

Brood Raiding in the Fire Ant, *Solenopsis invicta* (Hymenoptera: Formicidae): Laboratory and Field Observations

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ABSTRACT One of the first activities of minim workers in incipient fire ant nests is mutual brood raiding, the reciprocal stealing of brood from nearby incipient nests. Brood raiding was observed in the fire ant, *Solenopsis invicta* Buren, in the laboratory and in the field. Raids were initiated by individual workers, usually from the larger nest, involved trail laying and following, and lasted from minutes to days. Aggression toward intruding workers was generally low and often absent. Workers in the losing nest occasionally raided for the intruding colony (traitor raiders). The colony with more workers was likely to win the raid. No other factors—number of queens, number or stage of brood, or minim relatedness—affected winning. Workers from the losing nest, and often queens too, defected to the winning one. In the field, reciprocal brood raiding was a major cause of incipient colony mortality. It took place along odor trails connecting various numbers of nests from a few centimeters to 20 m apart, and its effect was to aggregate the brood and workers from local populations of incipient colonies into a few locations. One brood raid lasted 38 d, with over 100 m of trail, and involved at least 80 incipient nests.

KEY WORDS colony founding, colony mortality, life history

IN THE MAJORITY OF ant species, colony founding is claustral: female alates, in isolation and without the aid of workers, rear the first brood from reserves stored in their bodies. During this period, most colonies are subject to high mortality, hence high potential for selection. The incipient period immediately following the claustral period is one of further stress, competition, and mortality. Phenomena such as pleometrosis (cooperative founding) and brood raiding can improve survival and success. Early accounts of *Solenopsis invicta* Buren (Khan 1966, Markin et al. 1972) and *Atta texana* (Buckley) (Echols 1966) noted that incipient colonies sometimes joined or could be joined artificially without much hostility. Bartz & Hölldobler (1982) found that workers from incipient colonies of *Myrmecocystus mimicus* Wheeler engage in reciprocal brood stealing ("raiding") with neighboring colonies. Subsequently, pleometrosis and brood raiding were reported in *Veromessor pergandei* (Mayr) (Rissing & Pollock 1987) and *S. invicta* (Tschinkel & Howard 1983, Tschinkel 1987). Rissing et al. (1986) thought brood raiding was likely in *Acromyrmex versicolor* (Pergande). Pollock & Rissing (1989) suggested that in all four of these species, brood raiding is a consequence of the combination of clumped colony founding in favorable microsites and adult territoriality. Tschinkel (1987) interpreted pleometrosis and brood raiding in light of the scramble competi-

tion in which the "weedy" *S. invicta* engages during the colonization of disturbed sites.

Brood raiding in *M. mimicus* (Bartz & Hölldobler 1982) and *S. invicta* (Tschinkel 1987) occurs with little or no fighting among workers, but fighting occurs in *V. pergandei* (Rissing & Pollock 1987). In all three species, losing workers defect to the victorious nest. Abandoned queens may leave their founding chamber and attempt to enter other incipient nests. Winning nests are usually nests with the most workers at the outset, those founded by groups of queens, highlighting the importance of pleometrosis.

In *V. pergandei*, *A. versicolor*, and *M. mimicus*, brood raiding has been observed only in the laboratory. Its occurrence and importance in the field have not been established. The purpose of this paper on *S. invicta* is to report the first field observations of brood raiding, and to describe raiding behavior in both field and laboratory. Data on the importance of raiding to the early population dynamics of the species is published elsewhere (Tschinkel 1992).

Materials and Methods

Newly mated queens were collected during mating flights in late spring and early summer. In the laboratory, they were allowed to rear incipient colonies at 30°C in test tubes filled halfway with water retained by a cotton plug; the

queen(s) themselves were retained by a second cotton plug in the mouth of the tube. Incipient nest tubes were placed in pairs in arenas whose sides had been coated with Fluon (Northeast Chemical, Woonsocket, RI) to prevent escape, and behavioral observations were carried out under the dissecting microscope. Workers were marked individually with paint spots. One to 2 d after painting, nests were opened and observed. Seventeen nest pairs were observed for a total of >100 h. Observations of 12 raids were sufficiently complete to warrant summarizing here. Because it is not possible to observe both nests of a pair at once, the record does not include all events in a raid.

Data were analyzed by Minitab (Ryan et al. 1976).

Results

Observations of Raiding Behavior in the Laboratory. The following is a composite picture of typical raids and their variation, divided into before-raiding, initiation of raiding, and raiding phases.

