

# Factors That Influence Individual Fecundity of Queens and Queen Production in Crazy Ant *Paratrechina fulva* (Hymenoptera: Formicidae)

by

Angela María Arcila<sup>1</sup>, Patricia Ulloa-Chacón<sup>2</sup>, & Luis Antonio Gómez<sup>3</sup>

## ABSTRACT

Some factors that influence both queens fecundity and queens production in *Paratrechina fulva* (Mayr) were studied. Queenright (monogynous, trigynous and hexagynous) and queenless colonies were employed for that purpose. A significant positive correlation between queen's weight and the number of mature oocytes was found. Although there is not a cause-effect relationship between these two variables, the positive correlation allow us to use weight as an indicator of queen's fecundity. Significant differences were found in the average number of eggs produced per queen, between monogynous, trigynous and hexagynous colonies. Specifically between monogynous and polygynous colonies, although no significant difference was found between polygynous colonies. A negative relationship was found between queen number per colony and individual oviposition rate. Production of queens in queenright nests was not observed. Immature development of queens, from larval stage, in queenless colonies ranged between 34-49 days. A high worker/pupae ratio is necessary for the production of queens in queenless colonies, but it is possible even from third instar larvae. Restriction of production of gynes by young queens may be an advantage for successful colony foundation.

Key words: Crazy ant, *Paratrechina fulva*, queen fecundity, queen number, queen production.

## INTRODUCTION

In spite of its introduction to Colombia almost 30 years ago (Zenner-Polania 1990), little is known about the biology of crazy ant (CA) *Paratrechina fulva*. This species has become an agricultural and ecological problem and this fact has stimulated a fairly good amount of research regarding both its biology and control.

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<sup>1</sup>Departamento de Biología, Facultad de Ciencias, Universidad del Valle, P.O. Box: 25360, Cali, Valle, Colombia, e-mail: angelarcila@hotmail.com

<sup>2</sup>Departamento de Biología, Facultad de Ciencias, Universidad del Valle, P.O. Box: 25360, Cali, Valle, Colombia, e-mail: pachacon@uniweb.net.co. Corresponding author

<sup>3</sup>Centro de Investigación de la Caña de Azúcar de Colombia, CENICANA, P.O. Box 9138, Cali, Valle, Colombia, e-mail: lagomez@cenicana.org

Only a few studies on the biology of CA have been published in Colombia so far. Most of them deal with its ecological impact and symbiotic relationships with other arthropods (Zenner-Polanía & Ruíz 1985, Zenner-Polanía & Martínez 1992, Zenner-Polanía 1994, Aldana *et al.* 1995) and just one with some aspects of its basic biology (Zenner-Polanía 1990).

Within ants, numerous variables have been found to influence the fecundity of individual queens: 1). External factors such as nutrition quality, temperature, humidity and photoperiod; 2). Internal factors related to the individual's age (for example weight); and 3). Social factors like the number of queens per colony.

*P. fulva* is a polygynous species with a variable number of egg-laying queens per colony (Chacón de Ulloa *et al.* 2000). Due to the importance of queens fecundity in the regulation and growth of colonies, we decided to focus on the study of some variables that influence the oviposition rate of queens of this ant species; an internal factor, the queens weight, and a social factor, the number of queens per colony.

Several studies have demonstrated the influence of age related factors, such as weight, on the fecundity of queens, reporting a positive correlation between these two variables (Petersen-Braun 1975, Mercier *et al.* 1985a, 1985b, Keller 1988, Tschinkel 1988, Ulloa-Chacón & Cherix 1989, Vargo & Fletcher 1989, Keller & Passera 1990).

On the other hand the effect of the number of queens per colony on their individual fecundity has been documented for various polygynous ant species, these studies report a negative correlation between queen numbers and egg-laying rate (Fletcher *et al.* 1980, Mercier *et al.* 1985a, 1985b, Keller & Passera 1989, Ulloa-Chacón & Cherix 1989, Vargo & Fletcher 1989, Keller 1993).

We also investigated the effect of different factors on the production of queens in queenless colonies of CA, specifically the number of workers taking care of the brood, larval instar of the brood and the age of queens from which the brood were coming. Although the replacement of queens by new inseminated queens is very unusual in ants (Passera *et al.* 1988b), it has been reported for a number of species similar in some aspects of their biology to *P. fulva*, among them *Monomorium pharaonis* (Linnaeus) (Petersen-Braun 1977), *Iridomyrmex humilis* (Mayr) (Passera *et al.*, 1988b), *Wasmannia auropunctata* (Roger) (Ulloa-Chacón & Cherix 1990) and *Tapinoma melanocephalum* (Fabricius) (Bustos & Cherix 1998), all recognized as important household or agricultural pests.

