Foraging and Spatiotemporal Territories in the Honey Ant *Myrmecocystus mimicus* Wheeler (Hymenoptera: Formicidae)

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Summary. The honey ant *Myrmecocystus mimicus* is a scavenger, forages extensively on termites, collects floral nectar, and tends homoptera. Individual foragers of *M. mimicus* usually disperse in all directions when leaving the nest, but there are also groups of foragers that tend to swarm out of the nest primarily in one direction. Such massive departures are usually at irregular intervals, which may last several hours. The results of field and laboratory experiments suggest that these swarms of foragers are organized by a group recruitment process, during which recruiting scout ants lay chemical orientation trails with hindgut contents and simultaneously stimulate nestmates with a motor display and secretions from the poison gland. Usually these columns travel considerable distances (4–48 m) away from the nest, frequently interfering with the foraging activity of conspecific neighboring colonies.

To prevent a neighboring colony from access to temporal food sources or to defend spatiotemporal borders, opposing colonies engage in elaborate display tournaments. Although hundreds of ants are often involved during these tournaments almost no physical fights occur. Instead, individual ants confront each other in highly stereotyped aggressive displays, during which they walk on stilt legs while raising the gaster and head. Some of the ants even seem to inflate their gasters so that the tergites are raised and the whole gaster appears to be larger. In addition, ants involved in tournament activities are on average larger than foragers.

The dynamics of the tournament interactions were observed in several colonies over several weeks – mapping each day the locations of the tournaments, the major directions of worker routes away from the nest, and recording the general foraging activities of the colonies. The results indicate that a kind of dominance order can occur among neighboring colonies. On the other hand, often no aggressive interactions among neighboring colonies can be observed, even though the colonies are actively foraging. In those cases the masses of foragers of each colony depart in one major direction that does not bring them into conflict with the masses of foragers of a neighboring colony. This stability, however, can be disturbed by offering a new rich food source to be exploited by two neighboring colonies. This invariably leads to tournament interactions.

When a colony is considerably stronger than the other, i.e., with a much larger worker force, the tournaments end quickly and the weaker colony is raided. The foreign workers invade the nest, the queen of the resident colony is killed or driven off, while the larvae, pupae, callow workers, and honey pot workers are carried or dragged to the nest of the raiders. From these and other observations we conclude that young *M. mimicus* queens are unlikely to succeed in founding a colony within approximately 3 m of a mature *M. mimicus* colony because they are discovered and killed, or driven off by workers of the resident colony. Within approximately 3–15 m queens are more likely to start colonies, but these incipient groups run a high risk of being raided and exterminated by the mature colony.

Although populations of *M. mimicus* and *M. depilis* tend to replace each other, there are areas where both species overlap marginally. Foraging areas and foraging habitats of both species also overlap broadly, but we never observed tournament interactions between *M. mimicus* and *M. depilis*.

The adaptive significance of the spatiotemporal territories in *M. mimicus* is discussed.

Introduction

Many ant societies are stationary. They spend their entire lives in one spot and only the young, winged reproductives disperse from the nest. In the surrounding terrain of the nest, foraging workers gather infor-

mation, energy, and matter. Hence space around the nest of an ant colony is a precious commodity and frequently has to be defended against competitors.

The territories of ant societies are defended co-operatively by the usually sterile worker casts. Whereas a solitary animal can at a given moment be in only one place doing only one thing, a colony of social insects can be in many places doing many different things by deploying its workers for division of labor. Thus the insect society achieves its optimal territorial strategy by the allocation of specific worker task forces to specific places at specific times (Hölldobler and Lumsden 1980).

Although important differences in the use of space exist among ant species (Hölldobler and Lumsden 1980; Levings and Traniello, in press), most territories previously studied can be called absolute territories, where the resident colony guards its entire territory throughout the foraging activity period, using overt aggression, aggressive displays, and 'keep out' signals, either alone or in combination, against intraspecific and sometimes interspecific intruders. I report here the results of the behavioral ecological analysis of the foraging strategy and the spatiotemporal territories of the honey ant species *Myrmecocystus mimicus*, which defend by ritualized combat only those portions of their home range in which they happen to forage and encounter conspecific competitors at close range.

Notes on the foraging behavior of *Myrmecocystus* are scattered throughout the literature (McCook 1882; Wheeler 1908, 1913; Leonard 1911; Creighton 1956; Cazier and Statham 1962; Cazier and Mortenson 1965; Snelling 1976; Schumacher and Whitford 1976; Chew 1977; Kay and Whitford 1978). Snelling (1976) summarizes these observations by stating: "The species of *Myrmecocystus* are, for the most part, generalized predator-scavengers, but have been able to utilize a resource only cursorily tapped by other ants in this habitat; the carbohydrate-rich secretions of plants. They gather nectar from floral and extrafloral nectaries, fruit juices and honeydew from aphids and pseudococcids." For *M. mimicus* in particular, Snelling notes that it is a diurnal species, "foraging most actively during the middle part of the daylight hours" as a scavenger. It also collects nectar from flowers and has been observed in attendance of aphids. Almost nothing is known about the foraging strategies, social organization of foraging, and partitioning of foraging space in *M. mimicus*.

Materials and Methods

Myrmecocystus mimicus is one of the honey ant species in which workers belonging to a special honeypot caste function as living storage containers. When their crops are heavily filled, their gasters can be expanded to the size of a pea or even larger. For a review of the literature, summary of the biology, and revision of the taxonomy of the formicine genus *Myrmecocystus* see Snelling (1976).

Myrmecocystus is restricted to the nearctic region of North America. Our study site was located in a mesquite-acacia community near Portal, Arizona, and Rodeo, New Mexico. This area is populated with at least four *Myrmecocystus* species, all of which show an intraspecific overdispersed distribution pattern (Alpert and Hölldobler, in preparation). The field work was conducted in 1974, 1975, 1977, and 1979 during June, July, and August. For laboratory experiments the colonies were reared from founding queens in test-tube nests, each tube measuring 15 × 2.2 cm. The water supply in the tubes was trapped at the bottom by cotton plugs. Several hardwood applicator sticks were fixed on the ceiling of each horizontally positioned tube to enable developing honeypots to suspend themselves from the ceiling of the artificial nest chamber. As the colonies grew, more nest-tubes were provided. The colonies were allowed access to foraging arenas (71 × 142 cm floor area) and were provided with freshly killed insects (mostly *Nauphoeta cinerea* cockroaches) and honey water. In this way, queenright colonies containing several hundreds of honeypots could be kept in the laboratory over several years. The evaluation of behavioral sequences was assisted by the use of a 16-mm Beaulieu movie camera and a single-frame analyzer. For measurements of the width of head and length of thorax, a Wild microscope with an electronic microlength measuring attachment was used.

Where not mentioned otherwise, the statistical evaluation was based on Student's *t*-test.

Results

Foraging Behavior

To determine food preference, the items carried into the nest by foragers were recorded at the nest entrance of three mature nests located more than 40 m apart during the annual peak foraging period shortly after the rainy season had started in July and August 1975 and 1977. A total of 27 observation hours randomly selected during the morning and afternoon were spent at the colonies. During these observations a total of 928 foragers were counted carrying termites, 167 foragers carrying other insects or insect parts, 20 foragers returning with seeds, and 632 ants entering the nest without carrying anything between their mandibles. Many workers of the last group, of course, may have transported liquid food in their crops. From these and numerous other observations it appears that termites are a major food source for *M. mimicus*.

