exposed area, they tend to crowd toward the center of the mill with the result that the more exposed side of the ring becomes narrower than the opposite side, and most of them turn rather sharply away from the rainy side when this becomes possible. Notwithstanding such difficulties, the rotation continues.

2:00 P.M.: (Fairly heavy rain, 12:15 P.M. to 1:50 P.M.) The place occupied by the ants at 12:00 is now thoroughly wet; however, the column continues its counterclockwise movement in a new spot 15 cm. closer to the building, where the cement is fairly dry. The group did not shift directly toward the building, but at angles in the counterclockwise direction. At 2:15 P.M. the ring wobbles as it rotates, so that its outer margin occasionally enters wet surface; in general, however, there is a small gap between its side and the wet cement. The entire assemblage moves at a slower pace than at 12:00 P.M. Once again there is a central cluster, which at 2:10 measures 4 cm. in diameter.

3:40 P.M.: (Sunshine after 1:50; now dark, beginning to sprinkle.) The circling proceeds counterclockwise, with the group about 8 cm. closer to the building than at 2:00 P.M. Some 60 of the ants have escaped the treadmill, only to wander in a loose network of columns on the outer side (i.e., farther from the building). Their number increases as the beginning of

rain noticeably disturbs ants on the exposed side of the circle. (Heavy rain from 3:45–4:00 P.M.)

8:30 P.M.: Somehow the group has divided into two distinct circling rings of ants. These rings, nearly equal in size, presumably were caused by the heavy though brief rain which came shortly before 4:00. Both groups rotate counterclockwise, with their outer margins about 20 cm. apart; both nearer the wall than was the exposed margin of the single ring at 3:45 P.M. In each group a few ants occupy the central area, where they huddle together or turn narrowly in irregular ways. During an hour of observation more are shunted into the central huddle, drawn from ants in the innermost file, where many have difficulty turning rapidly enough to evade bumping by others in line. At 10:00 P.M. the two rings still rotate counterclockwise, and in both, the central clusters have grown in size. The rate of general movement has become very slow.

September 5, 6:30 A.M.: On the spot of yesterday's phenomenon little or no circling is to be seen. The entire area is strewn with the bodies of dead and dying Ecitons. A few of the survivors wander about slowly, while no more than three dozen of them form a small (ca. 7 cm. D.) and rather irregular circular column in which they plod around slowly, counterclockwise. At 7:30 A.M. virtually none of the ants are on their feet. Circling has stopped, and various small myrmecine and dolichoderine ants of the neighborhood are busy carting away the dead.

Circumstances indicate that the Ecitons must have died of desiccation, after having been in nearly constant circular motion over an essentially dry area for more than 24 hours. They might have been able to survive much longer had they not shifted their ring away from the wet each time rain broke during the day. It is probable that these ants were marooned from the evening of September 3, since the raid stopped then and no other trace of the colony was observed in the vicinity after dusk on that day.

#### PROBABLE INITIATION OF THE *E. praedator* MILL

Although this case may be regarded as a special instance of trailing, it is far from simple, as analysis soon discloses. Unfortunately we lack direct information concerning the initiation of the circling; however, circumstances warrant the following supposition. It is very probable that the group was an offshoot of the swarm

raiding in this locality on September 3, operating at a distance from the main body and connected with it by only one or two shuttle trails when a heavy rain arose shortly before 2:00 P.M.<sup>1</sup> The downpour

<sup>1</sup> As measured by the station rain gauge near the library, 1.12 inches fell within little more than an hour before 3:00 P.M. on September 3. It is probable that the ants were cut off then, since the only other

would cause the ants to cluster, as Ecitons commonly do when exposed to rain, and would isolate them by flooding the area so that the trails connecting with the swarm could not be followed. (In the behavior of these ants on September 4, especially those that strayed away from the mill, at no time was there any indication that shuttle trails were in effective existence.)

The circling may have begun in the following manner. It is reasonable to assume that the isolated group or one main body of it was huddled in a roughly circular mass or confined to a small area during the downpour. (Such aggregations of Ecitons commonly form when rain breaks during a raid.) Then, when the rain stopped, the first ants able to run freely would be those situated on the margin of the huddle. Most of these individuals would tend to follow around the periphery of the group, through their typical response of turning toward the side of Eciton chemical and toward the side of continued tactual stimulation (i.e., furnished through brushing ants on the margin of the mass). A circular trail of Eciton chemical would thus soon be formed which these ants and newly aroused newcomers would follow in a canalized manner.

Favoring this hypothesis, there is a considerable body of evidence from laboratory observations and tests. When light strikes captive groups of *E. praedator* or others kept in laboratory nests, after a period of quiescence in darkness, a common response of those first set into action is to run around the margin of the cluster, with a persistent circular column often resulting. Occasionally contact alone is sufficient to produce this result, as was the case in Wheeler's observations of *E. schmitti* mentioned above. In his instance the ants established their treadmill around a glass jar and continued moving for 48 hours; under comparable conditions such columns may persist, though not operating continuously, for as long as a few weeks. I have observed a number of cases in the laboratory in which, for example, Ecitons

would trail persistently around the lower border of their cylindrical bivouac (e.g., *E. hamatum*, housed in tall wire nests), form an endless column around the inside wall of a circular nest, or trek around objects or clusters of ants in flat glass-covered nests. In a situation of the last type, an *E. hamatum* group consisting of about 40 workers and a queen would move for hours on end in a circular path around a 10-cm. square of cellulose sponge in the center of their nesting compartment, at frequent intervals during the 8-day life of the queen in captivity. This would soon begin, for instance, whenever they were newly exposed to light. The initial runs around the sponge were slow and hesitant, mainly in contact with the sides and involving sharp turns at the corners; however within two days the route had become circular, still leading around the sponge yet not touching it.<sup>1</sup>

The notion that the *E. praedator* mill began through the tendency of Eciton workers always to turn toward the side on which weak tactual stimulation is offered, and to move along beside a surface which maintains this contact, is supported by the following test. When *Eciton* workers running over a table top have settled into a course along the outer edge of the table (a common occurrence with *E. hamatum*, *E. burchelli*, and *E. praedator*), a smaller circular column of them may be set up by placing a glass jar of 10-25 cm. D. near the table edge so that some of the ants brush it with antennae or legs as they

<sup>1</sup> The workers in this case were responding to the stimulative effect of the queen as well as to the trail, as was shown by the fact that when she was present a compact group of them always hurried along closely behind and beside her (many clutching at her legs and body, or actually riding upon her), but always with a clear space ahead of her. When she was removed they continued to follow the trail, but now in an even column and at a slower pace. It may be added that normally the Eciton queen appears outside the bivouac only in the evening or at night, to participate in the movement of the colony to a new site. Then she follows the trail (used during the day as a raiding route) readily under her own power, accompanied by a horde of workers which greatly swells the normal width of the bivouac-change column. Far from being dragged along by workers to the new site, as many writers have assumed is the case, she furnishes her own power and usually pulls or carries workers with her. This applies to the species of *Eciton* (*sensu stricto*) which have been observed (*E. hamatum*, *E. lucanoides*, *E. burchelli*). In the early part of the rainy season, males have been seen following the bivouac-change route in a similar manner. It is very possible that Eciton mating occurs under these conditions.

rain of the day was a light one (.05 inch in all) coming just after 7:30 p.m. Before the latter rain came, the *praedator* raiders (as is usual) would have mainly withdrawn into their base trails and subterranean avenues leading to the bivouac.

pass. Ants that touch the jar lightly in this manner tend to leave the table-edge trail and follow the jar around its circumference, and a circular column results which in the end may absorb nearly all the strays on the table. The contact must be light, or the response is to turn away from the stimulated side, resulting in an eddy of the table-edge column away from the jar, but with no other change in behavior. If the jar is pushed too far into the initial column, so that the ants actually collide with it in passing rather than merely brushing its surface, they turn away and thus many get off on the vertical edge of the table, perhaps ending by the entire group trailing away on the floor.

