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Resource allocation, brood production and cannibalism during colony founding in the fire ant, *Solenopsis invicta*

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Summary. The colony founding characteristics of newly mated fire ant queens from monogyne colonies were studied in the field and in the laboratory under haplo- and pleometrotic conditions. Initial queen weight (live) was not correlated with subsequent progeny production. During founding, queens lost a mean of 54% of their lean weight, 73% of their fat weight and 67% of their energy content. The percentage of fat decreased from 44% to 33%. Queens lost weight or energy in relation to the amount of progeny they produced (Figs. 1, 2). The efficiency of the conversion of queen to progeny increased as more progeny were produced, leading to a decline in the unit cost of progeny (Fig. 3). The more minims a queen produced, the lower the mean weight of these minims and the faster they developed (Fig. 4). In a field experiment on pleometrotic founding, total brood increased with queen number, peaked between four and seven queens and declined with 10 queens (Fig. 5). Brood developed faster at the sunny, warmer site, but total production and queen survival was higher at the shady site. As queen density increased, production per queen decreased as a negative exponential in which the exponent estimated sensitivity of brood production to queen-crowding and the constant estimated the production by solo queens (Fig. 9). These effects of queen number were confirmed in laboratory experiments. The decrease of production per queen was small and not always detectable during the egg-laying phase, but brood attrition was always strong during the larval period and increased with queen number (Figs. 8, 10). While airborne factors may have contributed to this inhibition, most of the brood reduction was due to other causes, probably cannibalism. For a given number of minims, increased queen number increased the mean weight of these minims, an effect that resulted both from a lower minim production per queen and from cannibalism of dead queens by survivors (Fig. 11). Cannibal queens lost much less weight to produce a given number of minims than unfed control queens, and these minims were heavier (Fig. 12).

Key words: Pleometrosis – Formicidae – Worker size – Cannibalism – Haplometrosis – Colony development.

Introduction

Ant queens found new colonies in one of two ways: either accompanied by workers (dependent founding) or unaccompanied (independent founding) (Hölldobler and Wilson 1977). Among the majority of independently founding species, founding is claustral, meaning that the queen seals herself in the founding chamber and rears the first brood of workers by drawing on nutrient stores in her body (Hölldobler and Wilson 1990). The need for such large nutrient stores has led to higher levels of fat in species with claustrally founding queens than in those founding dependently (Keller and Passera 1989). Most of this material is sequestered between adult eclosion and the nuptial flight (Keller and Passera 1989).

In some claustral ant species, queens may improve founding success through pleometrosis (co-operative colony founding) (Hölldobler and Wilson 1977). The main features of colony founding in *Solenopsis invicta* have been described by Markin et al. (1972), including the existence of pleometrosis. Tschinkel and Howard (1983) showed positive relationships between queen settlement density and pleometrosis, and between pleometrosis and founding success. Pleometrosis may lead to lower queen mortality and greater worker production (Waloff 1957; Bartz and Hölldobler 1982; Tschinkel and Howard 1983). Larger numbers of workers in the first brood result in an advantage in the ensuing competition among incipient colonies (Bartz and Hölldobler 1982; Pollock and Rissing 1989; Tschinkel 1992a,b). Central to this competition is brood raiding, the reciprocal stealing of brood from neighboring incipient nests by workers (Pollock and Rissing 1989; Tschinkel 1992a). Victory usually goes to the nest with more workers, emphasizing the importance of pleometrosis and worker production. Workers soon execute supernumerary queens (Tschinkel and Howard

1983), but how they choose the single, surviving queen is unknown.

In most ants, workers produced by the founding queen(s) are distinctly smaller than any others in the life cycle and are called minims or nanitics (Hölldobler and Wilson 1990). Vander Meer (1986) suggested that minims are a behaviorally and biochemically distinct caste. Certainly, the role of minims in brood raiding suggests some distinctive minim behavior, but the degree to which this is limited to minims is not yet clear (Tschinkel 1992a). The small size of minims may be an adaptive feature of fire-ant life history: Porter and Tschinkel (1986) showed that for a given weight of workers, minims reared more brood than did minor workers of *S. invicta*. For many species of ants, rapid colony growth is an important element in survival and competition (Vargo 1988).

Pollock and Rissing (1989) have pointed out that, whether pleometrotic or haplometrotic, the sealed founding chamber is a closed system with fixed resources. For the denizens of the founding chamber, the question is how to allocate these fixed resources in order best to meet the needs of survival, worker production and the post-claustral brood raiding competition (Tschinkel 1992a, b). Natural selection should optimize the trade-off between worker number and worker size (Porter and Tschinkel 1986). Higher worker numbers favor success in brood raiding (Tschinkel 1992a) and colony growth rate (Tschinkel and Howard 1983), while larger worker size favors worker longevity (Porter and Tschinkel 1985a), stress resistance and defensive value. In addition, the queen must balance allocation of resources for worker production against those for maintenance of herself and her brood, and perhaps also for a reserve for post-claustral needs.

These allocations are, of course, adjusted over evolutionary time, but there is an indication that some adjustment may be possible within each founding chamber. Wood and Tschinkel (1981) showed that the small size of *S. invicta* minims was at least partly trophogenic in origin, because when newly mated queens were adopted into queenless nests, the size of workers in the first brood was larger than minims. Generally, similar conclusions were reached by Goetsch (1937) and Passera (1977) working with *Pheidole pallidula*, and by Petersen-Braun (1977) with *Monomorium pharaonis*. These findings suggest that the outcome of larval development within the claustral chamber may not be fixed, and may be modified by the rearing environment. The number of minims produced by founding queens has been shown to be important, but variation of their size may also affect such traits as their longevity and resistance to stress and dehydration (Hood and Tschinkel 1990).

During the claustral phase, developing larvae of most ant species are nourished at least partly through trophic eggs laid for the sole purpose of being eaten (Hölldobler and Wilson 1990; Baroni-Urbani 1991). Such trophic eggs are often non-embryonated. Voss (1985) refined a method for detecting embryonation in eggs. Both inseminated and virgin queens in mature colonies can lay non-embryonated eggs, especially in polygyne colonies (Vargo and Ross 1989), where they may play a role in reproductive competition and regulation. Embryonation of eggs as a regulatory mechanism in founding colonies is unexplored.

Although the potential for regulation within the claustral chamber exists, little is known about processes and relationships during this period. In this paper I relate queen weight, queen number, weight loss, minim number, minim size and development rate during the claustral period, clarifying patterns of the allocation of queen resources under haplo- and pleometrotic conditions. I also show that cannibalism of larvae and queens stretches the resources within the sealed founding chamber and affects allocation patterns.

Materials and methods

General methods. Queens were aspirated from the ground and under litter on the afternoons of large mating flights in Tallahassee, Florida, USA. All colonies in this area are monogyne. For colony founding, queens were placed singly or in groups, depending on the experiment, into one of two types of founding nests. The first consisted of small test tubes half filled with water retained by a cotton plug. After addition of the queen(s), these were retained with a second cotton plug in the mouth of the tube. The second type consisted of blocks of dental plaster $15 \times 15 \times 3$ cm with 25 flat-bottomed holes 1.5 cm in diameter in a 5×5 array. Queens were placed into the holes in numbers called for in the experimental design. For laboratory use, the sides of the plaster blocks were waxed to reduce drying, and the plates were covered, top and bottom, with glass and held at 30°C. Plates were moistened as needed. For field use, the plaster founding plates were unwaxed.

Data consisted of counts and weights of the contents of founding nests. For several analyses brood were lumped into "young brood" consisting of eggs and first-instar larvae, and "older brood" consisting of the remaining larval instars, pupae and adult minim workers.

Fat contents were determined by dry weight loss after ether extraction. Energy contents were calculated using 39.33 J/mg fat and 18.87 J/mg of lean weight (Peakin 1972).

Field experiment. Queens were collected on the afternoon after the mating flight of 10 May 1982, and placed in the founding plates in groups of 1, 2, 4, 7, or 10, arranged in Latin squares. The plates were covered with a fine-mesh brass screen, wired tightly and buried at the test sites. The sunny site contained scattered weedy vegetation, and received full sun most of the day. The shady site was under sweetgum trees less than 100 m from the sunny site. At each site, three founding plates, each containing five of each group size, were buried at 5 cm depth and three at 15 cm (six plates per site). This entire experiment was repeated a second time after the mating flight of 21 June 1982. In the first replicate, the plates at the sunny site were terminated after 30 days and those in the shady site after 40 days. For the second replicate, all plates were excavated after 35 days.

The experimental design thus consisted of the independent variables: queen number (5 levels); site (2 levels); depth (2 levels); founding plate (a blocking factor, 3 levels); replicate (a blocking factor, 2 levels). There were 300 nests in each replicate, 60 at each queen density. Each replicate used 1440 queens.

Staining eggs to detect embryonation. Five-day-old eggs were collected and stained with the Feulgen stain method of Schmuck and Metz (1931) as modified by Voss (1985). Because DNA is stained pink, this method allows non-developing trophic eggs to be differentiated from nucleated, embryonated eggs. Eggs were classified into unstained, non-embryonated eggs (class 0) and classes 1–3 containing increasingly developed embryos.

