80, 48 (1978); Ecole Normale Supérieure preprint, LPTENS 79/6 (March 1979); see also B. Julia, in *Proceedings of the Second Marcel Grossmann Meeting* (Trieste, July 1979, in preparation).

95. Yu. A. Gol'fand and E. P. Likhtman, *JETP Lett.* **13**, 323 (1971); D. V. Volkov and V. P. Akulov, *ibid.* **16**, 438 (1972); J. Wess and B. Zumino, *Nucl. Phys. B* **70**, 39 (1974); A. Salam and J. Strathdee, *ibid.* **79**, 477 (1974); *ibid.* **80**, 499 (1974); *Phys. Lett. B* **51**, 353 (1974); reviewed in A. Salam and J. Strathdee, *Fortschr. Phys.* **26**, 57 (1978).
96. Supersymmetry algebra extends Poincaré group algebra by adjoining to it supersymmetric charges Q_α which transform bosons to fermions. $\{Q_\alpha, Q_\beta\} = (\gamma_\mu P_\mu)_{\alpha\beta}$. The currents which correspond to these charges (Q_α and P_μ) are $J_{\mu\alpha}$ and $T_{\mu\nu}$—these are essentially the currents which in gauged supersymmetry (supergravity) couple to the gravitino and the graviton, respectively.
97. A. D'Adda, M. Lüscher, P. Di Vecchia, *Nucl. Phys. B* **146**, 63 (1978).
98. E. Cremmer *et al.*, *ibid.* **147**, 105 (1979); see also S. Ferrara, in *Proceedings of the Second Marcel Grossman Meeting* (Trieste, July 1979, in preparation).
99. P. Fayet, *Phys. Lett. B* **70**, 461 (1977); *ibid.* **84**, 421 (1979).
100. J. Scherk, Ecole Normale Supérieure preprint, LPTENS 79/17 (September 1979).
101. J. R. Oppenheimer, Reith Lectures, British Broadcasting Company (1953).
102. If one does not know G, one way to infer the parameter $\sin^2\theta(M)$ is from
$$\sin^2\theta(M) = \frac{\Sigma T_{3L}^2}{\Sigma Q^2}\left(= \frac{9\,N_q + 3\,N_l}{20\,N_q + 12\,N_l}\right)$$
Here N_q and N_l are the numbers of fundamental quark and lepton SU(2) doublets (assuming these are the only multiplets that exist). If we make the further assumption that $N_q = N_l$ (from the requirement of anomaly cancellation between quarks and leptons) we obtain $\sin^2\theta(M) = 3/8$. This assumption, however, is not compulsive; for example, anomalies also cancel if (heavy) mirror fermions exist (*106*). This is the case for $[SU(6)]^4$, for which $\sin^2\theta(M) = 9/28$.
103. J. C. Pati, A. Salam, J. Strathdee, *Nuovo Cimento A* **26**, 72 (1975); J. C. Pati and A. Salam, *Phys. Rev. D* **11**, 1137 (1975); *ibid.*, p. 1149; J. C. Pati, in *Theories and Experiments in High Energy Physics*, A. Perlmutter and S. Widmayer, Eds. (Plenum, New York, 1975), p. 253.
104. A. Salam (*68*); also Q. Shafi and C. Wetterich, *Phys. Lett. B* **85**, 52 (1979).
105. J. Learned, F. Reines, A. Soni, *Phys. Lett.* **43**, 907 (1979).
106. J. C. Pati and A. Salam, *Phys. Rev. D* **10**, 275 (1974).
107. H. Georgi, Harvard University report HUTP-29/A013 (1979).
108. M. Gell-Mann, unpublished.

Territorial Strategies in Ants

Bert Hölldobler and Charles J. Lumsden

Summary. Several features in social insects, particularly in ants, make the behavioral organization of territoriality considerably more complex than that of solitary animals. The establishment and maintenance of territories are based on a division of labor and a complex communication system. The analyses of territorial strategies in ants comprise the study of the design and spatiotemporal structure of the territory, as well as the social mechanisms through which the insect society pursues its territorial strategy. The geometric and behavioral organization of the absolute territories of the African weaver ants (*Oecophylla longinoda*) and harvester ants (*Pogonomyrmex*), and of the "spatiotemporal territories" of honey ants (*Myrmecocystus mimicus*) are described, and simple cost-benefit models are developed to illustrate the economic defensibility of each type of territory.

In studies of community biology, a territory is generally defined as an area that the animal or the animal society occupies exclusively and defends—using overt aggression, aggressive displays, and "keep-out signals" either alone or in combination—against intraspecific, and sometimes interspecific, intruders. Nonoverlapping territories produce relatively evenly dispersed spacing and usually indicate competition for some resource in limiting supply (*1*).

Territorial strategies are especially elaborate in animal species that live in well-organized societies. In social insects, the establishment and maintenance of territories are based on a division of labor and a complex communication system. Although it has been known for a long time that many ant species defend territories around their nests (*2*), only recently have biologists begun to analyze the diversity of their territorial strategies and the underlying communication mechanisms.

Theories of territoriality and space utilization have been based on results obtained from research with solitary animals (*1*, *3*). But in social insects, and particularly in ant societies, there are several unique features that often make the behavioral and spatiotemporal organization of territoriality considerably more complex.

Most ant societies are stationary; like barnacles or terrestrial plants they spend their entire adult lives fixed in one spot and produce winged reproductive forms to disperse away from the nests as the functional analogs of larvae and seeds. Foraging workers comb the surrounding terrain, where they gather information, energy, and matter and retrieve these resources to the nest. Thus, 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 cooperatively by the usually sterile worker castes. Whereas a solitary animal can at any moment be in only one place and can be doing only one thing, a colony of social insects can be in many places by deploying its workers and can be doing many different things because of the size of the worker cohorts and their 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.

Because of the division of labor between reproductive individuals and sterile worker castes, fatalities caused by territorial defense have a different qualitative significance for social insects as compared to solitary animals. The death of worker ants represents an energy and labor debit, rather than a destruction of a reproductive agent. Worker death might more than offset its costs by bringing or maintaining resources and colony security. Death can thus become a positive element in the colony's adaptive repertory.