Individual foragers of *M. mimicus* usually dispersed in all directions after leaving the nest, but there were also groups of foragers that tended to swarm out of the nest primarily in one direction. Such massive departures were usually at irregular intervals, which may last several hours. In fact, sometimes only very few foragers left the nest during a whole day, while in contrast the foragers of a neighboring nest might have been very active. This pattern
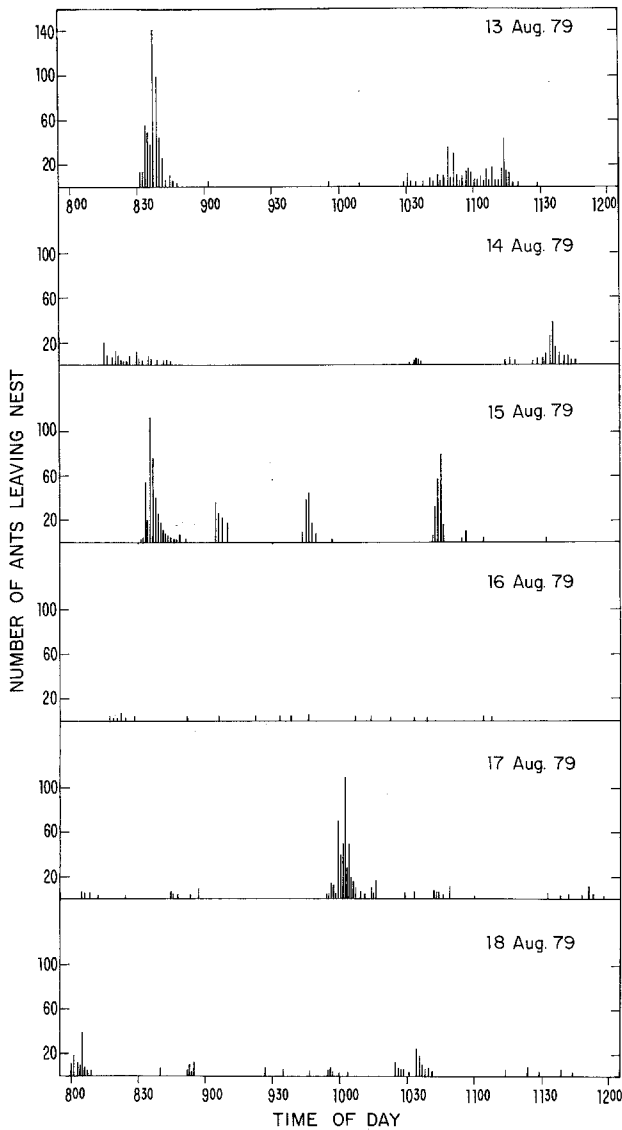
Fig. 1. Activity of workers departing from a *M. mimicus* nest on 6 consecutive days from 8:00 a.m. to 12:00 noon

is illustrated in Fig. 1, which gives a representative example of the activity of workers departing from a *M. mimicus* nest on six consecutive days from 8 a.m. to 12 noon. The climatic conditions and the overall activity in the population during these six days were quite similar, but the individual colonies showed remarkable differences.

Usually these swarms of foragers traveled considerable distances away from the nest ($\bar{x}$=23.6 m; SD = ±13.0; n=27; range 4–48 m) in a loosely organized column. Then individual ants dispersed onto an area of approximately 4–16 m². Frequently workers were seen digging in the soil either individually or in groups, and we often observed them pulling termites out of the soil or out of dried cowdung where the

termites were apparently foraging. These observations led us to the suspicion that the outrush of a group of foragers in one particular direction might be caused by a recruitment process. We hypothesized that individual scouts discover subterranean or exposed termite galleries, rush back to their nest, and recruit a group of nestmates to the area in order to search for and retrieve the termite prey. The following experiments were designed to test whether *Myrmecocystus* employs a recruitment system during foraging.

A feeding site about 100 × 100 cm was established 10 m from the nest entrance. Since previously most swarms of foragers had headed north and northeast, the experimental feeding site was placed in the opposite direction, south. In the following 30 min we counted all ants leaving the nest, and in particular those that departed southward toward the feeding site. After 30 min approximately 300–400 termites, either previously killed or slightly crushed in order to prevent them from moving away, were randomly scattered onto the feeding site. We continued counting the ants departing from the nest.

Shortly after the first foragers bearing termites entered the nest, the activity at the nest changed markedly. An increasing number of ants emerged from the nest entrance, and either returned into the nest or ran away from it in various directions, many of them to the north. A few minutes later, however, a column of ants departed from the nest and traveled swiftly toward the southern feeding site (Fig. 2). We could clearly observe that at least one ant, which moved with its body somewhat lowered, repeatedly touched the ground with its abdominal tip, as if it were depositing a trail pheromone (Fig. 3). Apparently this ant was the recruiting forager because it was usually surrounded by a continuously changing group of 20–30 workers and when directly contacted by a nestmate, frequently performed rapid jerking movements lasting 1–2 s (Fig. 4). Many ants moved short distances ahead of the recruiting ant, but they always turned back to cluster once again around the trailing nestmate.

When the ants arrived at the feeding site, many of them immediately grasped a termite and rushed back to the nest, while others started digging in the soil. Additional groups of foragers arrived at the feeding site until the supply of termites was exhausted and the foraging activity declined.

We performed this experiment 12 times using two colonies. Each time the feeding site was placed in a different direction. Five of these experiments failed because the dolichoderine ant *Iridomyrmex pruinosum* interfered with *Myrmecocystus,* preventing the honey ants from retrieving the termites from the feeding site (Hölldobler, in preparation). However, the seven
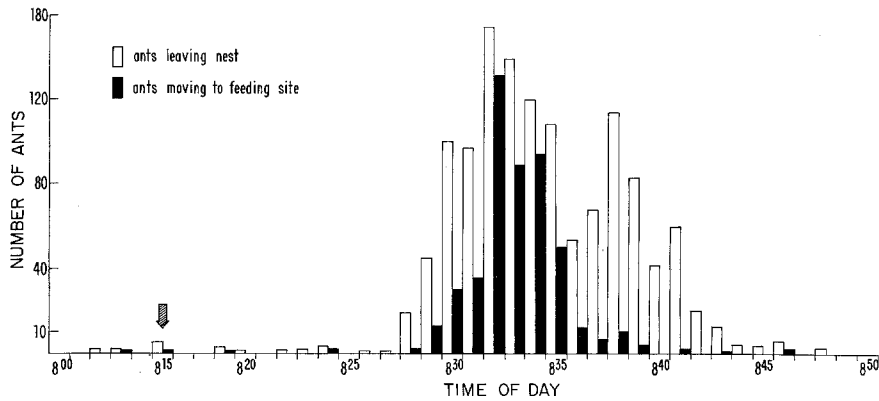
Fig. 2. Recruitment response of *M. mimicus* after a rich food source (termites) was offered in 10 m distance from the nest entrance. *Arrow* indicates the time at which the termites were presented
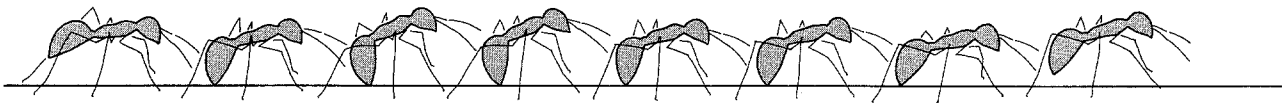

