

# Brood raiding and the population dynamics of founding and incipient colonies of the fire ant, *Solenopsis invicta*

WALTER R. TSCHINKEL Department of Biological Science, Florida State University, Tallahassee, Florida

**Abstract.** 1. One of the first activities of minim workers in incipient fire ant nests is mutual brood raiding, the amalgamation of nests through the reciprocal stealing of brood and defection of workers.

2. Discrete mating flights created cohorts of incipient colonies. About 25% of founding nests survived the claustral period of 16–48 days (depending on season). Early incipient colony mortality was 5–6% per day. Over 60% of this mortality was accounted for through brood raiding. Most colonies raided when each cohort first became active, and many raided more than once. Raid size (number of nests, duration, distance) tended to increase during the summer as colonies grew through raiding. After the raiding period, nest mortality rate dropped 3–10-fold. Only 1–3% of founding nests were still alive at this time.

3. Queens from losing or failed nests tended to abandon their nests and attempted to enter successful ones, often following raiding trails to do so. This emigration was at least as successful as non-emigration in ultimately achieving the status of reproductrix of a successful nest (about 4%).

4. Brood raiding is a dominant process in early population dynamics, probably accounting for most of the early nest mortality. Its effect is to change the venue and unit of competition from nest-against-neighbor to a shifting aggregation of queens, workers and brood involving entire local populations. Nest thinning is thus very rapid, and the boost to the size of winning nests very large, allowing raiding colonies to win the competition for territory, and to achieve the early colony maturity so important to this, and other, weedy species. The importance of winning brood raids may also have driven increased minim production through the evolution of pleometrosis.

**Key words.** Colony founding, colony mortality, mating flights, queen vagility.

## Introduction

Colony founding is a particularly stressful period in the lives of ants, and claustrally founding queens and colonies are subject to high mortality and strong selection. Improvement of survival and success has been achieved by phenomena such as pleometrosis (cooperative founding) (Hölldobler & Wilson, 1990) and brood raiding. Early accounts had noted that incipient nests of *S. invicta* (Khan, 1966; Markin *et al.*, 1972) and *Atta texana* (Echols, 1966) merged or could be joined with little hostility, but the life-history importance of this phenomenon was not re-

cognized until Bartz & Hölldobler (1982) reported that workers in incipient colonies of *Myrmecocystus mimicus* engaged, without hostility, in reciprocal brood stealing ('brood raiding') with neighbouring colonies. This behaviour was subsequently described in *Veromessor pergandei* (Pollock & Rissing, 1989) and *Solenopsis invicta* (Tschinkel, 1987, 1992) and seems likely in *Acromyrmex versicolor* (Rissing *et al.*, 1986; Rissing & Pollock, 1987). In all cases, the larger colonies tend to win the raids.

Tschinkel (1992) detailed brood raiding behaviour of *S. invicta* in the laboratory, and was the first to observe brood raids in a natural field situation. He noted that raiding seemed to be a major cause of incipient colony mortality. The purpose of this paper is to document the effect of brood raiding on queen and incipient colony survival, and on population dynamics.

Correspondence: Dr W. R. Tschinkel, Department of Biological Science, Florida State University, Tallahassee, FL 32306, U.S.A.

## Materials and Methods

*Quantitative observations of survival and raiding.* In 1985 and 1986 a 1200 m<sup>2</sup> plot was used for a study of colony founding, incipient nest survival and brood raiding. A 30 × 40 m grid was marked with dots of paint at 1 m ticks. The dates of mating flights and rains were recorded. The locations of founding chambers were marked. About 20 days after marking, the study site was patrolled almost daily and incipient nests that developed from marked colonies, as well as unmarked ones, were numbered with tags as soon as they were detected. Locations of tagged nests were mapped. In both years, at 5–14 day intervals, all tagged nests were checked for activity (freshly excavated soil or live workers). Those found inactive for two sequential checks were judged to be dead.

*Determination of queen departure from claustral chambers.* Traps were fashioned from pie plates and short sections of PVC pipe such that, when buried flush with the soil, a central earthen island 15.5 cm in diameter was surrounded by the fluon-coated moat of the trap. Five evenly spaced 3 × 60 mm holes were made in the earth of the central island, and a small fluoned cylinder placed around each hole. Queens placed within these cylinders had no choice but to nest in the holes provided, and almost all did so. Each central island received a nest of one, two, four, seven and ten queens, each density having been marked with a different colour paint. Two replicates of twenty traps each (100 nests, 480 queens per replicate) were set up using the queens from the mating flights of 5 May and 6 June 1988. By the following morning, almost all the holes had been occupied and sealed.

Traps were checked daily, and the colour marks of captured queens noted. At the end of 39 and 29 days for replicates 1 and 2, respectively, all founding chambers were excavated and censused. Overall, 79% and 63% of the emplaced queens could be accounted for. There was no relationship between accountability and density.

Data were analysed by Minitab (Ryan *et al.*, 1976).

## Results

### *Development rate and survival during the claustral phase*

Mating flights occur on warm days after significant rains (Morrill, 1974). In 1986 each major rain from May to mid-July was followed by a mating flight. Successive flights following closely tend to be smaller, as do flights later in the season, especially after mid-July.

Late on days after mating flights, founding chambers were easily recognized by the small circles of excavated pellets. Such chambers were marked after the mating flights of 28 June 1985, and 4 and 13 June and 5 August 1986. In 1985, 18% of the 151 marked founding chambers survived to produce minims (the incipient colony stage). In 1986, survival of founding nests was 31.7% ( $n = 400$ ), 20.7% ( $n = 363$ ) and 25.4% ( $n = 64$ ) from the three flights, respectively. Overall, mean 1986 survival to the incipient colony stage was 26.2% ( $SD = 7.8\%$ ).