Table 1. Initial weights (mg) and fat content of queens from the mating flights of 29 May, 3 June and 19 June 1991

Measures	Mating flight								
	29 May		3 June		19 June		*F* ratios		
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	*df*	Ratio	r^2
Live weight	16.3[a]	1.22	14.9[b]	1.23	15.1[b]	1.13	3, 100	42.9	22%
Dry weight	7.58[a]	0.69	7.92[a]	0.82	8.53[b]	0.62	3, 50	22.9	23%
% Dry weight	47.0[a]	2.65	52.5[b]	3.41	55.6[c]	1.57	3, 50	34.0	26%
Lean weight	4.24[a]	0.38	4.51[b]	0.40	4.65[b]	0.36	3, 50	15.1	17%
Fat weight	3.35[a]	0.43	3.41[a]	0.52	3.88[b]	0.36	3, 50	22.4	23%
% Fat	44.0[a, b]	3.01	42.8[a]	3.94	45.5[b]	2.24	3, 50	9.31	11%

The *F*-ratios and *df*s refer to comparisons among flights by ANOVA. All *P* values were less than 0.005 after application of the Bonferroni correction for table-wide significance. Means with the same superscript indicate pairs of values not significantly different (ANOVA)

Data analysis

Data were analyzed using Minitab (Ryan et al. 1982) by multiple regression using dummy variables, or by analysis of variance (ANOVA) and the Newman-Keuls Test. Occasionally data were transformed to stabilize the variance. A few outliers were deleted after analysis of residuals. The field experiment was analyzed by ANOVA using BMDP8V (Dixon et al. 1985).

Results

Haplometrotic founding

Initial queen weight, and fat content. Queens were collected after 3 mating flights in 1991 (29 May, 3 June, and 19 June). From each flight 50 queens were used to determine initial weights and fat content (Table 1).

Over all three flights, queen live weights averaged 15.4 mg (SD = 1.19), dry weights 8.01 mg (SD = 0.71), lean weights 4.47 mg (SD = 0.38), and fat weights 3.55 mg (SD = 0.44). Dry matter made up 51.7% (SD = 2.54) of the live weight, and fat made up 44.1% (SD = 3.06) of the dry weight. Similar live weights were reported by Fletcher and Blum (1983), Porter and Tschinkel (1986) and Markin et al. (1972) and are characteristic of the monogyne form of the fire ant.

For most measures, there were significant differences between mating flights (Table 1). For all measures except percent fat, the 29 May flight was significantly different from the 19 June flight, with the 3 June flight more similar to the earlier flight in some measures and the later flight in others. Dry, lean and fat weights increased with each mating flight. The 29 May queens contained the highest proportion of water, resulting in the highest live weight. The percent fat varied only little, although significantly.

Queen weight loss during founding After completion, in the laboratory, of colony founding by another 100 queens from each mating flight, the queens and their progeny were killed by freezing. Live, dry and lean weights of the queens were determined. Because it is not possible to take the initial dry weight of a queen that produced minims, only differences in mean queen weights before and after founding were determined by comparison between data sets. Queens lost a mean of 8.55 mg live weight (about 54%) during founding. Loss of dry weight averaged 64% (5.14 mg) revealing that the percent water of queens averaged about 12% higher after founding (59%) than before (47%). Loss of fat weight was about 2.59 mg, and was proportionally higher (73%) than the loss of lean weight (2.54 mg; 57%). This was reflected in a decline of queen percent fat from about 44% before founding to about 33% after. When these declines were expressed in energetic terms (joules), queens lost 67% of their energy content during founding.

Again, there were significant differences among the three flights. Queens from each subsequent flight lost less live weight (ANOVA, $F_{2,210} = 10.1$; $P < 0.001$; $r^2 = 9\%$), but this order was reversed for dry, lean and fat weights, reflecting the higher water content of queens from the first flight.

Together, these data show that colony founding results in very large losses of weight and energy content, that fat contributes disproportionately to these losses, and that queens from different mating flights can be significantly different in many or most of these measures.

Brood production in relation to queen characteristics. Dry and lean weights of grouped minims and grouped brood were then determined for the same 300 post-founding nests from the above experiment. Minims and pupae were counted. The parameters and the total r^2 values are given in Table 2. In the discussion below most r^2 values exclude the effect of mating flight and thus differ from the total r^2 in Table 2.

While it might be expected that heavier queens produced more minims, this was not the case (Table 2; regression 1). The number of minims was not significantly related to the initial queen weight (slope not significantly different from zero, 0.4% of total variation). While total progeny weight increased significantly with increased initial queen weight (Table 2, regression 4), this trend was weak and accounted for only 2.5% of the variation.

On the other hand, the number of minims increased significantly with increased weight lost by the queen during founding (Table 2, regression 2; Fig. 1). The regres-

Table 2. Coefficients for regressions of brood production variables, in the form $y = ax + b$

Regression number	Variables		*y*-intercept			Slope		Total r^2
	y	*x*	MF	*b*	SEM	*a*	SEM	
1	No. min.	Q live wt.	All	–	–	–	–	
			1	−2.36	9.90	–	–	9.4%
			2, 3	4.60	9.00	–	–	
2	No. min.	Q wt. loss	All	–	–	4.11	0.36	
			1	−23.9	3.43	–	–	44.8%
			2, 3	−15.8	3.15	–	–	
3	Wt. progeny	Q wt. loss	All	–	–	0.31	0.028	
			1	−0.87	0.27	–	–	41%
			2, 3	−0.45	0.24	–	–	
4	Wt. progeny	Q live wt.	All	–	–	0.15	0.040	
			1	−0.48	0.66	–	–	7.5%
			2, 3	−0.12	0.60	–	–	
5	Wt. progeny	Final Q dry wt.	All	–	–	−0.56	0.079	
			1, 2	3.57	0.22	–	–	22%
			3	3.83	0.24	–	–	
6	Tot. min. dry wt.	No. min	All	0.12	0.022	0.069	0.0012	96%
7	AS% min. of total progeny wt.	No. min.	All	–	–	12.2	1.25	
			1	13.5	1.30	–	–	84%
			2, 3	16.4	1.39	–	–	
8	AS% min. of total progeny wt.	Tot. prog. wt.	All	–	–	12.2	1.25	
			1	22.2	2.87	–	–	39%
			2, 3	27.9	5.74	–	–	
9	wt/min	No. min.	1	0.089	0.0016	–	–	
			1, 3	–	–	-6.57×10^{-4}	0.8×10^{-4}	
			2	0.11	0.0020	−0.0012	0.0001	50%
			3	0.094	0.0019	–	–	

MF = mating flight; 1 = 29 May, 2 = 3 June, 3 = 19 June. Q = queen, min. = minim, AS% = arcsine square root transformed proportion. All listed coefficients are significantly different from zero or from others in the regression after application of the Bonferroni correction for table-wide significance. A single slope difference became non-significant after this correction

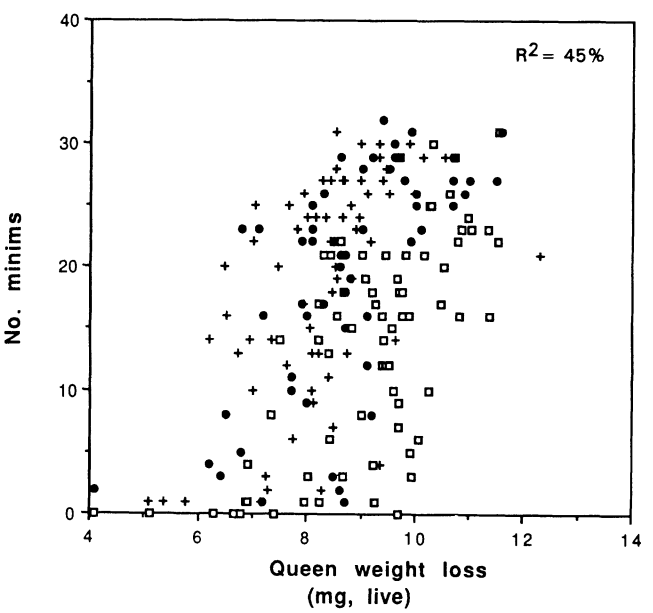

Fig. 1. Number of minims produced in relation to the live weight lost by the queen during founding. Data are from three different mating flights (29 May, *squares*; 3 June, *circles*; 19 June, *crosses*). The more minims a queen produced the more weight she lost (r^2 = 45%). The ranges of brood production and weight loss are high. Queens producing no brood nevertheless lost a substantial amount of weight

sion equation showed that queens that produced no minims lost up to 3.8 mg (29 May) and 5.8 mg (3, 19 June). Thereafter, every 1 mg of live weight lost resulted in a mean of 4.11 additional minims. Queen weight loss explained 27% of the variation in minim number.

Total weight of progeny similarly increased with queen weight loss (Table 2, regression 3). About 31% of the variation in progeny weight was accounted for by queen weight loss. Queens lost an average of 1.5 or 2.8 mg live weight in order to produce the first offspring individual. Thereafter, they produced 0.31 mg progeny (dry weight) for every 1 mg live weight lost. Because queens averaged about 50% dry weight initially, this meant that 0.6 mg dry progeny were produced for every additional (dry) 1 mg lost.

In energetic terms, queens lost 90 J without progeny production (intercept = –31.2). Over 70% of this can be accounted for as maintenance cost, using 0.029 J/lean mg/h (Tschinkel, unpublished data). Mean lean weight declined 57% over 30 days at 30°C. Thereafter, each additional joule lost resulted in 0.34 J of progeny (r^2 = 50%) (Fig. 2).