Before-Raiding Phase. Minim workers usually wandered into the foraging arena within minutes of nest opening, and entered and made contact with the other nest in 20–40 min (range, 10 min to 1 h). Initial contact usually involved antennation, but occasionally the intruder jerked back. The intruder remained in the host nest for seconds to hours, often engaging in mutual grooming or trophallaxis with host workers. Hostility toward intruders was either absent (3 of 12 raids) or very mild (6 of 12), varying from brief grasping and holding of an intruder's appendage or petiole to longer restraint by holding. At the highest level of aggression (3 of 12), at least one host worker grasped an intruder and flexed its gaster as if to sting, but stinging was never observed. Workers from some individual nests were consistently more aggressive than those from others, but most contacts between minims from different nests were not overtly hostile. In some cases, host workers failed to respond to intruders in any overt way, and remained quiescent.

In 7 of 12 raids, an intruding worker, usually from the larger nest, engaged the host queen in trophallaxis, and this often occurred during the before-raid phase.

In most cases, at least one of the intruding workers laid a trail upon returning home, sometimes reinforcing it several times. In five of six cases in which initial trail laying was observed, the trail-layer was from the larger nest. In one case, three workers from the larger nest laid trails, and in one case where the nests were of almost equal size, a worker from each nest laid a trail.

Initiation of Raiding Phase. Raiding began 10 min to 5.75 h (mean = 130 min; SD = 111 min; $n = 11$) after opening the nests. In 10 of 12 cases,

raiding was initiated by an intruder from the larger nest, who simply picked up a pupa, larva, or callow worker and carried it back to the home nest. In one case, a traitor worker from a smaller nest initiated a raid by carrying brood from its own into the larger nest. Brood stealing was sometimes passively blocked by the queen's or host workers' position over the brood, but active resistance to stealing was not seen.

Raiding Phase. Once the brood was deposited in the home nest, a worker occasionally appeared to alert nestmates by excited antennation, but often she simply returned to the host nest to steal more brood. In three raids, a single worker raided for one nest. In five raids, one of the nests provided no raiders. In the other seven cases, workers from the raided nest began to carry brood back from the raiding nest, so that a two-way traffic in brood developed. It was possible for a larva or pupa to be carried back and forth many times.

In only one case did all workers in a nest raid, and then the nests were both small but of almost equal size. In all other cases, only a minority (mean = 20%) of the workers in each nest raided at all. The number of raiding workers seems unlikely to explain victory in raiding because the number of raiders committed by the two nests did not differ much. The values were (large versus small): 3 versus 2; 2 versus 4; 1 versus 0; 4 versus 3; 0 versus 1; 3 versus 0; 1 versus 0; 3 versus 5; 6 versus 6 (but 3 were traitors); 4 versus 4; 3 versus 7 (all); 2 versus 0.

When a nest fielded multiple raiders, their activity was usually unequal. For the three well-quantified raids, the number of brood returned by three raiders from one nest were 15, 10, and 1. From another, they were 45 and 5, and from a third, 21, 6, and 4.

Raids were not usually observed to their termination, so neither the winner nor the duration of raiding is known for most of these cases. In at least four cases, raids lasted more than 12 h, and in one case, some of the same individual workers were still raiding after 6 d. The tempo of raids also varied enormously, from occasional leisurely trips by a single raider to very rapid and frequent raiding in both directions. When brood were not abundant, this sometimes meant that a pupa or larva was carried into a home nest and practically deposited into the mandibles of an intruder waiting to return it to its own nest.

An especially interesting phenomenon is that of "traitor raiders." In 4 of 12 cases, workers carried brood or callows from their own nest into the other nest, and in one case, this action even initiated the raid. In one case, three raiders from the larger (28 minims) nest raided for the smaller (17 minims) for most of the raid's duration, boosting the number of raiders for the smaller nest from six to nine and decreasing those raiding for the larger nest to three loyalists. Two of the traitors were even seen laying trails many times

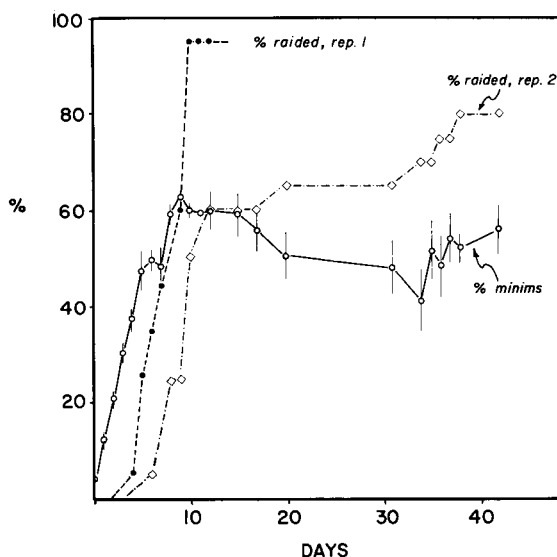


Fig. 1. Cumulative proportion of incipient nests that brood raided in relation to development stage (% minims). By the time the first brood of pupae had eclosed, most raids were complete. A second wave of raids coincided with eclosion of the second brood of minims. Ordinate shows both percentage of test pairs having raided, and percentage of unmanipulated nest population that is minims. Error bars = SEM.

while they continued to raid for the opposition. The smaller nest won this raid after about 20 h.

