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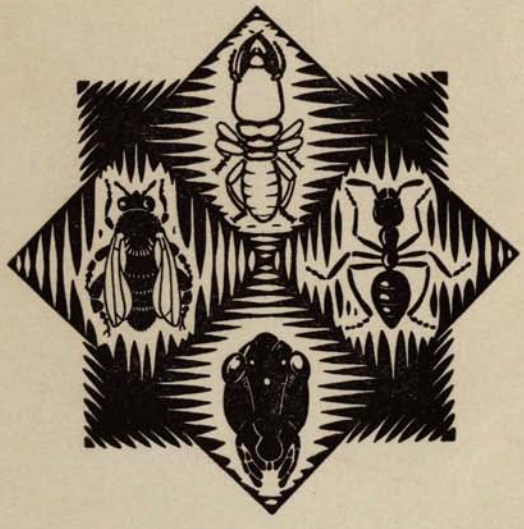

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THE ARMY-ANT QUEEN : KEYSTONE IN A SOCIAL SYSTEM[1]

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Although the Eciton queen does not directly lead the activities of her colony, her role is critical in the functional pattern (5). This queen is the unique reproductive female of her colony, with a prodigious egg-laying capacity almost from the time of emergence. Wingless throughout life, she differs from her sister workers not only in her much greater size and bulk, but in nearly all structural details (1, 2, 5, 9, 10, 11). She is truly irreplaceable in her social group (7, 8).

General Situation of the Queen in the Colony

The colony queen of these ants is never completely free from physical and social contact with workers. During daylight hours she remains in the midst of the curious temporary nest (or « bivouac ») formed of the clustered bodies of thousands of workers (3), usually stationed within a tight bolus of queen-affiliated workers in the upper center of the mass. Under normal conditions she is almost never exposed to light, even to the dim light of the tropical-forest environment, since she seldom emerges from the interior

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of the bivouac cluster except for an hour or two in the evening or night. Then she travels over 200 metres or more of meandering chemical trail, pushing along with a great wedge-shaped retinue of highly excited workers, to enter the new temporary nest which she will not leave until the next nighttime emigration brings her forth (4).

The army-ant queen is thus well-protected at all times. In the daytime she is surrounded by a thick wall of clustered workers, all capable of biting and stinging formidably when the bivouac is molested. At night, in the emigration, she runs along with workers surging about her, and even the slightest disturbance or impedance of progress may cause the queen to stop, whereupon excited workers promptly cluster over her. When an Eciton colony loses its queen, it is doomed (7). This is because the system of normal colony activities depends for its maintenance upon the presence of developing broods. In a functioning colony of Eciton hamatum, the queen produces, within a few days and in a single batch, more than 25.000 eggs, repeating this prodigious feat about every 36 days throughout the year (4, 5, 7, 8). In the ovaries of the queen of this species we have counted 2300 + ovarioles, and the queen of *E. burchelli* has an even larger number. The entire social function of the colony has evolved in relation to the cyclic reproductive pattern in the queen.

Relation to Activity Cycle

The army ants lead a cyclic pattern of life which centers about the queen's reproductive function. Investigation shows that members of any one great brood, all starting life and reaching each successive developmental stage nearly together, exert similar effects upon their colony (4). The brood influence proves to be most powerful in the colony. When a brood is passing through its larval stage of development, there are constant tactual and chemoreceptive stimulative relations between these active, voracious individuals and the worker population. The brood thereby exerts a « trophallactic » stimulative effect (12, 13) of great magnitude which excites the worker population greatly and continuously until the larvae are mature (6, 7). In fact, as the larvae grow, this stimulative effect increases steadily. But precisely at the time when the larvae become mature and spin their cocoons, their group stimulative influence falls sharply, and correspondingly the worker population is greatly reduced in its level of activity in normal colony function such as

raiding. The daily raiding forays then drop greatly in magnitude and the colony carries out no further emigrations. This condition of low activity persists until a further major brood change (the emergence of the callow workers) again sharply raises the level of trophallactic stimulative relations between adults and brood.

This social function of the brood must be kept in mind if we are to understand the time relations of the entire army-ant cyclic activity system. In *E. hamatum* the phase of large raids and nightly emigrations, the *nomadic* phase, lasts 16 or 17 days as a rule, and the *statary* phase of small raids and non-nomadic activity usually lasts about 20 days. This nomadic-statary cycle normally is maintained stably, without much varition in the length of its respective phases, as long as further new broods continue to appear at regular intervals. Since the queen always produces a new great batch of eggs midway in each statary phase, two important events synchronize at the end of this phase : 1) the emergence of the older brood from cocoons sets the colony into nomadic function and maintains this condition for a few days ; and 2) when this trophallactic energizing effect of the callow brood falls off after four or five days, the new brood reaches an early larval stage at which it becomes a social-stimulative factor capable of maintaining nomadic function in the colony (4, 6, 7).

