

# A comparison of queen oviposition rates from monogyne and polygyne fire ant, *Solenopsis invicta*, colonies

ROBERT K. VANDER MEER, LAURENCE MOREL\* and CLIFFORD S. LOFGREN Medical and Veterinary Entomology Research Laboratory, USDA-ARS, Gainesville, Florida, U.S.A.

**Abstract.** The oviposition rate of individual queens of *Solenopsis invicta* Buren (Hymenoptera: Formicidae) in relation to their weight and number of queens present in the colony was investigated by direct 2h observations. There is a strong positive correlation between the weight of a queen and its oviposition rate in both monogyne and polygyne colonies. However, the number of eggs laid per mg queen is higher for monogyne queens than for polygyne queens. This difference is more evident when the total weight of queens present in a colony is considered. The individual queen oviposition rate is negatively correlated with the number of queens in the colony. In addition, the weight loss per egg laid is significantly greater for polygyne than for monogyne queens, probably due to differences in egg size. These data suggest that oviposition is more efficient in monogyne than in polygyne queens at the individual level; however, at the colony level, polygyne colonies produce significantly more eggs. Comparison of colony level efficiency predicts that polygyne colonies must have at least nine queens to compete reproductively with a mature monogyne queen. Therefore, oligogyny does not appear to be a viable strategy for *S. invicta*.

**Key words.** Fire ants, monogyny, polygyny, oviposition rate, population dynamics.

## Introduction

The fire ant, *Solenopsis invicta* Buren, was accidentally imported from South America into the United States where it rapidly expanded to occupy virtually all of the southeastern and south central states (Lofgren *et al.*, 1975), as well as Puerto Rico (Lofgren, 1986). Fire ant colonies were once thought to be exclusively monogyne (one functional queen per nest). However, polygyne populations, first discovered 18 years ago (Glancey *et al.*, 1973), are now reported in many of the affected states (Fletcher, 1983; Lofgren & Williams, 1984; Glancey *et al.*, 1987). The two types of *S. invicta* populations differ in many ways. For example, polygyne colonies may contain

several hundred queens (Glancey *et al.*, 1975) and have higher worker and higher nest densities. Worker size distribution (Greenberg *et al.*, 1985), and probably the means of colony reproduction (Glancey & Lofgren, 1988; Vargo & Porter, 1989) are also different.

The fecundity of *S. invicta* queens is high compared with other ant species. A mature (i.e.  $\geq 3$  years old) monogyne queen can produce her own weight in eggs every 24 h (Tschinkel, 1986, 1988). This, and the large number of sexuals produced, contributes to the large colony size and remarkable ecological success of this species. The monogyne and polygyne queen's fecundity is correlated positively with its weight. In polygyne colonies fecundity is also correlated negatively with the number of queens in the colony, according to Vargo & Fletcher (1989). These authors suggest that there is mutual oviposition inhibition among queens. Monogyne queens are usually more phyogastric than polygyne queens and lay more eggs per individual (Fletcher *et al.*, 1980). Direct comparisons of oviposition variables of the two fire ant forms are essential

\* Present address: Department of Pathology and Laboratory Medicine, JHMHC Box 275, University of Florida, Gainesville, FL 32610, U.S.A.

Correspondence: Dr R. K. Vander Meer, P.O. Box 14565, Gainesville, FL 32604, U.S.A.

to an understanding of their population dynamics. Oviposition behaviour is identical for monogyne and polygyne *S. invicta* queens (L. Morel, unpublished data). In this paper, we directly compare the polygyne and monogyne queen's oviposition rate with queen weight and the number of queens in a colony.

## Methods

**Source of queens.** Polygyne *Solenopsis invicta* colonies were collected in north central Florida and maintained in the laboratory for at least several months prior to use (for description of the rearing technique, see Banks *et al.*, 1981). Monogyne colonies were reared in the laboratory from newly mated queens collected near Gainesville, Florida. Each colony selected for this study was considered mature and healthy, based on worker numbers and abundant production of all brood stages. Colonies were maintained and observations carried out at 27°C with ambient relative humidity.

**Monogyne queens.** Twenty-eight observations were made, from January to July, on twelve monogyne queens, with multiple observations (up to four) 1 week to 3 months apart on the same queen. All queens were weighed (Mettler H51Ar, Princeton, New Jersey) before each oviposition observation and, in sixteen cases, after the observation.

**Polygyne queens.** Thirty-two observations were made from May to June on polygyne queens from five different colonies. All queens in each colony were weighed, but only five to ten queens per colony were used for oviposition observations. The queens were picked randomly within five broad weight ranges and thus our sample of queens covered their colony's weight range. Selected queens were isolated in a cell, which contained their colony workers and brood, but no other queens. All queens were weighed before oviposition observations and twenty-seven were weighed after the observations. After the final weighing, the queen was marked with a copper belt (0.2 mm diameter) around her petiole and replaced in the holding cell, so the same queen was not observed twice. Each polygyne queen was tested only once and all queens from the same colony were tested within 48 h.

