TERRITORIALITY IN ANTS

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A territory is generally defined as an area which the animal or the animal society uses exclusively and defends against intra- and sometimes interspecific intruders. The behavioral organization and the adaptive significance of aggression and territoriality in animals remain among the central problems in the study of animal behavior. Territorial strategies seem to be especially elaborate in animal species that live in well organized societies. The territorial behavior of social insects in particular is based on a division of labor and on a complex communication system.

It has been known for a long time that many ant species establish and maintain territories, but only recently have biologists begun to analyze the diversity of their territorial strategies and the underlying communication mechanisms. Our first results demonstrate that the complexity of territorial and aggressive behavior in ants surpasses almost everything that we know about aggression in other animal species, with the possible exception of *Homo sapiens*. In the presentation to follow I will attempt to demonstrate that the diversity of territorial strategies is a direct consequence of different strategies of resource exploitation in ants. But first we have to consider the basic distinction between ant societies that have a single queen (monogynous) and those that have multiple queens (polygynous). Queens of truly polygynous species such as *Formica polyctena* or *Formica exectoides* are usually not aggressive to one another. In fact they are often found clustered together in large numbers, and so far as known all lay eggs and are not organized into dominance orders. Queens of monogynous colonies, in contrast, do not tolerate other queens in their vicinity. The difference is maintained among mature colonies: workers of polygynous colonies are usually not or relatively little aggressive to conspecific neighboring colonies. Sometimes the whole population of nests can be considered as one large polydomous colony, because workers, brood and even queens are frequently exchanged between different nests. On the other side, workers of most monogynous species discriminate aggressively against members of conspecific neighbor colonies, and they are often highly territorial.

By comparing the mating and colony-founding strategies we can further conclude that within-nest matings occur quite frequently in polygynous species, leading to a relatively high degree of inbreeding, with new colonies being mostly founded by a budding procedure. In monogynous species within-nest matings are extremely rare. Usually all alate sexuals leave the nest during the nuptial flight period, and individuals from many different nests mix in massive mating aggregations. This procedure assures a high degree of outbreeding. After mating the young females of most monogynous species found their colonies independently, usually far away from their mother colony. Consequently neighboring colonies, of many polygynous species, can be expected to be genetically much more closely related than neighboring colonies of monogynous species.

Although some of the ecological factors that favor polygyny and the abandonment of territoriality in ants have been identified (Hölldobler and Wilson, 1977), it generally appears true that insect societies have been biased toward monogyny in the course of evolution by natural selection. In theory, queens should prefer to retain personal reproductive rights and surrender none to their sisters or daughters, because they are more closely related to their daughters and sons than to their nieces, nephews, and grand offspring. Since one queen usually is able to supply as many eggs as a worker force can rear, extra queens would be an unnecessary energetic burden on the colony, an especially significant factor during the colony's early growth; monogyny should therefore also be of advantage to the workers. From this, a tendency to monopolize ecological resources on which the colony fitness depends seems to be the logical optimum, and indeed, many monogynous ant colonies have evolved specific strategies to secure nesting sites and foraging space in competition with conspecific neighboring colonies. In order to illustrate these and other principles in colonial organization, I will now describe three territorial strategies, the behavioral organization and significance of which have only recently been analyzed (Hölldobler, 1976; Hölldobler and Wilson, 1978).

WEAVER ANTS

The African Weaver Ant (*Oecophylla longinoda*) is one of the dominant ant species in forest canopies.

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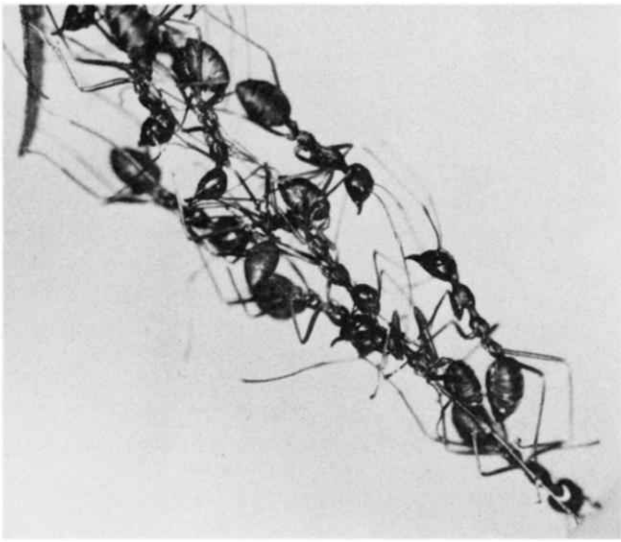

FIG. 1. Workers of *O. longinoda* form living bridges by linking their bodies into chains when exploring new terrain. The worker seen running over the lower portion of this bridge is laying an odor trail from her everted rectal gland directly onto the bodies of her nest mates. The trail will guide other members of the colony to a newly available foraging space. (From Hölldobler and Wilson, 1978.)

