

Production of trophic eggs by virgin workers in the ponerine ant *Gnamptogenys menadensis*

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Abstract. Most colonies (thirty-five out of thirty-seven) of the ant *Gnamptogenys menadensis* (Mayr) (Hymenoptera: Formicidae: Ponerinae) lack queens. Mated workers produce reproductive eggs, whereas virgin workers can lay only smaller trophic eggs (350 ovipositions observed). These two egg types are morphologically distinct (e.g. in the pattern of oogenesis and ultrastructure of membranes and micropyle) and relate to different ovarian characteristics (ovariole length, number of yolky oocytes and yellow bodies). When reproductives are removed, a small number of virgin workers switch to producing reproductive eggs, although only 3% of these develop into larvae. Once workers are mated, up to 50% of their eggs develop further. Trophic eggs are generally absent in social insects lacking physical castes, and we review adaptive explanations of its occurrence in *G. menadensis*.

Key words. Development, egg, nutrients, ovary, reproductive division of labour, social insect.

Introduction

Hymenopteran females can reproduce even if they are not mated, and their unfertilized eggs develop into males as a consequence of haplodiploidy. Nevertheless, in species living in societies, the majority of females are sterile and help to raise related offspring. In the ants, breeders and helpers are morphologically specialized, and workers have lost the ability to mate and produce diploid offspring in most species. Nonetheless, workers always retain ovaries (except in nine genera; Bourke & Franks, 1995), and they can produce male eggs (either in the presence of the queen or when they are orphaned; Bourke, 1988), or trophic eggs, which are non-viable and morphologically distinct from reproductive haploid eggs (Passera *et al.*, 1968; Camargo-Mathias & Caetano, 1995). Trophic eggs are a unique characteristic of social insects, and function to distribute nutrients to colony members which never forage, such as reproductives and larvae (reviewed in Wheeler, 1994).

Sexual reproduction by workers is known in 10% of species in the subfamily Ponerinae (Peeters, 1991, 1997). Workers can mate and lay fertilized eggs (they are termed 'gamergates' to distinguish them from queens), and in many species the queen caste has disappeared permanently. Even in the absence of a specialized breeding caste, there is reproductive division of labour in the colonies, with only a single (monogyny) or several (polygyny) gamergates occurring in each colony (Peeters, 1993). In queenless ponerines, as well as in wasps and bees lacking caste dimorphism, behavioural mechanisms regulate reproduction. The gamergates monopolise reproduction and subordinates usually have totally undeveloped ovaries. Nevertheless, in some monogynous species, a few virgin workers can produce male eggs infrequently in the presence of the gamergate (e.g. Nakata & Tsuji, 1996; Monnin & Peeters, 1997). These reproductive eggs are destroyed by the gamergate, and this is a distinct phenomenon from the consumption of trophic eggs.

Gamergates reproduce in most colonies of *Gnamptogenys menadensis* (Mayr) (Hymenoptera: Formicidae), and virgin workers lay trophic eggs (Gobin *et al.*, 1998). Trophic eggs are known from only two other ponerine ants with gamergates, namely *Pachycondyla krugeri* (Villet & Wildman, 1991) and *Amblyopone* sp. (F. Ito, pers. comm.). The production of reproductive and trophic eggs by nestmate workers in *G. menadensis* was studied, and its relationship to ovarian characteristics established. Experimental groups of virgin

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workers were created to investigate whether they can switch to producing male eggs when reproductives are absent. Ultrastructural differences in oogenesis associated with either egg-types were also compared.