When Does Raiding Occur? At what stage of colony development does raiding behavior appear? Clearly, adult workers must be present. The lag between their appearance and the onset of raiding was tested in the following experiment. Claustal nests founded by single queens were censused before emergence of the first minims when dark (older) pupae were present. They were assigned to one of two treatments: unmanipulated nests in which relatively large and small nests were paired in arenas; and manipulated, in which dark pupae were regularly removed as they appeared in the smaller nest of each pair and replaced with pale pupae. The manipulated nest never contained minims and was itself incapable of raiding. It was considered "bait" for the unmanipulated member of the pair. All nests were given continuous access to the arena and each other and were checked daily for raiding. Nests were censused daily. Each of the two replicate sets consisted of 10 manipulated and 10 unmanipulated pairs.

Raiding is one of the first orders of business for newly emerged minim workers (Fig. 1). By the time the first wave of minims has eclosed (about 8 d from the first minim eclosure), 95% of the pairs in the first replicate and 60% of the second replicate had raided. In replicate 2, after the first 60% raided, raiding did not commence again until the second wave of minim eclosion began at

about 30 d. This suggested that it is primarily young minims who raid. Raiding occurred at similar rates in the normal-bait pairs and the large-small pairs within a replicate and these were thus pooled, but they differed significantly between replicates (Fig. 1). On the other hand, the rate of eclosion of minims was almost exactly the same in both replicates, so that these data were pooled in Fig. 1.

Of special interest is the occurrence of raiding in the manipulated treatment in which the larger, normal nest interacted with a minimless nest containing only brood and a queen. The fact that these raids occurred with the same timing and frequency as those of unmanipulated pairs suggested that interaction with host minims was not a necessary condition for raiding to occur.

No shared character could be associated with the eight nests whose workers failed to raid. The reasons for not raiding are unknown.

Characteristics of Winning Nests. What does it take to win a brood raid? Brood raiding between pairs of laboratory colonies of experimentally manipulated composition allowed me to determine the characteristics of raid-winning nests. Nests were composed in two different ways: seminatural and random. In seminatural, minims were simply removed from an incipient nest to achieve the desired nest size. Brood were pooled over all nests and assigned as called for in the experimental design. Workers thus remained with their own mothers, at least until raiding began, but most brood were from other nests. In the random treatment, workers, brood, and queens from the entire experimental group were randomly assorted into nests of the desired composition before the experiment began. Ants in such incipient nests were mostly unrelated. Experimental nests were placed into arenas, allowed to acclimate for 24 h, and then unplugged so that raiding could take place. A raid was considered won when all brood were in one nest. In most cases, most of the workers were also found in the winning nest. The experiment was terminated after 24 h. The effect of composition was tested by pitting randomized nests against seminatural nests with the same composition. There was no significant difference in their likelihood of winning a raid (Table 1; binomial test).

When experimental colonies were only censused but otherwise unmanipulated, and paired large (mean = 19.3 minims) versus small (mean = 8.6 minims), large colonies won 11 out of 12 raids (Table 1). The outcome was similar when the size difference was created by experimental manipulation. When such semi-natural small nests (seven minims and eight brood) were challenged with large ones (20 minims and 40 brood), the large nests won most raids (Table 1).

Does the size of the numerical advantage affect the likelihood of winning? Randomized nests of 10, 20, and 40 minims with proportional brood

Table 1. Factors affecting victory in laboratory brood raids

	<i>n</i> (pairs of nests)	No. of raids	Odd treatment	No. raids won	Even treatment	No. raids won	<i>P</i>	No. queens joining victor
Nest composition (minims)	20	12	Natural	8	Random	4	ns	2
Colony size (unmanipulated)	20	12	Small (mean = 8.6)	1	Large (mean = 19.3)	11	0.003	0
Worker no. (seminatural)	20	19	Small (7M, 8B)	3	Large (20M, 40B)	16	0.005	5
Worker no. (randomized)	30	29	Ten	12	Ten	17	ns	10
	30	27	Ten	7	Twenty	20	0.010	6
	30	29	Ten	2	Forty	27	0.001	8
Brood ratio (15 minims, seminatural)	20	11	Low (5)	8	High (30)	10	ns	7
	20	15	High (30)	6	High (30)	9	ns	5
	20	19	Low (5)	9	Low (5)	10	ns	6
Brood state (seminatural)	20	11	Pupae	6	Larvae	5	ns	3
No. queens	15	14	One	8	Four	6	ns	2
End raid (first versus later brood)	9	9	Minims	4	Minims	5	ns	0
	10	10	Minims	3	Regular	7	ns	7
	10	10	Regular	7	Regular	3	ns	3

Full description of the experiments in text. Odd and even treatments refer to the numbering of the nests in each test pair. *P* values from binomial test with *P* = 0.5. M, minims; B, brood. Last column shows number of losing queens abandoning their own nest to join the victorious nest.

were set up. When nests of 10 were matched against others of 10, the winner was not predictable. When 10 were matched against 20, the larger won 74% of raids, and when 10 were matched against 40, the larger won 93% (*P* = 0.08; chi-square test).