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, the territorial defense should gain more energy than it expends (*3*). To this end, the territory can be ei-

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ther absolute or spatiotemporal. As Wilson (*1*) has expressed it: " . . . the resident can guard its entire territory all of the time, or it can defend only those portions of the territory within which it happens to encounter an intruder at close range."

From these considerations it follows that the analysis of territorial strategies in ants must comprise the study of the design and spatiotemporal structure of the territory, as well as the social mechanisms through which the insect society pursues its territorial strategy. The geometry of the territory and the social mechanisms by which the territory is established and maintained are inseparable.

Important differences in the use of space exist among species. Species foraging on relatively stable resources that are uniformly dispersed over a wide area have territories that are designed differently from those of species exploiting stable but patchily distributed resources. Distinct strategies are also associated with food sources that are either patchy, relatively stable, and predictable, or else they are frequently changing in location and are unpredictable. In this article, we suggest that the concept of economic defensibility can be used to understand the design of territories maintained by ant societies in these various environments. The species we discuss are ecologically dominant animals and have been studied extensively both in the laboratory and in their natural habitats. Adaptation to food sources that are distributed uniformly in space and are relatively stable in time is exemplified by the African weaver ant *Oecophylla longinoda*. Certain species of the harvester ant *Pogonomyrmex*, in contrast, utilize food sources that tend to be relatively stable but are often distributed patchily in space. Finally, the honey ants *Mymecocystus mimicus* use as a major part of their dietary input protein sources that occur randomly in space and time.

The models presented in this article are based on several major colony properties in order to show as clearly and simply as possible connections between territorial design and cost-benefit factors important to social insects. Oster and Wilson (*4*) have shown how powerful theoretical tools can be applied in order to elucidate the ergonomics of the caste systems and division of labor in insect societies. Our study provides the first attempt to predict territorial design in ants on the basis of the social mechanisms by which the territory is established and maintained.

Absolute Territories of African Weaver Ants

For blackbirds (*Euphagus cyanocephalus*) and a number of other animal species, it has been demonstrated that when resources are uniformly distributed and continuously renewing, it is advantageous to maintain a complete defense of whatever portions of the foraging area can be patrolled in reasonably short periods (*5*). We find a striking analogy to these absolute foraging territories in those of the African weaver ants (*O. longinoda*) although the mechanisms of establishing and maintaining the territories are very different.

Oecophylla longinoda is one of the dominant ant species in many African forest canopies. *Oecophylla* workers bind leaves into tight nest compartments with silk spun by the final instar larvae. One colony usually builds hundreds of such leaf nests, which are distributed over several nest trees and concentrated in the peripheral canopy of the trees (*6, 7*). Weaver ant colonies are monogynous; the single reproductive queen resides in one of the leaf tents, completely surrounded and protected by workers. Most of the other leaf nest compartments are filled with brood of all stages and hundreds of workers. The worker force of a mature *O. longinoda* colony can consist of more than 500,000 individuals.

Weaver ants are strongly predacious, using their cooperative ability to capture a wide range of large insect prey that venture onto their territory. Although the foragers tend to remain on the trees and surrounding low vegetation, they also hunt extensively on the ground; their territories are three-dimensional. *Oecophylla* workers patrol every part of their territory, tolerating only very few ant species on the trees they occupy. But most rigorously they exclude foreign colony members of their own species in aggressive interactions (Fig. 1) so severe that they create narrow, unoccupied corridors, which are in effect "a no ants' land" (*6–8*). In our study area in the Shimba Hills Reserve (Kenya), individual territories sometimes covered an area of up to approximately 1600 square meters comprising 17 major trees (*7*) (Fig. 2).

We were able to determine the territorial borders by repeatedly transplanting sets of 20 *Oecophylla* workers from one nest tree to another. So long as the trees belonged to the same territory, no conspicuous response was observed. But when the transplanted ants were released within the territory of a neighbor colony, a massive defense recruitment response was elicited in the resident ants. Individual ants that had encountered the foreign intruders ran back to some of the nearest leaf nest compartments in the tree canopy, laying a trail with secretion from the rectal gland (*9, 10*). When they encountered nestmates, they presented a vigorous jerking display similar to the initial fighting behavior between two individual opponents. We offered the hypothesis that the initial fighting pattern (or threat display) has been ritualized during evolution, becoming a symbolic signal to recruit nestmates for territorial defense (*10*). In fact, nestmates approached by a jerking recruiter ant became very excited and ran along the trail toward the battle site. After 30 minutes, often many more than 100 ants had assembled in this area and remained there long after all the "intruder" ants had been killed.

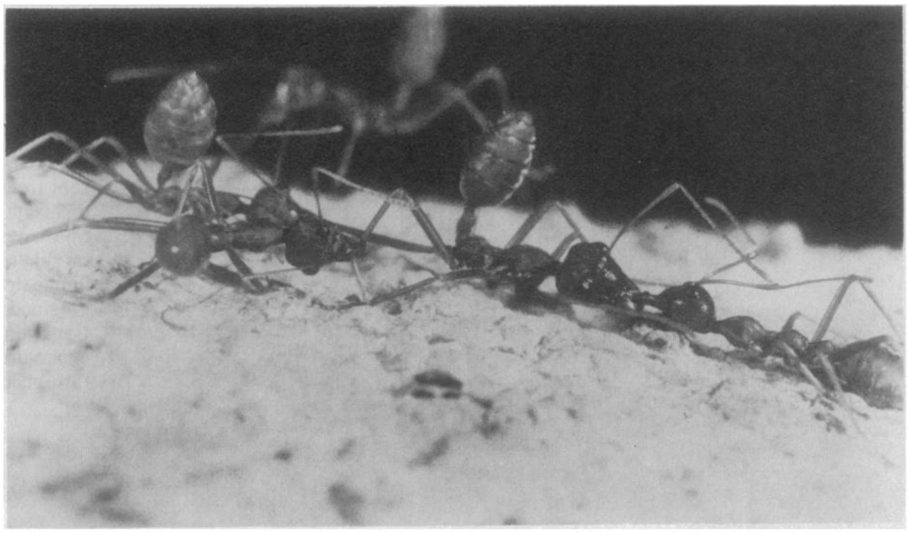


Fig. 1. Three *Oecophylla longinoda* workers attack a conspecific intruder.