**Observation procedure.** The queen to be tested, five workers near the queen, and five fourth instar larvae and/or prepupae were removed from the colony. The queen was weighed and placed, along with the brood and workers, in a 2 ml vial with a 100 µl insert (Sun Brokers, Wilmington, North Carolina). The insert limited the queen's movement. Brood and workers were placed with the queen to provide social interactions and minimize isolation stress. Observations were begun immediately by placing the vial under a dissection microscope equipped with fibre optic lighting. During the next 2 h, egg-laying was observed directly and the time recorded for each egg laid.

**Data analysis.** For monogyne queens the number of eggs laid in 2 h equals the number of eggs laid per 2 h per colony (E/2 h/C). However, for polygyne colonies the total number of eggs laid by each colony was estimated

using the regression line between the weight of the thirty-two polygyne queens and the number of eggs each of them laid during the 2 h observations. The number of eggs that corresponded to each colony's average queen weight (E/2 h/Q) was computed with this equation and multiplied by the number of queens present in the colony to give E/2 h/C. Best fit tests and statistical analyses were carried out with Cricket Graph (Cricket Software, Malvern, Pa.) and Statview II (Abacus Concepts Inc., Berkeley, Calif.).

## Results

### Weight of monogyne and polygyne queens

The weight of monogyne queens ranged from 11.6 to 25.5 mg (mean  $\pm$  SD = 19.5  $\pm$  3.9 mg;  $n$  = 27) prior to observation. The number of queens in polygyne colonies ranged from five to 109, with weights ranging from 6.7 to 16.4 mg (mean  $\pm$  SD = 10.8  $\pm$  1.5;  $n$  = 251). Polygyne queens used for oviposition observations weighed between 7.3 and 16.4 mg (mean  $\pm$  SD = 11.9  $\pm$  1.8;  $n$  = 30; see Table 1). For queens used in oviposition studies, polygyne queen weights were significantly less than monogyne queen weight ( $t_{35.7} = 9.19$ ;  $P < 0.001$ ). The average per queen weight in each polygyne colony showed a negative correlation with the number of queens present in that colony ( $R^2 = 0.83$ , d.f. = 3,  $P < 0.05$ ; Fig. 1). Significant differences were found between polygyne colonies when inter-colony queen weights were compared (see Table 1). The queen weights of the five queen polygyne colony varied greatly and were only significantly different from the 109 queen colony weights.

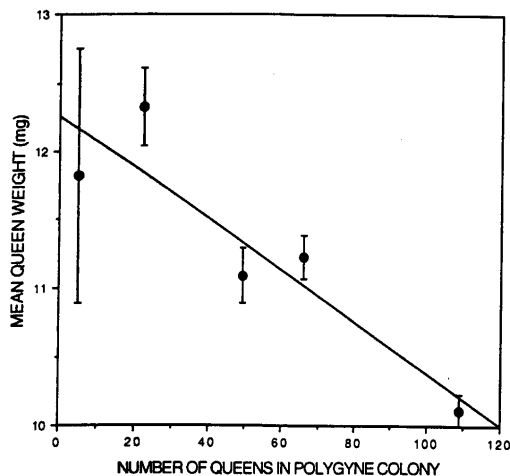
### Egg-laying rate versus queen weight

A strong positive correlation exists between monogyne or polygyne queen weight and the number of eggs laid

**Table 1.** Weight (mean  $\pm$  SD and range) and number of all queens ( $n$ ) in the indicated polygyne colony (C) and in the samples (S) tested from these colonies (I–V).