The previous experiments do not separate the effect of number of brood and minims. Seminatural nests containing 15 minims and either 5 or 30 brood were paired 5 versus 30, 5 versus 5, or 30 versus 30. This design tested the effect of worker-brood ratio on the likelihood of raiding, as well as testing the effect of brood number on the chance of winning. When nests with five brood were pitted against nests with 30 brood, there was no significant difference in the number won (Table 1), indicating that number of brood gives no advantage in raiding. There was also no difference in the number of pairs that raided in any of the three treatments, suggesting that the ratio of brood to workers is not a factor in causing raiding.

Brood stage also had no effect. When seminatural nests containing 15 minims and either 15 pupae or 15 larvae were tested against one another, neither type won more raids than expected.

Nests founded by more than one queen generally produce more minims than do singly founded nests (Tschinkel & Howard 1983). The effect of queen number, independent of minim number, was tested in seminatural colonies of identical size, containing either one or four queens. The four-queen nests won 6 of 14 raids, a proportion not significantly different from random. By itself, queen number therefore conveys no advantage in winning raids.

In summary, the likelihood of winning a raid is related only to the difference in the number of

minims between the nests. No other tested factor played a role.

What Causes Raiding to Cease? Field observations (see below) suggested that raiding ceased upon appearance of the first larger, non-minim workers. Nests were therefore composed of a queen, brood, and either 15 minim pupae or 15 nonminim pupae. The nonminim pupae were selected randomly from the smallest size class of pupae in mature laboratory stock colonies. These nests were paired in arenas in three combinations: minims versus minims, minims versus nonminims, nonminims versus nonminims. When the pupae had eclosed, nests were opened to allow brood raiding.

It was somewhat surprising that raiding occurred even in pairs involving only nonminim workers. There was no significant difference (χ^2 test) in the number won by any type of nest in any combination. These results suggest that raiding behavior is not a special characteristic of minims only, and this leaves open the possibility that tendency to raid is associated with a particular situation. Further experimentation is needed to answer these questions.

The queens of losing nests abandoned their nest in 98 of the 238 raids (41%) and entered the winning nest in 64 cases (27%). Winning nests in most of these cases contained all the members of both nests. Such queen emigration postpones the outcome of the competition, gives the losing queen another chance, and brings the site of competition into the winning nest. In these experiments, it also reunited the queen with her own workers, in most cases. The significance of queen emigration is further considered in Tschinkel (1992).

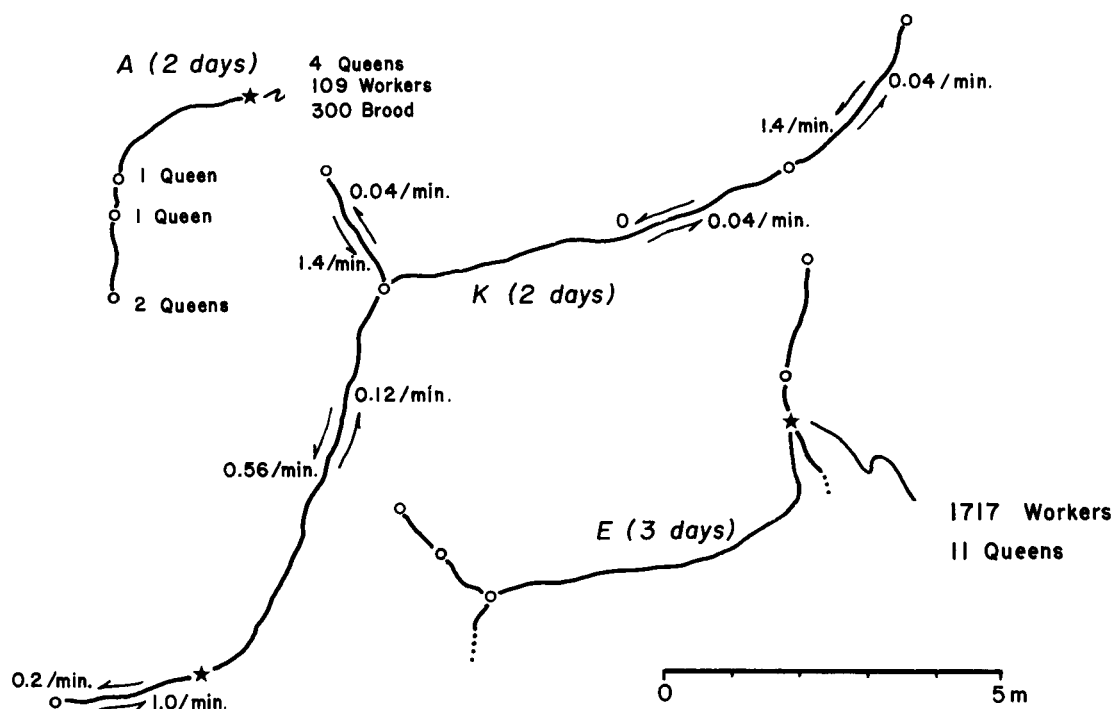


Fig. 2. Scale maps of three of the larger raids showing the winner (star), duration in days, and for raids A and E, the contents of the after-raid nests. For raid E, the reproductive status of the queens is given in the text. For raid K arrows show directions and rates of brood movement.