## MATERIALS AND METHODS

### Collecting ants from field colonies

Collections were made during June 1998 at Hacienda San Antonio (Buga -Valle del Cauca). Nests were found under dead leaves gathered between the roots of the trees. The leaf litter obtained was taken to the laboratory and ants were separated from it by flooding.

### Establishing laboratory colonies

Laboratory rearing of *P. fulva* was started without brood. Only adult queens and workers collected in the field were kept in plastic boxes (33x26x10cm) at 27°C and 80% R.H., their interior vertical surfaces coated with fluonâ (Polytetrafluoro-ethylene, ICI Fluoropolymers INC, Exton, P.A. 19341) to keep ants from escaping. Artificial nests made of plaster as described by Passera *et al.* (1988a) were placed inside the boxes. Colonies were fed with pure water, 50% honey-water solution, tuna fish and chopped *Diatraea saccharalis* larvae and entire adults or dead cockroaches.

Different kinds of colonies were set up at the laboratory, depending on the aim of the experiment being carried out as will be described ahead.

### Factors influencing the individual oviposition rate of queens

*Relationship between weight and oviposition rate of queens.* Oviposition test were not feasible with queens of *P. fulva*. Single queens died easily when isolated from their workers and when they were allowed to be attended by workers, these carried away the eggs making very difficult to count them. Because of this, we tested the possibility of using weight as an indicator of fecundity in these ants. A sample of 38 queens was obtained from the field at Natural Reserve Laguna de Sonso (Buga, Valle del Cauca) during May 1998, and weighed individually employing an analytic scale (+/- 0.1 mg), they were then dissected to record the number of mature oocytes.

*Number of queens per colony.* Three kinds of experimental colonies were set up. They were composed by one (Monogynous), three (Trigynous) or six (Hexagynous) queens and a fixed volume of 3ml (approximately 900 individuals) of workers per queen. There were three replicates of each treatment for a total of nine colonies. Colonies were observed during 10-11 weeks, every third day the number of laid egg masses (18 +/- 8.7 S.D. eggs) were counted. Average number of eggs oviposited per queen was estimated for each type of colony and comparisons were made.

### **Factors that influence queen production in queenless colonies**

Experimental units were composed only of workers and larvae. 18 colonies were used, half of them with 50 workers and 10 larvae (5:1), the other half with 300 workers and 30 larvae (10:1). In each case, three of them were set up with first instar larvae, three with second instar larvae and the remaining three with third instar larvae.

An additional group of nine colonies composed by first instar larvae and a worker/brood ratio of 10:1 were set up, varying only the age of the queen giving origin to the larvae (3 weeks, 2 months and 11 months old). For each queen's age three replicates were established.

*Worker/Larvae ratio.* Production of queens was compared under different worker/brood ratios. 18 queenless colonies previously described were used for that purpose. Colonies were examined every third day and number of gyne larvae, pupae and adults, if any, were recorded.

*Larval instar.* Production of queens was compared between groups of colonies with brood belonging to first, second or third larval instar. For reasons that will be explained later, only colonies with a worker/brood ratio of 10:1 (nine colonies) were used for comparisons.

*Queens age.* We wanted to test the potential of queens to produce larvae capable of developing into gynes throughout their fertile life. Only colonies with a worker/brood ratio of 10:1 and first instar larvae (higher percentage of differentiation into queens) were considered. Some of the data (three colonies) obtained from the previous test were used, corresponding to 6 months old queens. Additional information was obtained from queens 3 weeks, 2 months and 11 months old (nine colonies).

### **Statistical analysis**

All data were distributed normally according to the Kolmogorov-Smirnov's test, nonetheless, the number of mature oocytes was square root ( $\sqrt{x+1}$ ) transformed to adjust better to normality. To determine if there was a significant association between queens weight and the number of mature oocytes we calculated Pearson's correlation coefficient ( $r$ ). Means were compared employing parametric tests, homogeneity of variances was evaluated previously with Bartlett's test and for all the cases concerned there was no proof of non-homogeneity.