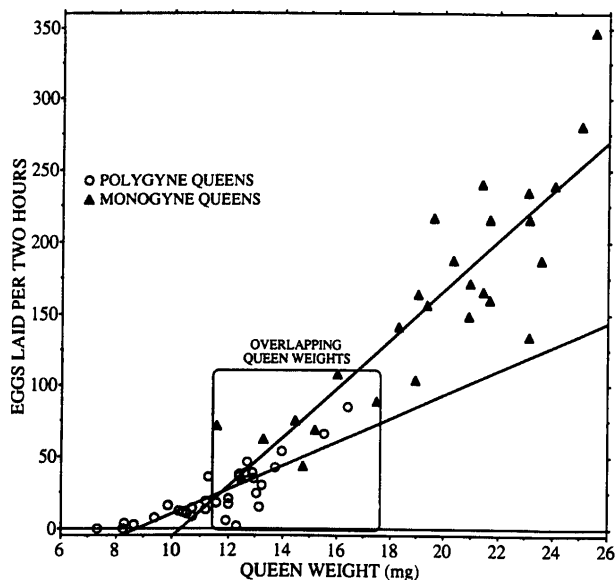
	$n$	Weight (mg)	Range
I C	5	11.82 $\pm$ 1.86	8.20–13.21
I S	5	11.82 $\pm$ 1.86	8.20–13.21
II C	22	12.32 $\pm$ 1.35	9.82–16.41
II S	5	13.19 $\pm$ 1.91	10.71–16.41
III C	49	11.09 $\pm$ 1.44	8.23–15.50
III S	5	12.72 $\pm$ 1.56	11.20–15.50
IV C	66	11.22 $\pm$ 1.32	8.43–14.30
IV S	7	11.25 $\pm$ 1.65	8.64–13.73
V C	109	10.10 $\pm$ 1.23	6.65–13.87
V S	10	10.54 $\pm$ 1.72	7.32–13.12

Comparison of inter-colony queen weights: II v. III ( $t_{69} = 3.404$ ;  $P < 0.001$ ); III v. V ( $t_{156} = 4.343$ ;  $P < 0.001$ ); I v. III (NS); I v. V ( $t_{112} = 2.893$ ;  $P < 0.002$ ).



**Fig. 1.** Relationship between the average weight of queens and their number in the five tested polygyne colonies. Equation of the regression line:  $y = -0.0189x + 12.26$  ( $R^2 = 0.84$ ,  $P < 0.05$ ). Bars represent the standard deviation.

during the 2 h observation period (Fig. 2). Best fit curve analyses showed that for the polygyne data set a linear regression gave the best fit ( $y = 8.39x - 73.80$ ;  $R^2 = 0.71$ ; d.f. = 1, 30,  $F = 72.98$ ;  $P < 0.001$ ). For the monogyne data the linear regression is defined by,  $y = 17.2x - 177.23$  ( $R^2 = 0.77$ ; d.f. = 1, 25;  $F = 85.64$ ;  $P < 0.001$ ). Although an exponential curve gave a better fit than a linear regression ( $R^2 = 0.81$  v. 0.77) for the monogyne data, the difference was not great enough to justify deviation from a simple linear regression. The number of eggs obtained



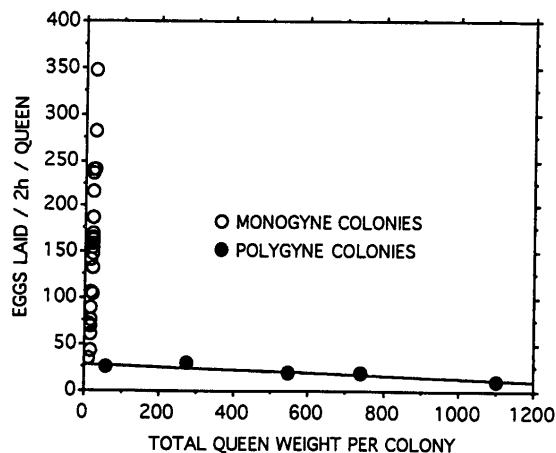
**Fig. 2.** Relationship between the number of eggs laid and queen weight for monogyne ( $n = 28$ ) and polygyne ( $n = 32$ ) queens. The data points of overlapping polygyne and monogyne queen weights are within the box.

in a 2 h period ranged from zero (two polygyne queens weighing 7.32 and 8.21 mg, and one 22.8 mg monogyne queen) to 347 (a 25.5 mg monogyne queen). The monogyne queen that laid no eggs, laid 216 and 134 eggs during two subsequent observation periods.

In the region of monogyne/polygyne queen weight overlap (Fig. 2), a linear regression provided the best fit for both data sets (polygyne:  $y = 14.37x - 153.44$ ,  $R^2 = 0.73$ , d.f. = 1, 16;  $F = 42.39$ ;  $P < 0.001$ ; monogyne:  $y = 7.495x - 38.475$ ,  $R^2 = 0.33$ ; d.f. = 1, 6;  $F = 2.93$ ;  $P = 0.14$ ). The slopes of the two regression lines were significantly different ( $t_{22} = 12.48$ ;  $P < 0.001$ ). For the overlap data, differences in egg-laying rates based on queen type were significant ( $t_{23} = 3.364$ ;  $P < 0.001$ ). However, queen weights for the overlapping groups were not significantly different ( $t_{23} = 1.54$ ;  $P > 0.05$ ). Therefore the difference in egg number is not due to queen weight, but the queen type.