Observations of Raiding in the Field. Brood raiding was observed at a naturally colonized 15-ha site during June–September 1985 and May–August 1986. The site had been cleared of forest and topsoil during winter 1984–1985, leaving sparse weeds and much bare soil. Two subareas separated by about 100 m were chosen as study sites. During the mating flights, which began in early May (Morrill 1974), these sites were colonized by several waves of newly mated queens who seemed to prefer sparsely vegetated, but not bare, areas. Vegetation was still sparse in 1986.

General Observations, 1985. The data consisted primarily of the location of nests and raiding trails and a census of the contents of some nests. Usually, raids were discovered in progress. Small or brief raids were difficult to spot, so my observations were probably biased toward larger raids.

Brood raids of all but the smallest sizes of colonies took place on odor trails connecting the nests involved in the raid (Fig. 2). Trails became largely inactive after midday, but were used again in the evening or the following morning, suggesting a long-lasting component in the trail pheromone. Worker density varied from a few per meter of trail to over 100. The trails varied in length from a few centimeters to many meters long. Minims carried brood of all types, but usu-

ally less than 10% of minims on trails carried any. Brood was often carried in both directions along these trails and into the participating nests. Initially, this directional movement was at similar rates, but eventually brood was carried more frequently in one direction than the other (Fig. 2, raid K). After some time, the nest with the net loss ceased activity, and workers were rarely seen to enter or leave it. Excavation of such nests usually showed them to be empty or to contain one or more queens without workers. On the other hand, excavation of the nests with the net gain of brood usually showed them to contain one to several queens, often with large numbers of minims and brood (Fig. 2).

In several cases (e.g., raids A and E), the winning nest population was clearly far beyond the capacity of a queen or group of queens to produce between May and July, and those nests must have been the result of aggregation through brood raiding. The head width–frequency distribution of the workers in nest 4 of raid E confirmed that they were all of the minim class (head widths 0.48 to 0.58 mm). Nest 4 must have been aggregated from more than six nests and was not the product of colony growth. Live weights and dissections clearly showed three types of queens: (1) Four queens weighed between 12.3 and 15.1 mg, contained 4 to 19 large ova and

much fat body; these were newly mated queens that had not yet passed through colony founding, but had found refuge in nest 4. (2) Six queens weighed between 6.4 and 7.9 mg, lacked fat body, and had one to six large ova; these were post-claustral queens who had lost the race for reproductrix because, (3) the last queen, weighing 11 mg and containing 300 vitellogenic oocytes in 150 active ovarioles, had clearly won.

The Mega-Raid. Brood raid B, first seen on 20 June 1985, continued for 38 d and ultimately involved at least 80 incipient nests. The progress of this "mega-raid" is shown in Figs. 3 and 4. At its peak, this raid contained over 70 m of active trail connecting many nests. Although nest 1 dominated the early phase of this raid, nests 47 and 49 ultimately became the sole survivors, and all workers and brood from at least 80 incipient nests aggregated into them.

During the first 24 d the increase of active trail suggested that raids catalyzed their own growth because the raid-caused size gain allowed raiding over ever-larger distances and numbers of nests (Figs. 3 and 4). The mean distance between raiding nests increased from 2.2 m at the beginning to 4.5 m on day 24. The decline of active trail after day 24 may indicate exhaustion of raidable nests, as also suggested by distances of up to 20 m between individual nests (mean distance = 9.5 m). On the first day of observation, brood moved at almost equal rate between the nests at the extremes of the raiding trail. On the second day, the raid had extended by four nests and become asymmetric: brood moved toward nest 1 2.5 times as fast as toward nest 10 at the other end of the raid. As the raid progressed, the contest became ever more asymmetric. Brood movement on the third day, although still bidirectional, showed that nest 1 predominated 5 to 1. On day 13, colonies 18 and 19 were first joined to the raid. Colony 1 was now so dominant that 91 brood were carried toward nest 1, but none the other way. Similarly, 25 brood were removed from colony 23 in a few minutes, with no reverse movement. On the twentieth day, the raid connected to colonies 49 and 47 (Fig. 3D). Colony 1 was eliminated almost overnight, and these two colonies dominated the remainder of the raid. On the last day of raiding (day 38), brood was carried toward the dominant nest (now no. 49) at the mean rate of 2.6 per min for several hours. Only a single pupa was carried the other way. When raiding ceased on day 39, the contents of at least 80 incipient nests had aggregated into nests 47 and 49 (Figs. 3A and F, Fig. 4).

