

WORKER REPRODUCTION IN THE PONERINE ANT *ODONTOMACHUS*
SIMILLIMUS

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PUBLISHED IN *SOCIOBIOLOGY* (1998) vol. 32, pp. 427-440.

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running title: worker reproduction in the ant *Odontomachus simillimus*

ABSTRACT

The occurrence of worker reproduction in queenright and orphaned conditions was studied in the monogynous south-east Asian ponerine ant *Odontomachus simillimus*. Age (physiological factor), body size and number of ovarioles (morphological factors) and antagonistic interactions among workers and egg cannibalism (social factors) were measured as possible correlates of reproductive activity. In presence of the queen, the majority of the dissected workers had weakly or undeveloped ovaries. Worker egg laying was only rarely observed and these eggs were offered to and eaten by the queen. After a two week orphanage period though, half of the workers had acquired moderately developed ovaries. Three weeks later, there was a drop in ovarian development of the majority of workers, but a small portion of the workers ($\pm 20\%$) acquired strongly developed ovaries. Observations have shown that these were also the main egg layers, so male production in the absence of the queen was performed by only a limited portion of the workers. Ovarian development of workers was not correlated with body size or number of ovarioles, but there was a clear relationship with age, the young workers being the reproductive individuals. Vigorous antennations among the egg layers and attempts to steal each other's eggs were observed and their significance as social factors regulating reproduction is discussed. Egg cannibalism occurred mostly during the first two weeks after orphanage, but its role concerning the regulation of worker reproduction is not clear.

KEYWORDS: ants, Ponerinae, *Odontomachus*, worker reproduction.

INTRODUCTION

In the social Hymenoptera, owing to their haplodiploid life cycle, females are more related to full sisters than to their own progeny. In the majority of ant species this has led to a situation where workers no longer produce their own daughters, but help their mother raise sisters (Hamilton 1964a,b). Although workers of most species cannot mate, they have functional ovaries in many species and are able to lay unfertilised eggs, which may develop parthenogenetically into males (reviewed by Fletcher & Ross 1985, Bourke 1988, Choe 1988). Since both queens and workers are more related to their own sons, there can be important reproductive conflicts over male production within social insect colonies (Trivers & Hare 1976).

The relatedness structure within a colony is the prime determinant of the nature and outcomes of such kin conflicts (Bourke & Franks 1995). In particular, under monogyny and single mating, a queen-worker conflict over male parentage is expected. This is because workers are in that situation on average more related to worker-produced than to queen-produced males (Trivers & Hare 1976), while the queen, from her side, transmits her genes twice as efficient through own sons than through grandsons. So both queen and workers would like to produce all males themselves. How the queen could reinforce her interests upon workers has been subject of considerable debate, but physical dominance ('queen policing', Oster & Wilson 1978)

arguably is the only evolutionary stable possibility (Keller & Nonacs 1993). The long build view that queens could suppress the ovarian activity of the workers by means of pheromones (e.g. Fletcher & Ross 1985, Bourke 1988) has been disputed on theoretical grounds (Keller & Nonacs 1993). Rather, queen pheromones should be regarded as honest signals to which workers reply in their own interests (Keller & Nonacs 1993). Such a situation where workers would not gain from producing their own males occurs when (1) more than 2,3 full-sib queens coexist in the colony, (2) the queen is multiple mated (Starr 1984, Woychiechowski & Lomnicki 1987, Ratnieks 1988, Pamilo 1991) or (3) the queen is singly mated but worker reproduction is costly (Ratnieks 1988). In the former two cases a worker's relatedness with an average worker-produced male is diluted and drops below the relatedness with an average queen-produced male, while in the latter case, the fitness benefits would not outweigh the costs. Under these conditions, the evolution of a system where workers prevent each other from reproducing would be promoted ('worker policing'; Ratnieks 1988). Queen and worker policing are therefore two mutually non-exclusive hypotheses that could explain why worker reproduction is rare in monogynous ants under queenright conditions, even when it commonly occurs in queenless colonies (Bourke 1988).