Materials and Methods

Gnamptogenys menadensis colonies were collected in Sulawesi as described in Gobin *et al.* (1998), transported to Belgium and kept in plaster nests at $25.5 \pm 2^\circ\text{C}$, with $75 \pm 15\%$ air moisture and a LD 12:12 h photocycle. Live fruit flies or small crickets were provided *ad libitum* in the foraging arena daily, as well as occasional supplies of sugar water. Colony members were individually colour-marked with Mitsubishi paint markers. Thirty-five out of thirty-seven colonies of *G. menadensis* were queenless, containing just over 100 workers on average, a few of which were gamergates (Gobin *et al.*, 1998). Egg-laying was monitored through direct observations in eighteen gamergate colonies for a total of 230 h and in two queenright colonies for 50 h. Virgin worker groups were created by isolating a number of workers (range 15–40) from the gamergate, and were observed directly for 300 h. Additionally, oviposition rates were determined by means of 24 h time-lapse video recordings of twenty-five gamergates (over 14 days), one queen (6 days), ten virgin workers (20 days) and five dominant virgin workers (18 days). To assess offspring production in experimental worker groups, the ratio of the mean number of larvae present in one week to the mean number of eggs present two weeks earlier was calculated. In this way, the time needed for eggs to develop into larvae was corrected for.

Workers of five colonies were killed by freezing and dissected within one month after collection to assess their ovarian development and insemination status. Workers of other colonies were dissected after several months of observation. Individuals that died prior to this were frozen for later dissection. In thirty individuals the three specific regions visible in a polytrophic meroistic ovariole were measured (Fig. 1): the germarium, the previtellogenic (non-yolky), and vitellogenic (yolky) growth stages of the vitellarium (Büning, 1994). Additionally, the length of the basal yolky oocytes was measured. All measurements are presented as mean \pm standard deviation. For histological and ultrastructural research, ten gamergates, twenty-five virgin workers and five dominant virgin workers were dissected in Ringer solution. Ovaries were subsequently fixed in cold 2% glutaraldehyde, buffered at pH 7.3 with 50 mM sodium cacodylate and 150 mM saccharose, postfixed in 2% osmium tetroxide in the same buffer, dehydrated in a graded acetone series and embedded in Araldite. Serial semi-thin sections were stained with methylene blue and thionin. Thin sections, cut with a Reichert Ultracut E microtome were stained with uranyl acetate and lead citrate in an LKB 2168 Ultrastainer, and examined in a Zeiss EM 900 electron microscope. Trophic and reproductive eggs were prepared in a similar way. Samples for scanning electron microscopy were dehydrated and dried using a Balzers CPD 030 critical point dryer, coated with a 40 nm gold layer and examined with a Philips SEM 515.

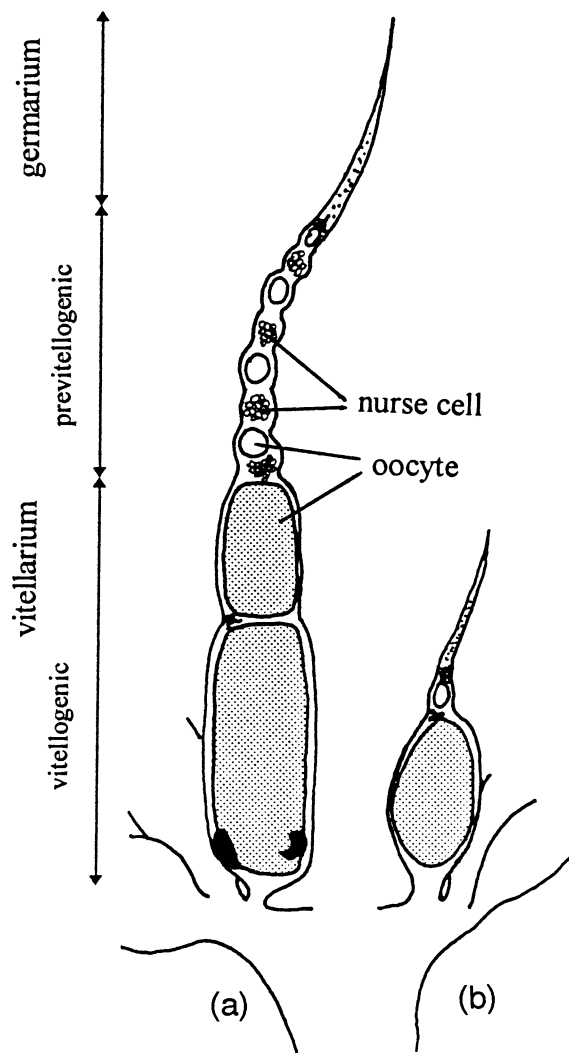


Fig. 1. Schematic drawing of a typical ovariole in (a) gamergates and (b) virgin workers of *G. menadensis*, with indication of the main growth regions. Yellow bodies are shown in black; yolky oocytes are speckled. Clusters of nurse cells are situated between successive oocytes in both types.