Egg-laying timed by extrinsic social events

The pacemaker function seems not to be endogenous to the the course of its activities. Her capacities and functions nevertheless are most essential to the social pattern. In particular, the foregoing facts indicate that the system of cyclic behavioral events in the colony somehow depends upon the egg-laying cycle of the queen for its timing. Hence, whatever governs the timing of the queen's reproductive cycle may be considered the crucial pacesetter of the cyclic social pattern (5, 7).

The pacemaker function seems no to be endogenous to the queen, and dependent upon some internal rhythm, as one might first suspect (5). Instead, we find that each new egg-laying episode is set off by an extrinsic change arising at a particular juncture in normal colony functions. The nature of this exogenous factor has been clarified by studies of brood-adult relations in the colony in relation to changes in the queen (7). When one of the great Eciton broods approaches larval maturity, the social-stimulative effect of

this brood upon workers nears its peak. The increased intensity of trophallactic relations between brood and adults now provides the indirect stimulative basis for the largest daily raids of the nomadic phase, and thereby, increasingly great quantities of booty are brought to the bivouac. But at the same time, more and more of the larvae (the largest castes first of all) soon reduce their feeding to zero as they complete their larval stage and begin to spin.

Thus, during the last few days of a nomadic phase, the larval brood energizes large colony raids, but uses less and less of the food thereby obtained. A food surplus arises, and the queen begins to feed quite voraciously. It is possible that the queen does not gorge automatically in the presence of plenty, but that she is started and also maintained in the process by intensified trophallactic attentions from the greatly enlivened worker population. Whitin the last three days of each nomadic phase the queen's gaster swells noticeably, first of all from a recrudescence of the fat bodies, then from an accelerating maturation of eggs. At the end of the phase, when the mature larval brood feeds no more and is occupied with spinning, the queen is so physogastric that the inter-segmental membranes of the abdomen are exposed as broadening white bands between the separated sclerites.

Even when the colony has entered the statary condition, with much smaller daily raids and no emigrations, the queen continues to advance in physogastry, and maturation of eggs accelerates. Since colony food consumption now is much reduced, the smaller raids bring in sufficient food to support the overfeeding of the queen until she is maximally physogastric. The point is that within these few days, although the larvae all have begun to spin and are taking no food, their spinning activities within the thin envelopes stimulate and energize the adult workers sufficiently to insure daily raids of moderate size. These occurrences, regularly associated with the termination of a nomadic phase, are adequate to prepare the queen for a massive egg-laying operation which begins about one week after the nomadic phase ends. All of the eggs for a great new brood are then delivered within about six days.

My theory therefore is that the queen is set off into each new egg-production episode, in a « feed-back » fashion, by events in the activity cycle which themselves are indirect results of the queen's own function at an earlier point in the cycle. The actual control of timing in the cycle thus would depend upon the duration of developmental stages in the brood as it matures under stable environ-

mental conditions in the colony bivouac (7). Between reproductive episodes, until the next appearance of a mature larval brood, the queen remains in a « resting » condition with fully contracted gaster. At such times, when no continued over-feeding can occur, the queen's fat bodies are minimal and the maturation of all eggs is checked at an early point by resorption.

The Queen as a Factor in Colony Organization

In addition to the queen's basic role in the colony activity cycle due to her reproductive capacity, she also serves as an important factor in colony unity. This function is clearly emphasized by the effect of removing the queen from the colony. Within an hour or two the workers begin to back-track, that is to follow the old chemical trail developed in the raiding foray of the preceding day and followed in the emigration of the preceeding night. Normally this trail is used only briefly if at all on the new day as further chemical trails are developed (7). But when a queen is removed from her bivouac, within an hour or two workers begin to file out along the abandoned route to the earlier bivouac site, from which they spread into radiating chemical trails used on the previous day, and in time may pass back into even older trails. To learn from which quarter a newly found colony has approached, we have only to remove the queen from the bivouac.