Fig. 3. Body postures of a recruiting ant. The sequence is taken from a movie filmed of 25 frames/s. Every seventh frame is reproduced. The recruiting ant streaks with its abdominal tip over the ground for 2–3 s and alternatively lifts it for 2–3 s
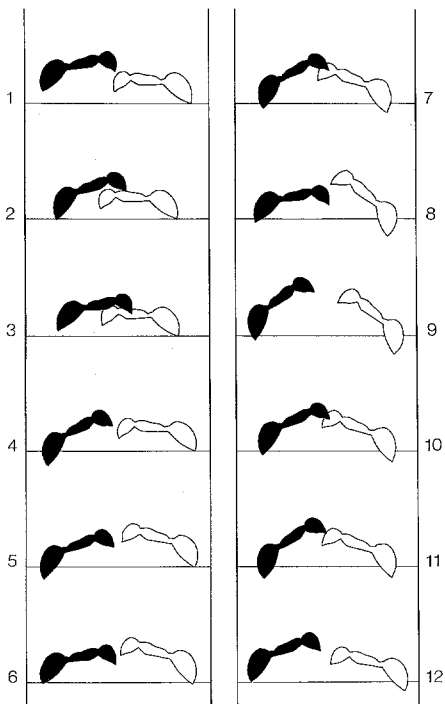

Fig. 4. Schematic drawing of the jerking display of a recruiting ant (*black*) when encountering a nestmate (*white*). The sequences are taken from a movie filmed at 25 frames/s. Every second frame is reproduced

remaining experiments yielded basically the same results as illustrated in Fig. 2. This demonstrates that *M. mimicus* employs a group-recruitment technique during foraging, at least in cases where the food source is rich enough to require a large number of

foragers to transport it to the nest. A similar recruitment response could be elicited with other prey objects such as grasshoppers or cockroaches (*Nauphoeta cinerea*), but termites were the preferred prey by a wide margin. Although *M. mimicus* is able to retrieve larger prey objects cooperatively in groups, they are much less efficient in doing so than, for example, *Novomessor* (Hölldobler et al. 1978; Markl and Hölldobler 1978). They are therefore more prone to lose large prey objects, which cannot be carried by one ant alone, to other ant species such as *Novomessor*, or to mass recruiting and chemically interfering smaller species such as *Iridomyrmex pruinosum*, *Monomorium minimum*, or *Solenopsis xyloni*.

As mentioned above, *Myrmecocystus* is known to collect nectar from flowers. We observed *M. mimicus* foraging on a variety of desert flowers, in particular several *Eriogonum* species and single hackberry bushes in the vicinity (*Celtis pallida*). Although individual foragers were observed leaving the nest independently to visit the flower patches or bushes, we often noticed columns of foragers suddenly leave the nest and travel toward the hackberry bush or to similar patchy nectar sources. These group departures were also led by trailing ants and continued to occur at irregular intervals while the bush was in bloom.

Recruitment Signals

The behavioral observations indicated that individual recruiting ants returned from a rich food source to the nest, laying a chemical trail by touching the abdominal tip to the ground. At relatively regular inter-

vals (after 50–70 cm) the scout ants stopped briefly, sometimes climbing elevated points, turning completely around and looking backward before continuing their homing run. This indicates that visual cues might play an important role in the home-range orientation of *M. mimicus*. When the scout ants arrived at the nest and a number of nestmates were already outside at the nest entrance, the recruiter ant was often seen to run excitedly in a random fashion from ant to ant and upon contacting these nestmates, to perform a rapid jerking display (Fig. 4). Apparently this excited the nestmates because some of them began to perform the jerking display themselves, whereupon their running speed increased markedly. After a few minutes the recruiting ant left the nest again in the direction of the food source. She was now surrounded and followed by a group of nestmates, which varied in number from about 20–50 ants to 100–300 ants. The recruiting ant still regularly touched the ground with the abdominal tip, repeatedly stopping for brief periods in order to turn around before continuing toward the food source.

Many formicine ants are known to lay chemical orientation and recruitment trails with substances originating from the hindgut (see review in Hölldobler 1978). We therefore tested whether the departure of forager columns could be triggered by artificial trails drawn with hindgut material from *M. mimicus* workers. The trails were 200 cm long and originated at the nest entrance. The concentrations of the hindgut contents applied on the trails varied from 0.5 to 10 hindguts in 1 ml destilled water or ether, and for each test the whole volume of 1 ml solution was applied to the trail. When the test colony was not in an 'excited' stage, i.e., when the colony was not stimulated by the performance of a recruiting nestmate shortly before the test, all 23 tests had a negative result since not one single ant followed the artificial trail. However, the results were different when artificial trails were laid while forager columns, organized and led by scout ants, were in full progress (i.e., once the ants had become initially aroused, presumably by the jerking behavior of the recruiting ants). We drew artificial trails (standard trail: 2 hindguts in 1 ml water or ether, drawn with a brush 250 cm long on the natural ground) intersecting the natural trail at 45° or 90°. A considerable number of workers departed from the natural trail and followed the artificial trail; (24 ± 17 followed the artificial trail; 86 ± 42 continued on the natural trail during a 2-min period; $n=15$). The ants did not respond to artificial trails laid with extracts from poison glands or Dufour's glands. Generally, a natural trail directly behind a recruiting ant was always more attractive than the artificial hindgut trail, even when we increased or

decreased the concentration of the trail substance. It is interesting that we never succeeded in distracting the scout ants from their course by offering artificial trails.

We continued to test the secretions of abdominal exocrine glands in the laboratory. Crushed individual glands, with glandular cells and reservoir dissected out of freshly killed ants by freezing, were offered on the tips of applicator sticks about 5 cm in front of the entrance of the laboratory nest. The response of the ants was recorded during the first 2 min after presenting the secretions. The major compounds of the Dufour's gland secretion of *M. mimicus* are undecane, *n*-tridecane, *n*-pentadecane, 2-tridecanone and 2-pentadecanone (Regnier and Hölldobler, unpublished work). We tested these compounds by releasing about 0.25 µl through a microsyringe in front of the nest entrance.

When presented with crushed Dufour's glands (20 tests), most of the ants responded with escape behavior and retreated into the nest. However, a few individuals rushed out of the nest and sometimes showed aggressive display behavior by walking on stilt legs, and when encountering nestmates, performing brief jerking movements with their whole bodies. Only 2-pentadecanone could produce a similar behavior response in two of eight tests. The ants behaved quite indifferently or retreated into the nest when any one of the other major compounds of the Dufour's gland was offered (eight tests with each).

Crushed poison glands (20 tests) triggered excitement in the ants. In 14 tests several workers rushed out of the nest, often contacting the applicator stick, and when we moved the stick away while keeping it close to the ground, several ants followed it for approximately 5–30 cm. Crushed hindguts (rectal bladders) did not elicit any noticeable reaction (12 tests), and trails drawn 100 cm long with crushed rectal bladders did not release spontaneous trail-following behavior (12 tests). However, when an applicator with a crushed poison gland on its tip was presented shortly afterward, and was moved along the hindgut trail without touching it, in 5 of 12 tests several ants followed it through the entire length of the artificial hindgut trail.