Because female alates mate and found in distinct cohorts, incipient colonies appear in corresponding cohorts (Fig. 1). Nests from each mating flight opened over a 10–14 day period, causing considerable overlap in emergence of the marked nests from the flights of 4 and 13 June, and possibly others. It seems likely that even after completing claustral development, nests wait for certain conditions before opening. The mean time from founding to nest opening (the claustral phase) decreased from 40–48 days for the A cohort (founded 5 May 1986) to 24–37 days for the B cohort (founded 4 June 1986), 16–31 days for the C cohort (founded 13 June 1986), and increased again to 30–34 days for the F cohort (founded 5 August 1986). The mating flight origins of cohorts D and E were uncertain, so no times were estimated. The shortening of the claustral period from May to June was probably the result of increased development rate as the soil warmed. The frequent rains of July and August caused soil temperature to decline again, and concurrently development time increased. Occurrence of appropriate conditions for nest opening may have contributed too.

### *Survival of incipient nests*

Incipient nest survival was followed both in 1985 and 1986. In 1985 eight cohorts of newly emerged incipient nests ( $n = 11–109$ ) were marked between 7 July and 21 August. All showed a sharp decline in survival during the first 40–50 days (Fig. 2), with a mean daily mortality of 6%. This was followed by a lower decline at 0.6% per day. At the time of this break in mortality rate (50 days post-incipient), only about 5% of the incipient nests still survived. This represents only 1.2% of the founding nests.

In 1986 the tagged cohorts (A–F) of incipient nests were linked to particular mating flights (Fig. 1). The percent surviving was similar among these cohorts (Fig. 2), with a mean mortality of 5.4% per day ( $SD = 1.5\%$ ). As in 1985, mortality after day 35–40 (18–23 July) seems to be somewhat lower ( $\bar{x} = 2.0\%$  per day,  $SD = 0.4\%$ ), perhaps because of the cessation of brood raiding (see below).

When the number of live nests (log scale) in each cohort was plotted against the date (Fig. 3), several additional facts became clear. Each successive cohort contained fewer incipient nests, a reflection of the declining size of mating flights after the first of the season. Sexual production peaks in April (Tschinkel, unpublished) while flight usually peaks in May or early June (Morrill, 1974), depending on weather. The combined effect of mortality and the succession of cohorts was to maintain the population of live nests between about 500 and 650 from 21 June to about 24 July. This corresponds to an overall mean incipient nest density of 0.42–0.54 per m<sup>2</sup>. The total number of incipient nests occurring over the entire 1986 season was 1690, a mean density of 1.4 nests per m<sup>2</sup>, though live nest density never exceeded a mean of 0.54 per m<sup>2</sup> (650 nests). At the last census (day 68, 20 August) there were still 260 live nests, a density of 0.22 per m<sup>2</sup> or about half the peak density of live nests.