Results

Egg-types and ovary development

Three hundred and fifty ovipositions in twenty colonies were observed directly. A small number of workers laid only elongate reproductive eggs (ninety-five observations) that normally developed into larvae. All other ovipositions involved small, round trophic eggs (255 observations) that were fed to the larvae. A similar distinction could be made in two queenright colonies, with the queen laying only reproductive eggs. Reproductive eggs are more robust, unlike trophic eggs which are flaccid and rupture easily when handled with forceps.

When laying eggs, *G. menadensis* workers bend their

Table 1. Differences in egg-type, egg-laying rate and appearance of ovaries and spermathecae of gamergates, virgin workers, and dominant workers in virgin worker groups. Only dominants which have laid reproductive eggs for at least 4 weeks were considered. Differences in ovary measurements were analysed using ANOVA, with *post hoc* comparison using a Tukey HSD test. Significant differences were assigned a different letter code, and non-significant differences received identical letter codes.

		Gamergate				Virgin worker				Dominant virgin worker			
Egg	Type	Elongate reproductive				Round or oval trophic				Elongate reproductive			
	Micropyle	Present				Absent				Present			
	Size (mm)	1.1 × 0.4				0.5 × 0.5–0.4 × 0.6				1.1 × 0.4			
	Approx. duration of extrusion (min)	10 (<i>n</i> = 15)				3 (<i>n</i> = 20)				10 (<i>n</i> = 11)			
Spermatheca	Status	Inseminated				Not inseminated				Not inseminated			
	Fat tissue	Not visible				Visible				Not visible			
Ovaries	Yellow bodies	Large dark yellow				Not visible				Small dark yellow			
		Mean	SD	<i>n</i>	Sig.	Mean	SD	<i>n</i>	Sig.	Mean	SD	<i>n</i>	Sig.
	Number of ovarioles	5.0	0.9	57	a	5.2	1.1	695	a	5.1	0.9	19	a
	Mean length (mm) per worker of ovariole	3.85	1.96	13	a	0.97	0.57	17	b	2.19	0.87	6	c
	basal yolky oocyte	0.76	0.56	13	a	0.32	0.32	17	b	0.79	0.30	6	a
	vitellarium (vitellogenic growth)	1.54	1.49	13	a	0.36	0.37	17	b	1.01	0.62	6	a,b
	vitellarium (previtellogenic growth)	1.30	0.85	13	a	0.11	0.56	17	b	0.44	0.45	6	b
	germarium	0.89	0.47	13	a	0.42	0.65	17	b	0.67	0.10	6	a
Egg-laying	Daily rate	1.42	0.95	20	a	0.29	0.14	23	b	0.77	0.35	10	c

abdomen underneath their thorax and extrude the sting in a typical oviposition posture. Both gamergates and virgin workers can remain in this position for 10–45 min before an egg becomes visible. Once the apex of an egg appears, trophic eggs are extruded significantly faster than reproductive eggs (Table 1). Gamergates lay on average five-fold more eggs per day than virgin workers (ranges 0.7–3.1 and 0.1–0.5, respectively; Table 1). The egg-laying rate of the queen of colony 51 was higher (3.6 eggs/day) than any gamergate monitored.

The dissections in this study show that only a limited number of workers are inseminated in each queenless colony (Table 2). The spermatheca reservoir in these workers is discernible as a bright white opaque bulb (mean diameter 0.13 ± 0.1 mm; *n* = 7), connected to the oviduct. Sperm is clearly visible when spermathecae are crushed between microslides and examined under high magnification. In virgin workers, the empty, translucent reservoir is surrounded by two small bundles of clear white fat cells. In contrast, these fat cells are not conspicuous in mated workers.