These results indicate the great importance of positive response to weak contact in the initiation of circular columns, supporting our hypothesis concerning the "spontaneous" formation of such a column in the open. In that instance, as suggested above, a turning toward Eciton chemical must have been involved as well. Such a combination of weak contact and Eciton chemical facilitates the formation of columns of this type; we have observed this repeatedly in the laboratory. Yet the fact that light contact alone will suffice to initiate proceedings suggests that it is not so much a matter of the nature of the stimulus as it is the intensity of stimulation that arouses the approach-turning response.

#### ANALYSIS OF THE PERSISTENT CIRCULAR COLUMN

After the column has been active for a time, contact with the surface no longer is essential, as is indicated by the case cited in which an *E. hamatum* group trailed in a circle around a square sponge. In a more striking demonstration, after Ecitons have formed a column around a glass jar on a glass substratum, removal of the jar leaves a regular circular procession which usually is able to maintain its formation for a considerable time. The chemical trail which is formed as the ants follow the surface becomes sufficient alone to canalize the column. Thus in a number of instances, Ecitons ceased trekking around the outside edge in running around the top surface of a square wooden block, gradually shifting to a course that cut the corners more and more, until finally they followed a circular course which neared the edge only at the center of each side.

It seems clear that other factors must complicate such behavior, beyond chemical and tactual stimulation as described. An interesting instance of freedom from the original contact which led to new complications was furnished by an *E. hamatum* group first observed running around a simple partition in their shallow glass-covered nest. After several hours it was noticed that they were actually describing a parallelogram around the partition, the

acute angles extending beyond the ends of the partition in the direction of turning (i.e., counterclockwise). (See fig. 2.) What happened was that after slavishly following the wall tactually for an hour or two, running speed gradually increased, and some of the ants began to overrun in rounding the corner. This brought them into contact with the side wall of the compartment, which they followed for a short distance before they turned back toward the partition (evidently responding to chemical stimulation). As their running speed increased, the ants steadily increased the distance they ran along the side wall before turning back toward the partition, and the path of their return to the partition (at first noticeably concave inward) came to be a straight line which brought them back to the partition at a point gradually closer to its opposite end. Finally the ants ran a course parallel to the compartment wall but not at all in contact with it, after rounding the end of the partition; turning from this line in an arcing course that straightened so that they neatly rounded the opposite end of the partition. At length they traced out the parallelogram with blunted corners shown in figure 2, in which they were near the partition only at its ends. In this rather complicated example, original contact with the partition and

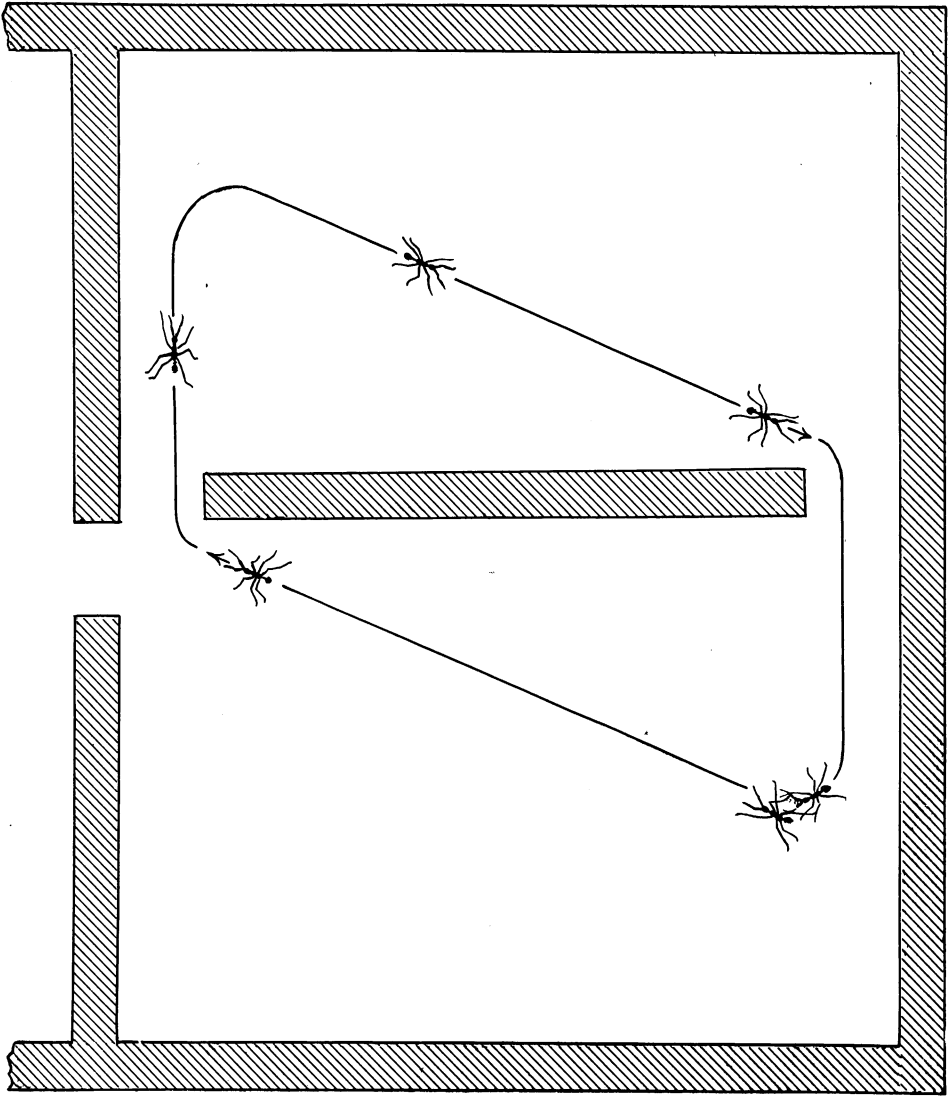


Fig. 2. Parallelogram course established by a group of *Eciton hamatum* workers around a partition in a shallow observation nest. The solid line represents the path eventually followed by the ants; the arrows indicate the direction of travel at a given time. (See text.)

newly encountered contact with the side walls were dispensed with as a chemical trail formed; however, as increasing saturation of the substratum facilitated faster running, this augmented the influence of a centrifugal-force effect generated in rounding the ends of the partition, accounting for their modifying the chemical trail to form the short sides of the parallelogram. The

turn back toward the partition through what became the long side of the parallelogram may be regarded as a result of turning toward chemical stimulation when the momentum effect had weakened sufficiently.