From these and other facts, we develop the concept of a queen odor which is attractive to all workers in her colony but most effective for a « queen-affiliated nucleus » of workers longest and most intimately associated with the queen. There is much supporting evidence. For example, when the queen is removed from the upper center of the colony bivouac we may segregate and mark distinctively the workers which have been clustered tightly around her, taking also a group of equal number from elsewhere in the bivouac. These workers are then placed in an experimental area into which the queen is later introduced. Without exception, it is the marked workers removed from the queen bolus of the bivouac which now soon preponderate near the queen and in the mass eventually formed around her.

Howerver, the specific chemical of the queen is attractive to all members of her colony. This can be tested readily by permitting the queen to rest for a given time on a piece of moistened blotting paper, then presenting the quartered pieces of « queen-chemical

saturated » blotter to workers of the colony. The workers are likely to gather on one or more of the saturated pieces, but not on fresh pieces of blotter spread at random among them.

Thus it is reasonable to believe that various chemical products specific to the queen's own organic processes form a composite which is highly attractive to workers, as a stimulus pattern specific to the queen of their colony. This postulation is supported by facts such as the following. Normally, when two colonies of the same Eciton species happen to cross paths in raiding, the workers do not inter-mix but seem markedly disturbed when they meet. Lines of agitated workers soon form at the border, and behind these the separate activities of the colonies are continued without any fusion of personnel. The outcome is very different if one of the colonies has lost its queen some time before the meeting. Then, when their columns meet there may be some indications of disturbance, but soon the workers of the queenless colony begin to intermingle freely with the others, which receive them readily on the whole, and eventually the queenless colony and the normal colony have fused into one.

Facts such as these point to two normal properties of an Eciton colony based upon the queen odor-pattern. First, the workers become habituated to the specific queen-odor of their colony, so that they cluster most readily in its presence and are disturbed by queen odors which differ from it. Second, the workers bear upon their own bodies persistent traces of the specific odor of their queen, which facilitate normal activities based on acceptance in their own colony, but which disturb and repel workers of other colonies. After the queen has been removed, it is evidently workers of the former queen-affiliated nucleus which are restless in her absence, hence likely to leave the bivouac center and circulate along all available trails. It is probably these workers which are most disturbed upon meeting a foreign colony, and in turn are most disturbing to the strangers, even some time after the queen has disappeared. But other workers in the colony evidently have less intense queen-odor traces which weaken sooner, as well as a lower queen-odor habituation which can fall off sufficiently in time. It is presumably the latter condition which permits a fusion of two colonies when one or both have lost their queens.

Although the biochemical influence of the queen appears to be an important factor in colony unity, it is by no means an invariable factor. The processes of trophallaxis normally provide a

means whereby this factor exerts its influence throughout the community, although to relatively different extents, gradient-wise, according to individual differences in the frequency and intensity of opportunities for association with the queen nucleus. A useful view of the situation may be gained by considering certain changes which may be expected to occur in the life of any colony.

The Process of Colony Division

Normally the attractiveness of an Eciton queen to her colony varies only minimally through each of the activity cycles, as successive worker broods are produced. Although strong at all times for her nucleus of workers, it seems to be somewhat stronger for the rest of the colony when very young worker larvae are present than when these larvae are nearing maturity. However, this suspected variation can have no more than a secondary significance and offers no apparent threat to the queen's general status in the colony.

The situation is very different when a sexual brood is produced (8). This type of brood contains no workers, but in *E. hamatum* consists of about 1.500 males and a very few young queens (only about six, we find). Almost always, sexual broods appear early in the dry season. No colony produces more than one such brood in a given year, and it also appears that the sexual brood is not necessarily an annual event in any Eciton colony. When this unique type of brood appears, colony reactions to the functional queen deviate significantly from the normal pattern of events with worker broods.

Even when the larvae of a sexual brood are still very young, an appreciable part of the worker population has become affiliated maximally with the brood and minimally with the functional queen. By the time the larval sexual brood is nearly mature, this deviation has sharpened to the point at which the colony (although still a unity in normal operations such as raiding and bivouacking) has two latent sub-sections : 1) a brood-free part of the bivouac in which is found the functional queen with her affiliated workers ; and 2) a section of the bivouac in which workers hold the sexual brood. No actual splitting of the colony has occurred, yet there are important behavioral differences between these two sections. One is in their reactions to the queen. If the queen is removed for a few hours at this time, she is readily accepted when introduced

to the brood-free zone, but difficulties may be expected when she is presented to workers in the brood zone, resulting in her non-acceptance there. Also, signs of worker cannibalism at the expense of the brood are noted at the border of the brood-free zone. Here, when the brood is enclosed, empty cocoons are often found among the clustered workers.