We investigated the occurrence of worker reproduction in the monogynous ponerine species *Odontomachus simillimus*, both in queenright and orphaned conditions. In the subfamily Ponerinae, the queen-worker dimorphism is seldom very pronounced (Peeters 1993) with ponerine queens and workers

often having morphologically similar ovaries. This is associated with the limited fecundity of queens and consequently the small colony size often recorded in this subfamily (Peeters 1993). In these small colonies of ponerine ants, male production by workers (both in queenright and queenless condition) is often associated with the formation of dominance hierarchies among the workers (reviewed by Heinze *et al.* 1994), which can be regulated by worker's age as in *Pachycondyla sublaevis* (Higashi *et al.* 1994). Worker fecundity can also be related to body size, as in *Plectroctena* sp. (Peeters & Crewe 1988). In the present study, we investigate the importance of various factors in the regulation of male production in queenless worker groups of *Odontomachus simillimus*, namely age (physiological factor), body size and number of ovarioles (morphological factors) and antagonistic interactions among workers and egg cannibalism (social factors).

In the pantropical (Brown 1976) ponerine genus *Odontomachus* (tribe Ponerini) worker male production has been studied in queenright colonies of *O. haematodes* (= *troglydytes*) (Colombel 1972), *O. chelifera* (Medeiros *et al.* 1992) and *O. rixosus* (Ito *et al.* 1996). This study is the first to address worker reproduction in *Odontomachus* in both queenright and orphaned condition.

MATERIAL AND METHODS

Field collection and culture methods

A founding queen of *Odontomachus simillimus* F. Smith, 1858 was collected in the Karaenta National Park in south-west Sulawesi, Indonesia in March 1996. Karaenta Park consists of limestone tower karst hills covered with secondary rain forest (Whitten *et al.* 1987). In the field, *O. simillimus* colonies inhabit ground nests, which are often located near the roots of trees.

In the laboratory, a colony of approximately 100 workers was raised from the founding queen, and housed in a 70 x 30 x 8 cm plastic box with a plaster floor in which 36 compartments covered with a glass plate served as nesting chambers. The nest box itself was closed with a large glass plate. The created worker groups were housed in smaller plastic boxes (17 x 14 x 7 cm), with 4 nesting chambers excavated in plaster. Since *Odontomachus* lives in the tropics, the colony was maintained under constant climatic conditions of $25,5 \pm 2$ °C, 75 ± 15 % air humidity and a 12h:12h day:night rhythm. The ants were fed *ad libitum* with live mealworms, crickets and fruit flies once a day.

Experimental treatment

Four queenless worker groups were created by random sampling of the mother colony. Each group contained 25 workers and 6-7 larvae. We took care not to transfer queen laid eggs to the worker groups, so that any worker reproduction would show up easily. A few weeks before creation of the

worker groups, all newly hatched workers in the mother colony (37 in total) were colour-marked immediately after emergence. These marked workers were then randomly distributed over the worker groups. In this way, age was known for at least part of the workers in each worker group so that effects of age could be examined.

Observation methods

In order to recognise the workers on an individual basis, every worker was colour-marked (Dejean & Lachaud 1991). The mother colony and the worker groups were observed to examine the occurrence of egg laying and oophagy. In the worker groups, we also looked for antagonistic interactions among workers. In ponerine ants, antagonistic encounters range from highly stereotyped antennal duels to climbing over the head or thorax of an opponent or violent pulling or biting (Heinze *et al.* 1994). In *Odontomachus simillimus* we observed vigorous antennations among nestmates, but workers who were antennated did not show any particular submissive behaviour, unlike the clear difference in behaviour between dominants and subordinates during antennal boxing as described in some ponerine ants (e.g. Ito & Higashi 1991, Medeiros *et al.* 1992, Ito 1993, Peeters & Tsuji 1993, Higashi *et al.* 1994, Heinze *et al.* 1996).