#### Egg-laying rate versus colony total queen weight

The difference in egg-laying rates between the two queen types is more striking when E/2h/Q is plotted against the total weight of queens present in monogyne and polygyne colonies (Fig. 3). The data for monogyne queens are the same as in Fig. 2. The estimated average number of eggs laid per 2 h per queen in each polygyne colony (E/2 h/Q) was calculated as indicated in the Methods section. For each polygyne colony E/2 h/Q was lower than for any monogyne colony, regardless of the total queen weight in that colony. Curve fitting trials showed that the best two fits were exponential and linear; however, since the exponential plots only increased the correlation coefficient by  $< 0.04$  units, linear plots were chosen for analysis. Both monogyne and polygyne egg-laying rate versus colony total queen weight data gave significant  $F$ -tests

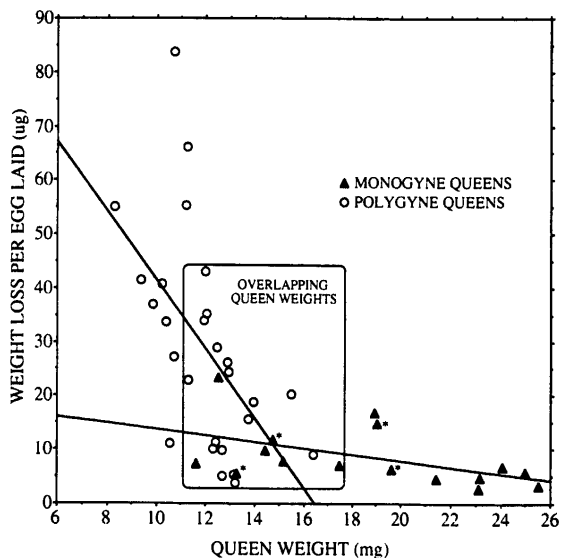


**Fig. 3.** Relationship between the number of eggs laid per queen and the total queen weight per colony (monogyne queens:  $n = 28$ ; polygyne queens:  $n = 32$ ). The data for polygyne colonies were estimated as described in the Methods section.

(monogyne:  $y = 17.2x - 177.23$ ;  $R^2 = 0.774$ ; d.f. = 1, 25;  $F = 85.64$ ;  $P < 0.001$ ; polygyne:  $y = -0.015x + 29.50$ ;  $R^2 = 0.801$ ; d.f. = 1, 3;  $F = 12.10$ ;  $P < 0.04$ ). The E/2h/Q for polygyne colonies decreases with increasing total queen weight and, as would follow, with increasing queen number ( $y = -0.16x + 29.6$ ;  $R^2 = 0.838$ ; d.f. = 1, 3;  $F = 15.49$ ;  $P < 0.03$ ). This is opposite to the dramatic increase in E/2h/Q for increased queen weight in monogyne colonies.

#### Queen weight loss versus number of eggs laid

The number of eggs laid is positively correlated to the weight the queen lost during the 2 h observation period for the entire data set (monogyne:  $R^2 = 0.24$ , d.f. = 1, 14;  $F = 4.46$ ;  $P = 0.05$ ; polygyne:  $R^2 = 0.25$ , d.f. = 1, 26;  $F = 8.77$ ;  $P < 0.01$ ). Monogyne queens, however, lose significantly less weight per egg than polygyne queens (mean  $\pm$  SD =  $8.8 \pm 5.5 \mu\text{g}$  and  $47.5 \pm 73.5 \mu\text{g}$ , respectively;  $t_{30.7} = 2.94$ ,  $P < 0.01$ ). The weight loss per egg laid by monogyne or polygyne queens is correlated negatively with queen weight (Fig. 4; monogyne:  $y = -0.59x + 19.68$ ;  $R^2 = 0.246$ ; d.f. = 1, 14;  $F = 4.56$ ;  $P = 0.05$ ; polygyne:  $y = -6.43x + 105.80$ ;  $R^2 = 0.33$ ;  $F = 12.32$ ;  $P < 0.01$ ). The regression line slopes for monogyne and polygyne queens, differed significantly ( $t_{43} = 8.36$ ,  $P < 0.001$ ) over the entire range of data, as well as for data restricted to monogyne and polygyne queens of overlapping weights ( $t_{20} = 22.3$ ,  $P < 0.001$ ). Moreover, in four of the sixteen monogyne queen observations (two in the monogyne/polygyne queen weight overlap region), defaecation accounted for part of the weight loss (see Fig. 4); therefore, the actual weight