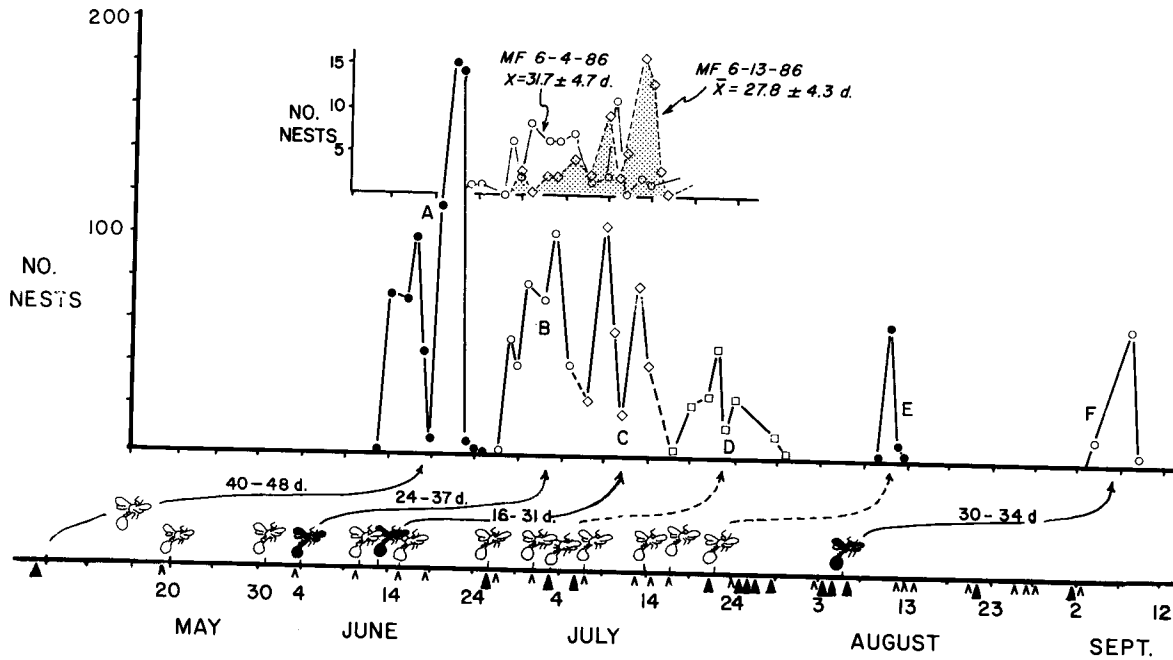


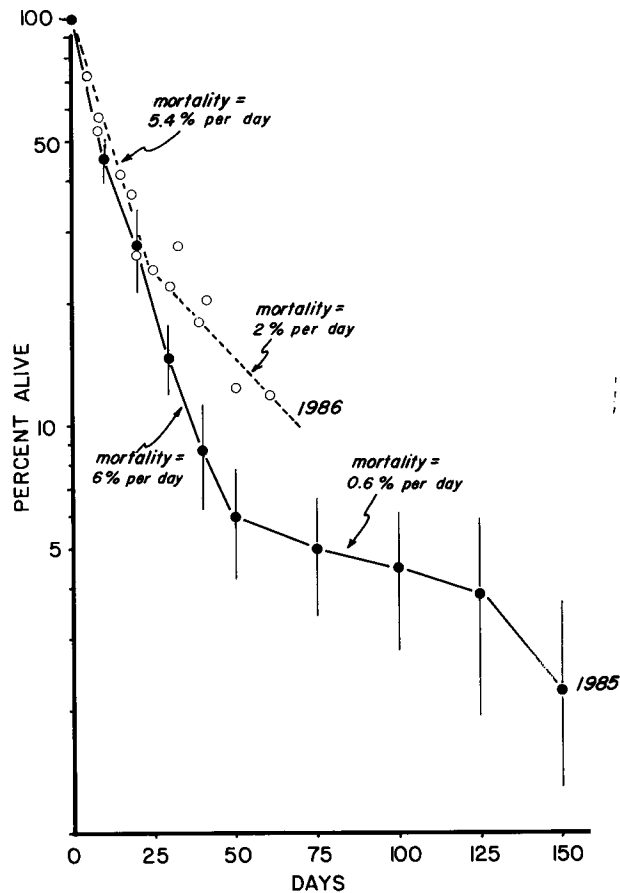
Fig. 1. Timing of mating flights, rain and the appearance of cohorts of incipient nests during 1986. All incipient nests were tagged as they appeared. A carat on the lower scale indicates rain and a filled carat heavy rain. Mating flights are shown by flying ants, with filled ones indicating those for which founding chambers were tagged. The inset shows the appearance as incipient nests of founding chambers marked at the time of the mating flights of 4 and 13 June. Although founded on a single day, the incipient nests were opened over 16–20 days. Size of mating flights and thus incipient nest cohorts declined during the summer. Most cohorts could be identified with a specific mating flight, although there was some overlap. Development time dropped until July then increased again.

#### Quantitative estimates of brood raiding

In 1986, beginning with the appearance of the first incipient nests (14 June), the site was patrolled for several approximately half-hour intervals during each morning, and randomly selected nests were checked for brood raiding. From fifty to 140 nests were checked during each half-hour check, but this number was sometimes less than ten for any individual cohort. As evidence of brood raiding, I used the presence of workers carrying brood along odour trails. Once detected, raids were rechecked every 15–45 min until they ceased. As long as they continued, these raids were excluded from the following half-hour samples of that day. Raiding was rare before dawn and after mid-day, and peaked during mid-morning with over 50% of the raids occurring between 8.30 and 10 a.m. The five to seven checks ( $\bar{x} = 5.5$ ) were thus made between dawn and noon. The number of brood raids observed during the morning checks was converted to an estimate of the number of raids in each cohort as follows. The sum of raids for each day was divided by the sum of the number of colonies checked (multiple checks were possible, and occurred randomly) to yield the raw proportion raiding. This proportion was adjusted for the means of the particular time periods making up that value, resulting in a mean number of raids per half-hour for each day. By multiplying by the number of half-hour time periods during which raids were censused (ten), an estimate of the raids occurring in each cohort was derived. The sum of these estimates over all days gave the total raids.

Fig. 4 shows the frequency of raiding by cohort and overall. All cohorts showed generally similar patterns. As the nests of a cohort first appeared, they participated heavily in raiding, peaking at 85–112 raids in a single day for cohorts A–C. During this period, incipient colonies were still making their first appearance. The high initial raiding can also be seen in the high proportion of colonies raiding during this period (Fig. 4, left). A raidless period from day 30 to 33 (13–16 July), was followed by a synchronized burst of raiding by all four cohorts. About 42% of all raids occurred during this 12-day period (approx. 25% of the total days over which raiding occurred). With the end of this burst of raiding, no further raids were observed in cohorts A–D throughout any of the remaining sample days. It is perhaps significant that the cessation of raiding coincides more or less with the decrease in mortality rate noted at this time (Fig. 2). Cohort E showed a single large raid on 15 August (day 63), but cohort F, which emerged 4–9 September, showed no raiding. Cohorts E and F were both very small and inadequately sampled and were omitted from most calculations.

The cumulative total of raids in each cohort is shown in Fig. 5. While not all raids result in the demise of all but one of the participating colonies (58% of colonies survived raids,  $n = 36$ ), this is the common outcome of most raids. Raid frequency is thus a measure of incipient colony 'mortality'. Because the number of raiding colonies in each cohort approximated or exceeded the number of colonies in the cohort (Fig. 5), raiding must be the most important cause of 'mortality' for these colonies. In total,

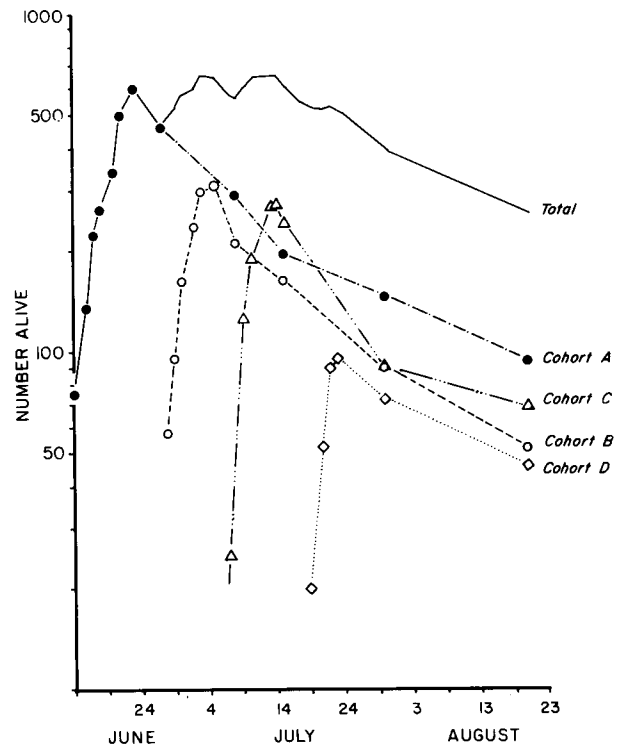


**Fig. 2.** Survival of incipient colonies during 1985 and 1986 (semi-log scale) showing mortality as per cent per day. In 1985 eight cohorts were tagged, but these were not identified with particular mating flights. Bars are standard errors. Mortality decreased sharply at about 50 days when about 6% of colonies were still active. Census data for the four mating flight cohorts of 1986 are shown as open circles, and the average survivorship as dotted lines. Again mortality decreased between 25 and 35 days.