The centrifugal-force factor, disclosed in the running of geometrical figures according to laboratory conditions, is to be

reckoned with when one studies trailing behavior under natural conditions. For example, its influence is disclosed when sharp turns around objects gradually shift outward as the trail develops, until the ants finally run at a distance from the previously "hugged" surface in rounding the corner. Or at other times, when a column at first turns off to one side promptly after having reached the end of a stick along which the trail leads, the course shifts in time so that finally the turn is made in a wide arc at a distance from the end of the stick. This type of modification commonly occurs along the course of trails used for a considerable time during the day. Depending upon: the slope of the incline which is mounted or descended, the momentum which may develop through passage along a fairly straight section of trail according to the smoothness of the terrain, and the running speed which may be in force in approaching and rounding a corner, numerous features in the initial and the later form of the route may be understood. In studying trail formation, one can never afford to neglect the simple mechanical principles underlying animal locomotion.<sup>1</sup>

Now we are in a position to attempt an explanation of how the *E. praedator* mill was kept going for more than 24 hours in the open. It is clear from the facts that this behavior involved more than the mere following of a circular chemical track; the shifting of the entire mill through a distance of about 30 cm. within less than 12 hours dismisses that notion. However, at any given time the ants were responding to a ring of chemical, as is shown by the partial disruption of travel introduced by occasional "Finger-versuch" tests (e.g., rubbing clean glass cloth over a portion of ring area vacant at the moment). In this phenomenon the chemical factor seems to have been merged with other influences in a rather involved manner.

The persistence of this circular column

may be understood in terms of the interaction of three component factors commonly influential in normal trail movements. These are: (1) a *pressure*, tactually exerted according to the principal direction of movement in the group, which minimizes variability of movement and tends to coerce "forward" progress in the group; (2) a *drainage* factor, the composite effect of chemical stimulation from the trail and tactual stimulation (as well as chemical) from travelers ahead and beside the given ant; (3) a *centrifugal-force* factor, the inertia of movement which tends to carry the ant away from the circle on a tangent with the circumference. The combined operation of these three factors holds the circular column together and accounts for the principal variations in its behavior.

The term "pressure" for our first factor is used here in the sense it was used when dealing with the phenomenon of organized swarm movement in Ecitons such as *E. burchelli* and *E. praedator*. "Its basis is the proneness of the Eciton worker to turn away from the side of strong or repeated tactual stimulation and to reverse her direction of progress if such tactual stimulation is encountered in head-on fashion" (Schneirla, 1940, p. 425). Thus through forcible bodily contact, an Eciton that happens to run against the preponderant direction of movement in a group is soon brought into line. If she happens to lag when in a hurrying column, forcible tactual stimulation from the rear spurs her onward. This factor must have played a major part in accounting for the fact that one direction of locomotion (i.e., counterclockwise) prevailed in our *praedator* mill. From laboratory observations we may say that a variable combination of circumstances (i.e., a "chance" situation) caused the majority to hit upon this direction of movement at an early point, and that deviates were gradually forced into the same direction through "pressure" until there was no longer any persistent clockwise movement in the group. A somewhat similar phenomenon is involved in a complex manner when a nomadic movement begins to develop toward evening in a raiding system of the

<sup>1</sup> For example, one such effect, the role of gravitation, has been studied by Barnes (1930) in relation to the lateral oscillatory excursions of *Lasius* in running. The influence of centrifugal force as considered here commonly leads Ecitons into behavior situations resembling those described as "centrifugal swing" in the maze behavior of *Formica* species (Schneirla, 1929, 1941).

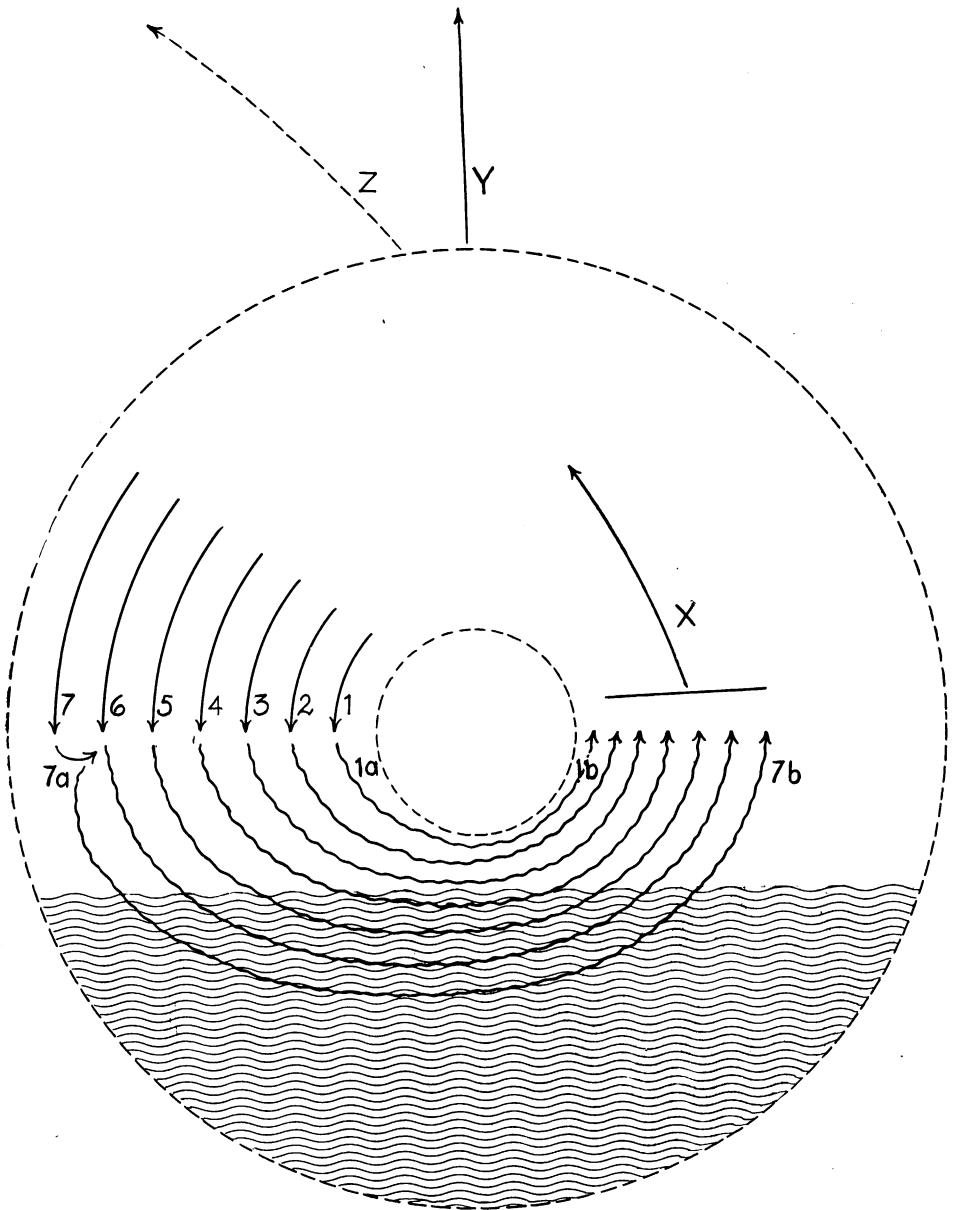


Fig. 3. Sketch representing the shift of the *E. praedator* ring as a result of wetting by rain in the area indicated by wavy lines. 1-7 Indicate the initial courses of concentrically traveling ants; 1a-7a their respective courses upon entering the area of disturbance; 1b-7b their respective courses upon leaving this area. 7a Indicates how individual ants are reoriented when they turn back from the wetted surface. X, the vector of pressure upon the upper portion of the ring; Y, shortest distance to wall under the eave; Z, direction in which the circle shifted in response to the rain. (See text.)

swarm raider *E. burchelli* (Schneirla, in press).