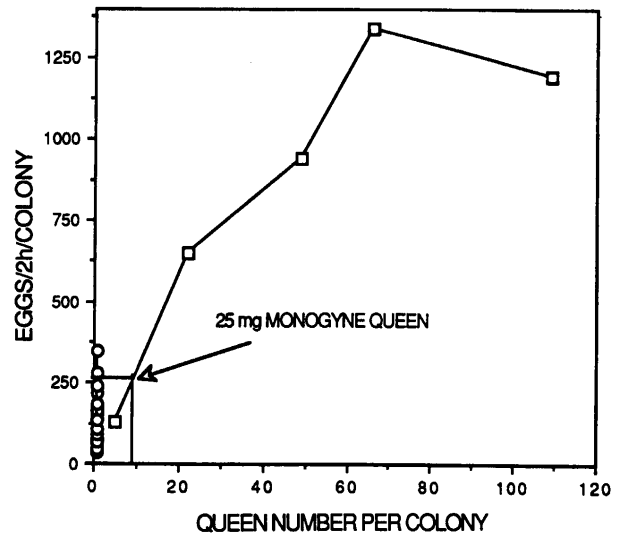


**Fig. 4.** Relationship between the average queen weight loss per egg laid and queen weight for polygyne ( $n = 31$ ) and monogyne ( $n = 16$ ) colonies. The overlapping polygyne and monogyne queen weights are within the rectangular box. A \* indicates when part of the weight loss was due to defaecation.

loss due to egg-laying is lower than the indicated values. For the queen weight overlap data (Fig. 4), there were significant differences between queen type and the weight lost per egg (mean  $\pm$  SD: monogyne:  $10.37 \pm 6.11$ ; polygyne:  $19.02 \pm 11.75$ ;  $t_{22} = 1.83$ ;  $P < 0.05$ ); however, the queen weights were not significantly different (mean  $\pm$  SD: monogyne:  $14.17 \pm 1.94$ ; polygyne:  $13.03 \pm 1.30$ ;  $t_{22} = 1.69$ ;  $P > 0.05$ ). Therefore, the difference in monogyne versus polygyne weight loss per egg is not attributable to differences in queen weight.

#### Monogyne/polygyne oviposition rate equivalency

For monogyne colonies, E/2h/C and E/2h/Q are equivalent, whereas for polygyne colonies E/2h/C is an estimate of eggs laid per 2 h for the sum of all queens in that colony. For each polygyne and monogyne colony, E/2h/C was plotted against the number of queens present in the colony (Fig. 5). The vertical line formed by the monogyne data represents the entire observed range of colony egg production for this queen type. The polygyne colony egg production plot shows a steep increase with queen numbers up to sixty-six. The value decreased slightly for 109 queens. Plotting the estimated egg production for a 25 mg monogyne queen on this graph indicates that approximately nine polygyne queens are needed to produce an equivalent number of eggs, suggesting the minimum number of queens per polygyne colony necessary to compete in worker production with a mature monogyne queen.



**Fig. 5.** Egg production for monogyne and polygyne colonies relative to the number of queens in the colony. The data for polygyne colonies (5, 22, 49, 66 and 109 queens) was estimated as described in the Methods section. The coordinate lines in the lower left-hand corner illustrates the estimated number of polygyne queens in a colony needed to lay the same number of eggs as a monogyne colony containing a 25 mg queen.

## Discussion

Monogyne and polygyne *S. invicta* populations are sympatric in the southern United States (Glancey *et al.*, 1987), but polygyne *S. invicta* have not yet been observed in their native South America (Jouvenaz *et al.*, 1989). The force behind the development of polygyne *S. invicta* populations in the United States is unknown. A variety of comparative studies are needed to understand the complex interactions that have led to polygyne *S. invicta* populations. This understanding is also important from a pest ant point of view, because polygyne *S. invicta* populations are more difficult to control than monogyne colonies (Glancey *et al.*, 1987; Drees & Vinson, 1990) and can have devastating effects on native arthropod fauna (Porter & Savignano, 1990). The present study provides the first detailed direct comparison of the oviposition rates of monogyne and polygyne *S. invicta* queens.

Despite a minimum of movement and handling, the removal of observed queens from the colony environment probably entailed stress. Consequently, our results likely constitute an underestimate rather than an overestimate of oviposition rates under natural conditions. Brood and workers were added to the observation vial to reduce the stress of isolation and provide social contact. Totally isolated queens do not release queen pheromone (Lofgren *et al.*, 1983), but pheromone release resumes in the presence of a few workers. This pheromone is produced in the poison gland and released through the sting apparatus (Vander Meer *et al.*, 1980). The relationship between the sting apparatus and oviposition behaviour (L. Morel, unpublished results) makes this a relevant observation.