Efficiency (fraction of queen weight-loss converted to brood) of the conversion of queen to progeny increased with the total weight of brood produced (Fig. 3), rising from 4% or 8% to about 35% (70% if converted to a

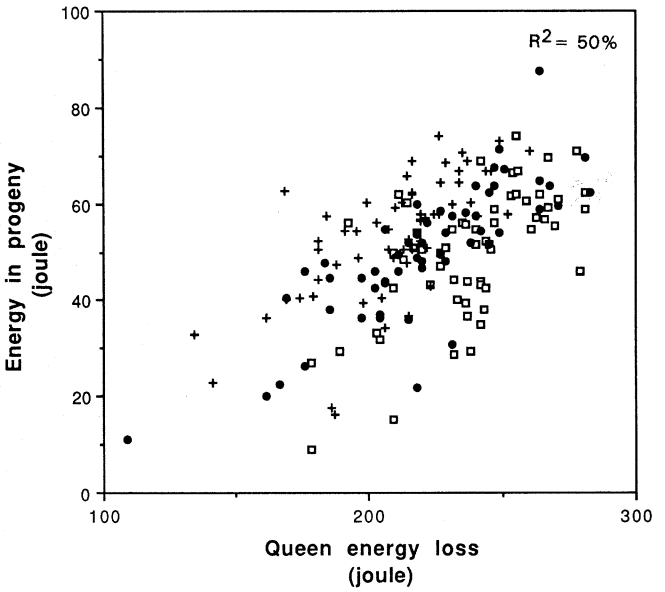

Fig. 2. Total energy in progeny in relation to the energy lost by the queen during founding. Data are for three different mating flights (as Fig. 1). The higher the energy invested in progeny, the more energy the queen lost (r^2 = 50%). The ranges of energy loss and brood production are quite high. Queens producing no brood nevertheless lost a substantial amount of energy, possibly as maintenance cost

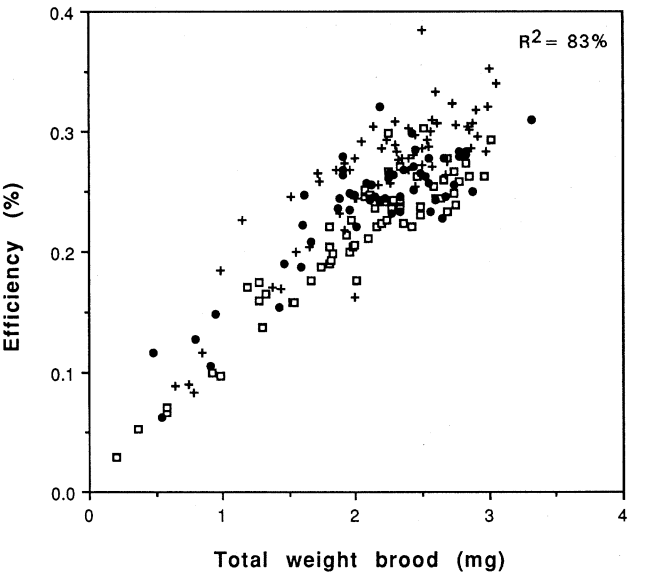

Fig. 3. Efficiency of brood production in relation to the weight of brood produced. Data are from three different mating flights (as Fig. 1). Efficiency was estimated as mg brood per mg queen weight lost. The cost of brood per mg decreased (efficiency increased) as more brood was produced (r^2 = 83%)

dry-weight basis). Variation in progeny weight accounted for 74% of the variation in efficiency while mating flight contributed an additional 9%. Thus, queens that produced more progeny did so at a lower unit cost, largely because of the large fixed cost that did not result in brood. This fixed cost is probably maintenance respiration.

When the basis was energy content, the efficiency of conversion of queen to progeny was much lower. Because the initial joule content of queens rearing progeny cannot be known, this conversion factor was calculated from the weight loss during founding, the mean energy content (J/mg) of queens before and after founding, and the progeny produced (J). Although efficiency increased significantly with increased weight loss (slope = 0.013; t = 5.08, $P<0.001$), this factor accounted for only 2.2% of the total variation, while mating flight explained 25% (see below).

All measures of brood production were significantly different for at least one mating flight, and the inclusion of mating flight in regressions added considerably to the explained variation (Table 2). While initial queen weight was not related to the number of minims produced, queens from the second and third flights produced significantly more minims, adding 9% to the explained variance. Similarly, this added 5% to the explained variance of regression 4 (initial queen weight and total progeny weight) and 17% to the regression 2 (number of minims vs. the queen weight loss). For the regression of progeny against queen weight loss, the second and third mating flight produced significantly more progeny than the first (t = 5.34; $P<0.001$) adding 9% to the explained variation.

Efficiency of conversion of queen to progeny, either in weight or energetic terms, was also significantly higher in queens from the later flights, adding 7% and 25% to the regressions of these variables against the amount of progeny (in mg or J).

As expected, total progeny weight was negatively related to the queen's final weight (Table 2, regression 5). For every additional 1 mg (dry) retained by the queen, total progeny weight was less by 0.56 mg (dry). Final queen weight accounted for 18% of the variation while mating flight added 4% more (22% explained).

First generation brood as a cohort. Inspection of brood status and numbers suggested that the total brood in experimental nests was a cohort – that is, larvae from the first batch of eggs developed together while few further larvae were produced until the brood consisted of a substantial fraction of minims. This means that the differences in counts of *total* brood represent largely differences in the size of this first cohort, not differences in the development rate. The temporal pattern of egg embryonation confirmed this. Five days after nest initiation, over 40% of the eggs were in stages 2 and 3 of development, while only about 4% were in stage 1, indicating that most of the embryonated eggs were among the first laid. The remaining 56% were non-embryonated trophic eggs laid later. These patterns are in general agreement with those described by Markin et al. (1972) and Voss and Blum (1987).

Progeny characteristics. As minim production increased, the individual weight and development time of minims decreased. When minim production was near zero, min-

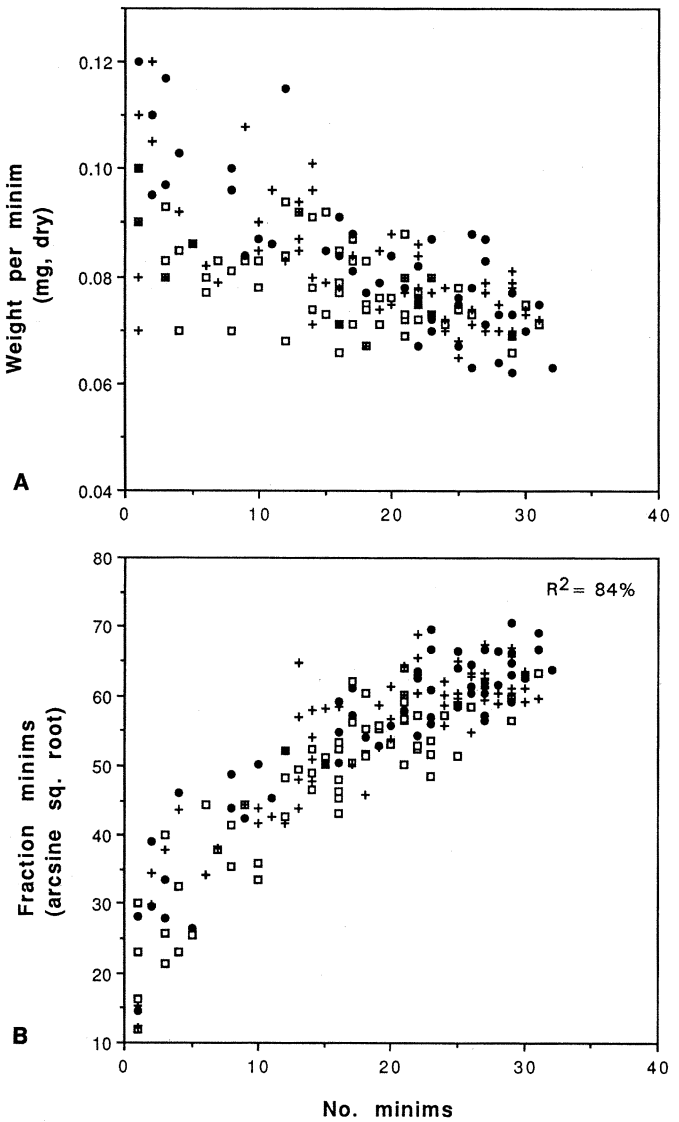

Fig. 4. **A** As minim production increased, the individual weight of minims decreased. **B** Minims developed faster when higher numbers were produced. Development rate was estimated as the fraction of the brood which were minims after a fixed elapsed time (r^2 = 84%). Data are for 3 different mating flights (as Fig. 1)

ims averaged between 0.09 and 0.11 mg dry weight (depending on mating flight). In groups of 30 minims, mean weight dropped to about 0.07 mg, a decrease of 22–36% (Fig. 4A; Table 2, regression 9). The number of minims accounted for about 38% of the total variation in their weight, the higher minim weight of the third flight adding 11% more (total 50% explained). Similar though somewhat weaker patterns emerged when total progeny weight was used as the x variable.