Although we could not duplicate these experiments in the field, due probably to the fact that poison gland secretions evaporate very rapidly, the field observations of recruitment behavior and the laboratory results support the hypothesis that the recruiting ants lay chemical orientation trails with hindgut contents, and that the recruitment signals consist of a jerking motor display reinforced by the discharge of small amounts of poison gland secretion. This would explain why the workers in a recruitment column con-

tinuously regroup around the scout ants; they are attracted by the poison gland secretion and as a result continue to receive reinforcing jerking displays.

From these findings we conclude that a significant part of the foraging activity in *M. mimicus* is regulated by a group recruitment process, in which recruiting ants lead groups of nestmates to a foraging site, even if this site is already part of the foraging area of the colony. The significance of this foraging strategy becomes more apparent in the light of intraspecific competition.

Intraspecific Interference Strategy and Territorial Tournaments

Using the distance between nearest neighbors as a measure of spatial relationships we calculated that in all our study sites *M. mimicus* colonies are over-dispersed. Their distribution departs from random expectation in the direction of uniformity with high statistical significance ($P<0.001$ to $P<0.01$; for statistical test see Clark and Evans 1954).

The nearest-neighbor measurements of one of the study sites illustrated in Fig. 5 were 10–29 m (mean: 17.8 m). In another study site the mean distance to the nearest neighbor was 26.4 m (21–45 m). Yet, as pointed out, foragers of one colony can travel considerably longer distances away from their nests; therefore, foraging areas of neighboring colonies can overlap widely. In *M. mimicus* this frequently interferes with the foraging activity of conspecific neighboring colonies.

When a scout ant discovers a rich supply of termites, e.g., under a piece of dried cattle dung, it directs a group of nestmates to this food supply. If another colony of *M. mimicus* is located near the food source and is detected by the foragers of the first colony, some of these individuals rush home and recruit an army of 200 or more workers to lead it to the foreign colony. They swarm over the nest and engage all of the workers emerging from the alien 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 to recruit reinforcements, while the other group of nestmates continues to retrieve the termite prey and comb the area for additional clusters of 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 declines and the intruding army finally retreats to its own nest. Although hundreds of ants are often involved during these tournaments, almost no physical fights occur. Instead, individual ants engage each other in highly stereotyped aggressive displays (Hölldobler 1976a). During
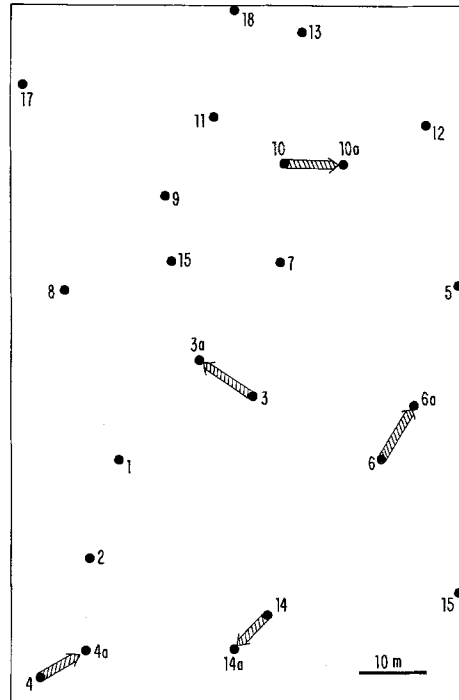

Fig. 5. Distribution of *M. mimicus* nests in one of the study sites. *Arrows* indicate raids during which the nests labeled *a* were abducted by the raiding colony
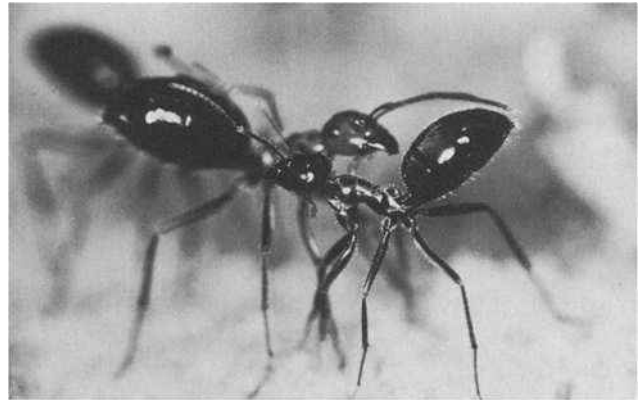

Fig. 6. Lateral display between two opposing *M. mimicus* workers

these contests the ants walk on stilt legs while raising the gaster and head. When two hostile workers meet, they initially turn to confront each other head on. Subsequently they engage in a more prolonged lateral display, during which they raise the gaster even higher and bend it toward the opponent (Fig. 6). Simultaneously, they drum intensively with their antennae on each other's abdomen and frequently kick with their legs (primarily the forelegs) against the opponent. This is almost the only physical contact, although each ant seems to push sideways as if trying to dislodge the other. After a few seconds one of the ants usually yields and the encounter ends. The

ants continue to move on stilt legs, soon meet other opponents, and the whole ceremony is repeated.

In a previous analysis (Hölldobler 1976a) we demonstrated that only conspecific members of a foreign colony elicit the prolonged display activity in *M. mimicus*. In a tournament situation encounters with nestmates lasted only 1–2 s and were terminated by a brief jerking movement of the body. They usually did not develop into a lateral display. The duration of individual encounters can vary considerably. In the initial phase of a tournament, for example, when the intruders moved onto the nest of a resident colony, the display activity was usually very hectic. The display encounters lasted only 1–3 s and could escalate into a real physical biting fight. An intermediate level of escalation was characterized by sham attack behavior where, after a brief lateral display, one ant lunged with open mandibles toward the yielding opponent without actually physically attacking it. In a more stable tournament situation such as in tournaments that demarcated a temporary territorial border between two colonies and where both colonies were represented by approximately the same number of workers, individual display encounters were often considerably longer (up to ~30 s); sham attacks and biting fights were extremely rare.

Frequently we noticed that displaying ants not only walked high with their legs in a stiltlike position, while simultaneously raising their gaster and heads, but also that some of them even seemed to inflate their gasters so that the tergites were raised and the whole gaster appeared to be considerably larger (Fig. 7). To be larger than the opponent seems to be important during the display fights. In fact, we observed several times how a displaying ant climbed a little stone and thereby was apparently more able to dislodge the opponent. If a large and a small ant were matched in a display encounter, the smaller ant usually yielded.

We had the general impression that the ants engaged in display activities in a tournament were on the average larger than the foragers. Of course, this might have been a deception caused by the ants pretension. We therefore collected 50 foragers at random from each of two opposing colonies and 50 ants from the tournament between the two colonies and then measured the width of the head and length of the thorax of each. As documented in Table 1, the tournamenting ants were indeed larger on the average than the foragers ($P < 0.001$).