Tschinkel (1988) demonstrated a positive correlation between the number of fourth instar larvae and the queen's egg-laying rate. Transfer of a material from larvae to worker to queen was implicated. It is doubtful that the five larvae added to the observation vial in our experiments would have meaningful stimulatory effects of this kind. Moreover, no workers were observed feeding the queen during the experiments. The lack of feeding by the queen leads to a steady decrease in egg-laying rate. The first and last half hour of the 2 h observation period often had lower egg deposition rates than the middle two half hours, probably due to queen disturbance and depletion of queen resources, respectively.

The five polygyne colonies examined in this study had five to 109 queens. The negative correlation between the number of queens and the mean queen weight in a colony confirms the results of Tschinkel & Howard (1978) and Vargo & Fletcher (1989). Similar negative correlations were discovered for the polygyne ants *Leptothorax curvispinosus* Mayr (Wilson, 1974) and *Plagiolepis pygmaea* (Mercier *et al.*, 1985). Fletcher *et al.* (1980) suggested three possibilities to explain this negative correlation in *S. invicta*: a lower queen-to-worker ratio meant less food per queen; or a queen pheromone system mutually inhibits queen fecundity; or both. Under field conditions, huge polygyne worker populations may create a resource crisis corresponding to the first situation. However, although

the rate of food flow from workers to queens could not be determined, ample food was always available in our laboratory studies. Worker attractiveness (queen pheromone) was correlated positively with queen weight for *Iridomyrmex humilis* (Keller, 1988) and *P. pygmaea* (Mercier *et al.*, 1985). Thus, a decrease in worker attractiveness with decreased queen weight could lead to a decrease in food flow to the queen. The involvement of the sting apparatus in *S. invicta* egg-laying behaviour (L. Morel, unpublished observations) and the release of queen pheromone containing venom during oviposition (Vander Meer *et al.*, 1980; R. K. Vander Meer and L. Morel, unpublished) suggests that queen weight, release of queen pheromone and queen fecundity are intimately linked. However, it is not yet possible to determine cause and effect. This queen weight/attractant hypothesis, postulated to explain similar phenomena in *I. humilis* (Keller, 1988) and *P. pygmaea* (Mercier *et al.*, 1985), may also be a circular argument. Additional studies specifically aimed at this question must be conducted.

A positive relationship between queen weight and fecundity has been demonstrated in the polygyne ant species *I. humilis* (Keller, 1988), *P. pygmaea* (Mercier *et al.*, 1985) and for polygyne *S. invicta* (Vargo & Fletcher, 1987). We found queen weight to be the major determinant of fecundity for both polygyne and monogyne *S. invicta* queens. The weight range of all *S. invicta* queens in this study was broad (7.32–25.5 mg); although there was overlap between the two forms, queens from polygyne colonies were responsible for the lowest weights, while monogyne queens were responsible for the highest weights. When fixed physical body measurements are compared (headwidth), polygyne queens are not smaller than their monogyne counterparts (S. D. Porter, personal communication). The large weight range reflects the potential reproductive variability of *S. invicta* queens, because 50–70% of the queen's weight may comprise ovaries (Tschinkel, 1988). Weight gain translates into an increased number of maturing follicles per ovariole and increased physogastry. The large number of ovarioles in *S. invicta* (up to 200) allows the potential for large variation in fecundity.

The egg-laying rate versus queen weight of the two *S. invicta* forms are governed by different regression lines when expressed as eggs laid per 2 h (Fig. 2). Significant differences in the egg-laying rate were also found where queen weights of the two forms overlap. Therefore, the egg-laying rate of polygyne *S. invicta* is not simply a low weight extension of monogyne queens. At least two explanations exist. There may be genetically based differences in the egg-laying physiology of the two *S. invicta* forms, or the polygyne status of a colony may influence the resident queens' oviposition rate. At the present time we can not differentiate between these two possibilities. When set up in the laboratory as monogyne colonies, queens of the typically polygyne ants *I. humilis* (Keller, 1988) and *P. pygmaea* (Mercier *et al.*, 1985) became heavier and laid more eggs than those in polygyne situations. However, these studies lacked true monogyne colonies for comparison.

Using the regression line equation between polygyne

queen weight and the number of eggs deposited, one would predict that a queen must weigh more than 8.81 mg to lay at least one egg. However, two of four test queens whose weight was less than 8.81 mg (8.30 and 8.64 mg), laid four and three eggs, respectively, in the 2 h observation periods. Therefore this regression line slightly underestimates values in the low weight range.

The number of eggs deposited per 2 h increased dramatically with increased weight of monogyne queens. However, as the total queen weight in polygyne colonies increased, the eggs deposited per hour per mg queen declined, remaining at a level below any of the monogyne queens. This demonstrates that queens from monogyne colonies are more efficient 'egg-laying machines' (eggs/queen) than are individual polygyne queens, although taken as a whole, queens in a polygyne colony out-produce a monogyne queen. Perhaps colony biomass constraints influence food flow to queens, and/or mutually inhibiting pheromones are produced, or genetic differences exist between the two forms.