Its colonies are exceptionally aggressive and territorial, tolerating almost no other ant species in the trees they occupy. They also exclude one another in aggressive interactions so severe as to create narrow, unoccupied corridors that are in effect "no ants' land." In our experimental studies we have identified no less than five recruitment systems used by *O. longinoda* to explore, seize, and exploit new terrain, constituting the most complex repertory thus far discovered in ants.

Workers of *O. longinoda* patrol the surroundings of their nest and nest tree restlessly. If a tree branch or another conspicuous object is placed near the nest tree, groups of workers, orienting visually, mass on the nearest twig or branch and attempt to reach the object by forming living bridges with their bodies (fig. 1). If they succeed, those crossing over begin to lay trails back and forth across the new space. Many return all the way to the nest, and while doing so lay trails directly across the bodies of the nest mates making the living bridge. This trail laying or long-range recruitment results in an outpouring of additional workers onto the fresh space; they begin to explore and patrol the new terrain on their own. The trail laying is achieved by an eversion of what we called the rectal gland. This organ is a specialized terminal sector of the rectal sac. In order to lay a trail the ant lowers her abdomen, rotates the terminal portion downward, and extrudes the rectal gland. The glandular applicators are then dragged lightly over the substratum, resting on a "sled" composed of two pairs of long bristles (fig. 2).

During territorial patrol a second form of communication is involved, which we called short-range recruitment. When workers encounter alien *Oecophylla* workers or other kinds of ants too large for them to seize and hold on the spot, they chase the intruder through distances of 15 cm or more while dragging the end of the abdomen (but not the anus) over the ground (fig. 2). This behavior is entirely different from ordinary trail laying employed during recruitment to new terrain and food discovery. Nearby workers are attracted over distances of up to 10 cm to the area where the display occurred and tend to settle there in loose clusters. The result is a change in the overall spatial pattern of *Oecophylla* workers in those portions of the territory through which the intruders have moved, from random distributions to moderately or strongly clumped distributions. In laboratory and field experiments clusters of workers were able to retain and subdue invaders in much

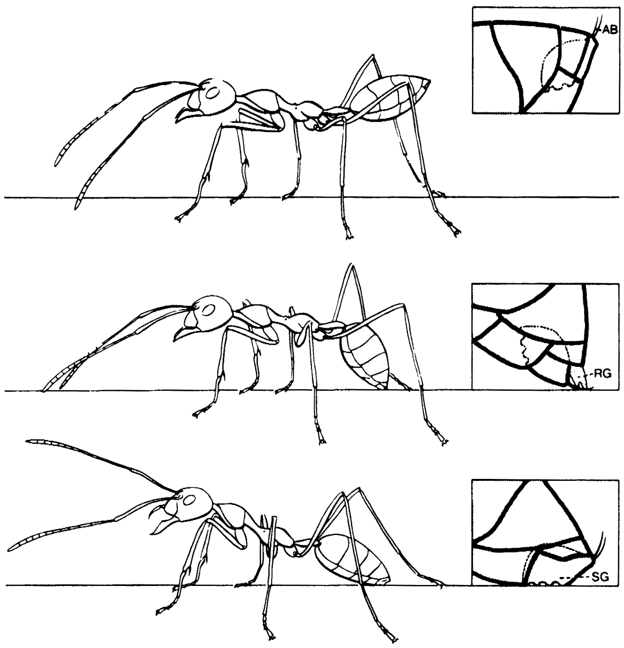

FIG. 2. The modes of application of pheromones from the rectal gland and sternal gland by workers of *O. longinoda*. Above: Ordinary running posture of a worker; as shown in the inset to the right, the terminal abdominal segment is held so that the sternal gland surface is covered by the penultimate abdominal sternite, and the rectal gland remains retracted within the wall of the rectal vesicle. Middle: Worker laying odor trail from the extruded rectal gland, which "rides" on the bristles of the acidopore, located just beneath the anus; the sternal gland surface remains covered. Below: Worker depositing sternal gland substance onto the substratum; the terminal abdominal segment has been rotated upward to expose the gland openings, while the rectal gland remains retracted. (From Hölldobler and Wilson, 1978.)