To gain a better understanding of the dynamics of tournament interactions, we observed several neighboring colonies over several weeks, mapping each day the locations of tournaments, the major directions of worker routes away from the nest, and
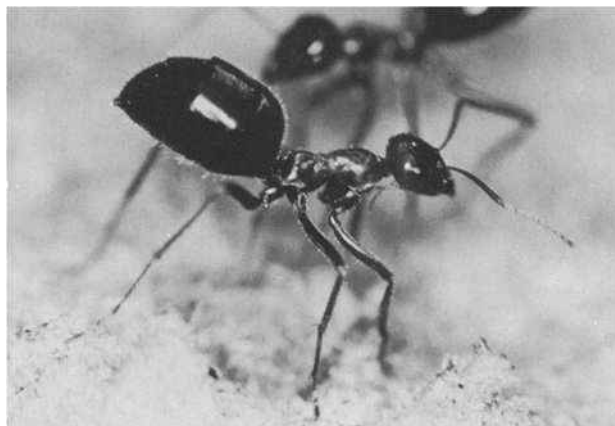

Fig. 7. Displaying *M. mimicus* worker with inflated gaster. Note that the tergites are raised so that the gaster appears to be larger

Table 1. The width of head and length of thorax were measured of three randomly collected samples, each containing 50 ants: foragers of two opposing colonies (colonies I and II) and workers engaged in tournament interactions between both colonies

	Width of head (mm)	Length of thorax (mm)
Colony I foragers	1.01 ± 0.2	1.74 ± 0.3
Colony II foragers	0.99 ± 0.2 $\}$ $P < 0.001$	1.72 ± 0.2 $\}$ $P < 0.001$
Workers from tournament	1.43 ± 0.2	2.26 ± 0.2

recording the general foraging activities of the colonies.

Figure 8 shows the interactions among three neighboring nests for a period of 3 weeks in July 1977, when the rainy season had already started and the foraging activity of *M. mimicus* was very high. In Fig. 8 (I) nest 3 is very active and interferes with nest 1 and nest 5, foraging in the immediate vicinity of these two nests. Several days later (Fig. 8, II) nest 3 is still engaging nest 5 in a tournament directly at nest 5, but the tournament between nest 1 and nest 3 has shifted toward nest 3 and nest 1 is now actively foraging. Seven days later (Fig. 8, III) nest 1 and nest 3 do not show any outside activity, but nest 5 is highly active for the first time since we began observing the three nests. From these observations (Fig. 8, I–IX) it appears that nest 3 is the most dominant colony, and frequently interferes aggressively with the foraging activity of its conspecific neighboring colonies. Nest 5 seems to be the weakest of the three colonies as its foraging activity is most frequently suppressed by neighboring colonies.
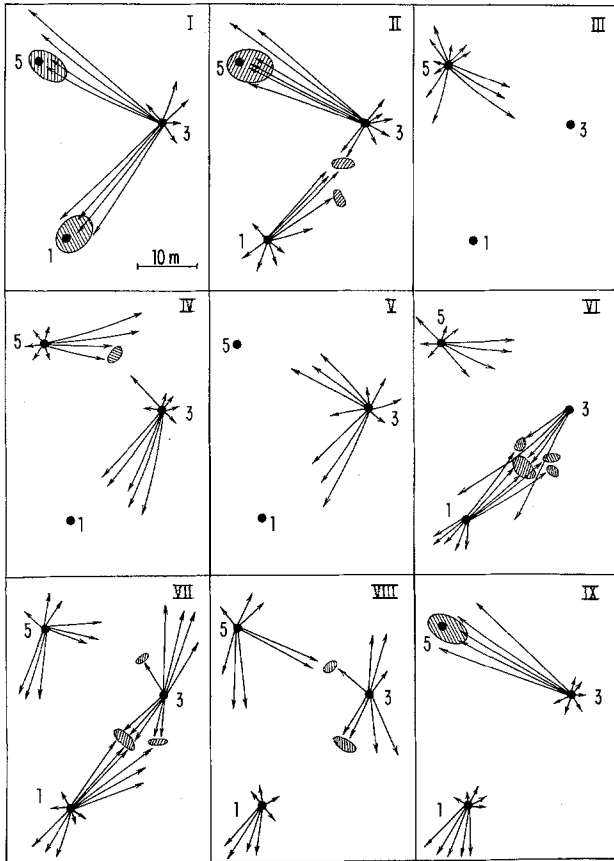
Fig. 8. Interactions among three neighboring colonies of *M. mimicus* during a period of 3 weeks in July 1977. *Shaded area* tournament area; *long arrows* main worker routes; *small arrows* minor traffic of workers. For further explanations, see text

Figure 8 illustrates a representative example of what we observed in our study area during the peak foraging period, which indicates that a kind of dominance order can occur among neighboring colonies of *M. mimicus*. Although on several occasions we noticed that one colony previously dominant over another could later be suppressed by this same colony (still later the situation could be reversed yet again), in most cases the direction of domination remained constant during the observation period of one season.

On the other hand, often no aggressive interactions among neighboring colonies could be observed, even though the colonies were actively foraging, as illustrated in Fig. 9 (I). We observed these three colonies for a period of 12 days and never noted any tournament interactions between them. What we called guard contingents were positioned daily at the same spots over an area not larger than 1 m². The contingents consisted of 1–6 workers that stood on stilt legs, often posing on top of little stones or waiting in the shade of little bushes during the hottest part of the day. They were usually out at these posts as early as 5.30–7.00 a.m., 1–2 h before the colony began foraging, and retreated to the nest at dusk. During their 'guarding' they repeatedly encountered individual foreign *M. mimicus* workers, which usually resulted in a typical display confrontation. However, in most cases the encounter lasted only 5–10 s before the intruder moved away again.

We recorded the major foraging directions taken by each colony (Fig. 9 long arrows). Although individual ants left the nest in all directions around the nest (small arrows), the masses of foragers of each colony departed in one major direction that did not bring them in conflict with the masses of foragers of a neighboring colony. The directional preference of each colony's foragers remained the same during the observation period of 12 days. The daily foraging activity varied among the three colonies, but generally the geometric partitioning of foraging ground between these three colonies appeared very stable.

In a special set of experiments we tested whether a new, rich food source would affect this stability. We placed several hundred termites midway between nest 1 and nest 3 (Fig. 9). Foragers of nest 3 quickly discovered the termites and retrieved them to their nest. Only very few foragers departed in the direction of nest 1. Within the first hour of the experiment nest 3 was retrieving about 25 times more termites than nest 1. Not one forager was observed transporting termites in the direction of nest 2. One day later we moved the feeding site (termites) closer to nest 1, (~5 m from nest 1, ~15 m from nest 3). Foragers
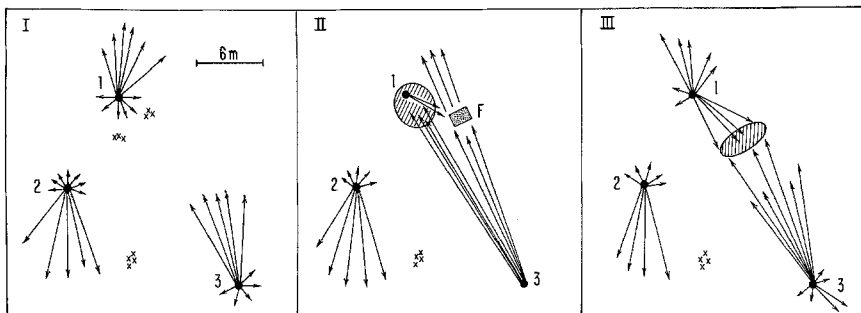

Fig. 9. Interations between three neighboring colonies of *M. mimicus*. *Shaded area* tournament area; *stippled area* food site; *long arrows* major foraging directions; *small arrows* directions taken by individual foragers; x guard posts. For further explanantions, see text

of nest 3 were already out, quickly discovered the termites, and began retrieving them. But in addition, several foragers of nest 1 carried termites to their nest. Within the first hour colony 3 sent three columns of workers to nest 1. We could clearly observe that these columns were led by trailing ants that frequently performed a vigorous jerking display when contacting nestmates. They literally swarmed all over nest 1. Workers of nest 1 were attempting to close the nest entrance. There were a few physical fights, but mostly we observed very hectic display confrontations. The foraging activity of nest 1 was effectively thwarted, and nest 3 continued to carry off termites in large numbers. Nest 2 was not affected by these activities at all (Fig. 9, II).