The weight lost per egg deposited was negatively correlated with the queen's weight in both monogyne and polygyne colonies, which is consistent with Tschinkel's (1988) demonstration that egg size (volume) decreases significantly with increasing weight of *S. invicta* monogyne queens. Direct comparison of our queen weight loss per egg/queen weight and Tschinkel's egg volume/queen weight regressions cannot be directly compared because of the different units involved. However, the ratio of two egg size estimates based on two widely different queen weight values can be compared. Tschinkel's (1988) egg volume/queen weight regression and our queen weight loss per egg/queen weight regression were used to calculate egg volume and weight loss per egg ratios. The egg volume and monogyne weight loss per egg ratios gave very close agreement. However, the polygyne data did not (ratio of predicted egg volume or weight from 15 and 25 mg queens: Tschinkel, 0.77; our monogyne, 0.46; polygyne, -5.88). The polygyne queen weight loss per egg/queen weight relationship is clearly different. Significantly different regression slopes for this data where the weights of the two queen types overlap is further evidence that polygyne queens are indeed different, and not simply representative of the low weight end of monogyne queen data. The higher values for weight loss in polygyne queens in the monogyne/polygyne queen weight overlap zone again indicate that oviposition is less efficient than for monogyne queens.

Our estimates for the egg production of monogyne queens agree reasonably well with those of Tschinkel (1988) and Williams (1990). Each study yielded results affected by the method used for measuring oviposition rate. Estimates of daily egg production for monogyne and polygyne colonies indicate that a minimum of nine polygyne queens are necessary to have the same fecundity as a mature physogastric (25 mg) monogyne queen. This result rules out the possibility of effective oligogyny in *S. invicta*, and is in accordance with the large number of queens usually found in *S. invicta* polygyne colonies (Glancey *et al.*, 1975; personal observations). These high

numbers more than compensate for the lower oviposition efficiency of individual polygyne queens, and produces enormous numbers of eggs for the colony. However, the selective advantage of polygyny over monogyny in *S. invicta* is still unclear.

It appears unlikely that monogyne/polygyne differences observed here, as well as those reported elsewhere (nestmate recognition: Morel *et al.*, 1990; nest distribution and worker size: Greenberg *et al.*, 1985), can all be adequately accounted for by lack of food or mutually inhibiting pheromones. Further studies should focus on why oviposition is more costly in polygyne colonies. Ovarian development must be compared between the two forms, using queens of the same weight. In addition, experiments must be designed to test whether or not a polygyne queen placed in a monogyne situation switches to an oviposition rate similar to that of a monogyne queen.

### Acknowledgments

We thank Edward Vargo, Harold Reed and John Sivinski for their valuable comments on the manuscript.

### References

- Banks, W.A., Lofgren, C.S., Jouvenaz, D.P., Stringer, C.E., Bishop, P.M., Williams, D.F., Wojcik, D.P. & Glancey, B.M. (1981) Techniques for collecting, rearing, and handling imported fire ants. U.S. Department of Agriculture, Scientific and Educational Administration, AAT-S-21, 1-9.
- Drees, B.M. & Vinson, S.B. (1990) Comparison of the control of monogynous and polygynous forms of the red imported fire ant (Hymenoptera: Formicidae) with a chlorpyrifos mound drench. *Journal of Entomological Science*, **25**, 317-324.
- Fletcher, D.J.C. (1983) Three newly discovered polygynous populations of the fire ant, *Solenopsis invicta*, and their significance. *Journal of the Georgia Entomological Society*, **18**, 538-543.
- Fletcher, D.J.C., Blum, M.S., Whitt, T.V. & Temple, N. (1980) Monogyny and polygyny in the fire ant, *Solenopsis invicta*. *Annals of the Entomological Society of America*, **73**, 658-661.
- Glancey, B.M., Craig, C.H., Stringer, C.E. & Bishop, P.M. (1973) Multiple fertile queens in colonies of the imported fire ant, *Solenopsis invicta*. *Journal of the Georgia Entomological Society*, **8**, 327-328.
- Glancey, B.M. & Lofgren, C.S. (1988) Adoption of newly mated queens: A mechanism for proliferation and perpetuation of polygynous red imported fire ants, *Solenopsis invicta* Buren. *Florida Entomologist*, **71**, 581-587.
- Glancey, B.M., Nickerson, J.C.E., Wojcik, D., Trager, J., Banks, W.A. & Adams, C.T. (1987) The increasing incidence of the polygynous form of the red imported fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae), in Florida. *Florida Entomologist*, **70**, 400-402.
- Glancey, B.M., Stringer, C.E., Craig, C.H. & Bishop, P.M. (1975) An extraordinary case of polygyny in the red imported fire ant. *Annals of the Entomological Society of America*, **68**, 922.
- Greenberg, L., Fletcher, D.J.C. & Vinson, S.B. (1985) Differences in worker size and mound distribution in monogynous and polygynous colonies of the fire ant, *Solenopsis invicta* Buren. *Journal of the Kansas Entomological Society*, **58**, 9-18.