1776 nests were estimated to have raided. Using a raid-caused mortality rate of 42%, this suggests that raiding accounted for the 'deaths' of 746 nests, or about 60% of the 1260 nests which 'died' (Fig. 3) during the period when raids occurred (14 June to 29 July). Because colonies do not limit raiding to their own cohorts, mortality for each cohort cannot be determined, but may increase in the later cohorts.

#### Characteristics of raids, 1986 (Fig. 6)

For the 30 × 40 m plot (site II) in 1986, fifty-four of sixty-six raids involved only two nests, but raids of up to seven were found. The mean was 2.5 nests per raid. More important, raids with more than two nests increased during the raiding period (Fig. 6). During the first 10 days, raids consisted of only two nests, but in the second 10 days,



**Fig. 3.** Number of incipient nests during 1986, by cohort and total. Successive cohorts are smaller, but the total number of nests remains between 500 and 650 for over 1 month.

three of sixteen raids had more than two, and this increased to five of twenty-one by the fourth 10-day period.

After detection, raids were checked at 15–45 min intervals. The duration of the raid was approximated by taking the average of the time from first detection to the last positive and the time from first detection to the first negative. The mean raid length for the forty-six timed raids (125 colonies) was about 75 min (SD = 85 min) and the median about 60 min. All but one of the nine longest raids (over 100 min) occurred in the second half of the raiding period from 17 July to 15 August ( $\chi^2 = 2.4$ ;  $P = 0.1$ ) (Fig. 6, top). About one-third of the raids lasted less than 25 min, and could thus escape detection in our sampling regime. However, considering the roughness of the estimate, an adjustment to the frequency of raiding did not seem justified.

The mean distance between nearest raiders increased significantly with time, from 0.32 m in the first 10 days, to 0.85 m between days 30 and 40 (Fig. 6). The single mapped raid on day 63 extended up to 3.3 m between nests. The overall mean distance between nearest raiding nests was 0.66 m (SD = 0.61;  $n = 62$ ). Nests did not necessarily engage their nearest neighbour in raids.

All together, the changes in raid characteristics suggest that the size increase which results from winning raids allows colonies to raid farther, longer and more nests. This makes raiding a potentially self-catalytic process and may

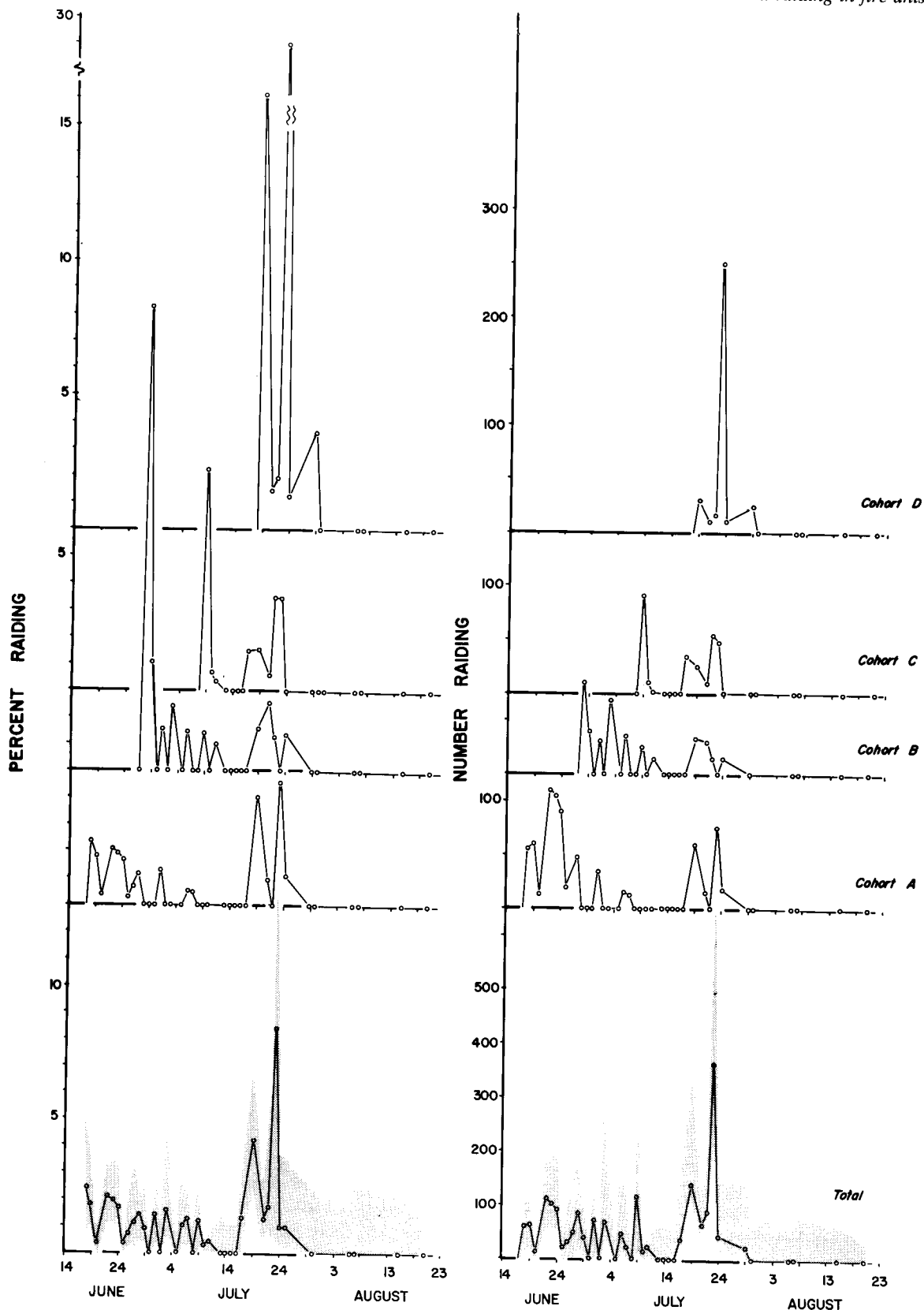
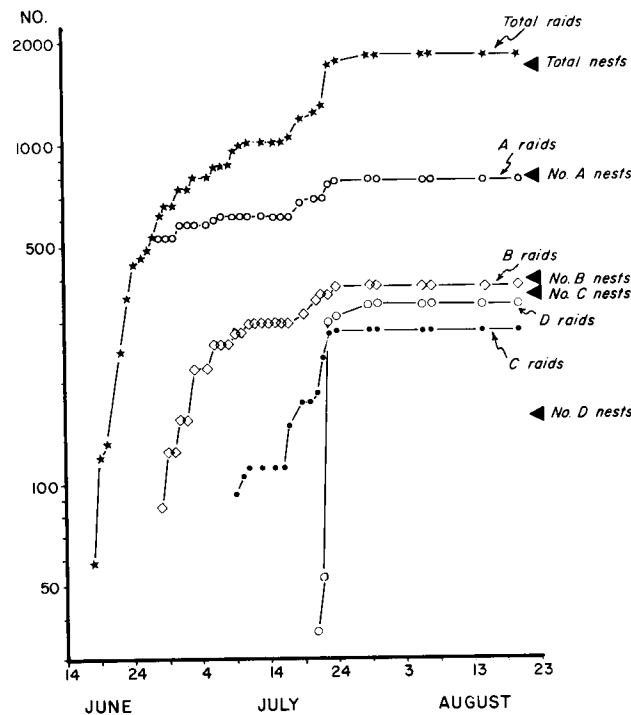