Within colonies, *G. menadensis* workers exhibit a great variability in ovariole number (3–9; Table 1). Queens have a slightly larger number of ovarioles (7–10). In colonies dissected shortly after field collection (Table 2), the ovaries of most workers contained yolky oocytes. Inseminated workers possessed better-developed ovaries than virgin workers, and were also the only individuals with distinct yellow bodies. In each ovariole, there was a succession of up to two yolky and four non-yolky oocytes, whereas virgin workers' ovarioles generally contained only a single yolky oocyte, sporadically

followed by a single non-yolky oocyte (Fig. 1). Mature oocytes in gamergates are cylindrical in shape, whereas those in virgin workers are round. Young virgin workers, up to two weeks of age, had undeveloped ovaries, whereas foragers had regressed ovaries, containing resorbed oocytes. In both queenright colonies, the queen was the sole inseminated individual and the only one with well-developed ovaries containing dark yellow bodies. Virgin alate and dealate queens had similar ovary development as virgin workers. Virgin egg-layers and gamergates differed significantly in all measurements of the ovarioles, although they had a similar number of ovarioles (Table 1).

Histology and ultrastructure

At a microscopical level, the early stages of oocyte development were identical in gamergates and virgin workers. Cell divisions in the germarium result in a cell cluster which will differentiate into a single oocyte and thirty-one nurse cells, completely surrounded by follicle cells. At the previtellogenic stage the oocyte will grow slightly without any visible yolk uptake. Vitellogenic growth starts when yolk is accumulated in vacuoles. When the oocyte reaches a length of about 0.5 mm, the surrounding follicle cells deposit an electron-dense vitelline membrane. However, distinct finger-like protrusions of the follicle cells still project through the vitelline layer into the oocyte, suggesting that the uptake of material by the oocyte still continues (Fig. 2a). When the oocyte reaches about 0.7 mm in length, a less electron-dense chorion begins to be deposited