The initiation of a raid on a new colony was seen only once. On day 15, a loose, oval cluster of several dozen minims progressed excitedly in a straight line beyond the last nest in the raid. When this raid swarm, which resembled the slave raid parties of *Formica sanguinea* Latr. or *Polyergus breviceps* Emery (Hölldobler & Wil-

son 1990), arrived at the apparent target nest, the raiders entered without hesitation and began to carry brood back along a trail within seconds.

During the later phase of the raid, the trunk raiding trails of the two dominant nests (47, 49) were gradually undergrounded (Fig. 3). When raiding ceased, these became the trunks of the underground foraging trails and the major routes to exploiting and expanding the colonies' new territory. This suggests that the shape of the initial territory was not simply oval or round, but was an octopus-like zone around the arms of the foraging tunnels. That the area between these arms was not yet in the colony's control was suggested by the persistence of live incipient nests in these areas. Territory probably grows first by the "filling-in" of these areas.

Raiding ended very suddenly. On 29 July, workers from nest 49 encountered workers from a more distant nest and attacked them in typical territorial defense behavior. Apparently the colony had changed overnight from raiding to territorial behavior, with battles in which workers grappled and stung as described by Wilson et al. (1971). Thereafter, although foraging continued along the same trails, raiding was never seen again. By the last brood raid, many workers in both nests 47 and 49 were clearly larger than minims and originated from later broods. Although this result suggested that later-brood workers are somehow causal in ending raiding, laboratory experiments showed that such workers, when reared in incipient nests, raid too (see above).

Queens were commonly seen following raiding trails. Their low weight (mean = 8.46 mg; sd = 2.07; $n = 40$), lack of fat, and sperm-filled spermathecae indicated that they were post-claustral queens. On several occasions, such queens attempted to enter incipient nests, succeeding without obstacle in some cases, being attacked in others. In at least three cases, wandering queens bore paint marks of an earlier experiment, proving their post-claustral condition beyond a doubt. The significance of these wandering queens is discussed in Tschinkel (1992).

Another follower of raiding trails was the interesting myrmecophilous staphylinid beetle, *Myrmecosaurus* sp. On three occasions, beetles were seen following raiding trails, and, on one occasion, a beetle was seen entering an incipient nest. This beetle is always associated with *S. invicta*, and it probably was introduced to the United States with *S. invicta* (Lofgren et al. 1975). The observed trail following may be part of its dispersal to new ant nests.

Discussion

Brood raiding is one of the first orders of business for incipient colonies and the major source of their "mortality." Of course, although the raiding colony ceases to exist as an independent