Although we stopped providing termites, the posture of the colonies remained the same for the next several days. Colony 3 kept colony 1 engaged in a display tournament directly at nest 1, blocking colony 1 from foraging. Foragers of colony 3 even ventured beyond nest 1 into the formerly preferred foraging area of colony 1. A week later both colonies were still engaged in a tournament, but the site of the tournament had shifted away from nest 1 toward nest 3, and colony 1 was again foraging (Fig. 9, III). Thus, territorial tournaments occur also in the zone between two adjacent M. mimicus nests, especially when both colonies are active at the same time. Alien foragers are then blocked from the respective foraging areas of each colony. These tournaments can last for several days, being interrupted only at night when workers of M. mimicus are normally inactive.

As in many similar instances where two colonies were engaged in a tournament, we noticed that the opposing parties sent out workers to the tournament site early in the morning (5:30–6:00 a.m), hours before the foraging activity started at neighboring nests. Mabelis (1979) reports similar observations for the wars fought by neighboring nest populations of Formica polyctena in the course of establishing territorial borders during springtime. These battles take place throughout the day and are interrupted only at night. Early next morning the armies of opposing colonies move straight to the battle field of the preceding day. In contrast to the tournaments of Myrmecocystus mimicus these territorial battles result in many casualties, and dead ants are retrieved into nests and eaten. We were also impressed by the lack of a clear distinction between territorial defense and predation in the repertory of the African weaver ant (Oecophylla longinoda). When intruders are killed, they are treated as prey and carried back to the nest and eaten. In fact, we regard recruitment to repel intruders and recruitment to retrieve prey by Oecophylla workers as merely ends of a continuum (Hölldobler and Wilson 1978).

In M. mimicus, too, the recruitment mechanisms to termite prey patches and to territorial tournaments appear similar, although in the latter a different group of workers seems to respond, and the jerking behavior of the recruiter ant seems to be more frequent and vigorous. We were not able, however, to quantify these rather subjective observations of differences in the recruitment mechanisms. In any case, the territorial tournament interactions between mature M. mimicus colonies are very distinct from territorial wars in F. polyctena or Oecophylla and intraspecific predation is extremely rare. The situation is different, however, when workers of a mature colony encounter a conspecific incipient colony in the vicinity of their nest.

Intraspecific Raids and Territorial Exclusion

When one colony is considerably stronger than the other, i.e., when it can summon a much larger worker force, the tournaments end quickly and the weaker colony is raided. During these episodes the foreign workers invade the nest, and the queen of the resident colony is killed (3 cases observed) or driven off (2 cases). The larvae, pupae, callow workers, and honeypot workers are carried or dragged to the nest of the raiders (Fig. 10). Many of the honeypots are injured during the raiding, but nevertheless are transported to the intruders' nest and may be eaten there. Field observations and laboratory experiments have led to the discovery, however, that the surviving workers as well as the honeypots and brood of the raided colony are incorporated to a large extent into the raiders' nest (Hölldobler 1976a).

To date, we have observed a total of 34 raids conducted by M. mimicus on conspecific neighboring nests in the field. These episodes constitute only about 8% of all tournament interactions observed. A total

Fig. 10. Honeypot worker being dragged by raider ant to the raiders' nest

Table 2. Raids conducted by mature *M. mimicus* colonies against conspecific incipient colonies. Number of larvae, pupae, and honeypots abducted to the raiders' nest

Date of observation	Larvae	Pupae	Honeypots	
			Alive	Dead
30-7-74 to 1-8-74	209	311	117	54
11-7-75	82	120	22	8
18-7-75 to 23-7-75	293	318	39	18
6-8-75	101	156	45	11
12-7-77 to 14-7-77	180	163	97	33
19-7-77	14	60	2	9
31-7-77	98	76	14	9
10-8-79 to 11-8-79	178	91	42	34

Fig. 11. Histogram illustrating the extermination frequency of *M. mimicus* founding queens and incipient colonies by conspecific established colonies, in relation to distance from the established colony

of nine raiding events were observed from beginning to end, and of eight events we have rather complete counts of larvae, pupae, and honeypots abducted into the raiders' nest (Table 2). From these data we conclude that the raided colonies were all younger, developing colonies. Also, we estimate that the raiding colony, which was always well-established and mature, was at least ten times larger than the raided colony. The incipient state of the raided colonies is also indicated by the considerably smaller average size of the workers in comparison to that of workers of the raiding colony. The larger workers, which are usually observed during tournament interactions, were very poorly represented in the raided colonies.

In all 34 cases the distances between the nests of the raided and the raiding colony (3.5–15 m; Fig. 11) were less than the mean nearest neighbor distance in the population. We observed seven additional raiding attempts on nests 16–26 m away from the raiders' nest (Fig. 11). Although these raids had all the features of success, with initial physical fighting, intrusion into the foreign nest, and even the robbing and transport of a few larvae and pupae to the raiders' nest, the raids were not infact successful. The resident ants rushed out of the nest and engaged the invaders in a very hectic display confrontation that occasionally escalated into physical fights, while other resident workers closed the nest entrance with stones, twigs, and debris. Apparently these colonies had already reached a size that enabled them to defend themselves successfully against raids from conspecific neighboring colonies.

During the colony-founding periods, we observed many freshly mated *M. mimicus* queens digging their founding nest chambers in the close vicinity of mature *M. mimicus* colonies. Many failed to establish nests, however, because they were discovered and killed or driven off by workers of the resident *M. mimicus* colony. During four summers we recorded a total
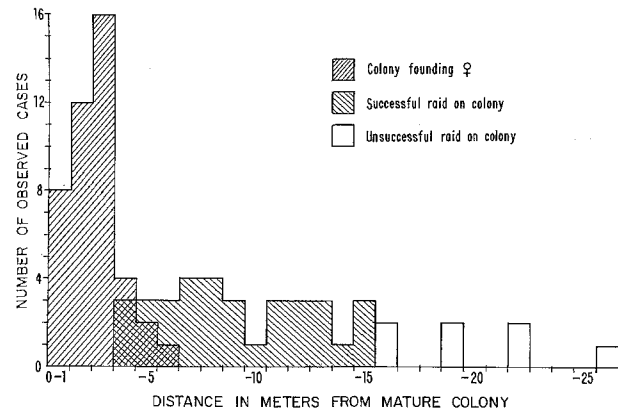
of 49 cases of *M. mimicus* queens being prevented from colony founding by conspecific workers. In all instances the queens attempted to dig their nest chambers within 0.5–5.5 m of a a major *M. mimicus* nest (Fig. 11).

From these observations in our study area we conclude that young *M. mimicus* queens are unlikely to succeed in founding a colony within a range of approximately 3 m of a mature *M. mimicus* colony. Within a range of 3–15 m queens are more likely to start colonies, but these incipient groups run a high risk of being raided and exterminated by the mature colony. The greater the distance to the nearest established conspecific colony, the greater the chance for the incipient colony to develop and reach a size large enough to be able to withstand raiding attempts of the neighboring colony.