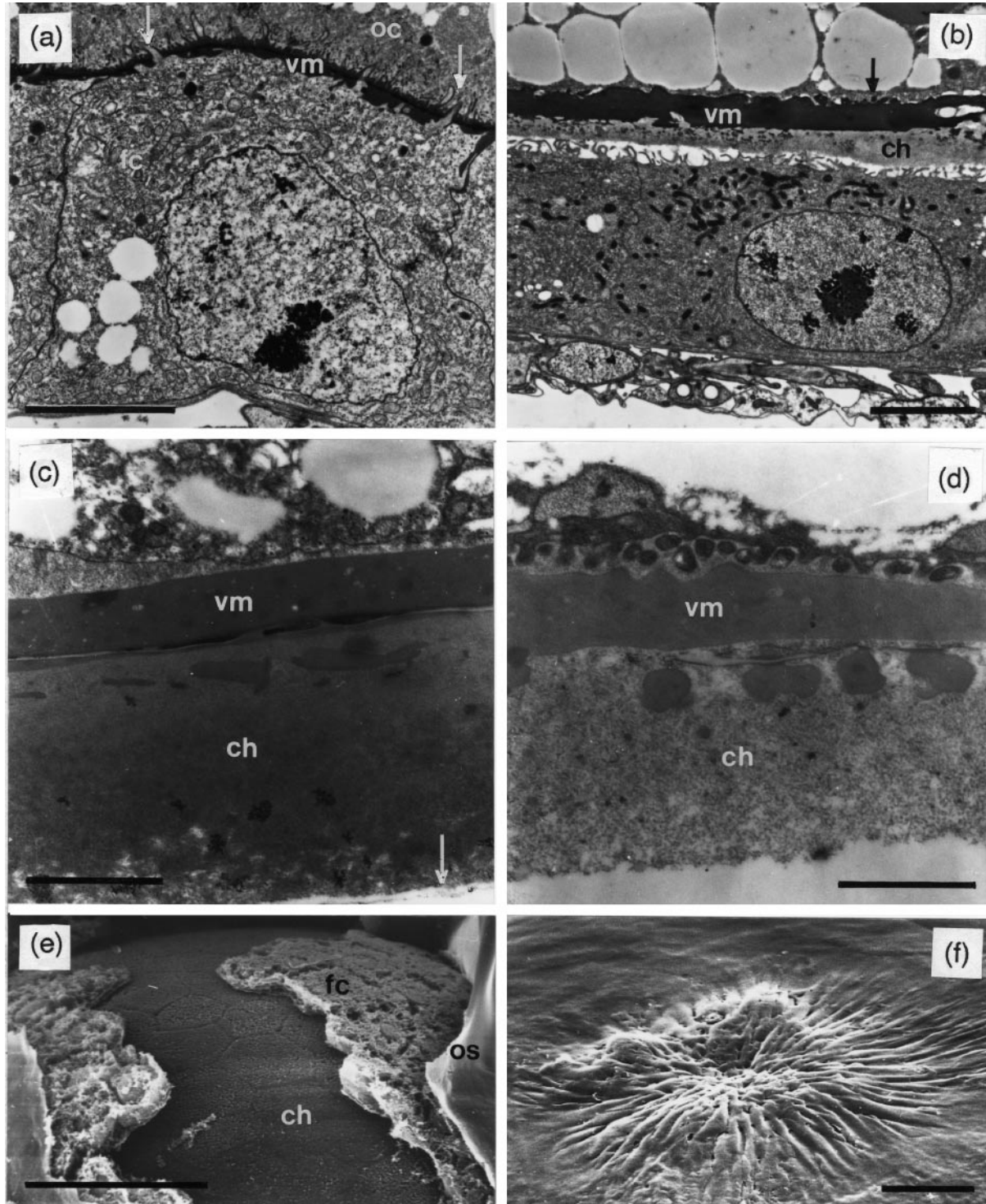


Fig. 2. (a) The beginning of vitelline membrane (vm) deposition is visible as small black droplets between follicle cells and oocytes. Distinct protrusions (arrows) from the follicle cells (fc) still penetrate the oocyte (oc) through this membrane, suggesting continuing material uptake by the oocyte. Scale bar = 5 μ m. (b) Early chorion (ch) deposition. Note the microvillar oocyte membrane (arrow). Scale bar = 5 μ m. (c) Chorion (ch) of a reproductive egg, showing the vitelline membrane (vm). Note the apical electronlucid layer (arrow). Scale bar = 1 μ m. (d) As (c) but for a trophic egg. The electronlucid layer is absent. Scale bar = 1 μ m. (e) Scanning micrograph of a mature trophic oocyte inside the ovariole sheet (os). The imprints of the follicle cells (fc) on the chorion (ch) are clearly visible. When laid, trophic eggs still show similar imprints. Scale bar = 50 μ m. (f) Scanning micrograph of the micropyle of a reproductive egg. Scale bar = 50 μ m.

Table 2. Ovarian development of individuals in five colonies of *G. menadensis*, dissected within one month of collection. Gamergates are mated individuals having ovaries with yolky oocytes and dark yellow bodies. Percentages of the total number of workers are given in brackets.

Colony code	Workers in nest	Workers dissected (%)	No. of gamergates (%)	Virgin workers with yolky oocytes (%)
A	12	10 (84)	1 (8)	4 (33)
5	19	15 (79)	3 (16)	9 (60)
12	41	36 (88)	3 (7)	22 (61)
25	80	54 (68)	6 (8)	42 (78)
44	296	80 (27)	5 (2)	50 (63)

between the vitelline membrane and follicle cells. Nevertheless, the oocyte membrane retains many microvilli, showing the oocyte can still take up material through both vitelline membrane and the unfinished chorion (Fig. 2b). At this point, development diverges between trophic and reproductive oocytes. Although trophic eggs have reached their maximal development, oocytes in gamergates will continue to grow, until they reach the size of reproductive eggs.