Observation sessions lasted 15 to 60 minutes and were performed between 9:00 a.m. and 8:30 p.m. The queenright colony was observed for 10 hours. Observation of the four queenless groups started 2 days after orphanage. Worker groups 1 and 2 were observed from 24 February until 10 and 11

March 1997 respectively (13 and 11 hours of observation respectively), after which all workers were dissected. Workers of groups 3 and 4 were observed 2 weeks longer (from 24 February until 26 and 27 March respectively; 20 and 19,25 hours of observation respectively) and were subsequently dissected. To identify the main egg layers in worker groups 3 and 4, 24 hour video-recordings were made at the end of the observation period (JVC Timelapse video-recorder, BR-S920E). To record which workers were attending the egg pile, the video recordings were also used for taking snapshots at 20 minute intervals for total periods of 24 hours.

Worker ovary dissections

Ovarian development was used as a measure of reproductive activity. To determine their ovarian development, 40% of the queenright workers (randomly chosen) and all workers in the worker groups were killed by freezing after the observation period and dissected in insect Ringer solution under a binocular microscope. The ovaries were isolated and drawings were made using a projection mirror. The yolky oocytes present in a worker's ovaries were counted and measured. According to the value of the sum of the lengths of the oocytes, ovarian development of the workers was classified into the following categories: weakly or undeveloped (<2 mm), moderately developed (2-6 mm) and strongly developed (6-12 mm). All ants present in a worker group were dissected the same day to avoid any changes in ovarian development caused by the removal of certain workers.

Size measurements and statistics

To investigate the effect of a worker's body size on her reproductive activity, standard head width of all workers in the four worker groups was measured under a binocular microscope. To calculate any correlation between ovarian development and body size, and between ovarian development and the frequency of antennation, we used the nonparametric Spearman rank correlation coefficient.

RESULTS

Worker egg laying

During the course of our study, no males were produced in the queenright colony. Two workers laid one egg each during 10 hours of observation. In both cases, the egg was offered to the queen and immediately eaten by her. The queen was not observed to steal any eggs or to cannibalise eggs from the egg pile.

On the contrary, there was abundant production of males in all orphaned worker groups. We already observed oviposition by workers two days after orphanage (table 1), although an egg pile of ± 3 male eggs appeared only 13 ± 2 days after orphanage.

The oviposition posture of an *Odontomachus simillimus* worker is very distinct and clearly recognisable. During egg laying, a worker sits still for 5-10 minutes with her abdomen raised and her sting extruded. When the egg

comes out of the gaster, the ant bends her abdomen forward and takes the egg in her mandibles. Usually, the egg is then placed on the egg pile. This process can take up to 30 minutes, during which many ants are trying to steal the egg. When the egg is successfully deposited, the egg layer often stays near the egg pile for a while or she carries the egg pile between her mandibles. 34-35 days after orphanage, a total of 149 and 155 eggs were laid in worker groups 3 and 4 respectively.

(TABLE 1 HERE)

Ovarian development

40% of the queenright workers (n=35) and all workers of the worker groups (n=82) were dissected and their ovarian development was determined.

(FIGURE 1 HERE)

In the queenright colony, 90% of the workers had weakly or undeveloped ovaries (figure 1). The remaining 10% of the workers had a moderate ovarian development, with 2 developing oocytes at most. None of the dissected queenright workers had strongly developed ovaries.

When orphaned workers were dissected 16-17 days after isolation from the queen (worker groups 1 and 2), almost 45% of them had moderately

developed ovaries (up to 6 developing oocytes in total); in the other half, the ovaries were still weakly or undeveloped (figure 1). Only one worker (in worker group 1) had strongly developed ovaries after this time. When workers were dissected 34-35 days after orphanage (worker groups 3 and 4), the number of workers having weakly or undeveloped ovaries increased again, while there was only a small part of the workers left which had moderately developed ovaries (figure 1). Approximately 20% of the workers now had strongly developed ovaries (up to 16 developing oocytes) and they were responsible for most (80-86%) of the ovipositions. Frequency of egg laying and ovarian development were significantly correlated ($R=0,836$ and $0,64$ in worker groups 3 and 4 respectively).