The weaver ants have achieved the exceptional control of their environment by the evolution of advanced social communication behavior. No less than five recruitment techniques, each entailing a distinct combination of chemical signals and locomotory communication patterns, are used by the ants to penetrate new territory and subsequently to defend it and to extract food from it (*10*). In our laboratory and field studies we discovered that *Oecophylla* scouts also recruit nestmates to unoccupied space, especially when the colony is growing and expanding (*7*, *10*). We found that when the ants ventured into entirely new terrain, they deposited drops of rectal sac fluid at a high rate all over the surface. Our experiments demonstrated the presence of a territorial pheromone in these markers.

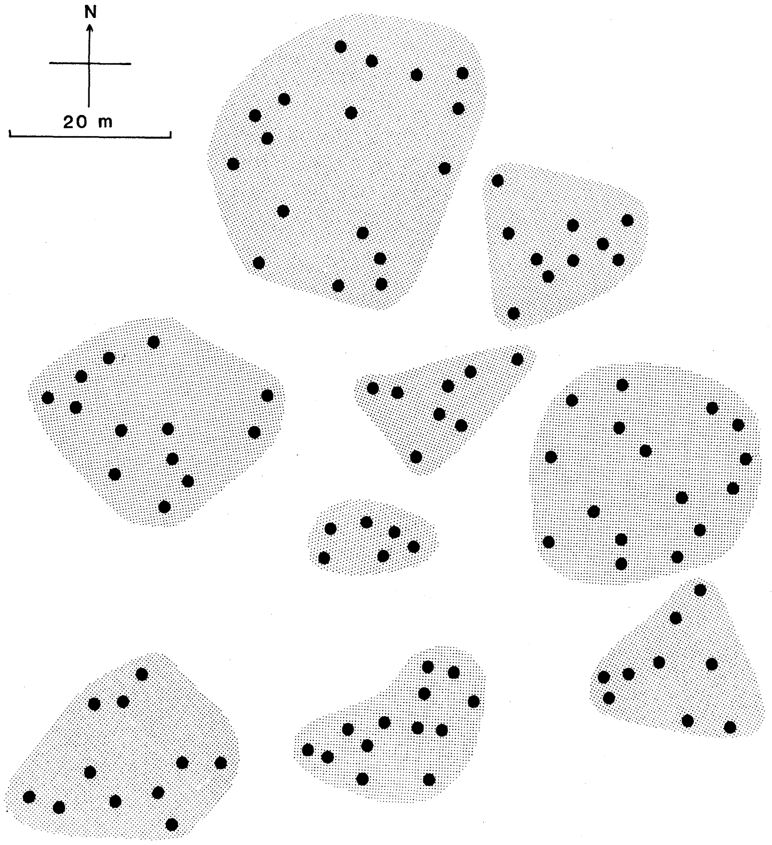
A true territorial pheromone can be defined as a substance used to mark the residential, mating, or foraging space of an animal and which induces an aversive behavior in intruders of the same species either by itself or in combination with other stimuli. The chemical home range markers of *Oecophylla* show all of these properties and must therefore be considered a true territorial pheromone. To our knowledge no pheromone belonging to this functional category had previously been demonstrated in social insects (*10*, *11*).

Interspecific Territoriality in African Weaver Ants

The weaver ant colony finds considerable advantage in excluding competitor colonies of all but the smallest or most dietarily different species. Indeed, *O. longinoda* is highly aggressive not only to conspecific aliens but also to many other ant species. At Shimba Hills, only a few ant species were found to coexist with *Oecophylla* on the same tree. Some other arboreal ant species (for example, *Camponotus* sp.) that were never found to coexist with *Oecophylla* on the same tree elicited as vehement a defense recruitment response in *Oecophylla* as

Table 1. Comparison of cost-benefit calculations of the four boundary defense models illustrated in Fig. 4. In all models C_k is a total cost to defend a boundary surface area per unit time, while B_k is the net foraging profit cropped per unit volume per unit time. For two-dimensional models, $k = 2$; for three-dimensional models, $k = 3$. In "cylindrical 2," the trees occur at a density of N trunks per unit area.

Item	Two-dimensional	Three-dimensional		
		Spheroid	Cylindrical 1	Cylindrical 2
Total cost rate	$2\pi r C_2$	$4\pi r^2 C_3$	$2\pi r h C_3$	$(N\pi r^2) 2\pi r_1 h_1 C_3$
Total benefit rate	$\pi r^2 B_2$	$\frac{4}{3}\pi r^3 B_3$	$\pi r^2 h B_3$	$\pi r^2 h B_3$
Net profit rate	$\pi r(B_2 r - 2C_2)$	$4\pi r^2\left(\frac{B_3 r}{3} - C_3\right)$	$\pi h r(B_3 r - 2C_3)$	$\pi r^2(hB_3 - 2\pi N r_1 h_1 C_3)$
Economic defensibility threshold	$r^* = 2C_2/B_2$	$r^* = 3C_3/B_3$	$r^* = 2C_3/B_3$	$B_3 = 2\pi N r_1 h_1 C_3/h$
Cost-benefit ratio	r^*/r	r^*/r	r^*/r	$2\pi N r_1 h_1 C_3/hB_3$
Figure	4a	4b	4c	4d



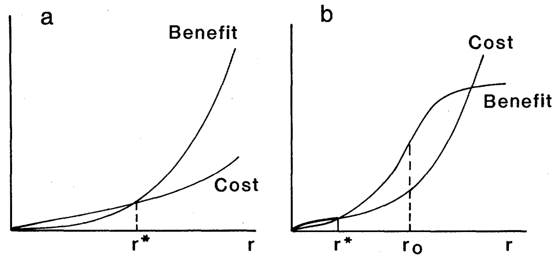


Fig. 2 (left). Territories of *Oecophylla longinoda* in the Shimba Hills Reserve study area. The solid circles represent trees occupied by *Oecophylla*, and the shaded areas delineate the individual territories (*7*). Fig. 3 (right). (a) Cost and benefit curves for boundary defense strategy on spherical territories. The symbol r^* represents the economic defensibility threshold. Maximum of benefit-cost is obtained for $r \rightarrow \infty$. (b) Toward large r, the benefit curve tips over, as a result of decreasing returns to scale in the economics of territorial expansion. Maximum rate of return occurs for territories of radius r_0.

conspecific aliens when they were introduced into a weaver ant territory. It is interesting to note that the *Camponotus* also responded with a defense recruitment of hundreds of nestmates when *Oecophylla* workers were released on a *Camponotus* tree. These results suggest that *Oecophylla* and apparently also the *Camponotus* react with a massive defense response only to certain ant intruders, such as the apparently most serious competitors for essential resources (nesting sites and food), and predators including the army ant *Dorylus* and the formicine *Anoplolepis longipes* (*7, 12*).