Fig. 4. Estimated proportion raiding (left), number of brood raids (right) by cohort and total. Number of raids was highest as each cohort emerged from the claustral phase. Raiding ceased after 46 days following a synchronized burst of raiding by all cohorts. Shading around 'total' indicates the 95% confidence interval.



**Fig. 5.** Cumulative number of colonies brood raiding (log scale), by cohort and total. Triangles at the right show the number of incipient nests in each cohort. Colonies can raid more than once, so cumulative number can (and does) exceed number of colonies. Most colonies raid at least once.

explain the origin of occasional very large raids, such as the mega-raid reported by Tschinkel (1992).

#### Fate of queens

Queens were commonly seen running on the ground surface on days when no mating flight had occurred. Sometimes the ground surface was dry, no rain having fallen in up to 5 days ( $\bar{x}$  days since rain = 2.8). Most of these queens weighed much less than flight-ready alates. Of the 152 queens collected in the plot, 78% weighed between 5 and 11.0 mg (median weight = 7.5 mg). Female alates of less than 12 mg rarely leave the nest during mating flights. On the other hand, queens that have founded colonies have a mean weight of 7.39 mg (SD = 1.25 mg;  $n = 40$  haplometrotic queens) suggesting that the vagrant queens have left founding nests during or after the claustral period. Dissection of some of these queens showed insemination, an absence of fat body and small numbers of developed ova, consistent with the post-claustral condition.

The rate and timing of queen departure from claustral chambers was determined in an experiment in which queens were trapped as they left their nests. Departure from chambers was low during the claustral phase (Fig. 7). By its end, only 6% of the queens in replicate 1 and 4% of those in replicate 2 had been taken in the traps. Queens from high density nests were no more likely to leave than

those from low density ones ( $\chi^2 = 5.57, 6.59$  respectively; d.f. = 4; n.s.).

Once the claustral nests were opened by the first minims, the rate of queen departure increased many fold (Fig. 7). The number departing was not related to density in replicate 1 ( $\chi^2 = 4.58$ ; d.f. = 4; n.s.). In replicate 2 there was a significant but inconsistent difference among the densities ( $\chi^2 = 20.1$ ; d.f. = 4,  $P < 0.001$ ): density 7 was higher and density 10 lower than expected. In both replicates there was a significant difference among traps, with five traps showing a significantly greater number of departing queens (replicate 1: expected number = 3.65; observed = 11, 13;  $\chi^2 = 45.5$ ; d.f. = 19;  $P < 0.001$ ; replicate 2: expected = 3.95; observed = 10, 9, 9;  $\chi^2 = 57.4$ ; d.f. = 19;  $P < 0.001$ ). In two of these five traps a raid had apparently taken place, and two had high levels of nest failure. The last may have had raids also, but the evidence was less compelling.

Why do queens leave and what effect does this have on their reproductive future? As noted above, queens do not consistently leave in relation to their chances of being the sole reproductrix in their home nest, i.e. in relation to density. The discovery of marked queens in nests not founded by them provided some interesting insight (Table 1). Nineteen of the 171 queens who left their founding chamber entered another nest in the same trap-island. The remainder were trapped in the moat, their future reproductive potential unknown and unrealized. Of the nineteen, nine were found in vigorous nests, that is, in nests containing a queen, brood and a number of minims. Of these, six were the sole queens in the winning nest of their trap-island, that is, they had already won over any other vigorous nests in their set, or had sufficiently more minims to do so. Based on the 171 queens leaving their chambers, this means that 3.5% won the competition for reproductrix of a successful incipient nest. In addition, two emigrant queens were in a single nest with two native queens, giving a 50% chance of an emigrant win. This would boost the success of emigrants to 4.1%. By comparison, of the 511 who remained in their founding chamber, twenty-two (or 4.3%) similarly won the competition. If one adds that some fraction of the emigrant queens trapped in the moat might also have succeeded, it seems likely that leaving the chamber is a strategy equally or more successful than seeing it through at home. Unfortunately, it is not possible to extrapolate the emigration and non-emigration strategies to a completely unmanipulated population because the trap island nests were unusually close together and isolated from other sets of nests, possibly favouring emigration success.