The vitelline membrane is of similar thickness in both reproductive and trophic eggs ($0.6 \pm 0.1 \mu\text{m}$, $n = 6$, and $0.7 \pm 0.2 \mu\text{m}$, $n = 5$, respectively; Fig. 2c,d). The chorion of reproductive eggs is thicker ($2.2 \pm 0.3 \mu\text{m}$, $n = 6$; Fig. 2c) than that of trophic eggs ($1.5 \pm 0.2 \mu\text{m}$, $n = 5$; Fig. 2d). In both egg-types, basal inclusions of similar electron-density as the vitelline membrane are found. Chorion layers of reproductive and trophic eggs have a different texture. Reproductive eggs have an additional thin electron-lucid layer on top of the chorion (Fig. 2c).

Scanning electron micrographs of reproductive eggs reveal a large micropyle region (diameter = 0.1 mm; Fig. 2f) on the egg apex. It consists of a rough dome-like structure with a central depression, perforated with many holes. Trophic eggs have no micropyle. Unlike reproductive eggs, clear imprints of the cell borders of the follicular epithelium remain visible (Fig. 2e).

Ovarioles of gamergates contain large accumulations of degenerating material at their base. In these yellow bodies, regressing cell structures can occasionally be observed. Although yellow bodies of virgin workers laying trophic eggs can rarely be distinguished during dissections, except in some older workers, at an ultrastructural level they are similar in structure but smaller than those of gamergates.

Experimental induction of male production

To investigate egg-laying of virgin workers in the absence of the gamergates, twenty experimental groups were created. In all of these, after 1–3 months a small group of workers became behaviourally dominant (Gobin *et al.* in prep.), and these started laying eggs with an increasingly elongate shape.

After 2–3 weeks, these became indistinguishable from reproductive eggs produced by gamergates, whereas eggs laid by subordinates remained trophic. In dominants which had not yet started laying reproductive eggs, ovaries were not different from those of subordinate workers. Small dark yellow bodies appeared < 2 weeks after the change, and mature basal oocytes had the typical elongate shape of reproductive eggs. At this point, the distal ovariole regions were not yet elongated and there was no increase in the number of oocytes. Virgin dominants dissected 4–8 weeks after the change in egg-type had increased lengths of both germarium and vitellarium, although their ovarioles were still less developed than those of gamergates (Table 1). At this point their egg-laying rate (range 0.3–1.3 per day) was greater than that of virgin workers, but still not as high as gamergates (Table 1).

Males were introduced into five virgin worker groups to allow mating with the dominant workers, that are sexually attractive (Gobin *et al.* in prep.). Shortly after mating, ovarian development did not differ between mated and virgin dominants within these groups. However, several weeks after male introduction, the mated dominants were the only ones that exhibited ovarian development similar to that of gamergates.

Reproductive eggs laid by dominant workers in virgin groups are cared for by workers in the same way as gamergate eggs. They are never aggressively destroyed. However, most of these eggs failed to develop and were eventually eaten. Only a couple of larvae emerged in these groups, even after > 250 days of monitoring (Fig. 3a). During all observations, only a single larva spun a male cocoon. In contrast, when dominant workers were allowed to mate, many larvae started to develop in the following weeks (Fig. 3b), eventually spinning cocoons out of which workers emerged. The ratio of larvae to cocoons present in worker groups in which dominants mated (median value = 0.47, $n = 5$) and those where dominants remained virgin (median value = 0.03, $n = 6$) differed significantly (Mann–Whitney *U*-test, $P < 0.05$).

Discussion

Gamergate colonies of *G. menadensis* are polygynous. Only inseminated workers lay elongate reproductive eggs, meaning that gamergates monopolise production of both worker and male offspring (from fertilized and unfertilized eggs, respectively). In two colonies with a queen, she was the only inseminated individual and the sole reproductive egg-layer. When either queens or gamergates are present, virgin workers produce only small trophic eggs, which are eaten by all larval instars. The imprints of the follicle cells on the chorion indicate that these eggs are laid at an immature stage of development. In *Plagiolepis pygmaea*, premature degeneration of the nurse cells and follicular epithelium result in small, non-chorionated trophic eggs (Passera *et al.*, 1968).