There are many indications that a considerable part of the worker population is strongly attracted to the sexual brood (and particularly to the young queens in this brood) on the basis of its unique stimulative properties. The greater strength of this attraction, as compared with attraction to a worker brood, is indicated by the vigorous manner in which adult workers respond to the sexual individuals in normal bivouac activities such as licking them and carrying them about, clustering over them in the bivouac, and transporting them in the emigration. Observations and tests indicate that this attraction is based especially upon chemoreceptive stimuli from the sexual brood, to which the workers become strongly habituated.

The processes lead to an overt colony division. First of all the young queens emerge from their cocoons from one to three days in advance of all the males. The workers cluster excitedly over the callow queens, but there is evidence of a gradation in this response. The first one or two new queens which emerge elicit worker responses resembling those to an adult queen in nature and intensity, but worker responses to the others are less intense on the whole, and are definitely ambivalent. Tests show that these young queens differ distinctively in their stimulative effect upon the workers.

A few days later, when emergence of the males energizes the colony sufficiently, a nomadic phase is initiated by a maximal raid and an emigration. This movement is not over a single raiding trail, with the colony remaining together as with an emerging worker brood, but leads divergently over two separate radial trails. When this emigration is finished, there exist two daughter colonies bivouacked in well separated places, each with its own queen.

For the detailed processes of this division the previously established polarization of the bivouac is of basic importance. As the raid develops during the day, the young queens and their nuclei of workers move out on one radial trail, the old queen with her nucleus on another radial trail. But as a rule only one of the virgin queens can make her way before the others to the peripheral place where the persistent cluster of the eventual daughter colony is

formed. The others are held back by a clinging and clustering of workers which impedes their locomotion, a distinctive reaction of workers to less-accepted queens which I have called « sealing-off » (8). When callow queens happen to make their way from the bivouac into the chemical trail along which the adult queen is passing to a new peripheral station, they are held back similary by a sealing-off reaction of the workers.

Most frequently in our studies, the adult queen of the old colony dominates one raiding line and becomes established in the new daughter bivouac formed on that line, and one of the virgin queens becomes established in the new daughter bivouac on another raiding line. In this complex of events there are factors at work which hold the fission process to a bilateral division into daughter colonies of nearly equal size, each eventually containing approximately half of the adult worker population, half of the callow males, and half of the young larval (worker) brood. These factors may be traced to a fission process which really begins during the development of the sexual brood, but remains latent until this brood emerges.

As for the remaining virgin queens, they are lost. The sealing-off process tends to press them back toward the bivouac site which is being abandoned, and away from the bivouacs of the two new daughter colonies. Gradually the workers disappear from the two divergent trails leading to the new bivouacs, leaving the supplementary virgins to their solitary fates.

The Supersedure of Old Functional Queens

In a minority of our cases, the adult functional queen of the parent colony is the victim of a sealing-off reaction and eventual abandonment, so that the two daughter colonies in that event have young queens. In one colony of *Eciton burchelli*, investigated in detail, a large tight cluster of workers was seen near the central division site, at the edge of one of the trails on which daughter queens had been observed. After many hours during which it shifted only slightly as the major colony division progressed, this cluster still held a place near the old bivouac site. Meanwhile, two separate clusters had formed on divergent raiding lines, each containing a callow queen. With colony division now a fait accompli, the tight cluster near the old colony site was examined. From it a single queen was taken, certainly an adult queen and probably the old colony queen. Her gaster was noticeably distended and

flabby in appearance. (An eventual histological examination disclosed that her tissues were in poor condition and the fat bodies of her gaster were abnormally enlarged). This no doubt was a case of supersedure, in which a queen of advanced age was replaced by one of her own daughters.

The reproductive capacities of this queen had not failed, since only about twelve days before her supersedure she had delivered a great batch of more than 35.000 eggs, a potential worker brood, close to normal in size for this species. A histological examination revealed masses of sperms in her spermatheca. However, there were indications that the organic changes of advanced age had reduced her stimulative attractiveness for workers so far that she could not compete with the leading members of the virgin group. Interestingly enough, most of the workers which remained persistently with the old queen were darker in pigmentation than the general population, indicating their own advanced age.