Interspecific Interactions in Myrmecocystus

Four species of *Myrmecocystus* occur sympatrically in our study area. Foragers of *M. mexicanus* and *M. navajo* are primarily active at night and rarely contact *M. mimicus* and *M. depilis*, which forage exclusively during daytime. Although populations of *M. mimicus* and *M. depilis* tend to replace each other, there are areas where populations of both species overlap marginally (Alpert and Hölldobler, in preparation) (Fig. 12).

Myrmecocystus mimicus and *M. depilis* are considered phylogenetically closely related, resembling each other in morphology, ecology, and foraging behavior (Snelling 1976; Kay and Whitford 1978). Our observations indicate that there is also a remarkable similarity in their selection of nesting sites as well as in their dietary spectrum, although *M. depilis* seems to be somewhat more efficient in group retrieval of
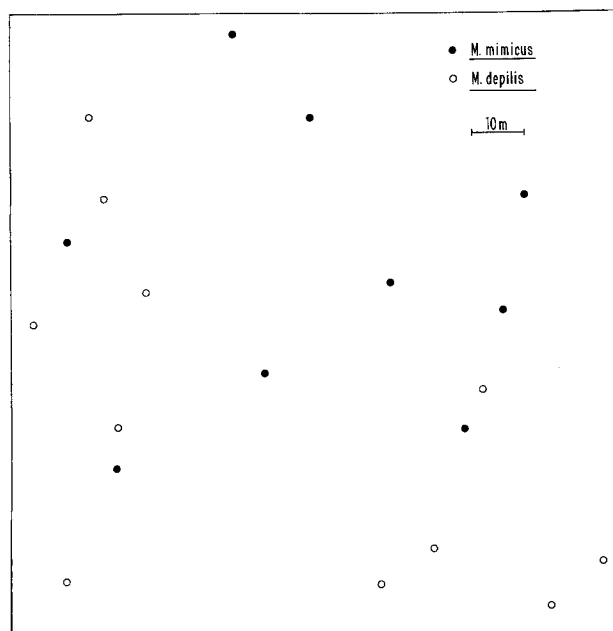
Fig. 12. Distribution of *M. mimicus* and *M. depilis* nests in one of the study areas
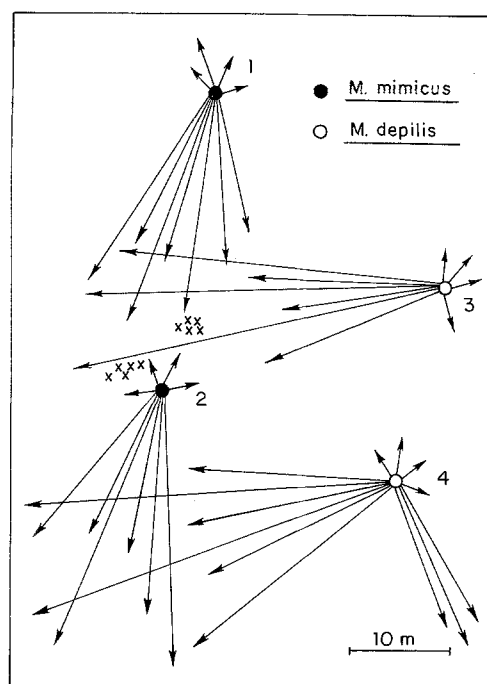

Fig. 13. Schematic illustration of forager routes of two *M. mimicus* colonies and two *M. depilis* colonies. Foraging areas (field of *Eriogonum*) of both species overlapped broadly. × guard posts of *M. mimicus*

larger prey objects, and *M. mimicus* appears to be more specialized on termites (Alpert and Hölldobler, in preparation).

Foraging areas of both species frequently overlap broadly (Fig. 13), but we never observed tournament

interactions between *M. mimicus* and *M. depilis*. On the foraging ground, workers of both species seem to avoid each other when they meet. Even when we arranged a rich feeding site (termites and grasshoppers) halfway between a *M. mimicus* and *M. depilis* nest (6 m from each nest), foragers of both nests retrieved the prey, occasionally pulling on the same prey object in opposite directions, but we never observed prolonged physical fighting or display interactions. The situation changed, however, when the feeding site was shifted into the close vicinity of either one of the nests. When we moved the feeding site from the halfway position to a spot 1–2 m from the *M. depilis* colony, foragers of *M. mimicus* soon followed. The reaction of the resident *M. depilis* was quite remarkable. Many workers stopped running for a few seconds, leaned to the side, bending the gaster forward and performing a rapid trembling motion. This peculiar behavior always coincided with the arrival of large numbers of *M. mimicus* foragers. Presumably this is an alarm behavior because an outrush of additional *M. depilis* workers followed, and many *M. mimicus* foragers were attacked by several *M. depilis* workers at once. The resident ants grabbed the intruders and pulled them into their nest where they were presumably killed. In contrast, when we lured large numbers of *M. depilis* workers to the *M. mimicus* colony by shifting the food source toward a *M. mimicus* nest, the resident *M. mimicus* appeared to be less aggressive. Some of them attacked the intruders and dragged them away from the nest area instead of pulling them into the nest. In both cases, however, the intruding colony's foraging activity at the feeding site was effectively hindered, and the traffic of foragers from the neighboring colony declined sharply.

These experiments, were repeated with four different pairs of neighboring *M. mimicus* and *M. depilis* colonies, and we conclude that within a circumference of 1.5–2.00 m around the nest entrance, both species tend to physically attack foragers of the other species. Otherwise, foraging areas of both species overlap broadly, and display confrontations and physical aggression are very rare.

During observations of eight tournaments between neighboring *M. depilis* colonies, we noticed that in comparison with *M. mimicus*, tournament interactions seemed to be less frequent and lasted only about 30–120 min. The display confrontations were considerably more hectic, and aggressive encounters more easily escalated into physical fighting.

In the following experimental series we again tested intra- and interspecific aggression in both species under more controlled conditions by transferring 50 workers of a neighboring colony into an arena (1.50 × 1.50 m, walls 20 cm high) built around the nest

entrance of a resident colony. When we placed 50
M. depilis workers into the arena of a conspecific
neighboring colony (21 m distant), we counted 43 dis-
play confrontations and 12 physical fights within the
first 2 min. Resident ants rushed out of their nest
in large numbers, and fighting escalated into heavy
prolonged biting fights. Many of the intruding ants
were pulled into the resident ants' nest. We repeated
the same procedure a total of 36 times with 12 differ-
ent *M. depilis* colonies. In 19 experiments we recorded
initial display behavior, then increased physical fight-
ing. In 12 experiments physical fighting commenced
promptly without any initial display encounters, while
in 5 experiments the release of foreign conspecific
ants did not elicit any response as apparently the
resident ants were not active at this time.

This pattern of response is remarkably different
from that of *M. mimicus*. In a series of similar experi-
ments with the latter species we found that display
confrontations always prevail over physical fights
(Hölldobler 1976a).

When we introduced 50 *M. mimicus* workers into
the arena at a *M. depilis* nest, *M. mimicus* usually
reacted with avoidance and escape behavior upon en-
countering resident *M. depilis* workers. Occasionally,
however, *M. mimicus* responded with a brief typical
display behavior and were then often attacked by
M. depilis, which pulled them into the *M. depilis* nest.
The same pattern prevailed when we introduced
50 *M. depilis* workers into the arena near a *M. mimi-
cus* nest, with the following exception: when *M. mimi-
cus* attacked *M. depilis*, they did not pull them into
the nest but instead dragged them away from the
nest entrance.