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shorter periods of time than are single defenders (fig. 3).

How is new space recognized? Weaver ants have excellent visual orientation, and they are able to remember the appearance of many details in their nest environment. Merely shifting the foraging arena through 90° is enough to release the recruitment process into new space. We also noticed when workers discovered entirely new terrain they deposited drops of rectal sac fluid at a high rate all over the area. This behavior contrasts with that of most other ant species, which discard rectal material in kitchen middens or other restricted areas outside the nest. This led us to suspect that the *Oecophylla* workers deposit a special scent to mark their home range and perhaps even to advertise their territory. We tested this hypothesis by the following procedure. A colony was first allowed to mark the papered floor of an arena for a period of several days. Then the ants were removed overnight, and the arena was shifted slightly to one side to make room for a second, identical arena that had been marked by an alien colony of *Oecophylla*. The alignment of the two arenas otherwise remained the same as that of the original arena in its undisplaced position. The colony was then given access to both arenas simultaneously. The results suggest the presence of a colony-specific pheromone. The first workers to enter the alien arena displayed greater caution and a significantly higher rate of aggressive posturing (fig. 4). The exploring ants showed a particular interest in the anal spots, inspecting them with their antennae. Furthermore we could demonstrate that the fecal chemicals provide

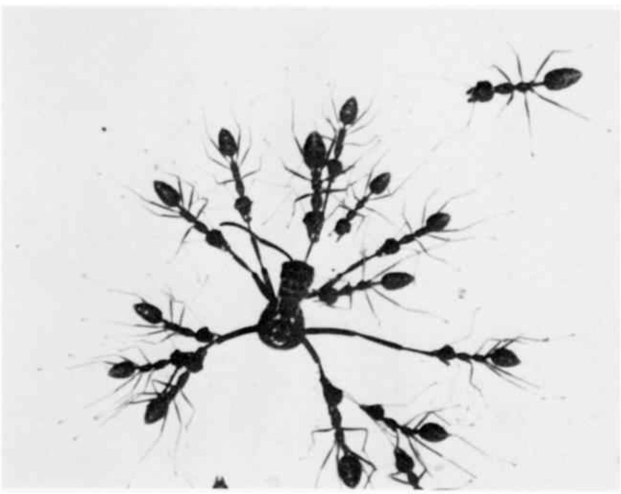

FIG. 3. A worker of the African tree ant *Polyrhachis militaris* has been spread-eagled and immobilized by *Oecophylla* workers. The capture of this large ant requires the initial cooperation of at least three *Oecophylla* workers, and the effort is abetted by both long-range and short-range recruitment of defending nest mates to the vicinity. (From Hölldobler and Wilson, 1978.)

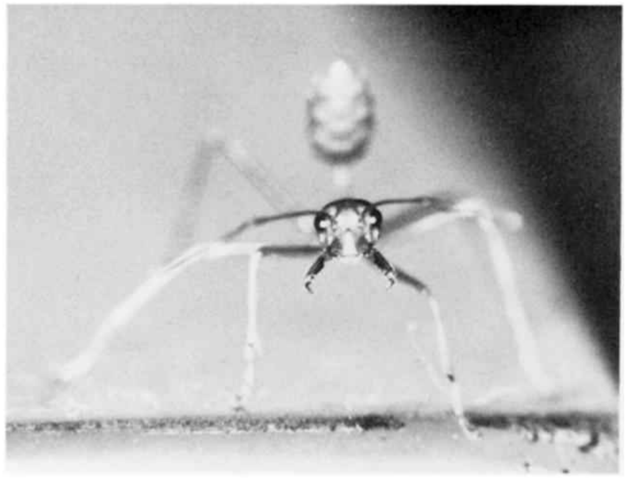

FIG. 4. Aggressive posture of a major worker of *O. longinoda*. (From Hölldobler and Wilson, 1978.)

an advantage to the defenders during territorial combat. We arranged a series of eight wars between colonies in arenas spotted previously by one selected colony or another. In each case the "owners" were less hesitant in foraging over the terrain and quicker to recruit nest mates when they encountered strangers. As a result they gained the initial advantage and secured more ground during the initial fighting. In African habitats such battles sometimes last for days, with the opponents massing along lines of defense that slowly shift back and forth as one colony or the other is able to press its advantage. Once the territorial borders are established, however, very little fighting between neighboring colonies can be observed. The territorial pheromone seems to have a deterring effect on workers of neighboring colonies.