The decline in individual minim weight was correlated with the decline in their development time. Because queens begin egg-laying on the same day and all nests of a replicate were later terminated on the same day, development rate was estimated by the proportion of the total progeny weight which was adult minims. The proportion was arcsin square root transformed and regressed against the square root of the number of adult minims (best fit) (Table 2, regression 7). As the number of adult minims increased from near zero to 30, the proportion of progeny weight present as minims rose from 6–8% (depending on mating fight) to 79–83% (Fig. 4B). Minim number accounted for 83% of total variation in percent minims, with mating flight adding only another 1%. When total progeny weight was used as the x variable, patterns were similar, although the explained variation dropped to 39% (Table 2, regression 8).

In overview, queen live weight failed to predict production during founding, but queens of higher fertility lost more weight and produced more minims, which developed faster and weighed less than minims of queens with lower fertility.

Pleometrotic founding

Field experiment. Queen number, site and depth explained 11% of the variation in total brood. Queen number had a highly significant effect on the total number of brood produced (exclusive of eggs) (ANOVA, data transformed to $\ln(y+1)$, $F_{4,16} = 19.33$; $P<0.001$) (Fig. 5). At all sites and depths, total production climbed from single queens to a maximum at about four to seven queens, and then declined as queen number increased to ten. The decline was more rapid and the peak sharper for nests at the sunny site, resulting in a significant site-by-queen number interaction ($F_{4,64} = 3.87$; $P<0.01$; 9.4% of explained variance). Total production was also 20% higher at the shady site in both replicates ($F_{1,16} = 7.06$; $P<0.05$; 8.2% of explained variance). A replicate-by-depth-by-queen interaction accounted for another 11% of the explained variance ($F_{4,64} = 4.70$; $P<0.005$). Overall, queen number explained about half of the variation in total production, with site and depth making smaller contributions, either directly or in interaction with queen number.

Brood development rate was estimated as the fraction of brood which were adult minim workers (arcsin square root transformed). Brood development rate was not significantly affected by queen number but was much higher at the sunny site (site: $F_{1,360} = 300$; $P<<0.001$) and at shallower depth (depth: $F_{1,360} = 45.5$; $P<<0.001$). In the sun, brood was 57% (SE = 2.0) minims at 5 cm and 46% (SE = 2.5) at 15 cm, while in the shade, brood was 24% (SE = 1.6) minims at 5 cm and 11% (SE = 1.4) at 15 cm. Site accounted for 61% of the explained variation in fraction minims, while depth accounted for 9.2%. A significant replicate and replicate-site interaction resulted from allowing the shade treatment in replicate 1 to run 10 days longer than the sun treatment, a source of artifact not repeated in replicate 2. When this run-length effect is eliminated, the results of the two replicates were similar.

The probable source of these development rate differences was soil temperature, which varied dramatically according to site and depth. The mean afternoon temperatures (1200–1500 hours) at the sunny site were 39°C at 5 cm and 33°C at 15 cm. Under sunny, dry conditions, the temperature at 5 cm occasionally reached 45°C. Mean afternoon temperatures at the shady site were 26°C

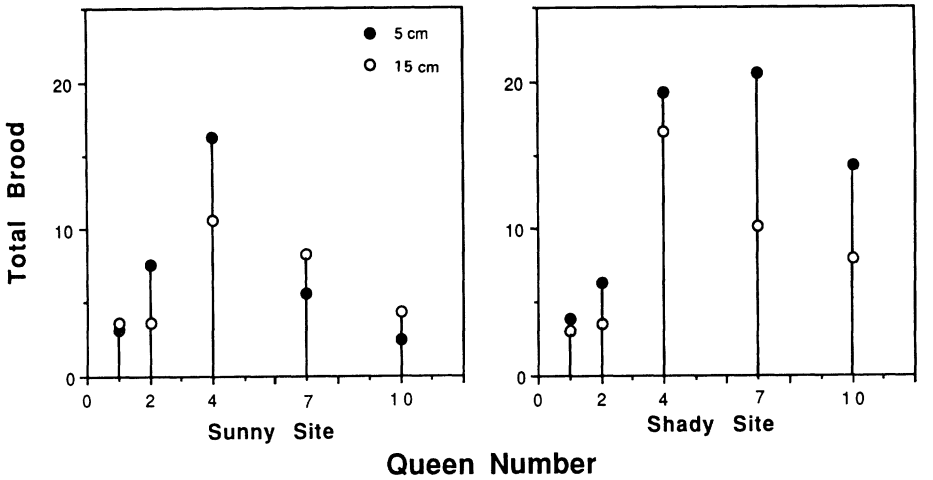

Fig. 5. The relationship of total brood to queen number, site and nest depth (*filled circles*, 5 cm; *open circles*, 15 cm) in the field experiment. Queen and site had the largest effects, with production reaching a maximum between 4 and 7 queens at the shady site

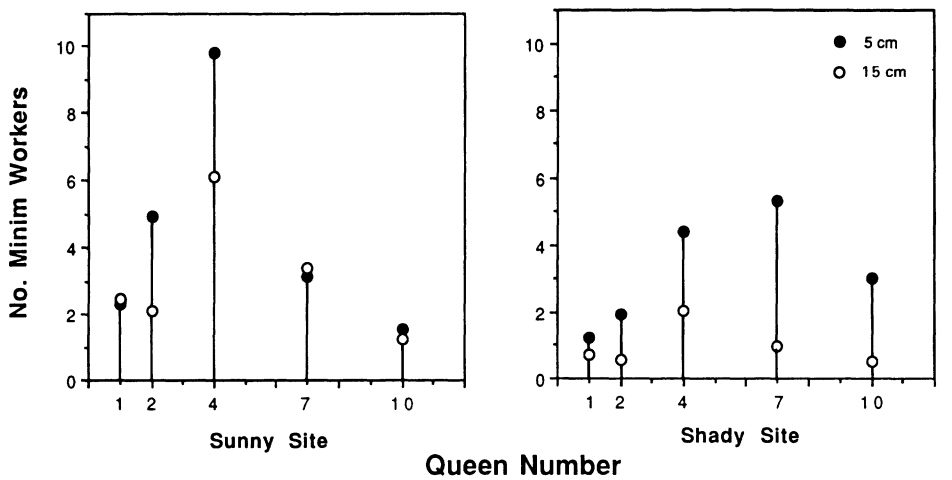

Fig. 6. Production of minims in relation to queen number, site and nest depth (*filled circles*, 5 cm; *open circles*, 15 cm) in the field experiment. Minim number was maximum for 4-queen nests at the shallow, sunny site, though this was not the site with highest brood production

and 25°C at 5 and 15 cm, respectively. Morning temperatures averaged about 29°C at the sunny site and 25°C at the shady site, with little difference by depth. Soil moisture was also different, perhaps as a result of the temperature differences. At the sunny site, the soil contained 2.2% and 3.2% water at 5 and 15 cm, respectively. At shady sites these values were 3.5 and 3.8%. While it may not have a direct effect on development rate, drier soil heats more rapidly, amplifying the temperature difference between sites.

From the point of view of post-claustral colony success, especially success in brood-raiding (Tschinkel 1992a) the early production of a large number of adult minims is of great importance. When the minims open the nest, brood not in the form of adult minims is of no value in winning brood raids. Queen number had the largest effect on the number of minims ($F_{4,64} = 17.1$; $P < 0.01$), accounting for 25% of the explained variation. As with total brood, minims reach a maximum at intermediate queen numbers. Replicate had a significant effect ($F_{1,16} = 22.98$; $P < 0.002$; 20% of explained variance) because shade treatments ran 10 days longer than sun in replicate 1. Replicate 2 avoided this artifact and is shown in Fig. 6. Site and depth affected the number of minims significantly (depth: $F_{1,16} = 14.9$; $P < 0.005$; 13% of explained variance; site: $F_{1,16} = 12.8$; $P < 0.005$; 11% of explained variation), with shallower and sunny treatments having higher numbers of minims. Modest interactions (5 and 4% of explained variance) of queen number with site and depth were associated with the very sharp peak at four queens found in the sunny, shallow treatment. Small but significant replicate by site or depth interactions were also found. Overall, while the sunny site had lower total brood production, the higher development rate resulted in higher adult minim production within a fixed time, and a more sharply defined optimal queen number. Because early production of large numbers of adult minims is important to colony founding success, the observed patterns may indeed be important for success.