Generally, we can conclude that intraspecific terri-
torial aggression in *M. mimicus* and *M. depilis*, ex-
pressed by either display tournaments or physical
fighting, is considerably stronger and more pro-
nounced than interspecific interactions between both
species, although in some areas colonies of *M. mimi-
cus* and *M. depilis* exist in close proximity and often
use the same food sources. This is well illustrated
by the following remarkable example (Fig. 14), a sin-
gle case that we think important enough and in such
striking accord with the experimental results to war-
rant presentation.

Both the *M. mimicus* colony 1 and *M. depilis* col-
ony 2 were gathering nectar from the flowers of a
hackberry bush. Although there were guard contin-
gents of *M. mimicus* around the bush, we never ob-
served a display confrontation between *M. mimicus*
and *M. depilis*. When a *M. mimicus* guard encoun-
tered a *M. depilis* worker, it chased the *M. depilis*
forager for a distance of a few centimeters. Only rarely
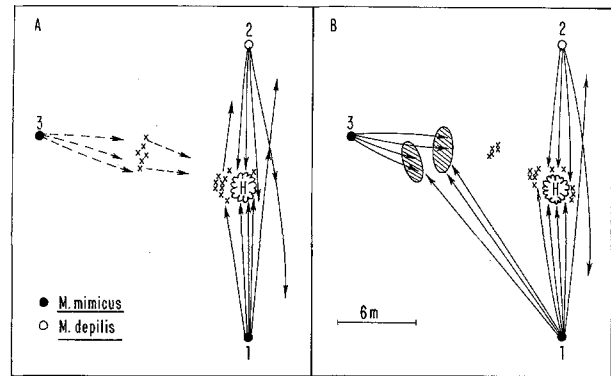did such encounters escalate into a physical fight,

Fig. 14. Schematic illustration of forager routes and interactions
between neighboring colonies of *M. mimicus* and *M. depilis. H*
hackberry bush; x guard posts of *M. mimicus; arrows* routes of
workers; *shaded area* tournament area. For further explanations,
see text

and then only briefly. In any case, both species for-
aged on and around the hackberry bush.

The situation was very different for *M. mimicus*
colonies 1 and 3. Guard posts were also positioned
between colony 3 and the hackberry bush, and individ-
ual foragers of colony 3 occasionally ventured beyond
this guard post toward the hackberry bush. After
we had observed this situation for 4 days (Fig. 14A),
with no observation on day 5, we were surprised to
discover on day 6 a large tournament precisely at
the spot where we had previously noted the guard
posts between nest 3 and the hackberrry bush (Fig.
14B). We repeatedly observed columns of ants from
nest 1 and nest 3 moving toward the tournament
area. At the same time, colonies 1 and 2 continued
to send foragers to the hackberry bush, and colony
2 (*M. depilis*) did not seem to be affected by the
territorial interactions between the two *M. mimicus*
colonies.

As mentioned above, populations of *M. mimicus*
and *M. depilis* tend to replace each other between
habitats (Alpert and Hölldobler, in preparation).
Nevertheless, we were surprised to find so little terri-
torial interaction between both species in areas of
overlap. Interspecific overdispersion in ant species
with similar ecological niche dimensions has been well
documented (see review by Levings and Traniello,
in press). Also, we have demonstrated that both *Po-
gonomyrmex barbatus* and *P. rugosus* behave territor-
ially like one species in areas where populations of
both species overlap (Hölldobler 1976b). This is cer-
tainly not the case between *M. mimicus* and *M. depilis*.

Discussion

Natural selection theory suggests that an animal
should only establish and maintain a territory whose

size and design make it economically defensible. In other words, territorial defense should gain more energy than it expends (Brown 1964; Brown and Orians 1970).

We suggested earlier that this concept of economic defensibility can be used to understand the design of territories maintained by ant societies (Hölldobler and Lumsden 1980). For example, species foraging on relatively stable resources that are uniformly dispersed over a wide area have territories designed differently from those of species exploiting stable, but patchily distributed resources. The honey ant *Myrmecocystus mimicus* uses termites as a major food source. The temporal and spatial distribution of the termite galleries 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, in contrast, for example, to the weaver ant *Oecophylla* (Hölldobler 1979; Hölldobler and Lumsden 1980). Since there are no well-established territorial borders, aggressive mass confrontations with conspecific competitors are much more common in *M. mimicus* than in many other ant species, where conspecific neighboring colonies establish and maintain separate foraging territories. Although fighting in the latter group can at times be heavy and costly, once the territorial borders are established, physical confrontations decline sharply (Hölldobler 1976 b, 1979; Mabelis 1979). If the frequent massive aggressive interferences between neighboring colonies of *M. mimicus* were as violent as the physical combat in some of the other territorial species, they would result in a constant and heavy drain on the worker force. Thus, the display fight tournaments seem to be the more economical strategy to defend spatiotemporal territorial borders. Only when one colony is considerably weaker does it risk being overrun by the adjacent stronger colony, having its queen killed, and its workers either killed or enslaved by the stronger colony (Hölldobler 1976a). This and the extermination of founding queens by conspecific workers of adjacent mature *M. mimicus* colonies lead to overdispersion of *M. mimicus* colonies.

The overdispersion of colonies is not necessarily a reflection of territoriality, however, nor does it result directly from defense of foraging areas or resources. As we pointed out (Hölldobler and Lumsden 1980), a general rule of thumb is that animals faced with chains of deficits and surpluses on fixed territories should dissolve such boundaries and let foraging ranges overlap. We have seen that this constraint applies in part to honey ants. Furthermore, for territorial risk-prone colonies there is a basic economic formula that will determine whether fixed territories pay

off in the long run. For scarce, quickly exhausted resources, this situation appears unlikely. The alternative to fixed territories is a foraging system with floating, temporary territorial boundaries of the kind observed in honey ants. Although the colony will lose a fraction of termite clusters in its region to competitors, it will gain others in the region of the competitor colony. Since defense costs are now much reduced, and even further reduced by the ritualized display fight strategy, floating boundaries and overlapping ranges become a preferred option.

Ritualized display fighting is probably more common in ants than previously noticed. It was observed in *Prenolepis imparis* (Traniello, unpublished observation), where it might have the same ecological function as in *M. mimicus*. In fact, observations by Talbot (1943) suggest that *Prenolepis imparis* also defends spatiotemporal territories. We observed it in the dolichoderine ant *Iridomyrmex pruinosum* (Hölldobler, in preparation) where it occurs near the boundaries of separate polydomous nest populations and at food sources where foragers from separate nest populations encounter. In the Australian meat ant (*Iridomyrmex purpureus*) Duncan-Weatherley (1953), and later Greenslade (1975a, b), observed antagonistic behavior between members of neighboring colonies, which superficially resembles that of *M. mimicus*. In a more detailed description Ettershank and Ettershank (in press) pointed out, however, that the behavioral patterns and sequences are quite different in *I. purpureus*. My own independent analysis of the display behavior of *I. purpureus* supports this conclusion. In contrast to *M. mimicus*, the territories of *I. purpureus* are quite stable (Greenslade 1975); therefore, the behavioral-ecological significance of the display fight strategy in *I. purpureus* is probably different from that in *M. mimicus*.

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