HARVESTER ANTS

Generally the partitioning of space in the field between ant colonies is effective in reducing aggression between individuals belonging to the same species but to different colonies. However, the pattern of space partitioning can be very different and depends largely on the foraging strategies of the species. The Weaver Ants hunt for randomly dispersed insect prey in their territories, they search for it all over the area surrounding their nests and therefore exclude possible competitors from these foraging grounds. In contrast, some harvester ant species, such as *Pogonomyrmex barbatus* and *P. rugosus,* which are among the most abundant species of the southwestern United States, tend to exploit patchy food supplies and accordingly show a more complex partitioning structure. Foragers of these species travel on well-established trunk trails before diverging on individual excursions. After foraging the workers return to these routes for homing. Such trunk trails sometimes extend for more than 40 m; they are remarkably per-

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FIG. 5. Photograph showing a *P. rugosus* nest with two distinct trunk trails. (From Hölldobler, 1976.)

sistent over long periods of time and even survive heavy rainfalls (fig. 5).

In a series of experiments I demonstrated that the trunk routes originate from recruitment trails to newly discovered seed falls. The recruitment pheromone, which is relatively short-lived, is discharged from the poison gland and deposited with the extruded sting on the ground. Because the seed patches are frequently quite stable, the ants continue to travel along the former recruitment trail to these foraging sites. Laboratory and field experiments have revealed that enduring chemical signposts are also deposited along the trail which, together with the visual markers, serve as orientation cues long after the recruitment signal has vanished. An extensive field study in Arizona revealed that such trunk trails used by *P. barbatus* and *P. rugosus* during foraging and homing have the effect of avoiding massive aggressive confrontations between neighboring colonies, while at the same time enlarging the foraging area for patchy food supplies. They channel the mass of foragers of hostile neighboring nests into diverging directions before each ant pursues its individual foraging effort. The trunk trails, together with the immediate surrounding of the nest entrance of mature *P. barbatus* and *P. rugosus* nests, can be considered to be the "core area" of the colony's territory. It is the area of the heaviest regular use within the home range and is kept clear of members of other conspecific colonies. If, by experimental means, two trunk trails of neighboring colonies are brought into contact, heavy aggressive mass confrontations occur (fig. 6). Although foraging areas of nearby colonies can overlap, fighting in the overlap zone is usually limited to individual confrontation between two foragers. Fighting inside the core area tends to be much more prolonged and vigorous than that at the foraging ground. One additional interesting observation should be mentioned here. In a series of experiments I displaced a number of ants from a trunk trail to near the nest entrance of a nearby conspecific colony. As expected, fierce fighting almost always ensued. Surprisingly, however, the fighting did not continue for long at the same spot; instead the displaced ants were rather dragged or even carried by the nest inhabitants 10 to 18 m away from the nest and then released. The inhabitants quickly returned to their nest, whereas the displaced ants searched around randomly, and only a few were observed to find their way back to their own nest. From these and similar experiments we can conclude that the farther away from its nest the intruder is, the less vigorous are the aggressive confrontations with the defenders. Only when neighboring colonies are located too closely together will increased aggressive interactions eventually lead to emigration of the weaker colony. In several cases I witnessed such a colony expulsion. Thus, although the major function of the trunk route foraging system seems to be to facilitate the exploitation of patchily distributed and relatively stable food sources, the topographic design of the route system of one colony

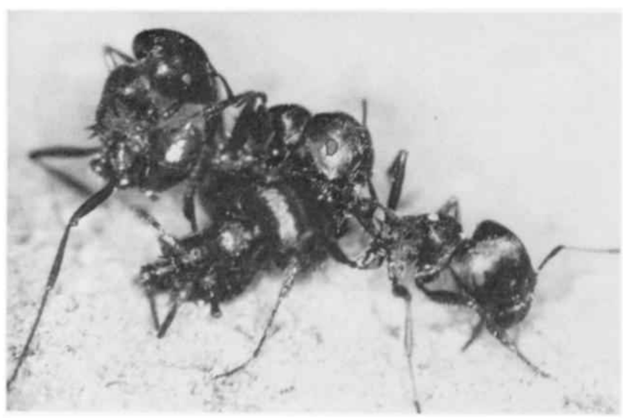

FIG. 6. Fighting between *P. rugosus* workers belonging to neighboring nests. (From Hölldobler, 1976.)