Body size and number of ovarioles

Head width measured in 82 workers of the worker groups varied between 1,74 and 2,31 mm ($M= 2,05 \pm 0,09$ mm). There was no correlation between head width and ovarian development or number of ovipositions. Almost all dissected workers had 8 ovarioles per ovary. Very rarely we counted 7 or 9 ovarioles and this was not related to reproductive activity.

Age

After 16-17 days of orphanage, the youngest workers in worker groups 1 and 2 (18-43 days old) had moderately developed ovaries, while the other workers had moderately or weakly or undeveloped ovaries. 34-35 days after orphanage, all the youngest workers of worker groups 3 and 4 (43-59 days

old) had acquired strongly developed ovaries. Workers older than 60 days had weakly or undeveloped ovaries.

Attendance at the egg pile

In worker groups 3 and 4, we recorded in 74 snapshots whether the ants were attending the egg pile or were present somewhere else in the nest. There was only one egg pile per nest, which was usually located in the corner furthest away from the entrance. In worker group 3, five workers were almost constantly present near the egg pile (95-100% of snapshots). Four of these workers had strongly developed ovaries, the fifth one had a moderate ovarian development. Two workers were near the egg pile in 65,5 % of snapshots on average and their ovaries were moderately developed. The remaining ants were seldom seen near the egg pile and had weakly or undeveloped ovaries. In worker group 4, six workers were attending the egg pile in 86-97% of snapshots. Five of them had strongly developed ovaries, while one had moderately developed ovaries. Other workers having moderately developed ovaries were attending the egg pile in 36-71% of the snapshots, and workers with weakly or undeveloped ovaries were again seldom seen near the egg pile. In both worker groups, we found a significant correlation between attendance at the egg pile and ovarian development ($R=0,802$ and $0,902$ respectively).

Oophagy

Egg cannibalism was largely observed during the first two weeks of orphanage (table 1). On 13 observations of oophagy, 8 eggs were eaten by a worker which later turned out to have strongly developed ovaries, two eggs were eaten by a worker whose ovaries were weakly developed and on 3 occasions the egg layer ate her own egg. Of the 13 eggs in total that were eaten, 6 had a more irregular form (squeezed on one side) compared to the eggs laid on the egg pile. On 4 occasions, an egg was stolen from the abdomen or the mandibles of an egg layer, though it was not eaten but simply inspected by the other worker and dropped on the egg pile later on. Most of the time, an egg layer defended her egg against workers who tried to steal it, but on 1 or 2 occasions she simply gave her egg away.

Behavioural interactions between nestmates

In the queenright colony, the queen was never aggressive towards the workers. Usually she was found near the egg pile and she often remained immobile for a long time.

In the worker groups, we observed vigorous antennations between ants. During such an interaction, the antennated ant could be indifferent, or she could reply by antennation. Antennated ants never showed any particular submissive behaviour, except on two occasions where an ant adopted a pupal posture when it was antennated (attacked?) by several workers.

In worker groups 2, 3 and 4 a significant correlation was found between the ovarian development of the workers and their frequency of being antennated ($R= 0,493, 0,641$ and $0,618$ respectively). In worker groups 3 and 4 also the frequency of antennation was correlated with ovarian development ($R= 0,501$ and $0,580$ respectively). So particularly workers with strongly developed ovaries antennated each other.

DISCUSSION

Queenright condition

In the queenright colony there were only 2 observations of worker egg laying and most workers appeared to have weakly or undeveloped ovaries. Two main mechanisms have been proposed to explain absence of worker reproduction in several Hymenoptera, namely 'queen policing' (Oster & Wilson 1978) and 'worker policing' (Ratnieks 1988).

The 'queen policing' hypothesis assumes that queens physically inhibit workers from egg laying. Ito *et al.* (1996) observed that eggs laid by workers in a queenright colony of the polygynous *O. rixosus* were aggressively seized and eaten by the queens. Queen policing is not likely to be of any importance in *O. simillimus*, since the queen was never observed to be aggressive towards the workers. Although the queen ate two eggs laid by workers, these eggs were not aggressively taken by her, but brought to her by the egg layer. A possible explanation for this difference is that the number of workers per

queens is much higher in *O. simillimus* (colony size of hundreds of workers) than in *O. rixosus* (number of workers: on average 142 ± 147 SD; number of queens: on average $26,2 \pm 26,2$ SD; Ito *et al.* 1996) so that queen policing could be less efficient in the former species. This explanation is supported by the findings of Colombel (1972) in the facultatively polygynous species *O. haematodes*, where workers seem to produce males in the queen's presence when the number of workers exceeds 50 per queen or when nesting space is particularly large.