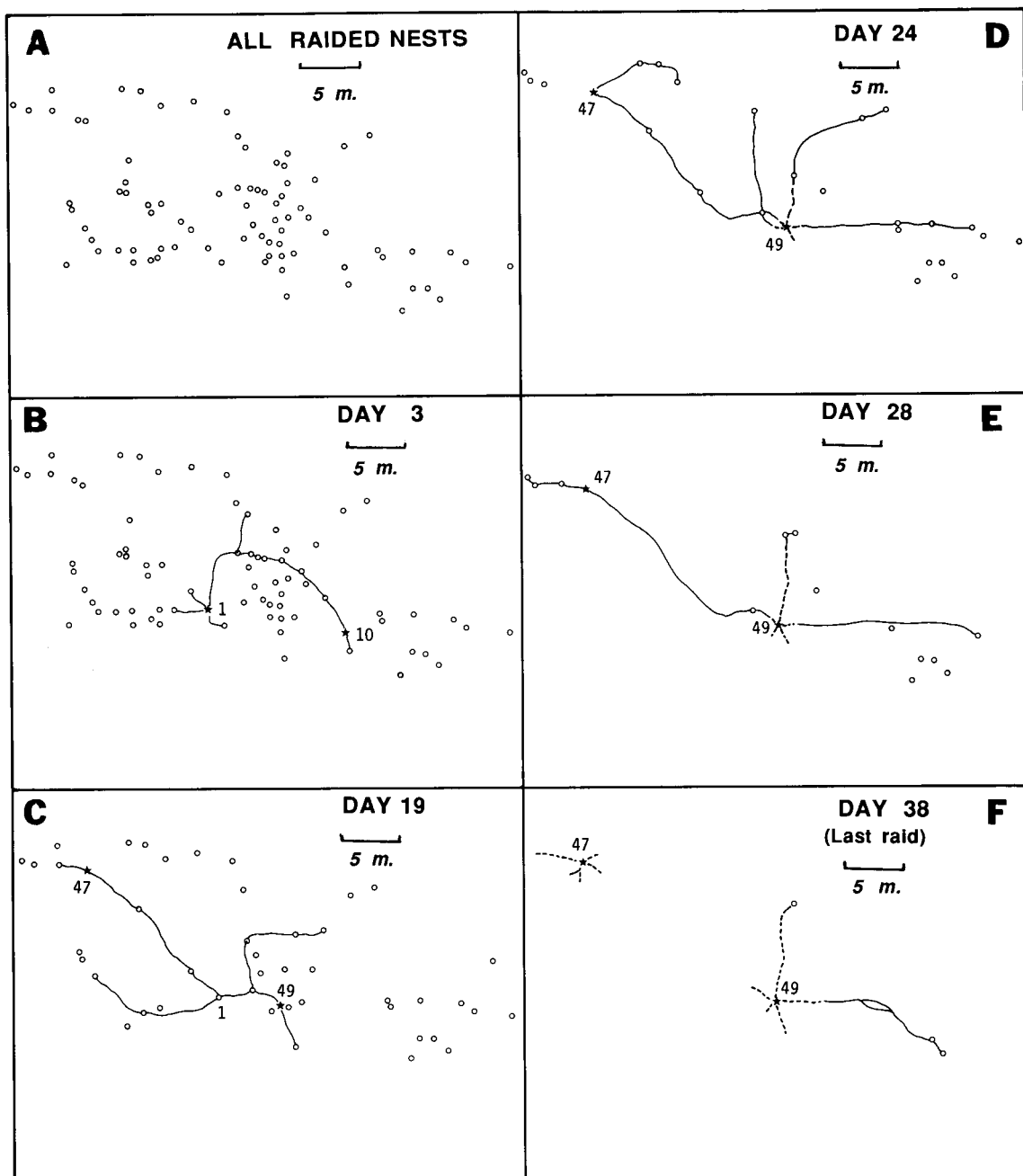


Fig. 3. Brood raid B (the "mega-raid"). Map A shows all incipient nests eventually raided. *Not all of these were present at the beginning.* Maps B–F show raid trails (solid lines) on selected days. Colonies eliminated by raiding were deleted from the sequential maps. Stars indicate dominant colonies. Dotted lines show underground portions of raiding trails that later became trunk underground foraging tunnels. Some incipient colonies within the mapped area were not raided and are not shown. On day 38, the site contained two large colonies (nos. 47 and 49) and a number of colonies that had not been involved in this raid, but are not shown.

entity, its workers and brood (and sometimes queen) have simply been incorporated into the raid-winning colony. This incremental increase in the size of raid-winning colonies allows raids to increase in size and extent as raiding continues (Tschinkel 1992), leading in (perhaps) rare

cases to raids of stunning proportions, such as the mega-raid in which thousands of 0.25-mg workers gamboled along up to 70 m of trail, burdened with brood weighing as much as themselves.

The winners of raids are usually the nests with more workers initially, whether these workers