Through the effect of *pressure*, in particular, one prominent change in the action of the *praedator* ring may be understood. When rain spattered upon one side of the assemblage, causing confusion and accounting for a noticeable faltering of ants entering that area, the circular column was kept in being especially through the influence of a forceful mass contact from the less exposed and more smoothly operating part of the mill. Ants that hesitated and turned when struck by rain were thereby forced to turn "forward" again and somehow rush through the damp area. Evidences of another special pressure effect were observed soon after the rain broke, an effect which seemed to contribute to the shifting of the entire circular mill toward the wall (i.e., farther under the wide eave of the building) during the downpour. Most of the ants running through the exposed area (i.e., the side away from the wall) not only speeded up noticeably, but also tended to turn short away from the side of disturbance instead of remaining in their respective concentric lines. Presently there were indications that the strong pressure effect thereby generated, concentrated upon the inner part of the circle when ants entered the drier area in the clockwise direction, was literally pushing the less exposed part of the mill toward the wall. By causing numbers of ants to run more widely outward while passing through the marginal section on that side, this unilateral pressure produced an eccentric torque or "twist" in the circling, toward the wall and counterclockwise (fig. 3). As a result of this effect and its various secondary consequences through the group, the entire mill gradually shifted its position at angles (i.e., in the counterclockwise direction, and not straight toward the wall) farther under the eave of the building. As new portions of surface closer to the building became chemically saturated by ants forced out centrifugally on that side, the entire mill could move into them, but most important, it was the dynamic interrelationship of the Eciton units in the mass that permitted the ring to retain its essential pattern

throughout the crisis. Then, after the rain, it regained its earlier symmetry.<sup>1</sup>

Although pressure is by no means the only agency accounting for persistent "forward" motion and the minimizing of deviations, the "push from behind" plays an important part in most of the group activities of these ants and should not be neglected here. Another function of pressure in the mill, a lateral component operating centripetally, will be considered presently.

Our second factor, "drainage," also holds a basic place in all Eciton mass movements, especially in the mass organization of swarm raiding (Schneirla, 1940, p. 425). This involves the propensity of the Eciton worker to turn toward the side of weak tactual and weak chemical stimulation, or toward these in combination. This positive response to weak tactual stimulation has been illustrated in the case of a circular column starting around the edge of a glass jar. General observation supports the view that gentle contact with another Eciton ahead elicits turning toward the side from which the stimulation comes; from the same source and from special tests comes support for the tendency of Ecitons to turn toward Eciton chemical, favoring the side of greater concentration.

For example, a large strip of bristol board was prepared in an Eciton-chemical gradient by regulating the passage of workers across it to have a maximum of crossings at one end and a minimum at the other, with graded frequencies between. Then in succession 40 *E. hamatum* workers were released at the edge, 20 at the "maximal-saturation" end and 20 at the minimal-saturation end, and were permitted to cross freely. More than 15 of the former crossed at the same end of the card; whereas the latter group crossed at points extending nearly the full length of the card. Thus the representative response of ants entering the weakly saturated zone was to turn into parts of the gradient in which Eciton chemical was more concentrated.

<sup>1</sup> Although the movement of the ring out of sunlight during late morning was not observed as it occurred, it seems very probable that this shift depended upon events somewhat similar to those described. The distorting effect in that case would depend upon the irritating action of bright light upon the Ecitons, causing them to speed up when entering the exposed area and turn away from the dazzle as promptly as circumstances permitted. Such responses are commonly observable in the everyday behavior of *E. praedator* swarms which are partially exposed to brilliant illumination (e.g., in sun-fleck areas).

The evident influence of the third factor, centrifugal force, is disclosed in figure 1, in which one or more lines of ants may be seen taking a path tangential to the rotating ring in the direction of turning. In the outer portion of the ring, where the ants run

centrifugal force increasingly effective as running speed increases, Eciton paths around square or irregularly shaped objects approximate a circle more and more closely. Through its effect, a *hamatum* path around a linear partition (influenced by initial

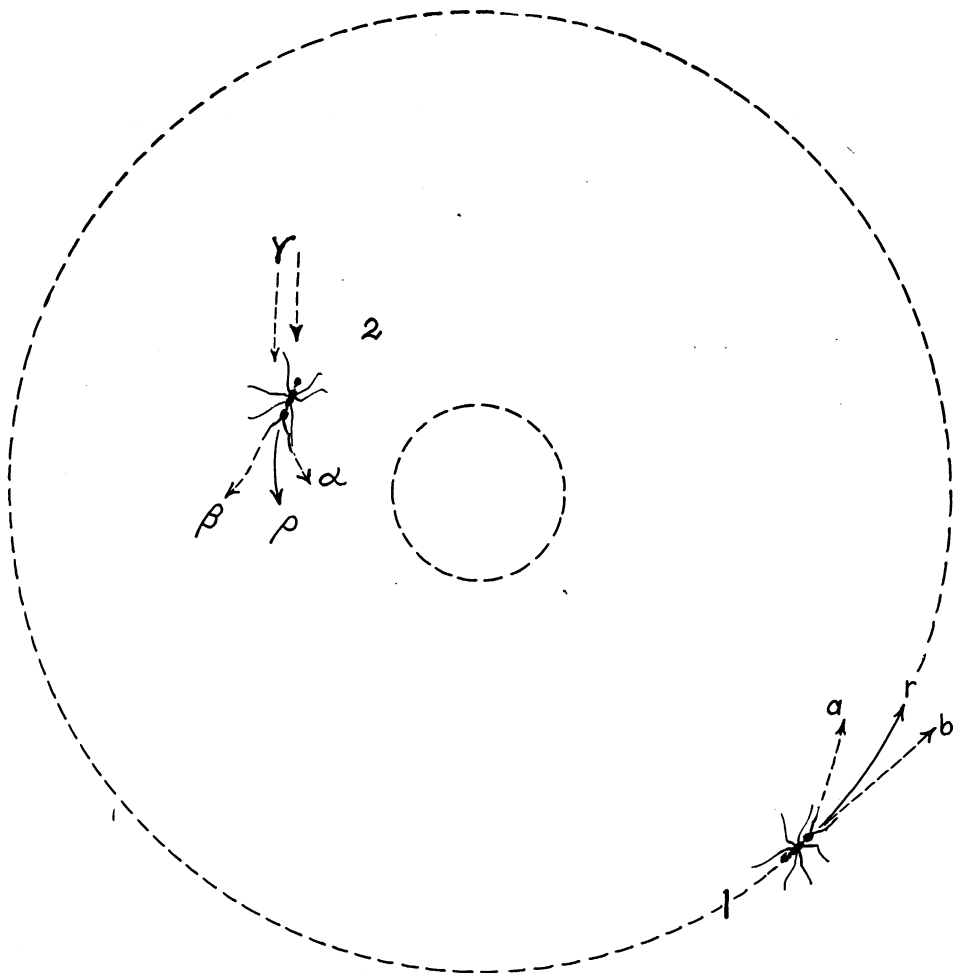


Fig. 4. Sketch to represent factors influencing the movement of ants in the *E. praedator* ring. 1, An ant moving on the margin:  $a$ , centripetal vector;  $b$ , centrifugal vector;  $r$ , the resultant circular course. 2, An ant moving in one of the inner lines:  $\alpha$ , centripetal vector;  $\beta$ , centrifugal vector,  $\gamma$ , pressure from outside and rear;  $\rho$ , the resultant circular course. (See text.)

most rapidly, the influence of this factor is most directly apparent in behavior, in that there is a persistent tendency for the marginal ants to "fray out" from the ring in the forward direction. We have mentioned laboratory cases in which, with

contact with end walls) became modified into a parallelogram (fig. 2). In such cases the interaction of our second and third factors is recognizable: a centrifugal-force effect leading the ant to run onward after turning a corner, and a response to Eciton

chemical when the centrifugal effect weakens.