The possibility of workers suppressing each other's reproduction ('worker policing') has been proposed as an alternative explanation. Workers could police each other by selectively attacking those workers with the highest degree of ovary development, by preventing each other the very act of laying eggs, or by eating each other's eggs (Ratnieks 1988). Although it is frequently mistakenly cited that worker policing would only be selected for when workers are on average more related to queen-produced than to worker-produced males (Ratnieks 1988), it could also occur under monogyny and monandry when worker reproduction would significantly diminish colony productivity or would entail costs related to mistaken destruction of female siblings (Nonacs 1993). *Odontomachus simillimus* is monogynous, but unfortunately no data are available on its mating frequency. Nevertheless, in ants effective mating frequencies higher than two are known to occur only in the highly evolved leafcutter ants (Fjerdingstad *et al.* 1998; Reichardt & Wheeler 1996; Boomsma & Ratnieks 1996), so the effective mating frequency in

the primitiver *O. simillimus* is unlikely to be higher than two. We did not observe any aggressive encounters between workers in queenright condition, nor any egg cannibalism, so we have no immediate indications for worker policing. A possible explanation is that the inherent proximate costs of worker reproduction are so high in this species that workers do not gain from even trying to reproduce ('self policing'; Ratnieks 1988). To study the importance of worker policing, manipulation experiments will be necessary. In future, we aim to test this idea by stimulating worker reproduction through orphanage with reintroduction of these workers into the mother colony and subsequent monitoring of the aggression within the colony (cfr. e.g. *Aphaenogaster cockerelli*, Hölldobler & Carlin 1989; *Gnamptogenys menadensis*, Gobin *et al.*, in prep).

Queenless condition

In presence of the queen, most workers had weakly or undeveloped ovaries, whereas two weeks after orphanage, half of the workers had acquired a moderate ovarian development. So workers' ovaries do not seem to develop in the queen's presence and seem to become functional only after queen loss.

Five weeks after orphanage, a clear differentiation appeared, with the majority of workers having weakly or undeveloped ovaries, and just a portion of the workers ($\pm 20\%$) having acquired fully mature ovaries. These workers were also the actual egg layers. In addition, several workers which had been observed ovipositing in the worker groups earlier, exhibited resorbed ovaries when dissected. These results show that reproductive activity gets regulated

among orphaned workers by a certain mechanism. Most probably this is a way to circumvent the productivity cost that would be associated with a situation where all workers would try to reproduce and none of them retrieving any food resources.

The reproductive activity of workers can be based on morphological factors, like body size or number of ovarioles. In *Odontomachus simillimus*, we found no correlation between body size and ovarian development of workers, unlike what has been found in workers of *Plectroctena conjugata* (Peeters and Crewe 1988), and there was no variation in number of ovarioles.

Secondly, in queenless groups of ponerine workers reproduction is often regulated by social factors, namely by dominance interactions or by egg cannibalism (reviewed by Heinze 1994). We observed vigorous antennation among nestmates, but it is not clear whether this can be considered as dominant behaviour. We found a significant correlation between ovarian development and the frequency of 'being antennated'. However, this correlation can partly be explained by the fact that workers especially antennated ants during oviposition, probably to try to prevent them from laying their egg. To investigate whether workers with strongly developed ovaries are actually recognised and preferentially antennated, the frequency of all antennations except those that occur during the act of egg laying should be recorded. The significant correlation between ovarian development and the frequency of 'giving antennations' indicates that especially workers with a strong ovarian development antennate other egg layers, though this may also

be partly due to the fact that egg layers who are ovipositing or carrying their freshly laid egg also antennate nestmates to prevent them from stealing their egg. Still, it is clear that workers did try to inhibit other workers from egg laying by antennating egg laying nestmates and trying to steal their eggs, and this may tentatively suggest social regulation.