This phenomenon of "enemy specification" in the alarm recruitment communication system of ants was only recently discovered in *Pheidole dentata* (*13*). From the new results obtained in our study with *Oecophylla* it now appears possible that the selective identification of either enemy or competitor is a more general phenomenon in ants and perhaps the major underlying behavioral mechanism by which the mosaic distribution of dominant ants is regulated (*7, 8*).

Economic Defensibility of Territories in African Weaver Ants

Social insects have frequently been compared to so-called central place foragers in solitary animals. Although this approximation is apt in many cases, we are intrigued by how far *Oecophylla* diverges from the classic central place model in the mechanisms by which it maintains territorial control. Their nests are not aggregated in one central location but are effectively decentralized throughout much of the territory that they control. This large territory can be patrolled and cropped over much of its volume simultaneously without the colony's incurring the costs of transporting prey from distant capture points to a single central nest deep within the territory. These factors allow us to formulate a different general model concerning the geometry of the "nest decentralization" and the economic defensibility of the *Oecophylla* territory.

A solitary animal, or even a social group with relatively few members, faces a challenge if a territory of considerable size is to be established and maintained: the defender cannot be everywhere at once. Invaders can often penetrate deep into the territory and even harvest resources before they are detected and expelled. This qualitative observation suggests that the solitary holder of a territory faces serious constraints in maintaining a large territory, particularly when the density of the invader is high. In contrast, *Oecophylla* is virtually everywhere at once throughout its territory. Invaders are detected at or very close to a colony's boundary. Consequently, the *Oecophylla* territorial system allows harvesting benefits from throughout the interior of its territory while restricting its defensive costs almost purely to its boundary or margin.

The strategic implications of such a system are far-reaching. To explore some of the consequences, consider a circular territory of radius r with uniformly distributed, temporally stable food sources (Fig. 4a). Similar conclusions hold for territories that approximate convex regions, as in the case of *Oecophylla* (Fig. 2) (*7*). A cohort of foragers, dispersed throughout the interior of the territory at density ρ_w, returns net foraging benefit $B_2 > 0$ per unit area per unit time. Because resources and workers flow locally into many leaf nests dispersed throughout the territory and not back to one central place located deep inside the territory, B_2, which includes the cost of food transport, does not decrease as r increases. Thus B_2 can be approximated by a constant independent of r.

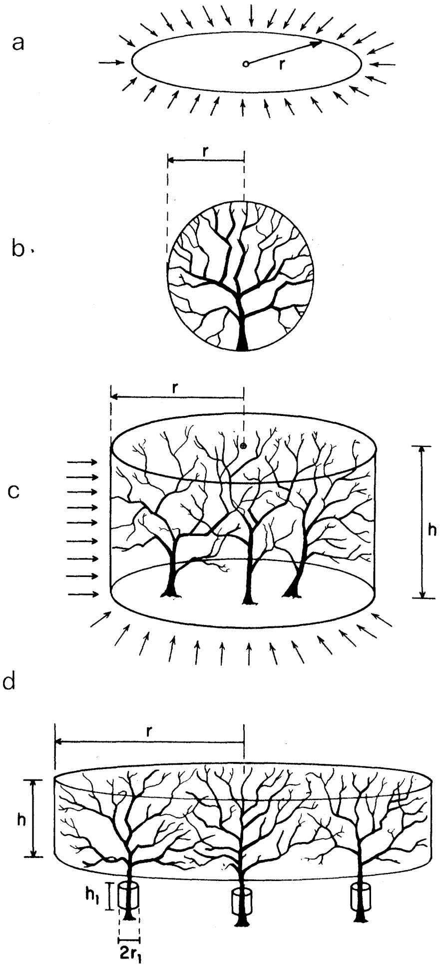


Fig. 4. A comparison of four boundary defense models for *Oecophylla*. (a) The two-dimensional model is that analyzed in the text. Its territory is circular with radius r. In three-dimensional models we have to consider several possibilities. (b) "Spheroid" is a spherical territory with radius r. This is appropriate to thick canopy systems in which the colony can expand outward from the queen nest in all directions for significant distances. (c) "Cylindrical 1" is a cylindrical territory of radius r and height h. All boundaries are defended and challenges come over the cylinder surface (arrows) but not the end faces, which are contained within the territory. (d) "Cylindrical 2," only the trunk surfaces leading up into the occupied canopy are defended. Trunk radius is r_1 and the defense occurs along a length h_1 of the trunks.

Since costs due to intercolony aggression occur primarily at the edge of the territory, let C_2 be the cost per unit time per unit length of boundary. Under these circumstances a territory of radius r yields benefit $B_2\pi r^2$ per unit time to a colony and costs it $2C_2\pi r$. A net ergonomic profit rate $\pi r(B_2 r - 2C_2)$ is produced by this strategy. Thus we find economic defensibility threshold $r^* = 2C_2/B_2$ beyond which the territory yields net positive return. Moreover, the net return is an increasing function of r. Once beyond r^*, the net profit rate is positive and continues to increase (Fig. 3a). The ratio of defense cost to net foraging benefit is just r^*/r and thus decreases monotonically with r. Colonies that use such a strategy should prefer the largest possible territory. Eventually, sufficiently large r is reached such that the egg-laying capacity of the queen is saturated and the colony, in addition, begins to control an unusable surplus of resource. Thus, the increment to benefit eventually approaches zero, and optimal economic defensibility occurs at an intermediate r, say r_0 (Fig. 3b). The very large number of workers that mature *Oecophylla* colonies can maintain suggests a large laying capacity in the queen and the potential for very large territories.