## **RESULTS AND DISCUSSION**

### **Factors influencing the individual oviposition rate of queens**

*Relationship between weight and ovarian development of queens.* Queen's weight ranged between 1.0 – 3.0 mg with an average value of (2.0 +/- 0.5mg), whereas the minimum number of mature oocytes was

1 and the maximum 60 with an average value of  $(13.4 \pm 12.9)$  oocytes). Pearson's correlation coefficient, revealed a significant positive association ( $r = 0.72$ ,  $P < 0.01$ ,  $N = 38$ ) between queen's weight and the number of mature oocytes. Although there is not a cause-effect relationship between these two variables, the positive correlation allow us to use weight as an indicator of queen's fecundity (Fig. 1).

Weight is a variable related to age, mode of colony founding (dependent with the help of workers or independent, queens alone); and number of queens per colony (polygynous or monogynous). In general terms weight is positively correlated with fecundity as reported by various authors (Petersen-Braun 1975; Mercier *et al.* 1985a, 1985b, Keller 1988, Tschinkel 1988, Ulloa-Chacón & Cherix 1989; Vargo & Fletcher 1989, Keller & Passera 1990), but throughout the life span of the queens their weight changes in different patterns. Monogynous species with independent colony founding show a tendency to lose weight until their first brood is reared, then both fecundity and weight increase as they age (Keller & Passera, 1990); in contrast polygynous species with dependent colony founding show different responses. *Plagiolepis pygmaea* shows no significant differences in weight or fecundity as queens age (Keller & Passera, 1990) whereas in *Iridomyrmex*

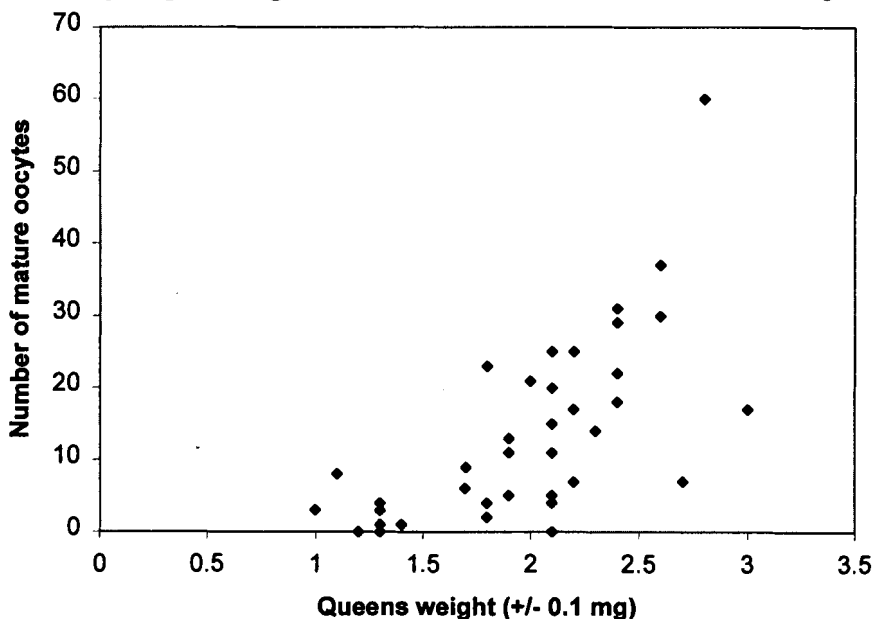


Fig. 1. Relationship between queens weight and number of mature oocytes on a field sample of *Paratrechina fulva* collected at Natural Reserve Laguna de Sonso (Bugá, Valle del Cauca) during May 1998.

*humilis* older queens weigh less than younger ones though their fecundity remains similar (Keller 1988, Keller & Passera 1990), *Wasmannia auropunctata* queens also lose weight as they age but their fecundity does not remain the same, it also decreases (Ulloa-Chacón & Cherix 1989).

During the time we did this investigation (two years), nuptial flights were never seen in the fields nor reported in any published work, although males have been observed flying. Based on results obtained about the way this ant colonizes sugar cane fields (unpublished results), it is possible that the type of colony foundation is dependent and therefore we expect the pattern of queen's fecundity and weight, in relation to age, to be similar to that reported for polygynous species with dependent colony founding. More research effort is needed on this subject.

*Number of queens per colony.* The highest production of eggs per queen was found in monogynous colonies (n=3) with an average of 21.1 (+/-) 11.5 eggs/day/queen, followed in descending order by the trigynous (n=3) 13.1 (+/-) 7 eggs/day/queen and hexagynous colonies (n=3) 8.2 (+/-) 4 eggs/day/queen.