Oophagy occurred largely during the first two weeks after orphanage. However, the significance of oophagy in the regulation of worker reproduction is not clear. Firstly, the fact that some of the eggs that were eaten had an irregular form makes us think that these could be trophic eggs. Secondly, although 61% of egg cannibalism occurred by workers having strongly developed ovaries, which would suggest that these workers eat each other's eggs to monopolise male production, sometimes egg layers ate their own egg, or the egg was eaten by a worker with weakly developed ovaries. In addition, on several occasions an egg was stolen, but it was not eaten, and simply deposited on the egg pile. Still, most egg layers defended their egg against stealing and the main egg layers were almost constantly attending the egg pile.

Finally, when we looked at age, we found that the reproductive individuals of a colony were almost exclusively young workers and all young workers (between 43 and 59 days) were reproductives. A comparable association between age and reproductive activity was also found in other ponerine ants (e.g. Tsuji 1990, Ito 1993, Higashi *et al.* 1994, Heinze *et al.* 1996). Also in *Odontomachus rixosus*, the variability in ovarian development of queens

seemed to correlate better with age than with individual interactions (Ito *et al.* 1996).

ACKNOWLEDGEMENTS

We are grateful to C. Collingwood for identifying the studied species. We also thank T. Wenseleers for making helpful comments on this manuscript.

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TABLES

Table 1. Records of worker egg-laying in the 4 worker groups. Date of the oviposition, the identity of the egg-layer and the fate of each egg laid are given. Some freshly laid eggs had an irregular form. Ants are individually characterized by their abbreviated colour code (B blue, G green, Or orange, P purple, R red, W white, Y yellow).

worker group	date	egg-layer	fate of egg
1 22 Feb-10 Mar	24 Feb	OrWW	eaten by PPP (irregular formed)
	4 Mar	YYY	eaten by PPP
	5 Mar	GPB	eaten by egg layer herself
	10 Mar	GRR	? (irregular formed)
	10 Mar	RBY	carried outside (irregular formed)
2 22 Feb-11 Mar	25 Feb	BGR	dropped on the floor
	27 Feb	WWW	eaten by BOrOr (irregular formed)
	4 Mar	YOrY	eaten by egg layer
	9 Mar	GBY	eaten by egg layer
3 22 Feb-26 Mar	11 Mar	WWW	egg pile
	6 Mar	OrWB	egg pile
	9 Mar	YYY	egg pile
	9 Mar	OrWB	egg pile
	11 Mar	OrYOr	eaten by BBB and YYY
	13 Mar	OrGG	eaten by YYY
	15 Mar	OrOrOr	egg pile
	15 Mar	OrWB	egg pile
	15 Mar	WPW	egg pile
	17 Mar	WPW	egg pile
	18 Mar	WPW	egg pile
	19 Mar	WPW	egg pile
	22 Mar	OrOrB	egg pile
	22 Mar	OrWB	eaten by WPW and OrOrB (irregular formed)
25 Mar	OrOrOr	egg pile	
26 Mar	PuPPu	eaten by WPW and OrOrB	
4 22 Feb-27 Mar	25 Feb	GPuW	eaten by YPP and larva
	26 Feb	BGW	eaten by OrOrOr and larva
	6 Mar	YYY	egg pile
	9 Mar	WBW	eaten by YPP (irregular formed)
	15 Mar	POrP	egg pile
	16 Mar	YYY	egg pile
	19 Mar	YYY	egg pile
	25 Mar	POrP	egg pile
	25 Mar	WBW	egg pile
	26 Mar	YPP	egg pile
	27 Mar	YYY	egg pile
27 Mar	YPP	egg pile	

FIGURE CAPTIONS

Fig. 1. Percentage of workers belonging to each class of ovarian development in the queenright colony, 16-17 days after orphanage (worker groups 1 and 2) and 34-35 days after orphanage (worker groups 3 and 4).

FIGURES

Fig. 1