- Jouvenaz, D.P., Wojcik, D.P. & Vander Meer, R.K. (1989) First observation of polygyny in fire ants, *Solenopsis* spp., in South America. *Psyche*, **96**, 161–165.
- Keller, L. (1988) Evolutionary implications of polygyny in the Argentine ant, *Iridomyrmex humilis* (Mayr) (Hymenoptera: Formicidae): an experimental study. *Animal Behaviour*, **36**, 159–165.
- Lofgren, C.S. (1986) History of the imported fire ant problem. *Fire Ants and Leaf-Cutting Ants: Biology and Management* (ed. by C. S. Lofgren and R. K. Vander Meer), pp. 36–47. Westview Press, Boulder, Colorado.
- Lofgren, C.S., Banks, W.A. & Glancey, B.M. (1975) Biology and control of imported fire ants. *Annual Review of Entomology*, **20**, 1–30.
- Lofgren, C.S., Glancey, B.M., Glover, A., Rocca, J. & Tumlinson, J. (1983) Behavior of workers of *Solenopsis invicta* (Hymenoptera: Formicidae) to queen recognition pheromone: laboratory studies with an olfactometer and surrogate queens. *Annals of the Entomological Society of America*, **76**, 44–50.
- Lofgren, C.S. & Williams, D.F. (1984) Polygynous colonies of the red imported fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae) in Florida. *Florida Entomologist*, **67**, 484–486.
- Mercier, B., Passera, L. & Suzzoni, J.-P. (1985) Etude de la polygynie chez la fourmi *Plagiolepis pygmaea* Latr. (Hym. Formicidae). I. La fécondité des reines en condition expérimentale monogyne. *Insectes Sociaux*, **32**, 335–348.
- Morel, L., Vander Meer, R.K. & Lofgren, C.S. (1990) Comparison of nestmate recognition between monogynous and polygynous populations of the fire ant, *Solenopsis invicta* Buren. *Annals of the Entomological Society of America*, **83**, 642–647.
- Porter, S.D. & Savignano, D.A. (1990) Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. *Ecology*, **71**, 2095–2106.
- Tschinkel, W.R. (1986) The ecological nature of the fire ant: some aspects of colony function and some unanswered questions. *Fire Ants and Leaf-Cutting Ants: Biology and Management* (ed. by C. S. Lofgren and R. K. Vander Meer), pp. 72–87. Westview Press, Boulder, Colorado.
- Tschinkel, W.R. (1988) Social control of egg-laying rate in queens of the fire ant, *Solenopsis invicta*. *Physiological Entomology*, **13**, 327–350.
- Tschinkel, W.R. & Howard, D.F. (1978) Queen replacement in orphaned colonies of the fire ant, *Solenopsis invicta*. *Behavioral Ecology and Sociobiology*, **3**, 297–310.
- Vander Meer, R.K., Glancey, B.M., Lofgren, C.S., Glover, A., Tumlinson, J.H. & Rocca, J. (1980) The poison sac of the red imported fire ant queens: source of a pheromone attractant. *Annals of the Entomological Society of America*, **73**, 609–612.
- Vargo, E.L. & Fletcher, D.J.C. (1987) Effect of the queen number on the production of sexuals in natural populations of the fire ant, *Solenopsis invicta*. *Physiological Entomology*, **12**, 109–116.
- Vargo, E.L. & Fletcher, D.J.C. (1989) On the relationship between queen number and fecundity in polygyne colonies of the fire ant, *Solenopsis invicta*. *Physiological Entomology*, **14**, 223–232.
- Vargo, E.L. & Porter, S.D. (1989) Colony reproduction by budding in the polygyne form of *Solenopsis invicta* (Hymenoptera: Formicidae). *Annals of the Entomological Society of America*, **82**, 307–313.
- Williams, D.F. (1990) Oviposition and growth of the fire ant *Solenopsis invicta*. *Applied Myrmecology: A World Perspective* (ed. by R. K. Vander Meer, K. Jaffe and A. Cedeno), pp. 150–157. Westview Press, Boulder, Colorado.
- Wilson, E.O. (1974) The population consequences of polygyny in the ant *Leptothorax curvispinosus*. *Annals of the Entomological Society of America*, **67**, 781–786.

Accepted 11 February 1992