Queen number had no significant effect on queen mortality ($F_{4,64} = 0.83$; n.s.) indicating that queens died of intrinsic or physical causes rather than the effects of crowding. Of variation in percent live queens (arcsin square root transformed) 6% was explained by site ($F_{1,16} = 38.6$; $P < < 0.001$): survival was 81% (SE = 3.2) in the shade and 48% (SE = 3.0) in the sun. Depth had no significant effect. It should be noted that after most

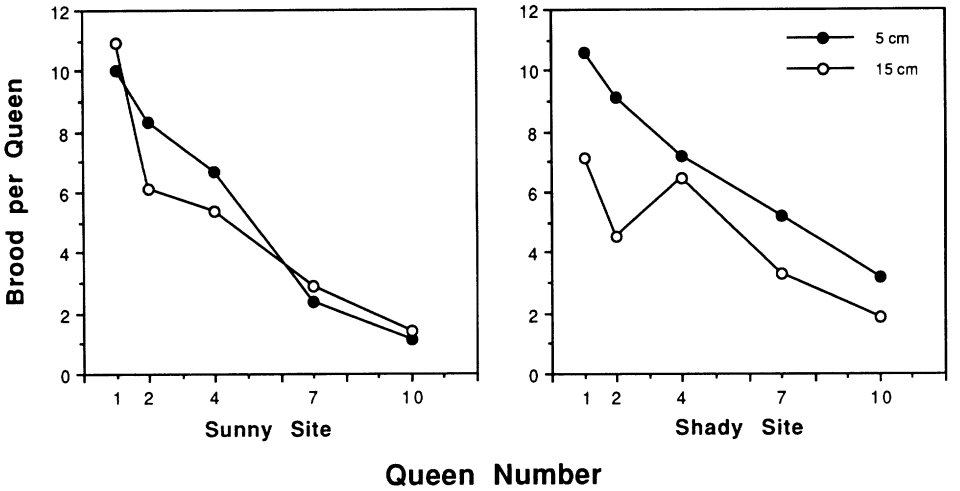

Fig. 7. Brood per queen in relation to queen number, site and nest depth (*filled circles*, 5 cm; *open circles*, 15 cm) in the field experiment. Brood per queen declined sharply with queen number. Depth also had a minor effect

minims have eclosed, they begin executing supernumerary queens, but these experiments were terminated prior to that stage.

The existence of a maximum for brood or minim production at intermediate queen numbers suggested that each queen's contribution must have declined rapidly as the number of queens in the group increased. This was confirmed by ANOVA of the brood per queen. Brood per queen showed a steady decline as queen number increased ($F_{4,64} = 26.7$; $P < 0.001$) (Fig. 7) and queen number accounted for 70% of the explained variation. Depth and replicate added another 5% each, with shallower nests being slightly more productive per queen. Analysis based on individual brood stages showed very similar patterns for all of these. Because site and depth had little or no importance, it appears that this decline in reproductive efficiency is the result of interactions among the ants in the founding chamber. This phenomenon is treated in greater detail below.

To succeed, a queen must not only survive, but produce brood as well. Successful nests were minimally defined as those with >0 brood and live queens. Note that there can be more than one successful queen in a nest. Both queens and nests enjoyed higher success in shade than sun. Nest success was maximal at intermediate queen numbers but queen success was independent of queen number.

Effect of queen number in laboratory experiments. Eight founding plates were stocked with queens at 1, 2, 4, 7 and 10 queens per group arranged in a Latin square. Queens were collected on 24 May 1983. Nests in all eight plates were first censused after 7 days. Four of these plates were terminated after 14 days and their contents censused and weighed. The other four were similarly terminated, censused and weighed at 24 days. Census data were transformed to $\ln(y+1)$. Both census and weight data were analyzed by ANOVA.

Census of young brood (eggs and first instar larvae) showed that their number increased in direct relation to queen number at all three census times (Fig. 8A). Queen number thus seemed to have little effect on egg production per queen (but see "Factors reducing queen fertility"

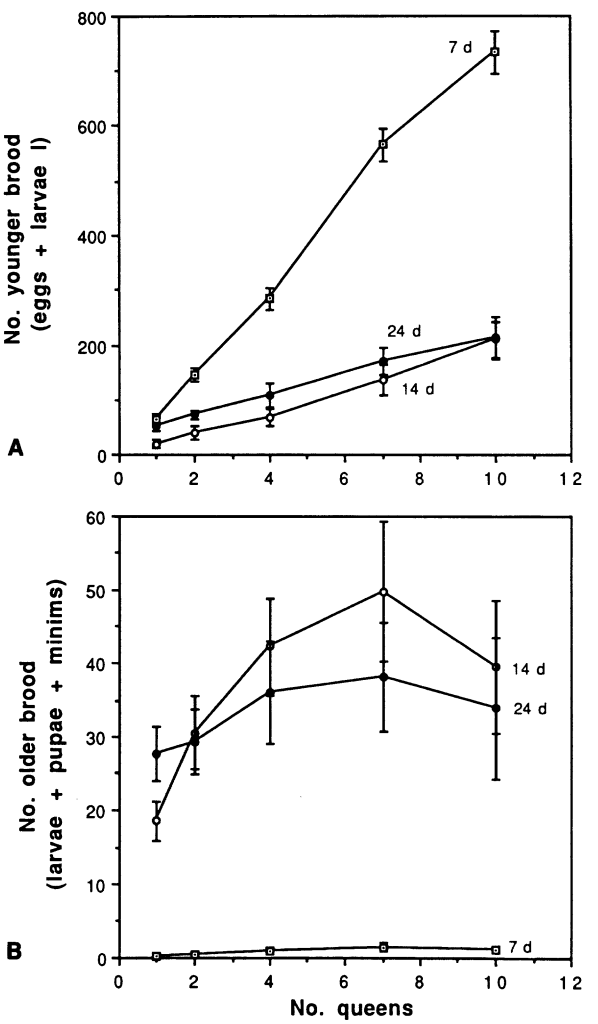

Fig. 8A,B. Brood counts in the laboratory experiment. **A** Young brood were a simple multiple of the number of queens, but **B** older brood showed a maximum at intermediate queen number. Nests were censused on days 7, 14 and 24. *Bars* indicate SE

below), though egg crop was significantly lower at 14 and 24 days than at 7 days.

On the other hand, the older brood production curve had an optimal character with respect to queen number (Fig. 8B), much like that in the field experiment (Figs. 5

Table 3. Parameters of the regression of ln (brood/queen) against $(-Q-D)$ for several experiments; brood/queen $= y$

Expt.	ln y	Day no. (condition)	K	Slope		Intercept			r^2	Dominant brood stage
				s	SE	ln N_1	SE	N_1		
Field	(L+P+M)/Q	30–40 (shade)	4	0.14	0.019	2.48	0.091	11.94	31%	pupae, minims (shade)
		30–40 (sun)	4	0.25	0.013					pupae, minims
Lab-83	(E+L1)/Q	7	8	0	–	4.22	0.089	68.0		eggs
		14	8	0	–	2.85	0.087	17.3	51%	larvae
		24	8	−0.046	0.013	3.98	0.095	54.0		pupae, minims
	(L+P+M)/Q	7	8	0.14	0.016	0.15	0.18	1.16		eggs
		14	8	0.23	0.019	2.76	0.21	15.8	71%	larvae
		24	8							pupae, minims
Embryo	eggs/Q	5	8	0.012	0.0036	4.63	0.040	103	8.4%	eggs
Poly	minims/Q	30	8	0.09	0.010	2.66	0.11	14.3	29%	minims, pupae

The slopes estimated the sensitivity of brood production to queen number, Q. The intercept, ln N_1, estimated the brood production of solo queens (N_1). $D = K-(K+1)/Q$ where K = a fitted constant (see text). E = eggs; L1 = first instar larvae; L = older larvae; P = pupae; M = minims. Field = field experiment; lab-83 = laboratory experiment on effect of queen number; embryo = embryonation experiment; poly = effect of queen number on minim weight experiment

and 6), with peak number increasing greatly from 7 to 14 days, then declining somewhat to 24 days. As in the field experiment, ANOVA showed that this peak was based on a decline in the brood production per queen. At 14 days, when the oldest brood began to pupate, there was a significant decline in mature larvae per queen ($F_{4,85} = 13.6$; $P<0.001$) and pupae per queen ($F_{4,85} = 4.09$; $P<0.01$) as queen number increased. At 24 days a substantial fraction of pupae had eclosed, and there were highly significant declines of production per queen of young larvae, mature larvae, pupae and adult minims ($F_{4,74} = 18.4$–30.6; all $P<0.001$). These patterns were similar when the total weight of brood was the dependent measure. Increased queen number caused a highly significant decline in the weight of brood per queen (ANOVA, $F_{4,163} = 58.7$; $P<<0.000$;1 $r^2 = 59\%$). Thus, as development of the pleometrotic colony proceeded, the brood contribution per queen declined continually over time, and this decline was more rapid for larger founding groups.

The lower production per queen was reflected in significantly higher final queen weights as queen number increased (ANOVA, $F_{4,169} = 16.7$; $P<0.001$; $r^2 = 29\%$), i.e., lower weight loss during founding. Whether this was the result of lower material donation rates or of cannibalism of brood or dead queens is considered below.

Fitting the production-queen number curve. The decline of production per queen with increased queen number generally resulted in a concave plot and was fitted reasonably well by a negative exponential function. Queens from different flights or under different conditions seemed to generate different parameters. I reasoned that the total progeny produced by an association should be a multiple of what queens produce by themselves, multiplied by a crowding sensitivity factor:

$$N = QN_1\, e^{s(-Q-D)}$$

where N is the mean number of progeny, Q is the number of queens, N_1 the mean number produced by solo queens, and s is a factor estimating sensitivity to crowding. When $s = 0$, crowding has no effect and N is simply a multiple of the solo queen contribution, N_1. As s becomes increasingly positive, brood production declines ever more rapidly with queen number. When s is negative, brood production is stimulated by crowding (not observed in *S. invicta*). In some cases, the decremental effect of each additional queen became smaller, so that the effect of each queen, $-Q$, had to be decremented by D, where D is itself a function of Q:

$$D = K-(K+1)/Q$$

and K is a fitted constant imparting increased non-linearity as K increases. The addition of 1 to the K in the quotient means that when $Q = 1$, the exponent equals 0 and $N = N_1$. When $K = 0$, the per-queen effect changes least with queen number. As Q becomes large D approaches K.