Significant differences were found in the average number of eggs produced per queen, between monogynous, trigynous and hexagynous colonies ( $F_{2,6} = 13.70$ ,  $P < 0.01$ ), and according to Tukey's multiple

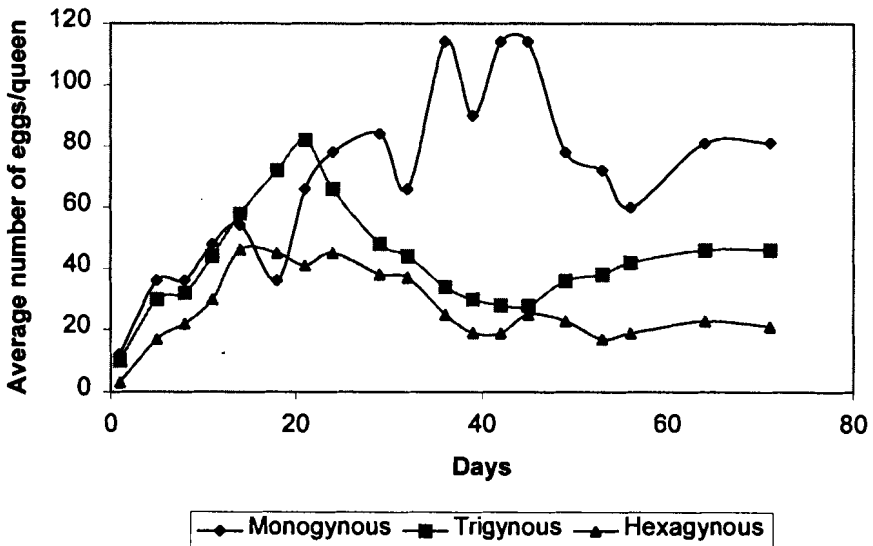


Fig. 2. Average number of eggs produced per queen daily in monogynous, trigynous and hexagynous colonies of *Paratrechina fulva* reared under laboratory conditions.

comparison test, specifically between monogynous and polygynous colonies (trigynous  $q_{6,3} = 4.53$ ,  $P < 0.05$  and hexagynous  $q_{6,3} = 7.34$ ,  $P < 0.005$ ), although no significant difference was found between polygynous colonies (Fig. 2).

These findings agree with the results reported by other authors (Yamauchi *et al.* 1982, Mercier *et al.* 1985a, Mercier *et al.* 1985b, Keller 1988, Ulloa-Chacón & Cherix 1989, Vargo & Fletcher 1989, Keller 1993).

Numerous hypothesis have been proposed to explain this negative relationship between queen number and their individual fecundity. The effect of colony size was studied by Wilson (1974 cited by Hölldobler & Wilson 1990) in *Leptothorax curvispinosus* and Mercier *et al.* (1985b) for *Plagiolepis pygmaea*, a greater relative number of workers taking care of queens in monogynous colonies, was responsible for a higher oviposition rate in contrast with polygynous colonies of the same species. In our experimental units the volume of workers per queen was the same, so we can not explain the differences found in terms of colony size. Nonetheless these differences could be related to other causes such as the ones described by Vargo and Fletcher (1989) for *Solenopsis invicta* and Keller (1988) for *Linepithema humile*, pheromonal inhibition between queens in the same colony that reduces egg production or a reduced attraction of workers to queens under polygynous conditions which causes a decrease in feeding and therefore a reduction in oviposition rate.

### **Factors that influence queen production in queenless colonies**

Production of queens in queenright nests was not observed during this study. This agrees with the information reported for similar ant species (polydomous and polygynous) such as *Monomorium pharaonis* (Petersen-Braun 1977), *Iridomyrmex humilis* (Passera *et al.* 1988b) and *Tapinoma melanocephalum* (Bustos & Cherix 1998). Not even when there was a decrease in egg production such as reported for *Monomorium pharaonis* (Edwards 1987).

The whole immature development (from larvae) of queens in queenless colonies ranged between 34-49 days, independent of the initial age of the larvae when isolated from their mother queen. Pupal stage only took between 6-13 days. Four larval instars were observed for the queens.

*Worker/Larvae ratio.* The production of queens was influenced by the workers/larvae ratio, just as reported for *Solenopsis invicta* (Vargo & Fletcher 1986). Out of two ratios tested (5:1 and 10:1), only the higher one resulted in the production of queens, even though average mortality was similar for both groups of colonies (less variable for the higher one)

Table 1. Influence of workers/larvae ratio and larval instar on the production of queens in queenless colonies of *P. fulva* reared under laboratory conditions.