The territories of *Oecophylla* are actually three-dimensional rather than two-dimensional. But so long as the territorial strategy is one of decentralized nests, with workers monopolizing the interior volume of the territory while confining defense costs to the boundary, there are economic defensibility thresholds; and the ratio of cost to benefit continues to decline along the curve r^*/r as the territory expands in size below saturation of the egg-laying capacity of the queen and the surplus limits of resources. Differences between the geometry of two and three dimensions and deviations from this idealized strategy impose quantitative differences in the details of territory design (Table 1 and Fig. 4).

There may also be territorial size limits beyond which such factors as transport of brood from the queen nest to other leaf nests in the colony becomes ergonomically impractical or the system of inter-nest coordination becomes too complex to maintain. The observed sizes of *Oecophylla* territories suggest, however, that the way stations offered by established leaf nests and the rather local nature of the nest-nest interactions within the territory make such limits relatively weak. It appears that there is a high selection pressure for expanding territorial space and thus increasing access to essential resources while simultaneously improving the relative economic defensibility of the territory. Indeed, the three-dimensional territories of *O. longinoda* are probably the largest territories known for all invertebrates.

Trunk Trail Territories of Harvester Ants

Generally, the partitioning of space 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. In contrast to the African weaver ants, some harvester ant species, such as *Pogonomyrmex barbatus* and *Pogonomyrmex rugosus*, which are among the most abundant species in the southwestern United States, tend to exploit patchy food supplies and accordingly show a more complex partitioning structure (*14-17*).

Foragers of the harvester species travel on well-established trunk trails before diverging on individual excursions (Fig. 5). After foraging, the workers return to these routes for homing. Such trunk trails sometimes extend for more than 40 meters; they are remarkably persistent over long periods of time and even survive heavy rainfalls. The trunk routes originate from recruitment trails laid to newly discovered seed falls. The recruitment pheromone, which is relatively short-lived, is discharged from the poison gland and deposited on the ground by foraging ants with the extruded sting. Because the seed patches are frequently quite stable, the ants continue to travel along the former recruitment trail to these foraging sites. Persistent chemical signposts are also deposited along the trail and, together with the visual markers, serve as orientation cues long after the recruitment signal has vanished.

Trunk trails of intraspecific neighbor nests never cross (Fig. 6). On the contrary, they usually diverge and channel the mass of foragers of hostile neighboring nests into diverging directions. The trunk trails, together with the immediate surrounding of the nest entrance of mature colonies, can be considered the "core area" of the colony's territory. Although foraging areas of nearby colonies can overlap, aggression in the overlapping zone is usually limited to individual confrontations between two foragers. However, when two trunk trails of neighboring colonies are brought into contact, heavy aggressive mass confrontations occur; and they continue until the trunk trails have diverged again. 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 depends greatly on the route maps of its neighboring colonies.

Fig. 5. A *Pogonomyrmex rugosus* nest with two distinct trunk trails (*15*).

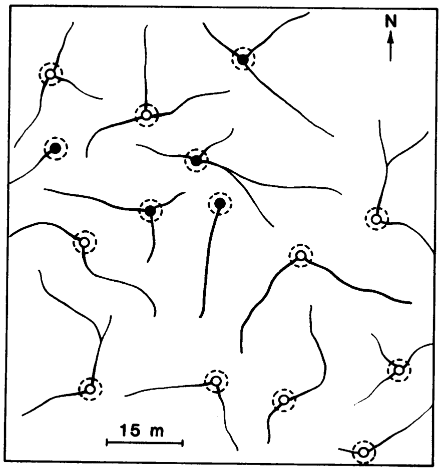


Fig. 6. Map of nests and trunk routes of *Pogonomyrmex barbatus* and *P. rugosus* in one section of the study site in New Mexico. Solid black circles, *P. barbatus*; open circles, *P. rugosus*.

Up to this point we have considered only the partitioning of foraging grounds by the trunk route system between colonies belonging to the same species. *P. barbatus* and *P. rugosus*, however, seem to have a wide niche overlap, and they seem to be identical with regard to food type, nesting site, and foraging activity period. Although populations of both species are largely separate geographically, overlap zones are known (*15, 18*). It is not surprising therefore that territoriality is strongly developed both within and between these two species, and that the foraging area is subdivided interspecifically by the trunk route system. These findings lead to the question of the cues used by the ants to discriminate between colonies of their own and other species (*19, 20*). The foragers not only have to be able to recognize members of their own colony and those belonging to another conspecific colony, they also need to identify other species that are potential competitors for essential resources.

Although not much is known about the mechanisms of species discrimination in ants, we have some analytical evidence of the species specificity in the mixtures of hydrocarbons of the Dufour's glands in *Pogonomyrmex*. It is interesting that *P. rugosus* and *P. barbatus*, which exhibit strong interspecific territoriality, have almost identical patterns in the mixtures of the compounds of their Dufour's glands, whereas other *Pogonomyrmex* species, whose territories overlap with those of *P. rugosus* and *P. barbatus*, have very different patterns (*21*).

Economic Defensibility of the Trunk Trail Territories

It is useful to compare the territorial strategy of the African weaver ant (*O. longinoda*) with that of species such as *P. barbatus* or *P. rugosus* that utilize spatially patchy but long-lived resources (Fig. 7a). To this end, the nest region can be visualized as a system of sectors (Fig. 7b) which define a polar coordinate system centered on the nest. Resource patches fall within the sectors. Let $C^{sec}(r, \theta)$ be the cost per unit time to the colony—in terms of the numbers of workers, their metabolism, and the mortality—to defend a sector of radius r and angular coverage θ. For most stages of *Pogonomyrmex* life-cycle, we expect $\partial C^{\text{sec}}/\partial r > 0$ and $\partial C^{\text{sec}}/\partial \theta > 0$, making C^{sec} an increasing function of r and θ. Thus a maximal net profit strategy in territorial design favors the smallest values of r and θ consistent with resource patch acquisition (Fig. 7, b to d). The resulting territorial design approximates a trunk trail system. The model is readily generalized to consider such details as efficiencies of food retrieval over narrow trails, the effects of nearby alien colonies, the presence of multiple patches in each sector, and time-varying costs.