The proportion of nest islands in which raiding had clearly occurred was eighteen out of forty. That is, the contents of one of the nests (usually the winner) exceeded normal expectations and other nests were mostly empty or contained queens only. In six traps, raiding may have occurred, but the evidence was not as compelling. These were excluded from the following chi-square tests because they could not be classified with respect to raiding. In addition to those raiding, six trap islands had one nest destined to win, but its composition was not obviously the

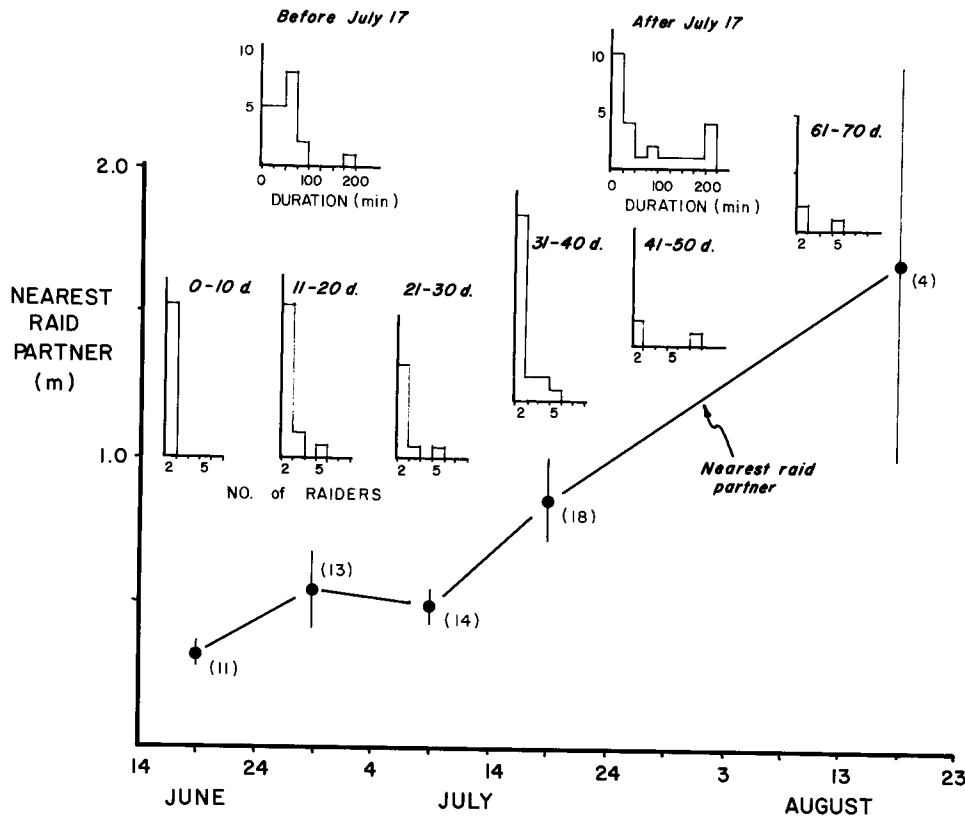


Fig. 6. Changing characteristics of brood raids during the summer of 1986. As summer progresses, raids involve more nests (middle rank of histograms), longer periods of time (top histograms) and longer distances. Eight of the nine raids longer than 100 min occurred after 17 July.

result of raiding. One trap had clearly raided, but the 'winning' nest was queenless, the live queens residing in other nests. Because these queens could vie for the 'winning' nest, this trap was included with the winners, bringing the total traps with winning nests to twenty-five, but leaving the number of traps with raids unchanged.

Emigrant queens were not significantly associated with raiding ( $\chi^2 = 0.46$ ;  $df = 1$ ; n.s.). On the other hand, such queens were strongly associated with traps in which there was a winning nest, whether this was the result of raiding or not. In all, 118 emigrant queens were found in the twenty-five traps with winners, but only thirty-five in the fifteen traps without winners ( $\chi^2 = 13.9$ ;  $d.f. = 1$ ;  $P < 0.001$ ). This suggests that emigration is an alternate strategy in which queens from failed nests engage as a last resort, whether that failure resulted from raiding or other factors. Of the nineteen queens which entered another nest in the trap experiment, sixteen came from losing or failed nests, one from an undecided situation and only two from winning nests ( $\chi^2 = 22.33$ ;  $d.f. = 2$ ;  $P < 0.001$ ). Results of laboratory raiding experiments (Tschinkel, 1992) also support this. The losing queen left her founding nest in 41% of the 238 raids and entered the winning nest in 27% of these raids. In the laboratory, most nests raided, so most winners were raiders too. Nest abandonment by queens was always associated with raiding. Queens were

never seen to abandon a winning nest. Those that moved into the winning nest were presumed to have a chance to win the competition for reproductrix, just as emigrant queens sometimes won in the trapping experiment.

## Discussion

In the fire ant, *Solenopsis invicta*, brood raiding has emerged as a major force in the population dynamics of incipient colonies, affecting early colony size and mortality. Like other brood-raiding ant species, newly-mated *S. invicta* queens tend to clump their founding chambers in the preferred microhabitat, disturbed sites in the case of *S. invicta*. In keeping with its weedy habits (Tschinkel, 1987), early competition among *S. invicta* colonies is essentially a scramble for space in the freshly available habitat. The rapid achievement of large colony size is crucial to winning this scramble. Brood-raiding boosts initial colony size many fold and allows colonies to achieve maturity and territorial dominance much sooner (Tschinkel & Howard, 1983). In the extreme, mature size can be attained in less than 1 year.