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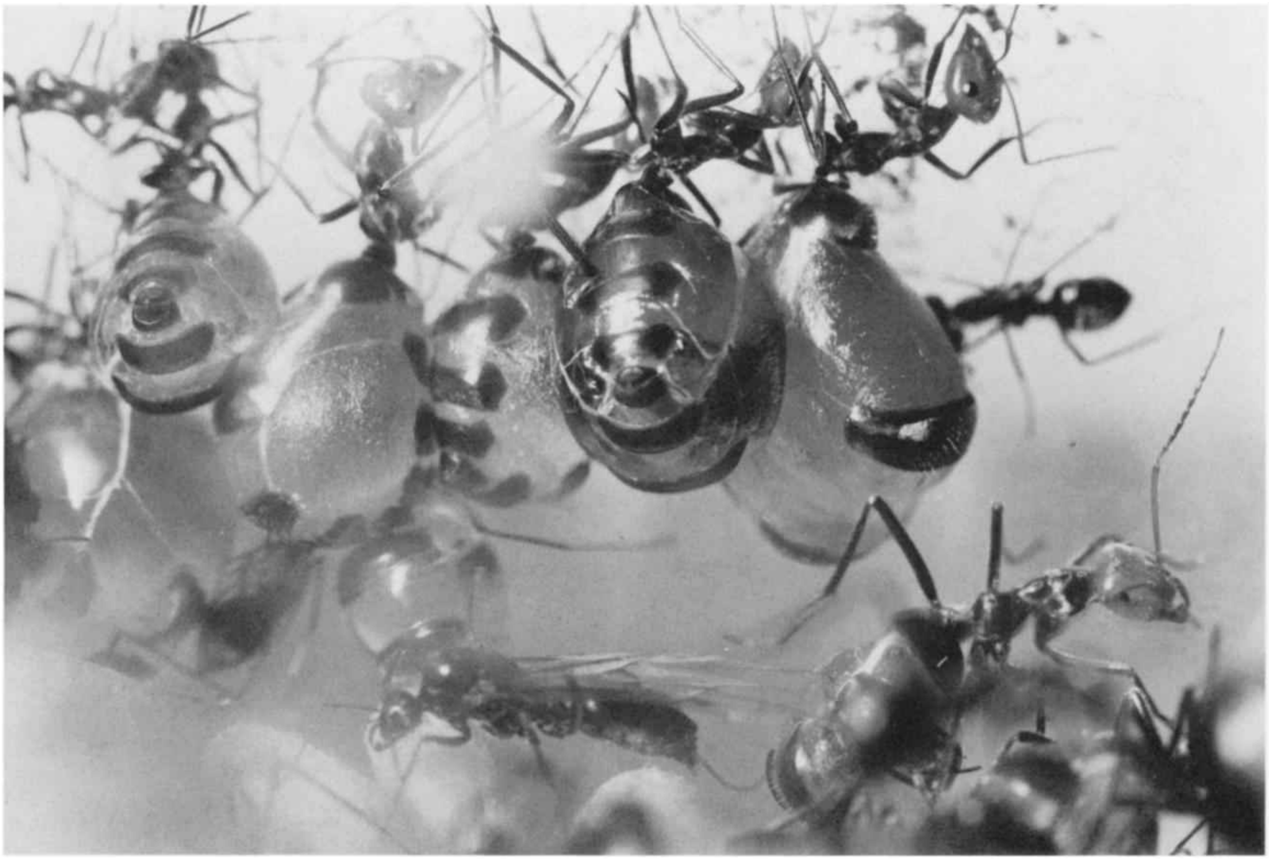

FIG. 7. The honeypot caste of *Myrmecocystus*.

depends greatly on the route maps of its neighboring colonies. If the trunk routes of two neighboring colonies approach too closely, fighting between the foragers will increase and this will eventually lead to a diversion of one or both trunk trails. Although the territories of *Oecophylla* and *Pogonomyrmex* have different designs, the outlines are relatively stable in the two genera. In both cases, the territorial borders are established by massive physical fights between neighboring parties, that lead to the death of hundreds of workers in both colonies, but once the borders have been stabilized massive fighting becomes rare.