If $B(r_i^o)$ is the net benefit derived from a resource patch at distance r_i^o from the nest in sector i and T_i is the length of time which sector i is kept open, then the net benefit accrued from the entire sector system is

$$B_{\text{net}} = \sum_i{}' [B_i(r_i^o) - C_i^{\text{sec}}(r_i, \theta_i) \cdot T_i] - \sum_i{}'' C_i^{\text{sec}}(r_i, \theta_i) \cdot T_i \qquad (1)$$

The sum Σ' is over sectors containing patches, while Σ'' runs over sectors which are defended but empty. Empty sectors represent pure cost and should be monopolized for zero time. Such a colony should, with the exception of scouts in the field, shut down empty sectors (Fig. 7, c and d). In some sectors the patch benefit B_i may not exceed the cost $C_i^{\text{sec}} T_i$. Hence the sector is not economically defensible and may be shut down. This can be the case when the patch is too small or not rich enough, or too far from the nest (which is a central place for *Pogonomyrmex*), or when a rival nest already occupies the patch and usurpation costs would be greater than the acquired benefit.

Our experimental field data agree well with these economic considerations. New foraging sites, which have not yet been discovered by competitors, are rapidly explored and occupied with the aid of an effective chemical recruitment system. In fact, the significance of the recruitment communication in harvester ants becomes especially apparent in view of the strong intra- and interspecific competition for the same foraging areas. We were able to demonstrate that the forager recruitment activity not only depends on a number of parameters of the food source—such as distance to the nest, density of the seed fall, and size of the grains—but also on the presence or absence of foreign foragers at the resource patch (*15*). Seed sites previously occupied by competing foragers were considerably less attractive than unoccupied seed sites.

Although most *P. barbatus* and *P. rugosus* colonies in our study area had extensive trunk trail systems, a number of nests, especially in areas with sparser vegetation, had no trunk trails (*15, 16*). This is a general trait of *Pogonomyrmex maricopa*, which we never observed to produce long-lasting trunk trails (*15*). In these cases ants usually leave the nest on their individual foraging excursions and disperse in all directions. However, as our experiments demonstrated, the foragers also show a high directional fidelity, although all sectors appear to be more or less equally frequented by the worker force as a whole. This suggests that the seeds are not accumulated in patches but rather are randomly dispersed. In other words, the individual sectors apparently are more or less equally productive. This foraging system obviously does not allow as subtle a partitioning of foraging grounds between neighboring colonies as the trunk trail system. Such colonies invariably show a much wider spacing pattern (*15*).

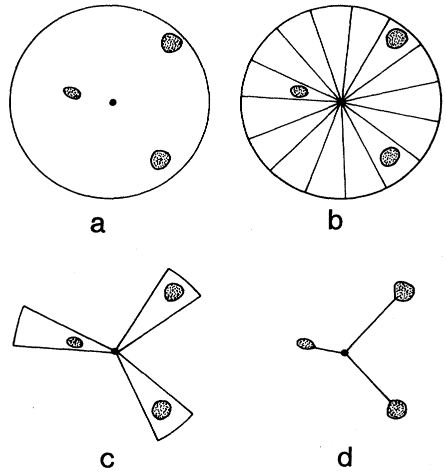


Fig. 7. Resource distribution and the development of the trunk route foraging system in *Pogonomyrmex*.

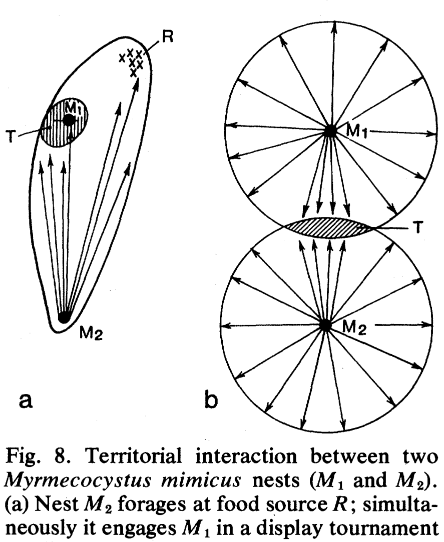


Fig. 8. Territorial interaction between two *Myrmecocystus mimicus* nests (M_1 and M_2). (a) Nest M_2 forages at food source R; simultaneously it engages M_1 in a display tournament (*T*) directly at the nest of M_1, thus, interfering with the foraging activity of M_1. (b) M_1 and M_2 foragers disperse in all directions around their nests. This can lead to territorial tournaments in an area located between both neighboring nests.

Thus the trunk routes of *Pogonomyrmex* are partitioning devices which curtail aggressive confrontations between neighboring colonies, while at the same time enlarging the foraging area for patchy food supplies. A similar foraging and partitioning system has been reported for several species of *Formica* (*22*), *Lasius* (*23*), and the leaf cutter ants *Atta* (*24*).

Trunk Route Foraging Systems of Other Harvester Ants

The trunk routes of the seed harvesting ant *Pheidole militicida* have much in common with those of *Pogonomyrmex* (*25*). They, too, originate from chemical recruitment trails and are stabilized by enduring chemical orientation cues and visual markers. Nevertheless, they are not as persistent as the foraging pathways of *Pogonomyrmex*. In fact, the route foraging system of *P. militicida* seems to be intermediate between that of *Pogonomyrmex* and that of *Veromessor pergandei*. *Veromessor* seems to employ a foraging strategy in which various sectors of the foraging area around the nest are successively exploited by the ants (*26, 27*). Like the *Veromessor*, *P. militicida* workers shift the direction of the foraging pathway or establish a new route when the seed supplies in a foraging area diminish. However, the shifts do not occur as regularly as in *Veromessor*, and no geometric pattern in the change of the foraging columns was detected. We have, however, no evidence that the trunk trails also serve for territorial partitioning as they do in the case of *Pogonomyrmex*. Although little is known about the territorial strategies of these species (*V. pergandei and P. militicida*), it is likely that they have less rigid territorial boundaries and that only those areas that are currently frequented by foragers are defended.