The occurrence of two morphologically distinct egg-types is related to the existence of two specific patterns of oogenesis. Gamergates (and queens) have long ovarioles with a succession of many oocytes in both previtellogenic and vitellogenic stages of maturation, and they have large dark yellow bodies. These

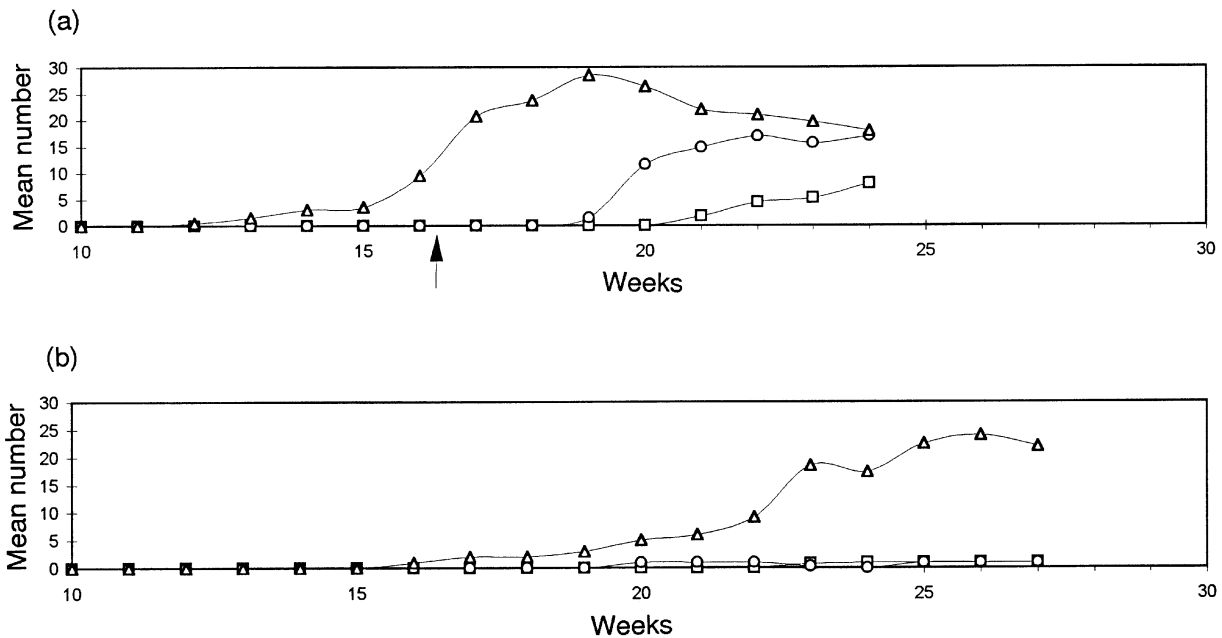


Fig. 3. Mean numbers of brood in experimental virgin worker groups of *G. menadensis*, given per week after separation of the gamergates. (a) Dominants were allowed to mate during weeks 16 and 17 (indicated by arrow), leading to the production of brood and eventually workers; (b) dominants remained virgin, and only a single larva emerged in week 20 and developed into a cocoon in week 23. The male emerged in week 27. □ = cocoons, ○ = larvae, △ = eggs.

features are an indication of active egg-laying (Peeters, 1993). Virgin workers always have short ovarioles, which can have a single yolky oocyte at their base, and have no visible yellow bodies, although the latter can be identified at a microscopical level.

When virgin worker groups are created experimentally, 7–12 weeks are needed before the switch in egg-type occurs in the newly dominant workers. Only after this time do the different regions of their ovarioles elongate, resulting in an increase in egg-laying rates. Even when dominant workers have laid few reproductive eggs, yellow bodies become visible in their ovaries. Yellow bodies are made up of remnants of nurse (Billen, 1985) and follicle cells (Büning, 1994). It can be expected that the larger yellow bodies in ovarioles producing reproductive eggs are a consequence of the greater size of the oocytes, which require more follicle cell material to enclose them. Higher egg-laying rates in gamergates will further enhance yellow body formation.