HONEYPOT ANTS

I will now describe a third territorial strategy in ants in which the territorial borders are kept very flexible. This strategy appears to have evolved as part of a foraging system designed to utilize patchily distributed but unpredictable or unstable food sources. The honeypot ant (*Myrmecocystus mimicus*) is abundant in the mesquite-acacia community of the southwestern United States, and like other members of its genus, it has a special honeypot caste, the members of which function as living storage containers. When their crops are filled to capacity, their gasters expand to almost the size of a cherry (fig. 7). One of the major food sources of *M. mimicus* are termites. When a scout ant discovers a rich supply of termites, for example under a piece of dried cattle dung, it directs a group of nestmates to this food supply by means of special recruitment signals. If another colony of *M. mimicus* is located nearby the food source, and is detected by the foragers of the first colony, some of them rush home and recruit an army of 200 or more workers to the foreign colony. They swarm over the nest and engage all workers, who emerge from the nest entrance in an elaborate display tournament, thus blocking this colony's access to the food supply. Frequently scouts leave the tournament to return to their colony in order to recruit reinforcement, while the other group of nestmates continues to retrieve the termite prey. Once the food source has been exhausted, and the foraging activity in this area declines, the tournament activity at the neighboring nest site also slows down and the intruding army finally retreats to its own nest. Frequently neighboring colonies of *M. mimicus* conduct territorial tournaments in a zone between their respective nests, thus preventing alien foragers from venturing into the respective foraging areas of each. The tournaments

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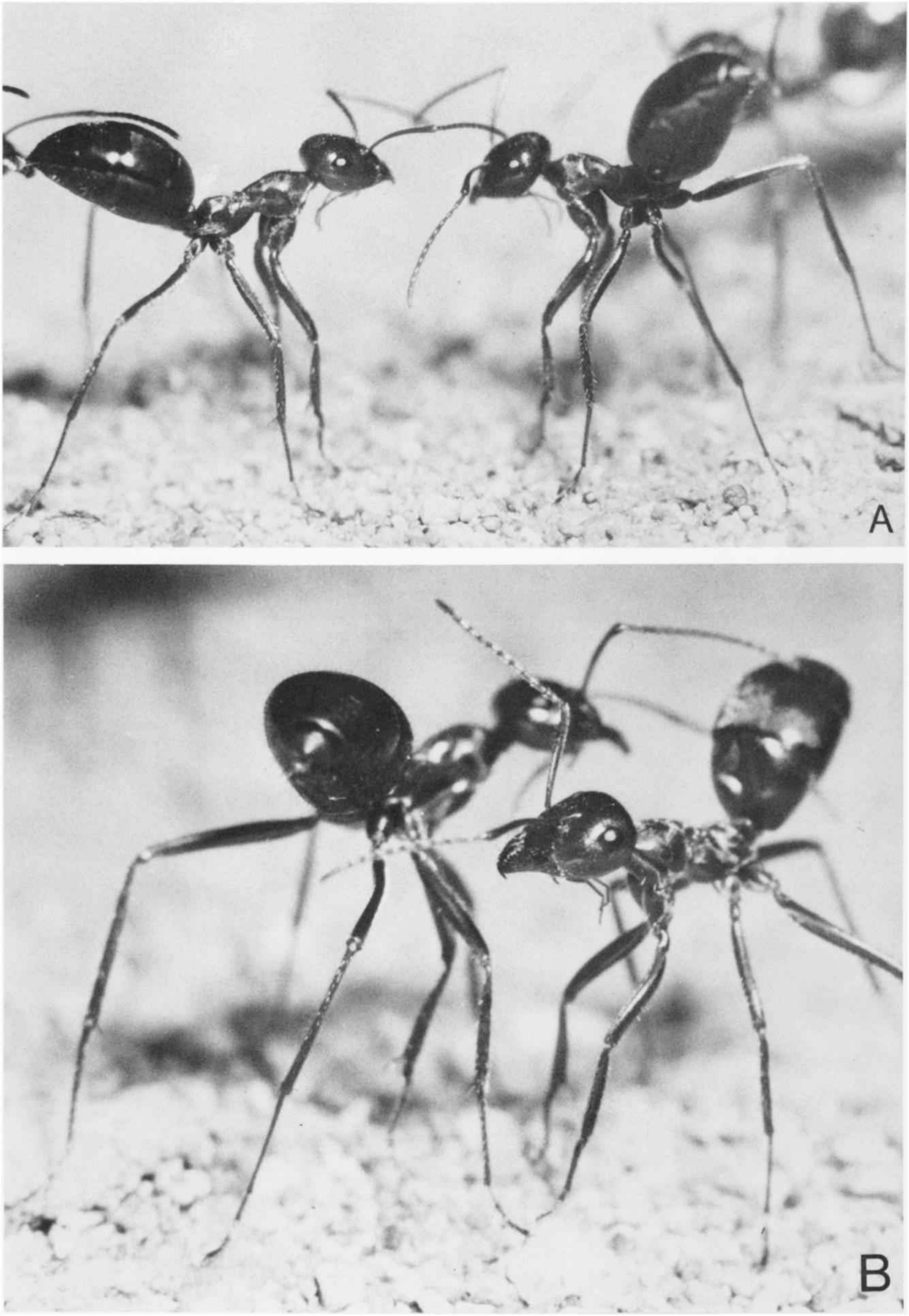