Spatiotemporal Territories of Honey Ants

If resident ants defend only those portions of their territory in which they happen to forage and encounter intruders at close range, the territorial defense is spatiotemporal. We will now describe a spatiotemporal territorial strategy of

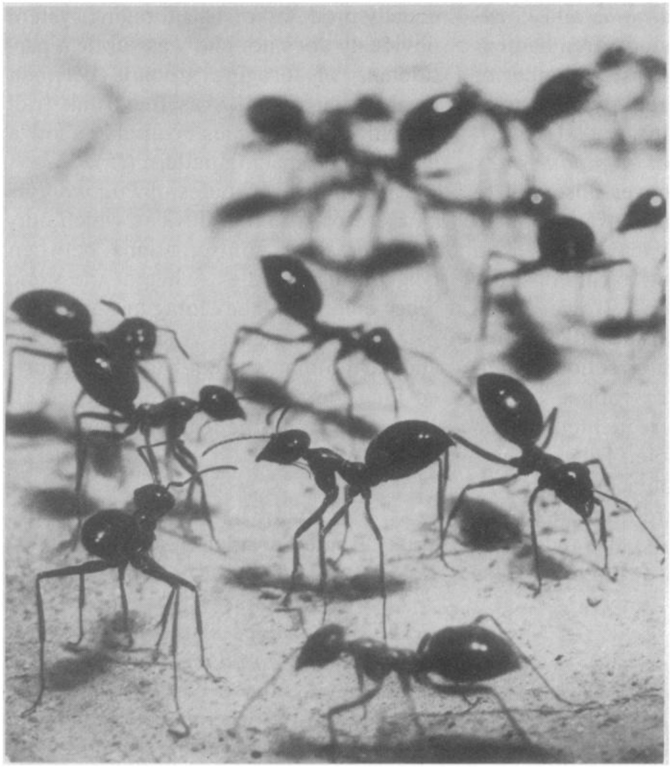


Fig. 9. Territorial tournament of *Myrmecocystus mimicus*. Worker ants of neighboring colonies confront each other in ritualized display fights during which they walk high with their legs in a stiltlike position, while simultaneously raising their gasters and heads.

honey ants (*Myrmecocystus mimicus*) that appears to have evolved as part of a foraging system designed to utilize patchily distributed but unpredictable or unstable food sources. *Myrmecocystus mimicus* is abundant in the mesquite-acacia community of the southwestern United States (*28*). Like other members of its genus, it has a special honeypot caste, the members of which function as living storage containers.

One of the major food sources of *M. mimicus* is 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 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 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 (Fig. 8a). 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 declines and the intruding army finally retreats to its own nest.

Although hundreds of ants are often involved during the territorial tournaments, almost no physical fights occur. Instead individual ants engage each other in highly stereotyped aggressive displays (Fig. 9). Each group of displaying ants breaks up after 10 to 30 seconds, but the ants continue to move on stilt legs. When they meet a nestmate they respond with a brief jerking display, but when they meet another opponent the whole aggressive display ceremony is repeated.

The answer to the question of how it is possible that scout ants can venture so deeply into the foraging area of a neighboring colony is provided by our field observations. Although individual foragers of *M. mimicus* frequently disperse in all directions when leaving the nest, they tend to swarm out of the nest at intervals. Such departures are usually spaced irregularly in time, and an interval between two can last as long as several hours. Sometimes only very few foragers leave a nest during a whole day, while in contrast the foragers of a neighboring nest may be very active. Then within a few days the situation is reversed. However, if a scout of a relatively inactive colony discovers a rich food source, such as an access to a gallery of a termite nest, it can quickly galvanize the colony into foraging activity by recruiting nestmates to the food source. But the termites may have already been discovered by foreign scouts of the very active neighboring colony, which then sends an army of ants to the competing nest in order to interfere with the first colony's foraging activity.

Territorial tournaments also occur 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 (Fig. 8b). These tournaments sometimes last for several days, being interrupted only at night when workers of this species are normally inactive.

When one colony is considerably stronger than the other, that is, when it can summon a much 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. Field observations and laboratory experiments have led to the discovery 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.

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 percent of all tournament interactions observed. A total of nine raiding events was observed from beginning to end, enabling us to make a fairly accurate count of the number of larvae, pupae, honeypots, and workers abducted into the raiders' nest. From these data we éstimate that the raiding colony is at least about ten times larger than the raided colony. Thus raiding seems to be primarily or perhaps even exclusively directed against younger, still developing colonies in the neighborhood. We suspect that during tournamenting the ants somehow assess the size of the opposing colony, which explains why scouts of both parties repeatedly recruit worker reinforcements to the area of conflict.

The Territorial Logic of *Myrmecocystus mimicus* Colonies

The adaptive significance of this peculiar territorial strategy is of interest. As already mentioned, one of the major food sources of *Myrmecocystus* is termites. The temporal and spatial distributions of the termite colonies 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. Instead it defends only areas into which it is currently conducting intensive excursions. This procedure obviously enables it to extend its foraging range considerably and leads to frequent incursions into potential foraging ranges of neighboring *Myrmecocystus* colonies. Since there are no well-established territorial borders, aggressive mass confrontations with conspecific competitors are much more common in *M. mimicus* than in *Oecophylla* or *Pogonomyrmex*. If these confrontations were as violent as physical combat in the latter species, they would result in a constant and heavy 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 does it risk being overrun by the stronger colony, having its queen killed, and being enslaved by the stronger colony (*29*).

The territorial logic of the *Myrmecocystus* colonies can be further analyzed with the aid of a geometric model. We consider a group of neighboring colonies located in an area A in which resources occur patchily in space and time and in an essentially stochastic manner. A honey ant colony pursuing a rigid territorial monopolization strategy would maintain exclusive use of an area α around the nest. If the cost of monopolizing a territory of area α costs the colony $C(\alpha)$ per unit time, then the total defense cost for a given interval T is $C(\alpha)T$.

During T, a number of resource patches (fractions of termite nests) will appear in the area A, patterned in a spatial distribution. In the simplest case, this distribution is random and each point in A is just as likely to receive a resource patch as is any other point. Let R be the total number of resource patches which, on the average, appear in A during the period T. Then the average density of resource patches is $\rho = R/A$ patches per unit area, and the probability that a honey ant colony will receive n of these on its area is

$$P(n) = e^{-\alpha\rho}(\alpha\rho)^n/n! \qquad (2)$$

For clarity let each patch return benefit B_0 to the colony. During T the colony acquires on the average a total of $\alpha\rho$ resource patches on its territory and thus harvests an average benefit $B = B_0\alpha\rho$. As resources become scarcer, ρ decreases and the size of territory required to harvest a given benefit B increases.