The form

$$(\ln N - \ln Q) = \ln N_1 + s(-Q-D)$$

yields a straight line with slope s and intercept 1n N_1 when (ln N–1n Q) is plotted against (–Q–D). Comparison of linear regressions of this form showed that intrinsic progeny production and sensitivity to crowding varied among different stages, flights and conditions (Table 3; Fig. 9). (The transformation [1n $(N+1)$–1n Q], which included groups producing no progeny, deviated strongly from normality and was fitted less well by this regression.)

Applied to the field experiment, the regression showed that production of older brood by queens in the shade was significantly less sensitive to crowding than those in the sun ($s = 0.14$ vs. 0.25; $t_{1,300} = 4.61$; $P<0.001$) (Table 3; Fig. 9A). There were no significant differences in the intercepts (t-test), showing that solo queens in all treat-

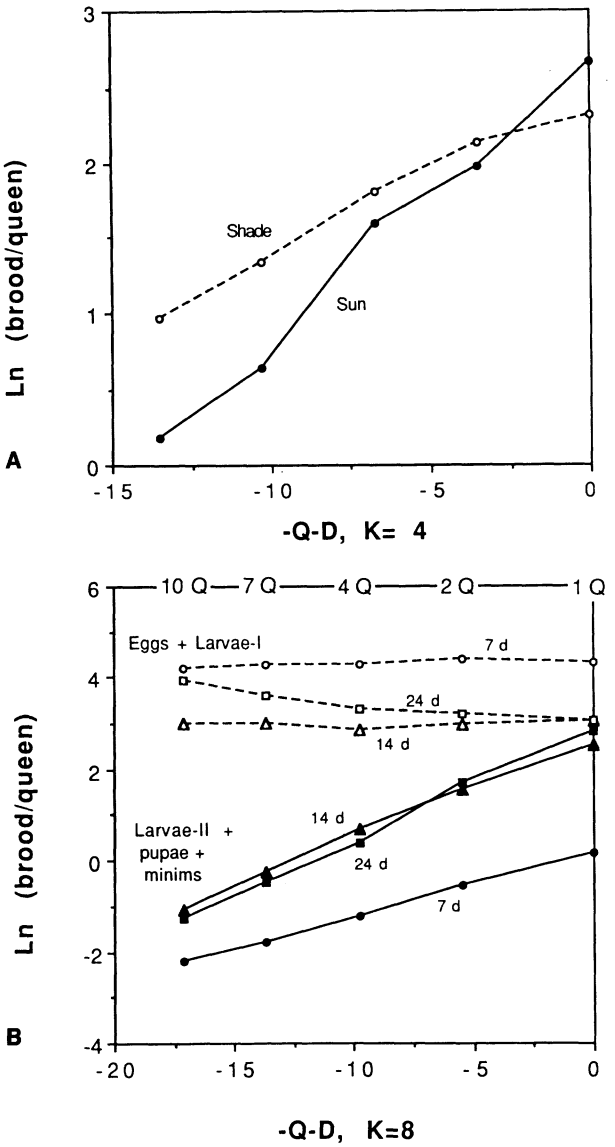

Fig. 9A,B. Brood production per queen plotted as the natural log of brood/queen against $-Q-D$, a variable derived from queen number and k = a fitted constant defining D (see text for details). This transformation produces linear plots and allows the slopes and intercepts to be used as estimates of sensitivity to crowding and solo queen production, respectively. **A** Data from the field experiment, showing that brood production at the sunny site was more sensitive to queen crowding. **B** Data from the laboratory experiment, showing little effect of queen crowding on young brood. This increased by day 7 and stabilized after day 14. Young brood declined and older brood increased from days 7 to 14

ments produced about 12 older progeny. Overall, variation in ($-Q-D$) and site explained 18% of the variation in (1n N–1n Q).

As brood developed, they increased in sensitivity to queen crowding. In both the laboratory and embryonation experiments, the slope for early brood was zero or quite low (0.02–0.08; Fig. 9B), indicating that the number of eggs in groups of queens was almost a simple multiple of the egg production of solo queens. This was true even at 14 and 24 days when older brood predominated (Table 3; Fig. 8). In another experiment (see "Factors affecting queen fertility" below), however, egg production declined

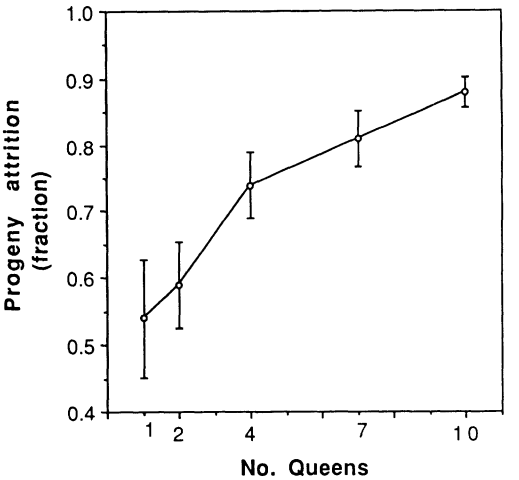

Fig. 10. Attrition of progeny in relation to queen number between day 7 and 14 in the laboratory experiment. Data based on counts of all individuals present, with 55% of the eggs present on day 7 assumed to be embryonated. Attrition increased with queen number, probably through cannibalism. *Bars* indicate SE

significantly with queen number, but the effects were small.

This was not true of older brood (larvae + pupae + minims) which showed a sensitivity to queen crowding in all experiments at all colony development stages, with slopes ranging from 0.14 to 0.40 (Table 3). For older brood in Fig. 9B the slope increased significantly from 0.14 to 0.23 ($t = 4.59$; $P < 0.001$) from 7 days to 14 days when mostly larvae were present, but did not increase from 14 days to 24 days (the pupal period) indicating that most of the attrition was probably of larvae, not pupae. Once larvae pupated, crowding had no additional negative effects.

Because older brood were reduced by crowding, while eggs were not, it followed that brood must have disappeared as they developed, and that the disappearance was proportionally higher in larger queen groups. The number of progeny present at 7 days that were still alive at 14 days declined by 44% for single queen nests. This attrition increased steadily with increased queen number, reaching 88% attrition in 10-queen nests (Fig. 10) (one-way ANOVA; $F_{4,91} = 6.40$; $P < 0.001$). This increase in attrition rate, and the higher final weight of pleometrotic queens are consistent with cannibalism of the vanished larvae.

The performance of solo queens (N_1) differed among experiments and changed over time (Table 3; Figs. 8 and 9). In the laboratory experiment, solo eggs dipped to a minimum at 14 days, while solo older brood rose from 0.81/queen at 7 days to 8.94/queen at 14 and 24 days. This is consistent with the cohort nature of the first brood noted above and by Markin et al. (1972). Solo production of eggs was also much higher than older brood, in part because only about half the eggs were embryonated, but also because there was 44% larval attrition even in solo queen nests (Fig. 10).

Effect of queen number on adult minim weight. Queens collected after the mating flights of 21 May, 3 July and 10

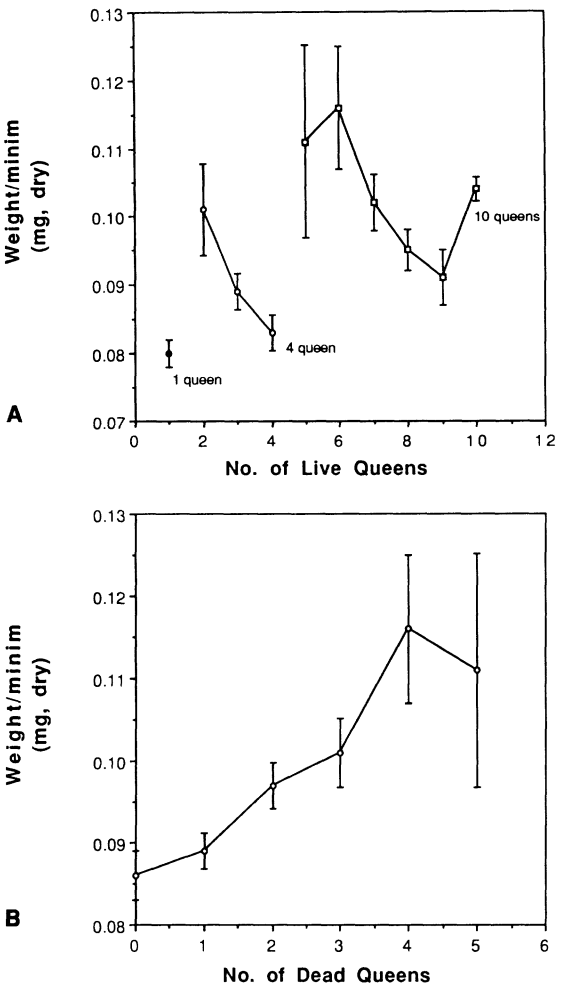

Fig. 11. **A** Weight per minim in relation to the number of queens alive at the end of the claustral period. Colonies were started with 1, 4 or 10 queens, as indicated. In the 4- and 10-queen colonies, the lower the number of live queens, the greater was minim weight. **B** Weight per minim increased in relation to the number of dead queens. Data from same colonies as Fig. 11A. *Bars* indicate SE

July 1990 were allowed to found colonies singly or in groups of four or ten. When most of the brood had eclosed, the colonies were killed for counting, drying and weighing.