To take stock, ants in the mill are kept in motion in the forward direction by a pressure from others just behind, an effect which is mutually exerted throughout the group. Upon this basis, the dynamic pattern mainly responsible for survival of the circular movement itself may be expressed most simply in terms of a combination of drainage and centrifugal-force effects. To illustrate this interactive set of influences, let us consider the case of an *Eciton* moving at the margin of the ring (fig. 4). Occasional contact with ants moving along on her left (i.e., inside, in the counterclockwise mill) together with a turning toward the side of distinctive *Eciton* chemical, would account for a centripetal vector in her movement (fig. 4, 1*a*). At the same time, depending upon running speed, her momentum would account for a *centrifugal force* which would tend to impel her directly ahead on a tangent with the circle (fig. 4, 1*b*). (As we have indicated, the effect of centrifugal force is directly evidenced at times in actual tangential departures of marginal ants from the ring, while the effect of the "drainage" factor is shown in the appearance of hesitancy and turning back toward the circle after short tangential excursions of this kind.) The circular course of marginal ants may be considered the resultant of these two vectors (fig. 4, 1*r*).

Although the case seems more complicated for travelers on lines within the outer border of the mill, we may assume that the same *drainage* and *centrifugal-force* pattern governs the circular course of all. However, for ants moving in interior files, there are indications that *pressure* effects are superadded. In their case, the centrifugal-force influence (fig. 4, 2*β*) is counteracted not only by a contact-chemical drainage effect (fig. 4, 2*α*) from ants turning away on the left (i.e., "inside," in the present case), but also by pressure effects through frequent and at times forcible contact with ants running on the right side (i.e., "outside"). The circular course (2*p*) may be considered the resultant of these three vectors. One feature we have mentioned, the indications of "friction" between fast

moving outer lines and adjacent slower moving inside lines, seems to illustrate the involvement of a bilateral tactual pattern for ants within the body of the mill. Assuredly, centripetal pressure must not be excluded here as a regulator of movement. We have noted that the circular mill expanded between 8:15 A.M. and noon. It will be recalled that a rise in temperature during this period would increase the running speed of all ants in the group, thus heightening the centrifugal-force effect tending to widen the circling of the respective concentric rings of ants.<sup>1</sup> But in addition, in accounting for the expansion of the mill, it seems necessary to consider the possibility that "inside" ants, by exerting an increased centrifugal pressure, facilitated the wider turning of outside lines; and that outside lines, in arcing more broadly, thereby reduced centrifugal pressure and permitted freer action to those within.

Now we may consider the *Ecitons* caught in the innermost line, near the hub of the wheel. We have remarked the fact that in early morning, near the end of the rain, and toward evening a central cluster was formed. At other times the central area was essentially bare, and when empty it was also larger. These were the times when higher temperatures accounted for a faster rotation of the mill as a whole, which checks with our suggestion that the faster motion of individuals increased the centrifugal-force effect and thereby spread the ring. However, when the ring contracted, individuals in the innermost line were forced by crowding (i.e., lateral pressure) of ants in the next outer ring to turn very sharply. This meant that some of the central ants were buffeted and crowded so forcibly that they were caused to circle in place. Turning variously at different angles these ants interfered with one another, an organized circling of the innermost members thereby became impossible, and they presently were thrown into a cluster. Very probably the relative slug-

<sup>1</sup> Shapley (1920) and others (Miller and Gans, 1925; Pratt, 1925) have shown for various species that the speed of ants traveling an established path increases with the temperature up to a given maximum.

gishness of the ants at such times (i.e., in lower temperature) contributed to the clustering tendency. Similarly, in normal foraging, when the coming of dusk slows the Ecitons, the nucleus of clusters at trail junctions is formed by disoriented ants caught and knocked about in the hectic

traffic at such points. We may say that Ecitons in the center of the narrowed *praedator* mill were passively tossed about by a movement in which they could no longer participate as synchronized units, and thus in a sense assumed the rôle of flotsam in the center of a whirlpool.

#### MILLING IN RELATION TO TRAILING UNDER NATURAL CONDITIONS

Instances of this kind in animal behavior are arresting not simply because of their bizarre character, but also because they may be utilized to review the factors of normal behavior in relief, as it were. In this example we have seen the operation, under special conditions, of the principal factors in everyday Ecton mass movement, i.e., pressure and drainage, together with the centrifugal-force effect. Studies of other *Ecton* species have shown how these factors are involved in the formation and use of ordinary raiding trails (Schneirla, 1938). Furthermore, the same concepts make understandable the integrative processes involved in the surprisingly direct advance of the relatively enormous *E. burchelli* swarm (Schneirla, 1940) and the smaller swarm of *E. praedator*. Despite very complex and at first sight utterly random eddying and cross-current movements among sub-groups in the swarm, by virtue of describable relationships of the pressure and drainage factors the whole body of ants is capable of a fairly straightforward advance through vegetation and over broken forest terrain. In the wake of every swarm there is a long fan-shaped network of columns (consolidation fan), which narrows posteriorly into a single column communicating with the bivouac. It is a relatively constant pressure, operating through this system and applied more or less evenly across the rear of the swarm by ants arriving from the bivouac, which enables the raiding mass to hold its laterally extended formation and at the same time continue its advance.

Why ants behind the swarm do not continue to roam throughout the wide lane saturated chemically by the swarm, but instead confine themselves to a progressively

narrower channel at distances farther in the rear, is explicable in terms of gradual changes in chemo-tactual response with further use of the ground. A turning of Ecitons toward others, thus as a rule keeping to circuitous columns and not spreading out widely, is noticeable in the rear of the swarm where forces are reduced in numbers. The center of the area is favored presumably on a chemical basis. Because of the way the swarm moves ahead, spreading out alternately on the flanks but with a fairly consistent crowding in the center, there is evidently a reduction in chemical saturation from the center toward both sides in the area pillaged by this body. Ants coming up in the rear evidently respond to this gradient by turning more readily toward the center of the wide lane than toward its borders. Their movements on the ground by favoring the central part increase the steepness of the gradient, thus provoking still more precise turns centrally by ants advancing behind them in the fan. At the rear of the fan, where the gradient must be steepest, all lateral trails disappear from use, as a rule, and only a narrow central route remains. In the behavior of Ecitons following this principal trail between bivouac and raiding front, there are many indications that the route is responded to as the region of greatest intensity in a bilaterally extended chemical gradient. A crowding away from the edges toward the center of the path is noticeable in moments of traffic congestion, especially when the route is new, and the fastest moving ants generally usurp the midline at the expense of burdened ones or slower moving individuals such as the clumsy major workers. Displaced laterally from the trail a few centimeters or more, in

the ensuing rambling of the *Eciton* there is a noticeable drift toward the main path, even if it is empty at the time. Displaced on the original ground, ants return to the central route far more quickly than when transferred to new ground with the trail (e.g., a section of it on a narrow leaf) located at a comparable distance.

Now although *Ecitons* are undoubtedly among the simplest of ants, psychologically considered, highly stereotyped in their activities, yet to the writer's knowledge a true circular mill has been observed in only this one instance under natural conditions. The *burchelli* or *praedator* swarm as it advances exhibits countless instances of vortexes, whirls, and eddying movements of short columns in the mass. Also, pushing out from the forward and lateral margins of the swarm are "pseudopodic columns" which frequently take eccentric courses, even looping back toward their origin points at times. When the consolidation fan takes form on ground first swept by the swarm, in its complex anastomosis there are always numerous remnants of circling courses formerly apparent in the swarm (Schneirla, 1940, fig. 1), which stand out for a time as loops and circular trails in the network. At times, on these circuitous portions of the system, one observes that given ants or trains of ants may travel one or more rounds in a loop before there is a change. However, in these cases, as when comparable circuits happen to form in the tree-like trail systems of *E. hamatum*, the complex of events soon modifies the circular path, so that true milling does not occur.