Because disturbance tends to appear suddenly on the heels of natural or man-made disasters, sites are colonized by large, synchronized cohorts of queens. Founding colony

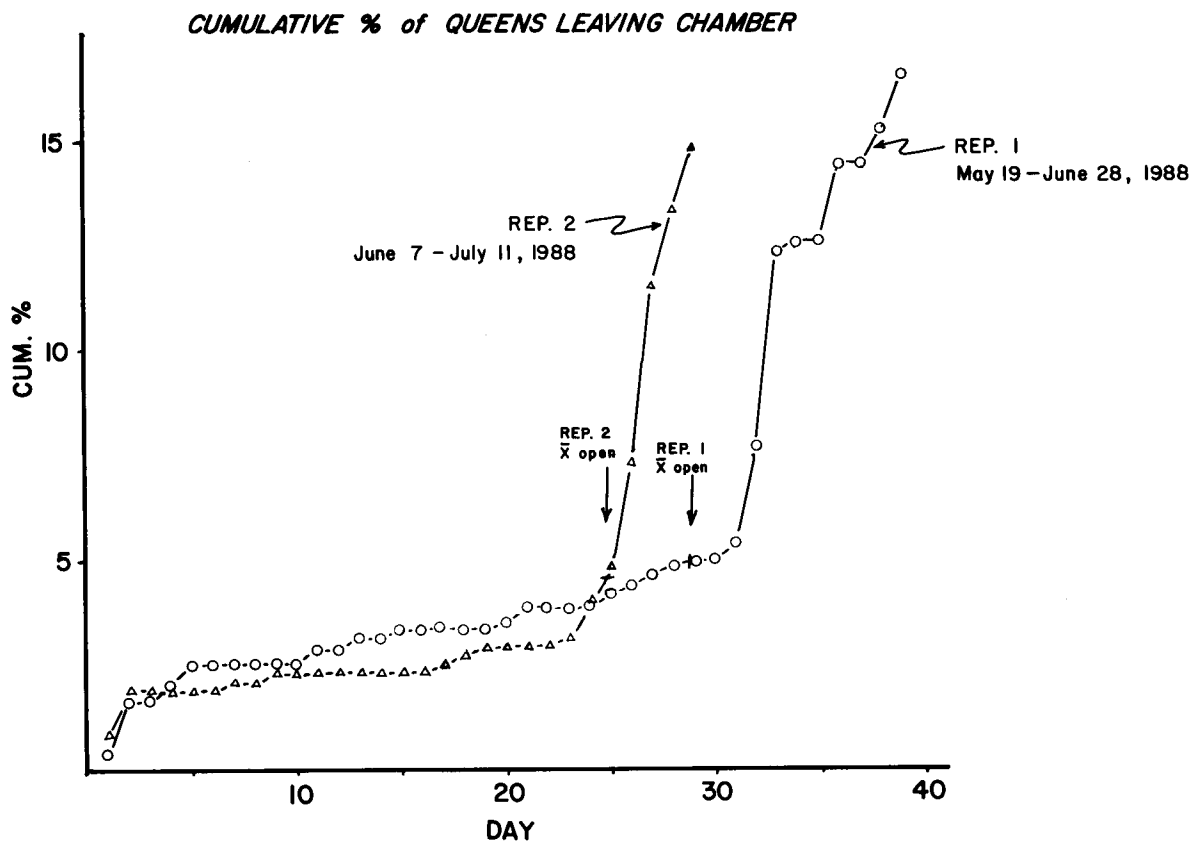


Fig. 7. The rate of queen departure from founding chambers increased at the end of the claustral period. See text for details. SD for mean days to nest opening were 4.8 days for replicate 1 and 5.1 days for replicate 2.

density usually far exceeds the ultimate density of mature, territorial colonies. For example, if we assume that the incipient colonies of cohorts A–D are the 25% of the founding nests which survived the claustral period, it follows that this plot of only 1200 m<sup>2</sup> was colonized by about 6800 founding nests, with a density of 2.64–0.53 nests/m<sup>2</sup> for cohorts A–D. Using the relationship between nest density and queens per m<sup>2</sup> (Tschinkel & Howard, 1983), it was calculated that perhaps 10,000–20,000 queens settled in this small area in the course of one summer. A resurvey of this site in 1989 showed that it was occupied by six mature colonies with another eleven close enough possibly to have some of the original plot as part of their territory. These colonies represent about 0.1% of the number of queens which attempted founding in this area in 1986.

My data show that the excess incipient colonies are eliminated very early in the history of the population, mostly by brood-raiding. Only 1–3% of the founding colonies survived after 50 days. Brood-raiding is one of the first orders of business for incipient colonies and the major source of their 'mortality'. Of course, while the raid-losing colony ceases to exist as an independent 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