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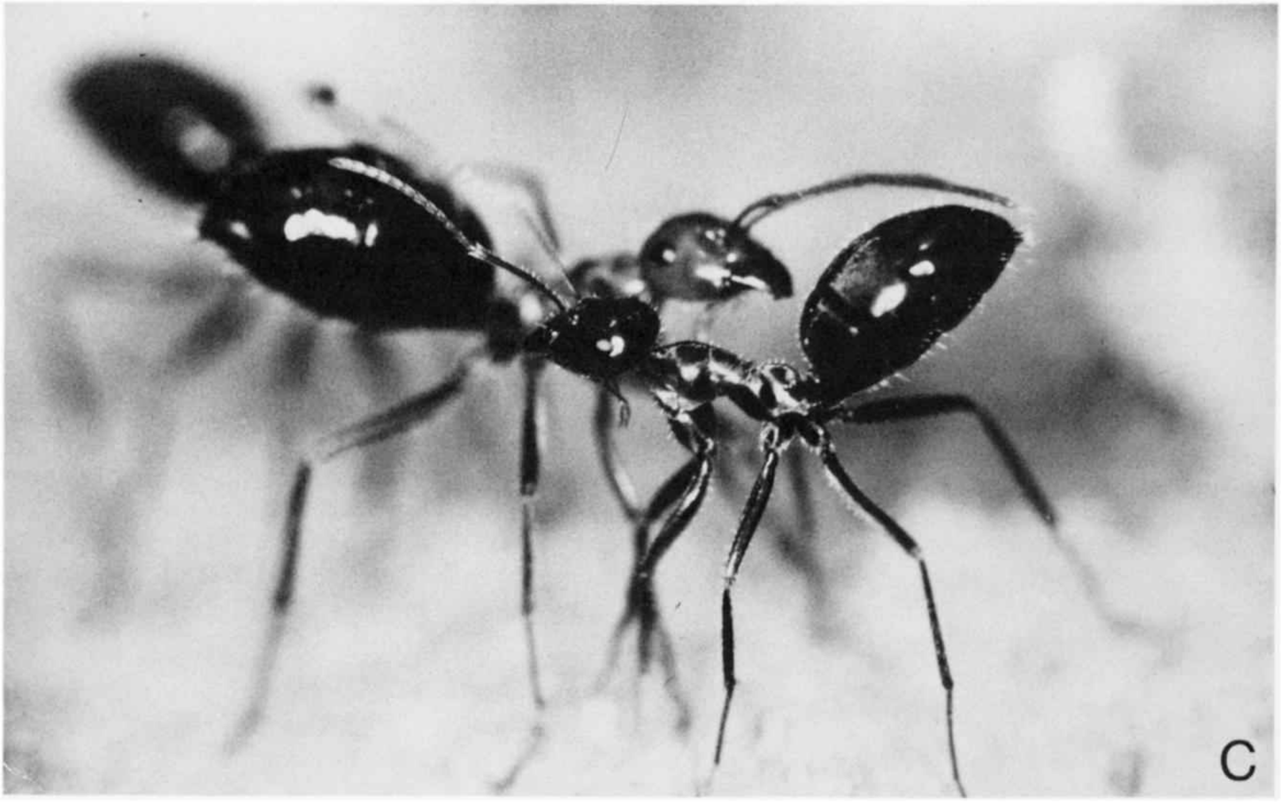