Actually, although all the chief factors underlying our instance of milling are readily recognized in trail following under natural conditions, circumstances operating in the forest environment militate strongly against any possibility of *Ecitons* being caught in a persistent local circling movement. Either the pressure of ants entering over connecting trails changes matters, or, if few newcomers arrive, the shuttle trails provide escape routes. The

raiding system of any *Eciton* species is a complex network of chemical trails connecting with the bivouac over well-traveled trunk routes, providing slight opportunity for any section of traffic to operate independently for long without being modified through its connections with adjoining sections. For this reason, no part of a raiding system can remain very long in a given pattern of action. In the case of our *praedator* mill the exception occurred, but there another unusual condition happened to be fulfilled: the ants were cut off from their colony when on or near *very homogeneous terrain*, the cement walk. Here the substratum was tactually neutral, presenting no irregularities which could intrude upon the symmetrical operation of pressure, drainage, and centrifugal-force influences around the ring. Afield, few if any situations ever approach very close to neutrality in this sense. To be accurate, the cement surface on which our *praedator* group chanced to rotate must be considered a quasi-artificial situation.

We find essentially the same idea in Wheeler's (1928b) interesting discussion of polymorphic specialization in ants, applied to the worker major of the harvester *Pheidole*.

"Some authors regard the soldiers, the highest high-brows of our ant series, as monstrous, or pathological forms on account of the excessive development of their crania. Certain facts might seem to lend support to such an opinion. If the soldier of *Ph. instabilis* be placed on its head on a perfectly smooth, hard, horizontal surface, the insect may be quite unable to right itself and may even die standing on its head. But this is a typical laboratory experiment. In its natural environment the soldier never encounters such surfaces. Closer study shows that all these supposedly monstrous forms are really exquisitely specialized and adapted for the functions they have to perform in the life of their respective colonies. The soldiers of the harvesting *Pheidoles* and *Pheidologetons* are needed not only as seed-crushers, but those of the latter genus have another very different function. Several observers have seen groups of the minute *Pheidologeton* workers sitting quietly on the huge heads of the soldiers and riding to and from the nest. The soldiers of the insect-eating *Pheidoles* dismember the tough prey before or after it has been carried into the nest. . . ." (p. 19).

## RELATIONS TO MILLING IN OTHER ANIMALS

## PARR'S ANALYSIS OF MILLING IN SCHOOLING FISHES

After the foregoing analysis of the *Eciton* mill had been sketched, in a search of the literature for cases elsewhere in the animal series my attention was drawn to a similar phenomenon in schooling fishes, described and analyzed by A. E. Parr (1927). A comparison of the *Eciton* mill in figure 1

from the known properties of the animal. Of course the Parr analysis takes priority as a theory of milling behavior in invertebrate animals; however, mention of it has been delayed until this point in order to emphasize the fact that a second investigator, working independently with

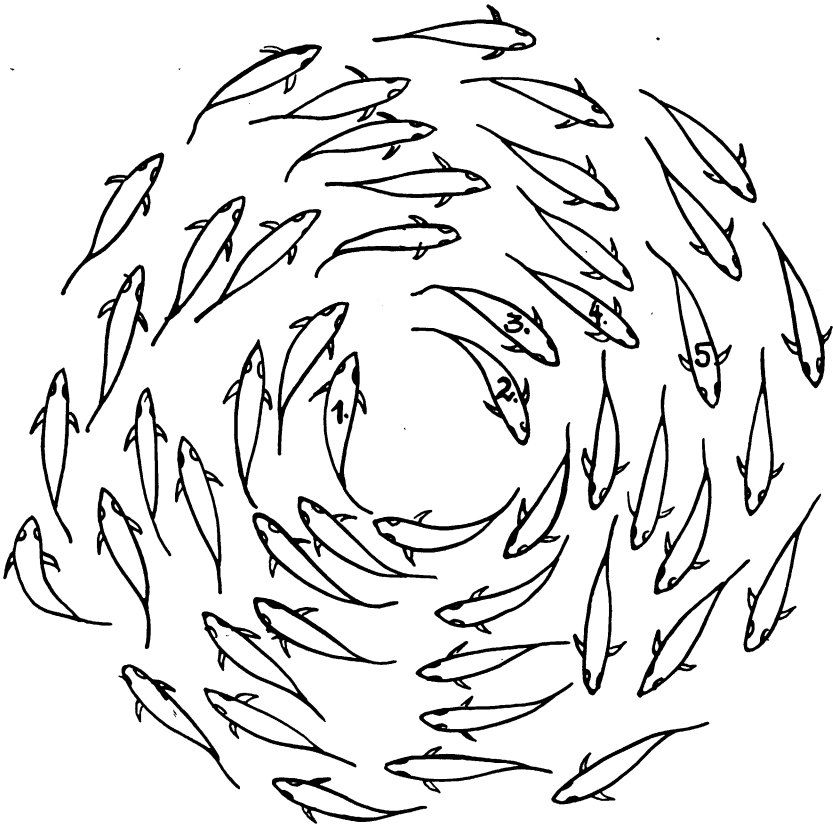


Fig. 5. Sketch of the circular fish mill described by Parr. (See text.)

with the sketch of one level of Parr's fish mill in figure 5 indicates a marked resemblance in these patterns of invertebrate and vertebrate behavior. Even more striking are the similar outcomes of analysis by the two investigators. Each of us evaluates his phenomenon as essentially one in the mechanics of animal locomotion in relation to available sensory patterns; each develops an explanation inductively

very different material, arrived at a theory which, notwithstanding the different setting, bears a surprising similarity to the Parr "bio-mechanics" explanation.

The theory offered by Parr to account for the formation and maintenance of a milling group of fish may be represented in résumé as follows. When a school of fish (e.g., mackerel) meets a deflecting surface and begins a sharp turn, individuals first

to head in the new direction are presented with a potent visual stimulus from those directly opposite and traveling in the original direction. This stimulation dominates over that from adjacent fish which have participated in the turn and are swimming on the outside in the new direction. Since the stimulative influence of companions swimming in the same direction is already adjusted to, the new stimulus is "much stronger" because it represents a more rapidly shifting pattern. Hence fish on the inside of the wheel continue to turn toward the inside. The nucleus of a mill is thereby formed through this mutual visual stimulation which keeps fish in the interior file turning toward oppositely swimming fish (fig. 5, 1 and 2). Soon individuals in files next the new center become influenced by the central individuals turning away from them interiorly, and they respond by turning toward that side, thus beginning to wheel

on the same principles as those causing the first circular movement of the central file. In each case, a similar turning of the adjacent outward companions in the school (fig. 5, 3, 4, and 5) prevents their stimulus effect on the given individual from opposing that of the adjacent interior file. The mill is maintained on the same basis: the circular movement of the central file acquires the nature of a continuous automatic process, and the tendency to turn as originally transmitted outward is maintained as each fish continues to respond to the inward turning of its adjacent inner companion. Once the mill is formed, the outermost file exerts a certain condensing influence upon the moving group, since the peripheral members are influenced solely by a one-sided attraction toward companions turning away on the inside, and thus act as a wall restraining any individuals happening to stray outward from interior files.