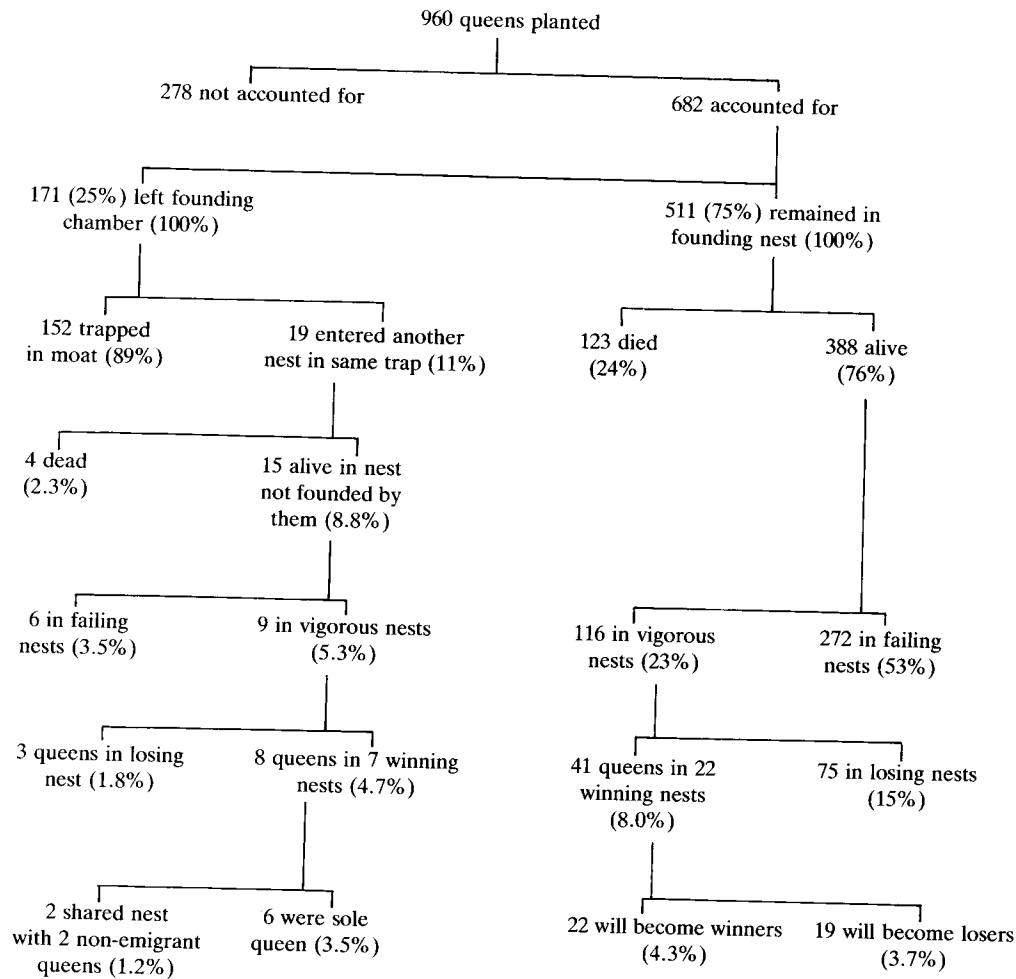
allows raids to increase in size and extent as raiding continues, leading in (perhaps) rare cases to raids of stunning proportions, such as the mega-raid in which thousands of 0.25 mg workers gamboled along up to 70 m of trail, burdened with brood weighing as much as themselves.

If my results are representative of unmanipulated populations, it is possible that emigration of queens to other incipient nests may be as successful a strategy as self-founding. This may be so because queens can choose incipient nests that have succeeded to some degree or other already. Whether queens can discriminate between vigorous and failing incipient nests, and choose between them is unknown. Nor is it known whether the resident queen has some competitive advantage during the reduction to monogyny. However, because most intruding queens probably come from failed nests, with no chance of success, even a small chance of success would be sufficient to select for taking the chance. Because queen emigration often takes place on the same trails as raiding, there is also a chance of mother and daughters being reunited.

While my data show that there were as many raids as incipient nests, this may still be an underestimate of raid frequency. In the larger 1985 raids, raiding often occurred in the evening. In 1986 we did not check for raids after mid-day. If evening raiding occurred at 20% the morning



**Table 1.** Founding success in the queen trapping experiment on basis of 960 queens. Percentages (in parentheses) were calculated on the basis of the number leaving or remaining in their founding chambers. Leaving is at least as successful a strategy as staying.



rate, this would mean we missed 350 raids. In addition, no checks were made on several days during the 1986 raid period, raising the possibility that 10–20% of the raids were missed. Finally, up to one-third of the raids were short enough occasionally to escape detection by our sampling. Overall, it is possible that the total raid frequency was 30–50% higher than estimated here.

The survivorship of most social insect colonies shows a type III pattern, that is, very high mortality of young colonies, followed by much lower mortality of mature colonies (Hölldobler & Wilson, 1990). In *S. invicta* and perhaps other raiding species as well, this early mortality is mostly the result of raiding. Unlike other type III species in which the dying feed predators or microbes, in ants, the 'dying' colonies directly cause the growth of the survivors. When raiding ceases, there is a decrease in the 'mortality' of the surviving colonies, which are much larger than they would have been without raiding.

*S. invicta* is an exotic species in the U.S.A. and reaches

high densities in optimal habitat, making the relevance of brood raiding and pleometrosis obvious. It appears that in selected habitats in its homeland in Brazil and Argentina, *S. invicta* can become as common as in the U.S.A. (S. Porter, pers. comm.; Wojcik, 1986), making it likely that brood raiding and pleometrosis are important evolutionary outcomes, not artefacts of translocation.

The picture of the establishment of fire ant populations that emerges from this and prior work (Tschinkel & Howard, 1983; Tschinkel, 1992) is a very dynamic one. Competition among nests leads to their aggregation into ever larger ones, and the competition among queens plays itself out in a locale shifting from raid-winner to raid-winner. The contest is over which of the original incipient nests will house most of the local population of minors and brood, and which of the founding queens will become the reproductrix of this amalgamated worker population. In a sense, when conditions favour raiding, colony founding in *S. invicta* is both pleometrotic and polydomous.

### Acknowledgments

For cheerful technical help under wilting Florida circumstances, I wish to thank Natalie Furman and Carrie Phillips. For helpful criticism of the manuscript, I thank Frances James, Eldridge Adams and Don McInnes. This work was supported in part by NSF grant BSR 8502969.

This is paper No. 22 of the Fire Ant Research Team.

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Accepted 4 December 1991