Colony number	Larval instar of larvae	Number of workers	Queens production (+) Absence (-)	Time* (days)	Percentage of larvae differentiated into queens	Mortality percentage Queens	Total
<b>workers/larvae ratio (5:1)</b>							
1	I	10	50	41	0	0	20
2				41	0	0	30
3				55	0	0	20
4	II	10	50	41	0	0	0
5				27	0	0	20
6				27	0	0	0
7	III	10	50	22	0	0	40
8				22	0	0	20
9				22	0	0	0
<b>workers/larvae ratio (10:1)</b>							
10	I	30	300	42	30	22.2	20
11				49	26.7	12.5	23.3
12				35	23.3	100	33.3
13	II	30	300	29	0	0	20
14				42	6.7	0	20
15				35	10	66.7	13.3
16	III	30	300	21	0	0	10
17				42	10	66.7	6.7
18				42	3.3	0	0

\* Observations were carried out until larvae pupated and emerged as adults

: 16.7 +/- 14.1% for (5:1) ratio and 17.4 +/- 8.3% for (10:1) ratio as shown in Table 1.

It seems that queens production is a very expensive task and implies a good investment of worker effort in the care of the brood that otherwise could only become workers.

**Larval Instar.** For a constant workers/larvae ratio (10:1), differentiation of female larvae into queens may occur at any larval instar (Table 1), although significant differences were found in the mean percentage of differentiation between the three instars ( $F_{2,6} = 22.35, P < 0.01$ ), specifically between the first instar and the second and third instar



larvae (II instar  $q_{6.3} = 5.63$ ,  $P < 0.025$ ; III instar  $q_{6.3} = 5.94$ ,  $P < 0.025$ ), but no significant difference was found between the latter. The percentage of queens differentiation is higher if isolation from mother nests takes place at an early stage of larval development (Instar I. 26.7 +/- 3.3%, Instar II. 5.6 +/- 5.1%, Instar III. 4.4 +/- 5.1%).

This flexibility in differentiation of female larvae into queens constitutes an adaptive advantage for fast colonization of short-lived environments or environments under disturbance regimes such as sugar cane fields or flooded lands, where this ants are usually found regionally.

**Queens age.** Based on the ability of queens to produce female larvae able to differentiate in to gynes. *P. fulva* queens can be classified as

Table 2. Influence of mother queen's age on the production of new queens in queenless colonies of *P. fulva* reared under laboratory conditions.

Colony number	Larval instar	Number of workers	Number of queens	Queens production		Time* (days)	Percentage of larvae differentiated into queens	Mortality percentage	
				(+) Presence	(-) Absence			Queens	Total
<b>&lt;3 weeks</b>									
1	I	30	300	-	-	51	0	0	20
2	I	30	300	-	-	51	0	0	30
3	I	30	300	-	-	36	0	0	30
<b>8 weeks</b>									
4	I	30	300	-	-	30	0	0	13.3
5	I	30	300	+	+	47	6.7	50	10
6	I	30	300	+	+	30	6.7	100	33.3
<b>24 weeks</b>									
7	I	30	300	+	+	42	30	22.2	20
8	I	30	300	+	+	49	26.7	12.5	23.3
9	I	30	300	+	+	35	23.3	100	33.3
<b>&gt; 44 weeks</b>									
10	I	30	300	-	-	39	0	0	30
11	I	30	300	-	-	39	0	0	20
12	I	30	300	-	-	39	0	0	33.3

\* Observations were carried out until larvae pupated and emerged as adults.

physiologically young (< 3 weeks old), mature (8-44 weeks old) or senile (> 44 weeks old). As shown in Table 2. Only mature queens produce larvae that have the potential to develop into gynes with a percentage of differentiation between 4.5 +/- 3.9%, for 8 weeks old queens and 26.7 +/- 3.3%, for 24 weeks old queens. Comparable results have been reported for *Monomorium pharaonis* (Petersen-Braun 1977) and *Myrmica rubra* (Brian & Hibble 1964).

These findings give us a clear insight of the adaptable nature of this ant species. *P. fulva* inhabits short-lived environments, the characteristics of the biology of its queens represent an advantage that does not need to be stressed. Colonies are potentially perennial since queen production is possible even from third instar larvae, given a high number of workers per larva. Furthermore copula can take place within the original nest. The restriction of production of gynes by young queens may be an advantage for successful colony foundation, in this way investment in costly gynes is avoided in colonies unable to cope with this expense, increasing the possibilities of success.

The polydomic nature of colonies of *P. fulva* gives these species the chance of production of new queens in worker-brood aggregates free from queen's inhibition and therefore the possibility of rapid colonization. These features are shared by a number of highly successful ant species already mentioned in the introduction, all recognized for being household or agricultural pests.

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