#### A COMPARISON OF MILLING IN FISHES AND IN ARMY ANTS

These phenomena of circular milling in schooling fishes and in army ants are strikingly similar, as a comparison of the respective analyses above suggests. In particular, in both cases a tendency to turn toward a dominant centripetally operating stimulation seems to be paramount. However, there are a number of differences worthy of consideration. One is in the dominant sensory mechanism of the milling, which in the schooling fishes thus far studied (Parr, 1927; Breder and Nigrelli, 1935; Shlaifer, 1942) has been identified as vision. In connection with his study of mobile aggregations in the herring *Jenkinsia*, Breder (1929) has pointed out that fishes schooling on the basis of vision approach only as close to one another as the distance at which clear optic resolution occurs. At shorter distances a negative response is given. In contrast, the army ants maintain their formation in dependence upon a pattern of diverse tactuochemical stimulative factors. This undoubtedly admits certain differences in the detailed mechanism of circling, such as the

influence of a tactual "pressure" from behind and from the next outer file in the Eciton mill, not demonstrable in the fishes. Although from Parr's analysis this factor of proximal stimulation would seem negligible or absent in the visually based fish mill, it is barely possible that it may acquire at least a limited importance in the exceptionally dense mills formed by the more tactual catfishes (*Ameiurus*). When in schools, as Parr (1927) states, young catfish are spaced at intervals governed by the span of their tactile barbels.

This difference in the dominant sensory modality may be involved in accounting for an apparent difference in the initiation of mills in Ecitons and in fishes. As far as our cases go, the circling in visually dominated fish appears to begin centrally and grow centrifugally, whereas through various relevant considerations we were led to regard the *praedator* mill (not observed in its origin) as having begun peripherally and developed centripetally. Of course, it is quite possible that more extensive studies may show that the mode of initiation, cen-

tral or peripheral, is not an invariable matter for either animal. Of far greater importance than this is the above-mentioned similarity in the maintenance of the two mills. Both may be understood as cases of predominantly unilateral stimulation of involved individuals, with Ecitons turning in stereotyped manner to the side of light contact and more effective Eciton chemical, the mackerel toward the side of visual stimulation.

Other differences between the milling of these two animals deserve mention here. An obvious difference is that although fish schools and milling when it occurs commonly operate in three dimensions, the Eciton mill is necessarily a two-dimensional affair which is more rigidly localized in one plane of space. This suggests a further prevalent difference which very probably is important for the frequency with which milling occurs under natural conditions, that is, the relative heterogeneity of the

two-dimensional working surface of the ants, in sharp contrast with the great homogeneity of the aquatic medium of pelagic fishes. A homogeneous environment tends to accentuate and to facilitate stereotypy in behavior, by permitting the peculiarities of the animal to establish relatively rigid patterns which dominate its behavior in given monotonous ways over considerable periods of time. In contrast, notwithstanding the fact that the properties underlying Eciton behavior are in themselves highly conducive to stereotypy (Schneirla, 1940, pp. 447 ff.), the varying situations of a tropical-forest environment militate strongly against the persistence of monotonous patterns such as the circular-trail formation. It is otherwise with fishes such as the herring, which not only possess the organic prerequisites for stereotyped behavior, but also happen to live in an environment which admits the predominance of these properties in given patterns for considerable periods of time.

#### CONTRASTING PATTERNS IN ANT ORIENTATION IN RELATION TO MILLING

Actually the mechanism of Eciton orientation, although complex in its own terms, represents nearly the extreme of simplicity in ant way-finding. It bears a close relationship to the stereotyped modes of orientation which characterize the invertebrates in particular, reaction types which, although highly involved, have been studied very successfully through the experimental examination of direct relationships between the energy pattern of stimulation and the dynamics of locomotion.<sup>1</sup> The Eciton system of orientation reduces essentially to a generalized chemotactically controlled pattern, apparently without much learning involved beyond the initial approach response to Eciton chemical. Contrasted with the cases of many other collective foragers, especially among the social insects, this army ant system appears highly rudimentary.

Formicine orientation on its higher levels exemplifies the condition which Maier and

Schneirla (1935, chap. 7) have termed "provisional orientation," in that the animal's behavior in a given field of stimulation is dominated in appropriate and plastic ways by circumstances which initiated the trip, and by a capacity to modify the route through previous experience in the situation. For example, the common garden ant *Lasius niger americanus* runs its trails according to the prevailing circumstances of chemical, visual, tactual, and muscle-sense (kinesthetic) stimulation, improving through learning in successive runs over the same general route. Since Lubbock's pioneer studies (1882), it has been known that *Lasius niger* follows its trail not on a chemical basis alone, but also according to the direction of light rays. Although there are grounds for believing that the *Lasius* forager may learn to move according to these sensory patterns, there remain largely unanswered a number of questions concerning the ant's ability to adapt her movements to changing outer conditions. One such question concerns how this ant

<sup>1</sup> For a survey of evidence on these basic forms of orientation, see in particular the valuable work of Fraenkel and Gunn (1940).

(together with a number of other species of similar foraging activities) is able to use a given route through a considerable period with light direction one of her orienting cues, notwithstanding a gradual change in the angle of the sun's rays through the period. Part of the answer seems to lie in their ability to utilize particular serial tactual cues such as the edge of a boulder or stick in a given section of terrain. Furthermore, in certain localities they may learn to depend upon slope of the ground as one cue, and Brun (1914) showed that *Lasius* adapts differently to such properties according to the nature of its relatively broad chemical trail. Also, if the ant returns repeatedly from feeding on nectar, there arises an end-for-end (i.e., polarized) difference in the chemical trail to which she becomes able to respond (for example, she readily differentiates the two directions after being displaced from the trail). If, however, larvae (*Lasius* larvae, experimentally placed at a distance) are being carried back to the nest, she becomes more dependent upon the non-chemical cues (e.g., direction of light) and becomes seriously disoriented if light, tactual cues, or slope of the path is changed. In contrast, Ecitons, as we have pointed out, follow their foraging trails mainly on the basis of a generalized ability to move toward a common chemical product. In their case an ability to learn a particular route according to direction of light or other special cues existing on the given pathway seems to be absent, as far as the writer's tests have shown.

Thus the Ecitons represent the primitive type of collective foragers among ants, which follow their trails in a slavish, stereotyped manner without the involvement of a special learning of the route, while *Lasius* represents the more highly specialized type of collective forager which is capable of learning a route in dependence upon prevailing sensory conditions. Under appropriate conditions Ecitons follow a circular trail persistently, but we may venture to say that no particular success would meet an attempt to elicit such behavior when *Lasius* individuals are the subjects.

The contrast is even greater if we com-

pare simple collective foragers such as *Eciton* with true individual foragers such as ants of *Formica* or *Camponotus* species. These ants are capable of learning individual routes to foraging areas in different directions from the nest, and can get through despite terrain changes (e.g., digging up the ground, laying down new surfaces) which would completely block *Eciton* or most collective-foraging ants. Field tests show that a *Formica* individual may set off from a food place toward the nest (50 yards or more away), first traveling mainly in dependence upon a clump of trees (visual stimulation of the ocelli), then pass through a low stretch of terrain mainly in dependence upon direction of light (stimulation of the compound eyes), then shift mainly to chemical cues upon a broad "ant road" a dozen or more yards from the nest (getting through on a visual basis if the ground has been disturbed), and finally reach the entrance to the nest by utilizing tactual cues, slope of ground, and a chemical gradient in complex combination (see Brun, 1914; Schneirla, 1929). In the laboratory, *Formica incerta* subjects are quite able to master a fairly complicated maze even when diffuse illumination reduces visual cues to a decided minimum and chemical cues are rendered highly unstable through frequent shifting and changing of the alley linings (Schneirla, 1943). Attempts to secure a mill phenomenon comparable to the *Eciton praedator* circular trail could never succeed with ants of these species.