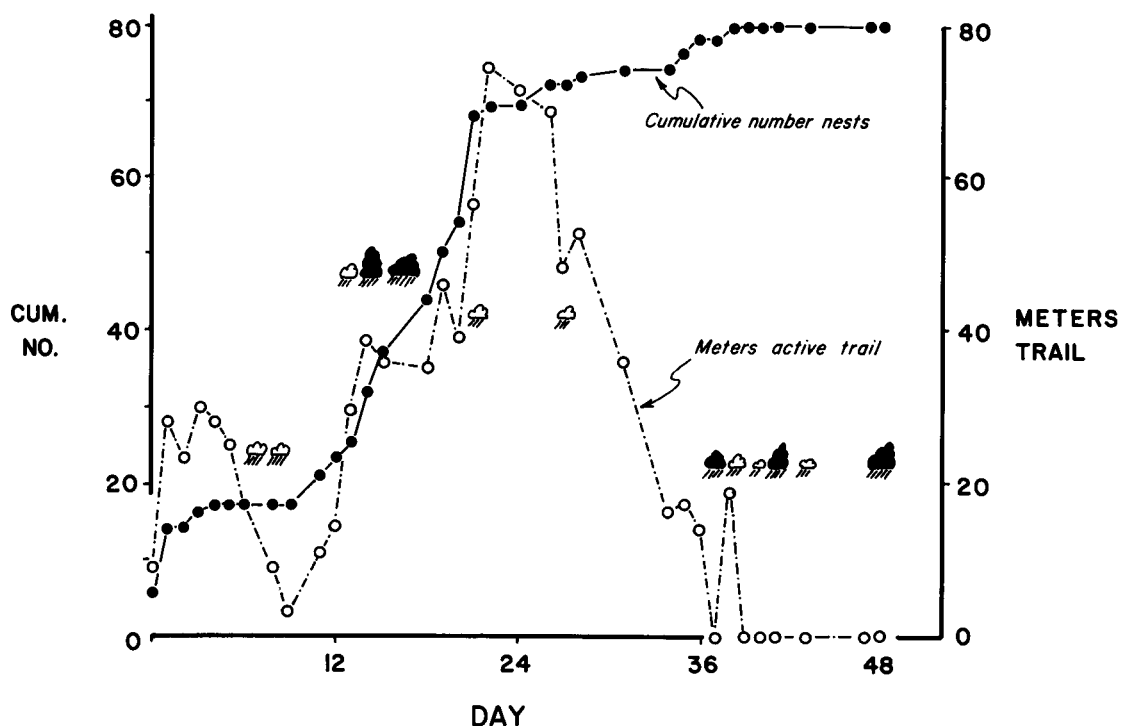


Fig. 4. Progress of raid B (the "mega-raid"), showing the cumulative number of nests raided and the meters of active raiding trail. Clouds show incidence of light (open) and heavy (filled) rain. The raid was first seen on 20 June 1985, lasted at least 38 d, and involved at least 80 incipient colonies that aggregated into two nests by the end of the raid.

were produced in the nest or acquired through previous raids. Intuition suggests that this is because the larger colony can afford to field more raiders, but my laboratory observations on first-time raiders do not bear this out. The number of minimis taking part in raids is not very different for large and small colonies. Victory in raiding may thus be grounded in some other aspect of colony size, or is somehow based on a mutual assessment of relative size. It should, however, be remembered that the victor in most of the observed laboratory colonies was not known. These results need confirmation and extension to determine why larger colonies win raids.

The phenomenon of "traitor raiders" is puzzling. If these are simply "errors" by workers, they are fairly common ones. On the other hand, if this is an evolved trait, it suggests that workers do not necessarily "perceive" their best interests to be in their natal nests. It certainly appears that the competition plays itself out in a rather large arena. The existence of traitors may also fit in with the possibility that the outcome of raiding is decided by some form of size assessment among minimis rather than by some numerical process such as relative brood-transporting ability.

As the size difference between raid partners increases, the raids are more and more one-sided, appearing more like simple pillage in the

extreme. This tight link between initial worker number and successful raiding led Pollock & Rissing (1989) to suggest that pleometrosis, with its larger worker production, evolved in response to the need to win brood raids. However, Tschinkel & Howard (1983) showed that larger initial size carries benefits even in the absence of brood raiding, suggesting that pleometrosis probably did not evolve solely in response to brood raiding.

The advantages of brood raiding to the winning nest are obvious. It boosts colony size with a very small effort and eliminates a future competitor. Less obvious is how the defection of workers from the losing to the winning nest, with the abandonment of their own mother, came to evolve. Of what advantage could it be to sterile workers to help an unrelated queen reproduce? There are several possibilities. Perhaps "nest" is equivalent to "brood" for workers, causing them to reaggregate around the brood in the winning nest. Alternately, losing queens often also abandon their own chamber and attempt to enter other incipient nests, suggesting that defection evolved because it is possible for workers to rejoin and serve their mother in another nest chamber (Pollock & Rissing 1989). Whether these probabilities are large enough to cause the observed system to evolve is unknown. It is possi-

ble that queen reassortment is nonrandom, because queens were often seen following raiding trails. Their workers would have defected by such trails, so this may tend to keep the queen and her workers together. In this context, traitor raiders would merely be speeding this competitive reassortment to its end.

Raiding probably has a cost that was not measured in this study—workers are exposed to desiccation, heat, and predators during raids. Occasionally, they may be subject to aggression from other raiders. Although I did not specifically determine minim mortality under raiding and non-raiding conditions, dead minims were commonly seen in laboratory arenas after raids.

An unanswered question is whether post-incipient colonies raid. At present it is believed that they behave in a strictly territorial manner, attacking workers from other colonies who intrude into their territory (Wilson et al. 1971). However, in *M. mimicus*, Hölldobler (1981) found that raiding can occur at any stage, provided there is at least a 10-fold difference in colony size. It may thus be that incipient colonies are simply too small to prevent the intrusion of workers from other nests, because they cannot afford to lose workers in fights. Raiding ceases when nests become large enough to be able to afford colony and territory defense. Even so, colonies might still be able to breach the defense of much smaller ones, after which they would raid the brood in a manner similar to the raids of incipient nests. The major difference would be that raids of larger nests would be preceded by fighting and loss of workers. It seems possible that such raiding by workers from larger *S. invicta* nests has gone undetected, so far. Such behavior would explain why even workers from large colonies, when reared from pupae in incipient nests, will raid. It remains to be seen whether the absence of hostility among minims is the result of small colony size or is intrinsic to the minims.

The picture of the establishment of fire ant populations that emerges from this and other work (Tschinkel & Howard 1983; Tschinkel 1987, 1992) is a dynamic one. Competition among nests leads to their aggregation into ever larger ones, and the competition among queens plays itself out in the shifting locale of the winners of brood raids. The contest is over which of the original incipient nests will house most of the local population of minims and brood, and which of the founding queens will become the reproductrix of this amalgamated worker population.

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