As before, groups of four queens produced significantly more minims than did single queens ($\bar{X}$ = 30.6 and 18.4, respectively), but in this experiment groups of ten were highest ($\bar{X}$ = 50.3).

A one-way ANOVA showed that the mean weight per adult minim increased significantly with queen number ($F_{2,187} = 30.3$; $P < 0.001$) suggesting that with more queens more material was invested in each minim. Further analysis showed a more complex phenomenon. ANOVA of mean minim weight against the number of queens still alive at the approximate end of the larval feeding period (14 days), showed that *within* the four- and ten-queen groups, adult minim weight was higher in nests with *fewer* live queens ($F_{9,96} = 3.4$; $P < 0.005$) (Fig. 11A). Conversely, minim weight rose 23% as the number of dead queens at 14 days increased from 0 to 5 (regression; r^2 = 18%) (Fig. 11B).

Because these simple analyses did not segregate the effect of the number of minims (see above) a more complete analysis of covariance was run. Queen number was used as the treatment factor. Many of the dead queens appeared to have been partially eaten, so the number of pieces (head, thorax, gaster) eaten and the number of minims were used as covariates.

The ANCOVA showed that all three factors had significant effects on adult minim weight (queen number, $F_{2,92} = 22.7$, $P < 1 \times 10^{-5}$; number minims, $F_{1,92} = 8.09$, $P < 0.006$; number eaten, $F_{1,92} = 7.53$, $P < 0.01$). Each additional queen increased mean minim weight by 0.0012 mg, each additional minim decreased it by 8×10^{-4} mg, and each piece eaten by surviving queens increased it by 0.0005 mg. Queen number accounted for 74% of the explained variance in minim weight, number of minims for 13% and number of queen pieces eaten for 12%. A total of 37% of the variance was explained.

A one-way ANOVA of only those nests without queen mortality at 14 days confirmed the positive effect of queen number itself on weight per minim, which increased from 0.080 mg for single queens to 0.083 for four-queen groups and 0.10 for ten queens ($F_{2,43} = 5.74$; $P < 0.02$; r^2 = 22%).

Regression showed that queen number, total weight of adult minims and number dead at 14 days all had significant effects on final queen weight ($F_{3,51} = 15.7$; $P < 0.0001$; r^2 = 57%). Each additional queen increased the final queen weight by 0.14 mg and each dead queen by 0.14 mg. Each additional minim decreased the weight per minim by 0.000084 mg. About 69% of the explained variation was accounted for by queen number, 4% by dead queens, and 27% by number of minims.

How might these factors operate to affect adult minim and queen weight? As shown above for single queens, minim weight declined as the number produced increased. As queens founded in larger groups, they produced less brood per queen, resulting in heavier adult minims and less queen weight-loss. Perhaps more resources per larva or cannibalism of some larvae caused minim weight to increase with queen number even when no queens died to provide additional food. When cofoundresses did die, they provided additional nourishment, contributing to lower weight loss of surviving queens and higher weight per minim.

Does queen cannibalism contribute to brood production? Newly mated queens from the mating flight of 26 June 1991 were set up singly in 300 nest tubes. To 100 of these, a piece of killed queen was added at 3-day intervals (previous piece removed) (cannibal group). To another 100, a piece of tenebrionid beetle larva of equivalent size was added (carnivore group), while the last 100 served as controls and were only opened and re-closed at 3-day intervals. When most of the brood had eclosed to adult minims, the nests were killed by freezing for weighing and counting.

Treatment and number of adult minims had significant effects on the weight per minim (Fig. 12A) ($F_{9,147} = 61$; $P << 0.001$; r^2 = 54%). Minims produced by cannibal queens averaged 0.022 mg (24%–30%) heav-

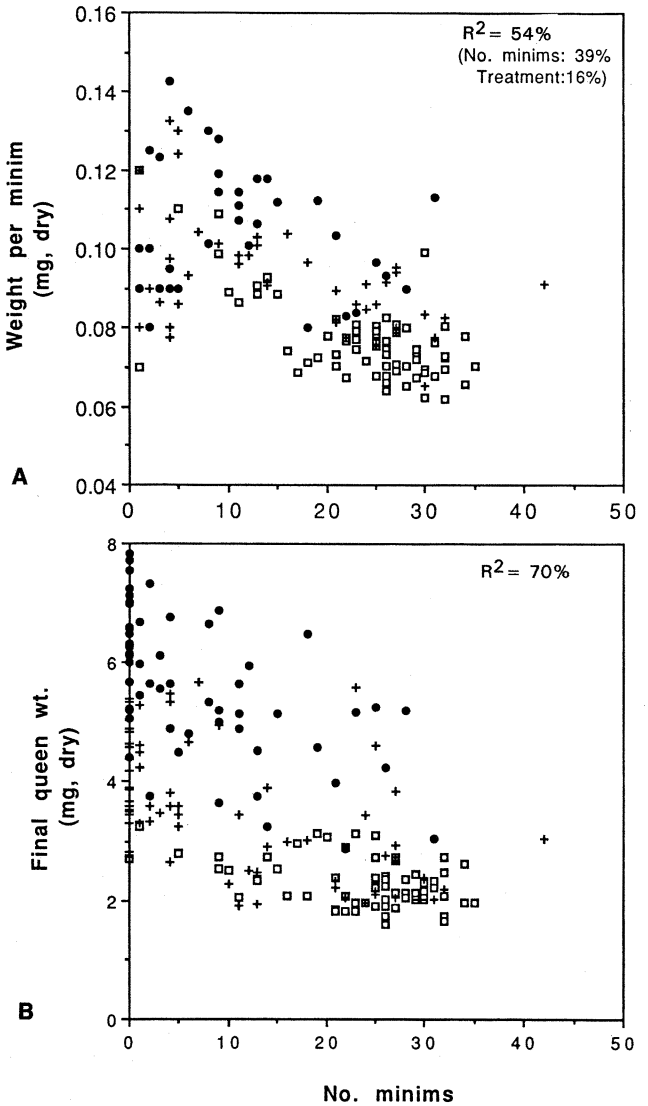

Fig. 12. A Weight per minim in relation to feeding and the number of minims produced by solo queens. Queens allowed to feed on queen pieces (cannibals, *full circles*) produced heavier minims than those fed beetle larvae (carnivores, *crosses*). Both groups of minims were heavier than unfed controls (*open squares*). (Total $r^2 = 54\%$; for number of minims, 39%; treatment, 16%.) **B** Queen weight at the end of the claustral period was much higher for cannibal than carnivore queens, and both were higher than unfed controls ($r^2 = 70\%$)

ier than those from control queens, while those from carnivore queens were 0.01 mg (11–14%) heavier. Both were significantly greater than the controls (*t*-test: $t = 7.25$, $P < 0.001$ and $t = 4.05$, $P < 0.001$, respectively).

As previously, weight per minim declined significantly with number of minims. Each additional minim caused a drop of 0.00061 mg in mean weight. Number of minims accounted for 39% of the total variance, while treatment accounted for 16% (total 54%).

In addition to producing heavier minims, queens given access to food lost less weight than controls (Fig. 12B). For equal minim production, carnivore queens weighed 0.72 mg more than did controls, while cannibal queens weighed a whopping 2.48 mg (76%) more (both significantly higher than controls $t = 4.91$, $P < 0.001$, $t = 15.1$, $P < 0.001$, respectively). Queen weight loss was 0.54 mg per mg of minims and did not differ by treatment (i.e., slopes were not significantly different). Weight of minims accounted for 26% of total variation of final queen dry weight, number eaten 11% and treatment for 35% more (70% explained).

The number of pieces offered to carnivore and cannibal queens was, of course, the same. However, queens ate parts of a significantly larger number of beetle larval pieces ($\bar{X} = 3.82$) than of queen pieces ($\bar{X} = 2.78$) ($t_{99} = 2.87$; $P < 0.01$). Nevertheless, queen pieces were significantly more effective in raising final queen weight and weight per minim, suggesting that queen pieces were either fed on more heavily than larval pieces, or were much more effective in achieving the observed results, or were partially eaten without detection.

Factors reducing queen fertility. How and at what stage does the reduction of contribution per queen in pleometrotic associations take place? It was shown above that queen number had only very minor effects on egg-laying. However, the decline of larvae/queen with increased queen number could have been the result of a decline in the proportion of nucleated eggs (i.e., higher fraction of trophic eggs). Queens were placed as above into founding plates in groups of 1, 2, 4, 7 and 10, and were allowed to lay and incubate eggs until the first eggs were almost ready to hatch (about 5 days). The eggs were stained (Voss 1985) to detect embryonation and the data analyzed by ANOVA after transformation to $\ln(y+1)$.

As noted above, the number of eggs increased almost, but not quite, as a simple multiple of queen number (Fig. 8). Of greater interest is the finding that the number of embryonated eggs per queen declined significantly with increased queen number ($F_{4,94} = 2.64$; $P < 0.05$; $r^2 = 33\%$), but so did the total number of eggs per queen ($F_{4,94} = 3.55$; $P < 0.01$; $r^2 = 34\%$). As a result, there was no significant effect of queen number on the fraction of eggs embryonated, about 55% ($F_{4,94} = 0.185$; n.s.). As group size increased, individual queens laid somewhat fewer eggs, on average, or fewer survived for 6 days, but a constant fraction of these were embryonated. Reduction in reproductive output thus began with egg-laying in this experiment but did not involve embryonation. The experiments in Figs. 8 and 9 found no such effect of queen number on egg production, suggesting that these small effects may sometimes be undetectable.