Thus among ant species one finds a relatively wide range of foraging patterns, from a stereotyped following of mass chemical trails to a highly specialized learning of individual routes largely independently of any chemical tracking. Of course, a detailed study of phenomena such as the *Eciton* circular trail shows that even the "elementary" types of trail-following behavior are far from a simple matter of running along a line of chemical. However, in *Eciton* species the milling phenomenon discloses susceptibilities for stereotyped behavior which are truly representative of characteristic psychological limitations appearing in their normal foraging activi-

ties. We have ventured to predict the impossibility of obtaining a true case of milling behavior in more advanced collective foragers and in individual foraging

species of ants, mainly because of their capacity for variable behavior in way finding which largely excludes such activities.

### CONCLUDING REMARKS

Studies of mass behavior phenomena such as milling make their chief contribution in the light cast upon the general problem of levels of integration in social behavior. It is not the pattern in and for itself, but its relation to other properties of individual and group behavior in the same animal, which merits special investigation.

The milling pattern arises when animals moving within the same area yield in common to the influence of routine stimulus-response mechanisms arising through group locomotion. These characteristics mark it as a very rudimentary form of group organization. In themselves, circular columns and other types of milling are simply monotonous group activities of little immediate adaptive significance save for the expenditure of energy, standing very low in the general scale of group-behavior patterns.

As for the eventual adaptive value of milling, in different cases it may be positive (e.g., by increasing protection from enemies), negative (e.g., by displacing essential behavior functions), or may have no special significance. The biological value of such group behavior, a problem of considerable importance, must be worked out in terms of the general life economy of the respective animal forms in which it appears. In the present connection interest attaches to the nature of milling and its relation to other behavior resources in the given animal.

Analyses of milling in two animals have shown us that in such group functions the component individuals are dominated by action-engendered stimulus effects to which they respond in very reflex-like ways. Studied in itself, obviously, this type of group behavior does not necessarily provide us with a true picture of the given animal's capacities for more versatile adjustments under different conditions. It is apparent that the mere occurrence of

the milling pattern may be a misleading sign of psychological inferiority, since it may well obscure capacities for plastic, opportune adjustments not dominated by those native factors which account for milling.

It happens that the army-ant circular column really typifies the nature of the animal, even though *Eciton* milling is undoubtedly rare under field conditions. Detailed study of *Eciton* behavior under forest conditions shows that the individual is subject to fixed and prevalent, intrinsic (i.e., native) limitations canalizing its behavior quite narrowly. However, in its complex environment, the animal is provided incidentally with innumerable possibilities for variation in behavior through the heterogeneity of forest and jungle terrain. Such diversity in surrounding stimulation permits a limited repertoire of stereotyped individual reactions to function in the group setting in highly adaptive ways. Any beginning of monotonous behavior, as we have seen, consequently is certain to be interrupted in some manner, so that it becomes merely one of a series of diversified events in the *Eciton* raid. Thus it is environmental change that frees this animal from the direct consequences of its native individual limitations.

The frequency with which milling and similar rudimentary group functions appear in any given animal must be held as a fact of uncertain significance, until the limitations of the animal and its potentialities for new adaptive behavior are better known. For example, the fact that milling occurs with considerable frequency in schooling fishes is, of course, no certain indication that they stand psychologically below army ants, in which we have found the potentialities for such behavior great, although milling itself is highly exceptional under natural conditions. To be sure, the capacities of some fishes such as the herring

do appear to be rudimentary and highly limited, yet there are other schooling fishes in which milling occurs frequently, although at the same time the resources for variable and complex behavior are definitely wider than in the herring (Breder and Nigrelli, 1935).

On its face, then, simplified group behavior such as milling suggests merely a capacity for a psychologically reduced behavior under the given conditions. With respect to the general problem of social behavior, it is a reasonable proposition that the appearance of such elementary group patterns may disclose psychological limitations which are binding lifetime limitations, or may indicate merely a special propensity for routine mass activities under particular conditions, with a possible capacity for higher type adjustments when occasion warrants. Unfortunately this principle is frequently neglected in sociological writings.

In mammalian groups, the milling type of behavior has been featured in folklore presumably because of its spectacular character, as in descriptions of massed bison rushing in a frenzied stampede from prairie fire, sheep jumping fences blindly in column, and other instances of pell-mell surging by a horde of animals. This scarcely represents the normal and typical state of affairs in an adequate way. The scattered literature (Alverdes, 1927; Murchison, 1935) suggests that responses to the movement of other animals keep the group together and thus provide a basis for its activities, yet the simple stimulus-and-response relationships of mass formation appear to occupy a subordinate rôle in the ordinary activity patterns of any mammalian aggregation. It is mainly at times of sudden and great excitement that the highly simplified milling pattern dominates group behavior to the exclusion of other factors. For the most part, group activities in lower mammals appear to be plastically adaptive and rather finely adjusted to the given situation, as is evident from careful studies such as Darling's (1937) work with red deer and Carpenter's (1934) with howler monkeys. In general, the milling pattern seems to be a highly

subordinate aspect of herd behavior in lower mammals.

It is a matter of considerable interest that an animal as limited in its capacity for new learned behavior as the army ant seems to be may largely escape the non-adaptive consequences of great susceptibility for circular-pattern mass activities *only* by virtue of the incidental fact of environmental heterogeneity. In contrast, the far superior resources of mammals for trial and error learning are available, in addition to mere ecological variety, for admitting appropriate group adjustments that largely hold the milling type of behavior in the background. This should be the case in their group activities in the natural environment, where opportunities to learn new patterns are not subject to the limitations that hold in barnyard and stock pen.

It may be observed that the point applies even more emphatically to the social potentialities of man himself. Yet from the point of view of what may be termed the "herd instinct" school of sociological theorists, certain writers (e.g., LeBon, 1917; Trotter, 1915), operating on a subjective and non-experimental basis, have insisted upon the inevitability of emotionalized, individually degraded, regimented patterns in the group behavior of mankind. We find Trotter carrying the notion of "herd impulse" to the extreme of assuming that human subservience to the attitudes of the group is inborn, with the child instinctively responsive to what Trotter mysteriously calls the "voice of the herd." This idea is comparable to that other hoary mysticism, the "gregarious instinct," which accounts for animal aggregations by postulating an inborn tendency to aggregate.

On whatever level of the animal series we work, a scientific approach requires us first to examine the causes of monotonous patterns such as milling when they appear, then to study their relation to the potentialities of the animal for other types of behavior. From this point of view, it is apparent that the "herd instinct" school has erred not only in evading the question of how such behavior originates, but also in underestimating the resources of higher

animals for group versatility under new conditions. Particularly in the case of man, when milling behavior becomes undesirable or obnoxious, it is well to consider the canalizing, straitjacket influence of social institutions fostering group tendencies for such behavior. An enlightening study of such influences as prevalent in contemporary Germany has been carried out by Freeman (1940).

It may be observed that while army ants are constitutionally susceptible to the pre-dominance of circular-column behavior and can be freed from it only by the incidental fact of environmental variation, man is by no means susceptible in the same sense, with his cortical basis for versatile corrective patterns which under encouragement may reduce milling to the minor rôle of an occasional subway rush.

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