FIG. 8. The stereotype display patterns of *Myrmecocystus mimicus*. A. Stilt-walking and head-on confrontation. B. Beginning of lateral display. C. Full lateral display and antennal drumming. (From Hölldobler, 1976.)

sometimes last for several days, being interrupted only at night when workers of this species are normally inactive. During the territorial tournaments hundreds of ants engage in highly stereotyped display fights. The ants walk high on legs held in a stilt-like position while raising the gaster and head. When two hostile workers meet, they turn to confront each other head on. Then they engage in a more prolonged lateral display, during which each raises the gaster even higher and bends it toward its opponent. Simultaneously, the opponents drum their antennae intensively on each other's abdomen and kick each other with their legs. These exchanges constitute the majority of the physical contact, although each ant also seems to push sideways with its body, as if to dislodge the other one (fig. 8). After 10 to 30 seconds one of the ants usually yields, and the encounter ends. The ants continue to move on stilt legs, quickly meet other opponents, and the whole ceremony is then repeated.

How do these territorial tournaments originate? When foragers venture into an alien territory, they encounter the residents at frequent intervals, whereupon they invariably commence a display fight. Subsequently, some scouts return to their colony while dragging their abdominal tips over the ground. Laboratory and field experiments have shown that these individuals lay a chemical trail with a pheromone originating from the rectal sac. But this pheromone alone does not alert the nestmates to follow the trail. The recruiting scout performs, a jerking motor display when encountering nestmates. This display seems to strongly excite the nestmates; they group around the recruiting ant, which subsequently guides them along the trail to the combat area. Meanwhile scouts of the other party may have also recruited a force of nestmates to the tournament site. When the opposing worker forces meet, they initiate massive display tournaments. Real physical fights occur only rarely and usually end fatally for both opponents. When one colony is considerably stronger than the other, i.e., when it can summon a considerably larger worker force, the tournaments end quickly and the weaker colony is raided. During these raids the queen is killed or driven off. The larvae, pupae, callow workers, and honeypot workers are carried or dragged to the nest of the raiders. This process often requires several days and is terminated only when the raided colony ceases to exist. Field observations and laboratory experiments demonstrated that the surviving workers as well as the honeypots and brood of the raided colony were incorporated to a large extent into the raiders' nest. Since all cases of slave-making in ants hitherto recorded have involved two different species, this is the first evidence for intraspecific slavery in ants and hence is worthy of close analysis.

What is the adaptive significance of this peculiar territorial strategy? One of the major food sources of *Myrmecocystus* is termites. Although they occur typically in patches, their temporal and spatial dis-

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tribution is highly unpredictable. Since there is little point in defending an area that is unlikely to provide adequate food in a given time, *Myrmecocystus* does not establish fixed territorial borders around its entire foraging range, but rather defends only areas in which it currently conducts intensive foraging excursions. This procedure obviously enables it to extend its foraging range considerably and leads to frequent incursions into the potential foraging ranges of neighboring *Myrmecocystus* colonies. Thus, since there are no well-established territorial borders, aggressive massive confrontations with conspecific competitors are much more common in *Myrmecocystus* than in *Oecophylla* or *Pogonomyrmex*. If these confrontations were as violent as the physical combats in *Oecophylla* or *Pogonomyrmex,* they would result in a constant, tremendous drain on the worker force. Thus the display fight tournaments seem to be the much more economical strategy to defend temporal territorial borders. Only when one colony is considerably weaker will it be overrun by the stronger colony, their queen will be killed, and the worker force will be enslaved by the stronger colony. This, of course, raises the question: Why do the defeated workers join the victors? Obviously the larvae, pupae, and also the almost immobile honeypots have little choice, but why the adult workers? I do not have a ready answer to these questions. We are currently testing several hypotheses. One is that the workers, after having lost their own mother queen, may choose to join the victors because there is a good chance that the queen of this colony is one of their aunts. Thus it might still pay in terms of inclusive fitness to stay alive and help raise the offspring of an aunt. Another possibility is that the workers start to lay eggs by themselves. Since the workers are not inseminated, their eggs will develop into males, which will participate in nuptial flights and inseminate virgin reproductive females. In this way the workers have still a chance to contribute to the gene pool, despite the loss of their mother queen. I hope our future work will shed more light on these questions.

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