If the colony requires a minimum return B^* on its territorial investment during the period T, then the fixed territory of area α is economically defensible on the average if

$$\rho B_0 - B^*/\alpha \geq C(\alpha)T/\alpha \qquad (3)$$

The surplus yield per unit area must exceed the defense costs per unit area during T. For environments with scarce resources, ρ will be small, and these conditions are unlikely to be met.

The expected return B characterizes the average benefit accrued over a very large number of repeats of the period T. For any single period T, the appearance of resource patches in a fixed territory is a sampling from $P(n)$ and will lie close to B each period only if $P(n)$ peaks sharply around its mean $\alpha\rho$. For $P(n)$ with the Poisson structure (Eq. 2), however, the variance σ^2 is as large as the mean itself

$$\sigma^2 = \alpha\rho \qquad (4)$$

and the harvestable return to the colony can vary significantly from period to period. Similar conclusions follow for related distributions. In such an environment, holding fixed territories is a high-risk strategy in the sense that variance on return is of the same magnitude as the return itself. For many periods T, there will be either a resource surplus on the territory, which can exceed the colony's handling capacity, or a substantial resource deficit, which will make the defense effort a heavy drain. If the colony can handle surplus and ride out hard times (which is evidently possible due to the honeypot caste), the effects of this short-term stochasticity can be smoothed out somewhat and net benefit B predicted by Eq. 2 would be more closely realized. Economic problems of defensibility would then again be addressed by Eq. 3. But a colony locked into a fixed territory is at the mercy of the fluctuations in the resource. A colony struck by chance with a long chain of "hard time" periods would be eliminated if it is unable to search further afield for resources.

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 for 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 appears unlikely. The alternative to fixed territories is a foraging system with floating, temporary territorial boundaries, as has been 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.

References and Notes

1. E. O. Wilson, *Sociobiology: The New Synthesis* (Belknap, Cambridge, Mass., 1975); A. P. Covich, *Annu. Rev. Ecol. Syst.* **7**, 235 (1976); N. B. Davis, in *Behavioral Ecology*, J. R. Krebs and N. D. Davis, Eds. (Sinauer, Sunderland, Mass., 1978); T. W. Schoener, *Annu. Rev. Ecol. Syst.* **2**, 369 (1971).
2. C. Elton, *J. Anim. Ecol.* **1**, 69 (1932). For reviews see: M. V. Brian, *Social Insect Populations* (Academic Press, New York, 1965); C. R. Carroll and D. M. Janzen, *Annu. Rev. Ecol. Syst.* **4**, 231 (1973); C. Baroni Urbani, in *Social Insects*, H. R. Hermann, Ed. (Academic Press, London, 1979), vol. 1, pp. 91–120.
3. J. L. Brown, *Wilson Bull.* **76**, 160 (1964); ——— and G. H. Orians, *Annu. Rev. Ecol. Syst.* **1**, 239 (1970); J. L. Brown, *The Evolution of Behavior* (Norton, New York, 1975).
4. G. F. Oster and E. O. Wilson, *Caste and Ecology in the Social Insects* (Princeton Univ. Press, Princeton, N.J., 1978).
5. H. S. Horn, *Ecology* **49**, 682 (1968).
6. M. J. Way, *Bull. Entomol. Res.* **45**, 93 (1954).
7. B. Hölldobler, *Z. Tierpsychol.*, in press.
8. D. Leston, *Proceedings of the Third International Cocoa Research Conference. Accra* (1969), pp. 205–221; *Annu. Rev. Entomol.* **15**, 273 (1970); *Cent. Overseas Pest Res. Misc. Rep.* **19**, 311 (1973).
9. B. Hölldobler and E. O. Wilson, *Science* **195**, 900 (1977).
10. ———, *Behav. Ecol. Sociobiol.* **3**, 19 (1978).
11. ———, *Proc. Natl. Acad. Sci. U.S.A.* **74**, 2072 (1977).
12. F. L. Vanderplank, *J. Anim. Ecol.* **29**, 15 (1960).
13. E. O. Wilson, *Science* **190**, 798 (1975).
14. B. Hölldobler, *Proc. Natl. Acad. Sci. U.S.A.* **71**, 3274 (1974).
15. ———, *Behav. Ecol. Sociobiol.* **1**, 3 (1976).
16. D. W. Davidson, *Ecology* **58**, 725 (1977).
17. For review see J. H. Brown, O. J. Reichman, D. W. Davidson, *Annu. Rev. Ecol. Syst.* **10**, 201 (1979).
18. D. W. Davidson, *Ecology* **58**, 711 (1977).
19. W. Hangartner, J. W. Reichson, E. O. Wilson, *Anim. Behav.* **18**, 331 (1970).
20. B. Hölldobler and C. Michener, in *Evolution of Social Behavior: Hypotheses and Empirical Tests. Life Science Research Report 18, Dahlem Konferenzen 1980*, H. Markl, Ed. (Verlag Chemie GmbH, Weinheim), pp. 35–58.
21. F. E. Regnier, M. Vieh, B. Hölldobler, *J. Insect Physiol.* **19**, 981 (1973); B. Hölldobler and F. E. Regnier, unpublished results.
22. G. J. De Bryn and A. Mabelis, *Ekol. Pol.* **20**, 93 (1972); G. J. De Bruyn, *Neth. J. Zool.* **28**, 55 (1978); R. Rosengren, *Acta Zool. Fenn.* **133c**, 1 (1971).
23. J. Traniello, *Naturwissenschaften* **67**, 361 (1980).
24. S. P. Hubbell, personal communication.
25. B. Hölldobler and M. Möglich, *Insectes Soc.*, in press.
26. R. A. Bernstein, *Ecology* **56**, 213 (1975).
27. S. W. Rissing and J. Wheeler, *Pan-Pac. Entomol.* **52**, 63 (1976).
28. R. R. Snelling, *Nat. Hist. Mus. Los Angeles Cty., Sci. Bull.*, No. 24 (1976), entire issue.
29. B. Hölldobler, *Science* **192**, 912 (1976).
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