It seemed possible that the negative effect of grouping on reproductive output per queen was partly mediated by an airborne factor such as a pheromone. This was tested by two experiments – one in which the chambers were divided by fine screening so that queens shared the airspace but had no physical contact, and the second in which extracts of queens were applied to filter papers which were used to line the chambers of solo queens. While the first experiment indicated that airborne factors might account for about a quarter of the reduction in output per queen, the second experiment failed to confirm a role for an extractable, airborne factor. Most of the decline in output per queen must result from factors re-

quiring queen contact. Whereas contact pheromones might play a role in the inhibition of queen fertility in founding associations, it seems unnecessary to invoke pheromones to explain the decline in brood output per queen. The observed brood attrition suggested cannibalism. Brood cannibalism is common in ants (Hölldobler and Wilson 1990).

Discussion

In *Solenopsis invicta*, as in the majority of ants, colony founding takes place in the isolation of a sealed chamber. Founding queens may join others but the founding chamber never contains workers until the first brood ecloses. Whether alone or in groups, once the queens are sealed in the founding chamber, their total material and labor resources are fixed. Their success, individually and as a group, may depend on how they allocate their resources to worker production, maintenance and post-claustral reserves. In spite of its apparent simplicity, a number of physical and social influences affect the nature of the first brood and the post-founding queen and therefore the success of the queens and associations.

In this study, the fate of founding nests was followed until most minim workers had eclosed. Although production of minims means that the queens have been successful in founding up to that point, becoming the reproductrix of a mature colony requires that the queen survive several ensuing phases: execution of supernumerary queens by minim workers (Tschinkel and Howard 1983); brood raiding and queen usurpation in which neighboring incipient colonies attempt to steal each others brood, and queens of losing nests attempt to usurp those of successful ones (Tschinkel 1992a, b); early colony growth and territorial competition in which small colonies can be overrun by larger ones (unpublished observations). Clearly, "success" during the phase which is the subject of this paper is still far from assuring a queen's ultimate reproductive success. Factors contributing to an individual queen's ultimate success are of great interest, but were not the subject of this paper.

Groups of co-founding queens are more successful during the claustral and incipient periods than are single queens (Tschinkel and Howard 1983; Tschinkel 1992a). In nature, pleometrosis was shown to be driven by local queen density and microtopography (Tschinkel and Howard 1983). Queens were more likely to join when local density was higher, leading to a highly clumped distribution of queens in nest chambers. Before the claustral chamber is sealed, there is a great deal of joining, leaving and mutual inspection (pers. obs.), raising the possibility that queens are making active choices among potential co-foundresses on the basis of accumulated information. Some of the potential effects of those choices have been described in this paper, but whether these effects are translated into greater ultimate success is known only in the case of worker number (Tschinkel 1992a). The benefits of joining an association depend upon the number of queens already in the group, the overall density (and therefore future competition) in the area and perhaps on physical factors. Whether queen behavior and physiology integrates all this complex information is presently unknown.

Queen "condition" varied significantly among mating flights, and these differences were detectable in queen weight, fat content, and in the production of brood. Queens lost more than half their weight during founding. Energy loss was almost 70%, and queens were 11% leaner after founding than before. This level of weight and energy loss is in line with other ant species that found colonies claustrally and independently (Keller and Passera 1989).

Predicting a queen's minim production from her physical characteristics would be of interest. However, queen live weight had no predictive value for queen fertility. This brings into question the assumption of Nonacs (1992) that a queen's weight is predictive of her reproductive competitiveness. The mean dry weights of queens from the different mating flights correlated weakly with the differences in mean production, but these relationships are of no use in the prediction of individual fertility. It is clear that brood production is greatly affected by variables not measured in this study, other than weight. Within a single cohort of queens, brood production varied from none to 32 minims, and this was accompanied by a weight loss of 4–12 mg, and an energy loss of 110–280 J.

Choice of founding nest site carries a trade-off: queens produced more brood and survived better at the cooler, shady site, but they produced minims much earlier at the sunny site, even though their total production was lower there. It seems likely that early adult minim production is more important than total brood, because pre-adult brood convey no advantage during brood raiding (Tschinkel 1992a). The lower total production at higher temperatures may result from proportionally higher maintenance costs at warmer sites.

Why are some queens so much more productive than others? Considering the importance of high minim production to the success of incipient colonies (Tschinkel 1992a), it is difficult to argue that low production is adaptive. Several possibilities can be suggested. Perhaps unproductive queens could be productive under other conditions (and vice versa). This hypothesis would, of course, be more than a little difficult to test. Perhaps under some conditions, low productivity could be advantageous, by reserving more stored nutrients in the queen and allowing longer post-claustral periods without feeding. Queens often found nests in bare areas before much plant growth has occurred, and it is my impression that incipient colonies do succumb to starvation sometimes.

Another possibility is that low production by an individual is advantageous when founding in groups, again because more body reserves remain at worker eclosion, allowing the individual a longer period in which to compete for reproductive dominance. Perhaps much of the variation simply represents the spread of norms of reaction in populations of newly mated queens.

The size of minims was not fixed, but decreased in nests with more minims. Although Wood and Tschinkel (1981) showed that the size of minims could be increased

by rearing them in worker-containing nests, the present data show that influences within the founding chamber prior to worker eclosion also affect minim size. The nature of these influences is similar to factors affecting worker size in colonies throughout their lives. Porter and Tschinkel (1985b) showed that when a fixed number of workers was allowed to rear larger numbers of larvae, the resulting pupae were smaller. They suggested that as the ratio of care-givers to larvae decreased, the final size of larvae declined because each received less care, on average. In the founding nest, the more larvae a queen produces, the less care she can lavish on each, and the smaller the resulting worker. Tschinkel (1988) has applied these observations to the explanation of the ontogeny of worker polymorphism in *S. invicta*. Mean worker weight increases smoothly over 6 orders of magnitude of colony size, including the founding chamber, suggesting that a single mechanism, perhaps resembling mass action, determines worker size from the founding chamber to the largest colony.

Weights and census of queens and brood suggest that the claustral period in pleometrotic nests may not be as peaceful as suggested by Rissing and Pollock (1987) in *Veromessor pergandei*. In this species, queens coexisted peacefully until the end of the claustral period, when fighting broke out. In *S. invicta*, grouping does not have large effects on egg-laying by individual queens, but the larger the group the higher the larval attrition rate during the claustral period and the fewer the surviving brood per queen. Because queens in such groups end the claustral period with higher body weights, it seems likely that brood are cannibalized. The question of who eats whose brood is an interesting one, and opens the possibility that queens compete even within the claustral nest through differential larval cannibalism. Groups of ten queens typically produced only 10–25% as much brood per queen as did solo queens, suggesting a great deal of brood attrition before the pupal stage.

Cannibalism of queens was also shown to be an important factor contributing greatly to the post-claustral weight of surviving queens, and to minim weight. In most experiments, queen mortality rate was not related to queen number, so it seems likely that queens die of "normal" causes and are not killed by chamber-mates. Those that die, however, are often cannibalized and appear to contribute to the improved weight and perhaps post-claustral condition of the cannibals. Higher weight per minim may have positive effects on minim longevity and resistance to stress, perhaps helping the colony survive the incipient period.

There are interesting parallels between polygyny in founding colonies (pleometrosis) and in mature colonies. In mature polygyne colonies, as in one of the two pleometrotic experiments in this study, the fecundity per queen was inversely related to the number of functional queens in the colony (Vargo and Fletcher 1989). Vargo (1992) showed that the queens in polygyne colonies mutually inhibit each others' fecundity by means of a pheromone. It seems possible that a similar mechanism, perhaps even the same pheromone, operates in pleometrotic associations. However, pheromone levels and effects would have to be much lower, because fecundity inhibition was not always detectable. On the other hand, polygyny results in larger workers during founding, but smaller ones in mature colonies.

Non-embryonated, trophic eggs are laid by both inseminated and uninseminated queens in polygyne colonies. Vargo and Ross (1989) showed that polygyny reduced the embryonation rate of inseminated queens, but not uninseminated ones, whose embryonation rates were much lower to begin with. They suggested that mutual inhibition may be involved in this reduction. Oviposition rate did not affect embryonation rate. I did not test for embryonation by individual queens, but found that the overall embryonation rate was not affected by queen number. Thus, whereas both embryonation rate and egg laying rate are elements of fertility reduction in polygyne colonies, only egg-laying rate reduction operates in founding associations, and weakly at that.

Finally, does founding chamber size increase with number of queens in a pleometrotic association? If so, it would suggest that space/queen may be an important factor, because crowding could affect queen interaction, efficiency of brood care and disease. Plaster casts of founding chambers showed some increase in chamber size with queen number, but certainly less than proportional. The chamber volume per queen in all experimental nests was much larger than that in all natural, queen-dug nests. On the other hand, nests in soil with their vertical tunnel allowed more effective disposal or storage of dead queens, dead brood and waste. In field excavations, dead queens were often found immediately under the soil surface in the driest part of the nest, with the live ants in the lower extreme. What role these factors play in founding success merits future research.

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