Initiation of Function in Daughter Queens

A new colony queen, a recently accepted virgin, evidently has a somewhat precarious position in her new colony at the start. She is well accepted only by a relatively small nucleus of workers, so that if she is removed from her central cluster and returned to a marginal place in the bivouac or near a raiding trail, she is likely to be sealed off and eventually abandoned. An adult queen, similarly tested, invariably is reaccepted without difficulty. However, since the worker nucleus affiliated with the young queen always remains closely about her, there is time for the gradual development of a more complete habituation in the colony to her specific odor.

The young queens are certainly virgin at the time of colony division, but evidently are fertilized at some time within the first week in the nomadic phase of their colonies. The mating process is complex, since first the males must fly out from their parent colonies, then wander about as dealates until a chemical trail of their species is encountered on which a host colony may be entered. Finally, it is probable that in the Ecitons the actual mating can occur only at night during a colony emigration, when the essential high level of excitement is reached as some male is able to penetrate the agitated retinue of workers surrounding the queen.

Daughter queens captured in the first nomadic days of their colonies prove to be unfertilized, but those taken after about one

week are found with masses of sperms in their receptacles when examined histologically. Hundreds of thousands of sperms are present, no doubt sufficient for a year or more of full reproductive function. In one year, a queen of *E. hamatum* produces about 10 broods each containing 25.000 or more workers. We know that adult queens may be refertilized, but do not know whether refertilization is an annual event.

New Eciton queens seem to begin their adult reproductive functions promptly and fully. We find that daughter colonies with young queens pass through a nomadic phase of nearly the normal duration for the species, then enter a statary phase in the usual manner. The early stages of physogastry are apparent in the young queen at this time, and midway in the statary phase a batch of eggs is delivered by her which is as large or nearly as large as that produced by any adult queen at the corresponding time. Therefore, the principal events appear to be much the same as with adult functional queens.

The Functional Life of an Eciton Queen

The army-ant queen evidently continues a full reproductive function in a regular manner for a considerable time unless some accident intervenes. We have followed numerous colonies of both *E. hamatum* and *burchelli* for more than 4 months, during which the queens invariably continue to deliver great new broods at the characteristic intervals. In all operative colonies, at all times, this is the case. Processes of maximal reproductive function evidently continue throughout the life of the Eciton queen in her colony.

Normally, this life seems to be a long one. We have been able to keep queens on record for considerable periods of time by marking them in a permanent and distinctive manner. According to code, one or two minute triangles of exoskeleton are cut with iridectomy scissors from the edge of abdominal sclerites. The cut edges darken somewhat, so that one can recognize marked queens without a lens when they are removed later on from their colonies.

Many recoveries have been made after several months, and a few after one year. Our longest record thus far is that of an *E. hamatum* colony (H-15) of which the queen was marked on Dec. 23, 1947. This queen was reidentified by means of her distinctive mark on April 3, 1952. She was still in vigourous condition and

normal reproductive function on May 25, 1952, when her colony was last seen. Queen H-15 therefore had a functional life of at least four and one-half years, in which an estimated total of 45 broods (i. e., probably more than 1.125.000 workers) had been produced. How much longer her useful life span may have been, cannot be said. Other evidence suggests that the case may not be exceptional among the Ecitons.

Summary

An intricate functional system centers about the single queen of an Eciton colony. Her reproductive function is a basic and indispensable factor in the activity cycle of the colony. This is because each of the great broods, when in the larval condition, powerfully energizes colony activity through trophallactic stimulative relations with workers. Thus, nomadic phases appear periodically in colony life, with intervening statary (sessile) phases. Delivery of successive broods by the queen, at regular intervals, is due to an extrinsic factor, an over-feeding precisely in connection with cyclic changes, and not to an endogenous rhythm in the queen herself. Basic aspects of colony organization, such as the maintenance of a stable bivouac or temporary nest, and distinctive worker reactions to their own colony against others, are attributable to trophallactic relations between workers and queen. Worker reactions to a specific queen-odor play an important role in colony unity. The properties of the unique bisexual brood are such that a considerable part of the colony affiliates on a chemoreceptive basis with this brood, while a part remains affiliated with the adult queen. The colony fission is at first latent, but becomes actual when the sexual brood emerges. A hierarchy among the young queens in their attractiveness for workers is a critical factor in colony division. In this process iwo daughter colonies are formed, evidence that at times an adult queen of advanced age may be superseded by a virgin queen. Virgin queens are fertilized within a few days after division is completed, and full reproductive function begins in synchronization with the first cyclic change thereafter. This begins a period, possibly as long as five years, in which this queen serves as a key factor in the social life of her colony.

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