Although the elongate eggs produced by dominant virgin workers become indistinguishable from those produced by gamergates, only exceptionally do they develop into larvae. In contrast, when dominants of *G. menadensis* mate, egg viability immediately increases to 50%, and all develop into workers. More detailed data on the primary sex ratio of gamergate colonies will be required to determine if egg mortalities are limited to the male sex. A high mortality of haploid eggs is to be expected if a male-killing agent or recessive lethal alleles are present (Smith & Shaw, 1980; Hurst, 1990; Hurst *et al.*,

1997). Inefficiency in transmission or expression of this agent or a low frequency of lethal recessive alleles could then explain the occurrence of males.

Virgin workers of *G. menadensis* are unable to compete with gamergates for reproduction and thus specialize in trophic egg production. Similarly, in the polygynous *Rhytidoponera* sp.12 and the monogynous *Pachycondyla krugeri*, virgin workers have a limited degree of ovarian development but cannot produce males in the presence of the gamergate(s) (Peeters, 1987; Villet & Wildman, 1991). West Eberhard (1981) interpreted trophic eggs to be advantageous from a worker's perspective, because it is a means to keep their ovaries active for male production should current reproductives die. Evidence for this is found in queenright colonies of *Aphaenogaster cockerelli*, *Plagiolepis pygmaea* and *Oecophylla longinoda*, in which workers produce only trophic eggs that are eaten by the queen or larvae. Once the queen disappears, they start laying viable eggs that develop into males (Passera, 1980; Hölldobler & Wilson, 1983; Hölldobler & Carlin, 1989). In the Ponerinae, data from *Pachycondyla apicalis* (Dietemann & Peeters, unpublished) support this idea, but not that from *G. menadensis*.

In the ants, there is an inverse relationship between the existence of either trophallaxis or trophic eggs as means of food exchange within the society (Wilson, 1971). Trophic eggs are efficient to funnel proteins necessary for vitellogenesis towards reproductives. They also enable colony members to store and distribute nutrients and overcome seasonal food shortages (Voss *et al.*, 1988; Crespi, 1992). Trophic eggs

produced by workers are common in many ants (Hölldobler & Wilson, 1990) and various stingless bees (Meliponinae; Sakagami, 1982). In some stingless bees, trophic egg-laying is used as a deceptive strategy by workers in the conflict over male production (Sakagami, 1982). Unlike ants, stingless bee workers can lay trophic eggs and reproductive eggs sequentially in the presence of the queen (Koedam *et al.*, 1996).

Although trophallaxis is generally absent in the Ponerinae, trophic eggs are known in five queenright genera (Peeters, 1997). In the queenright *G. moelleri*, *G. dammermani* and *G. costata*, worker-laid trophic eggs are fed to the larvae (B. Gobin, unpublished data). The occurrence of trophic eggs thus appears to be a widespread trait in this genus. Gamergates are found instead of queens in many colonies of *G. menadensis*, suggesting that the latter are selected against (Gobin *et al.*, 1998), but the benefits associated with trophic eggs should remain unchanged. This idea needs to be tested, once a phylogeny of some species in this genus becomes available.

The occurrence of trophic eggs in *G. menadensis* and a few other ponerine ants with gamergates (*Pachycondyla krugeri*, Villet & Wildman (1991) and *Amblyopone* sp. (F. Ito, pers. comm.) contrasts with their absence in bees (Xylocopini, Certinini, and Euglossini) and wasps (Polistinae and Polybiini) lacking dimorphic castes. Crespi (1992) argued that if all members of a colony have similar morphology and thus equal potential to reproduce, individuals will never give up an opportunity to take part in male production. This should also be true of queenless ants, except that their lack of a reproductive caste is a secondary modification (Peeters, 1993). Various wasps and bees never developed morphologically distinct reproductives, and it is thus necessary to distinguish between the evolutionary origins and maintenance of trophic eggs.

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