



# Policing behaviour towards virgin egg layers in a polygynous ponerine ant

B. GOBIN\*, J. BILLEN\* & C. PEETERS†

\*Laboratory of Entomology, K. U. Leuven

†CNRS UMR 7625, Laboratoire d'Ecologie, Université Pierre et Marie Curie

(Received 18 November 1998; initial acceptance 18 January 1999;  
final acceptance 13 July 1999; MS. number: 6058R)

The majority of colonies of *Gnamptogenys menadensis* in Sulawesi lack queens and several workers ('gamergates') mate and reproduce instead. Virgin workers lay morphologically specialized trophic eggs which are fed to larvae. Some of these virgins switch to male eggs when gamergates are experimentally removed. Three distinct patterns of oogenesis thus result in: (1) trophic eggs; (2) reproductive eggs (unfertilized) laid by virgin workers; and (3) reproductive eggs laid by gamergates, whose ovarioles are always longer than those of virgin workers. We investigated the behavioural regulation of ovarian activity in virgin workers by temporarily excluding gamergates. In 12 groups of 35–45 virgins, a few workers became dominant and started to lay reproductive eggs. Once gamergates were reintroduced, sterile workers attacked and immobilized workers with enlarged ovaries (confirmed by dissection of 173 individuals), which often died as a result. Gamergates were never aggressive towards new egg layers. Aggression was not triggered by divergence in colony odours, as it was absent in control experiments in which six colonies were divided in half, with each part containing gamergates, and reunited after 50 days. Our results show that sterile workers discriminate against new egg layers, given that their ovaries are not as developed as those of gamergates. Olfactory detection of different levels of ovarian activity thus appears possible. Mesh experiments indicated that the putative pheromones are nonvolatile and require physical contact for transmission. Aggressive behaviour directed at reproducing workers can be interpreted as worker policing. In *G. menadensis*, worker policing results in virgins laying only trophic eggs.

© 1999 The Association for the Study of Animal Behaviour

Social insects are striking examples of cooperative behaviour among animals, yet the existence of genetic differences between colony members leads to conflicts over reproduction. In the Hymenoptera, haplodiploidy allows the production of male eggs without mating. This generates asymmetrical patterns of relatedness between adult females and their male or female offspring. A social consequence of haplodiploidy is that disharmony is less likely over the origin of females (one's own mother is always favoured) than of males (Ratnieks 1988). A female always prefers herself as the source of a colony's males over her mother, sister or half-sister. Why then do the virgin females in a colony often refrain from producing sons? In species with lowered relatedness among nest-

Correspondence and present address: B. Gobin, Zoologie I, Universität Erlangen-Nürnberg, Staudtstrasse 5, D-91058 Erlangen, Germany (email: [bgobin@biologie.uni-erlangen.de](mailto:bgobin@biologie.uni-erlangen.de)). C. Billen is at the Laboratory of Entomology, K. U. Leuven, Naansestraat 59, B-3000 Leuven, Belgium. C. Peeters is at CNRS UMR 7625, Laboratoire d'écologie, Université Pierre et Marie Curie, 7 quai Saint Bernard, F-75005 Paris, France.

mates (e.g. when reproductives mate two or more times), any given worker's relatedness to an average worker-produced male is lower than that to an average queen-produced male. Virgin workers should then try to stop each other from reproducing. Behavioural interactions among workers promoting a queens' sons over the worker's sons are known as worker policing (Ratnieks 1988). Equally, nonkin factors, for example, policing as a mechanism to increase colony efficiency (Frank 1996), could lead to such prevention of reproduction. In the honeybee, *Apis mellifera*, worker policing can be expressed as either physical discrimination (e.g. Visscher & Dukas 1995) or oophagy of unfertilized eggs (e.g. Ratnieks & Visscher 1989). While only anecdotal evidence exists for worker policing in ants (Hölldobler & Carlin 1989; Crossland 1990), the genetic and behavioural correlates of worker policing in this subfamily have recently received increased attention (Walin et al. 1998; Monnin & Peeters 1999; Kikuta & Tsuji, in press).

In ants, adult females are typically morphologically specialized as queens or workers. Only in a few species

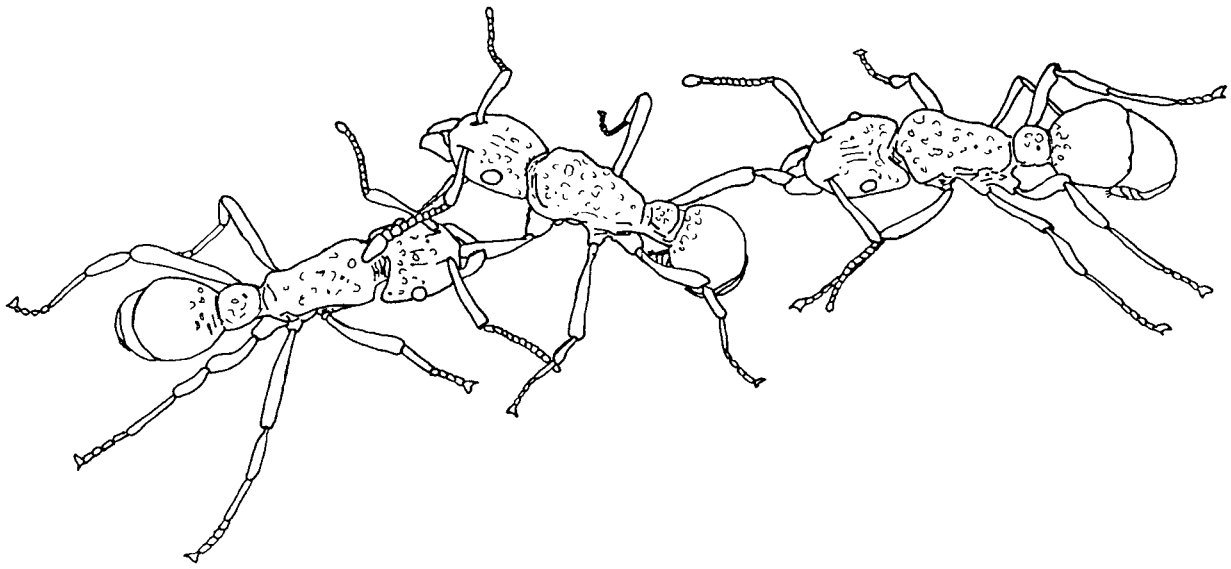


Figure 1. Drawing of two workers immobilizing a nestmate by biting its limbs.

from the subfamily Ponerinae have the latter retained a functional spermatheca, and such workers can reproduce sexually (they are then termed 'gamergates' to distinguish them from queens; Peeters 1993). In *Gnamptogenys menadensis* (tribe Ectatommini), all workers have the morphological structures needed to mate, but the majority of workers in a colony remain virgin as a consequence of behavioural regulation. A few dominant workers copulate and produce all the male and female progeny (Gobin et al. 1998b). Because of polygyny, nestmate relatedness is lowered in this species. Virgin workers do not reproduce, but many lay trophic eggs, which are eaten by larvae. Trophic eggs are morphologically distinct (round;  $0.5 \times 0.5$  mm; incomplete chorion; no micropyle) and embryos never develop (Gobin et al. 1998b). What prevents virgin workers from producing male eggs in the presence of gamergates, given that gamergates show little antagonism to virgins? If the gamergates are removed from a colony, virgin workers start interacting aggressively and some switch to producing reproductive eggs (elongate;  $1.1 \times 0.4$  mm; Gobin et al. 1998b).

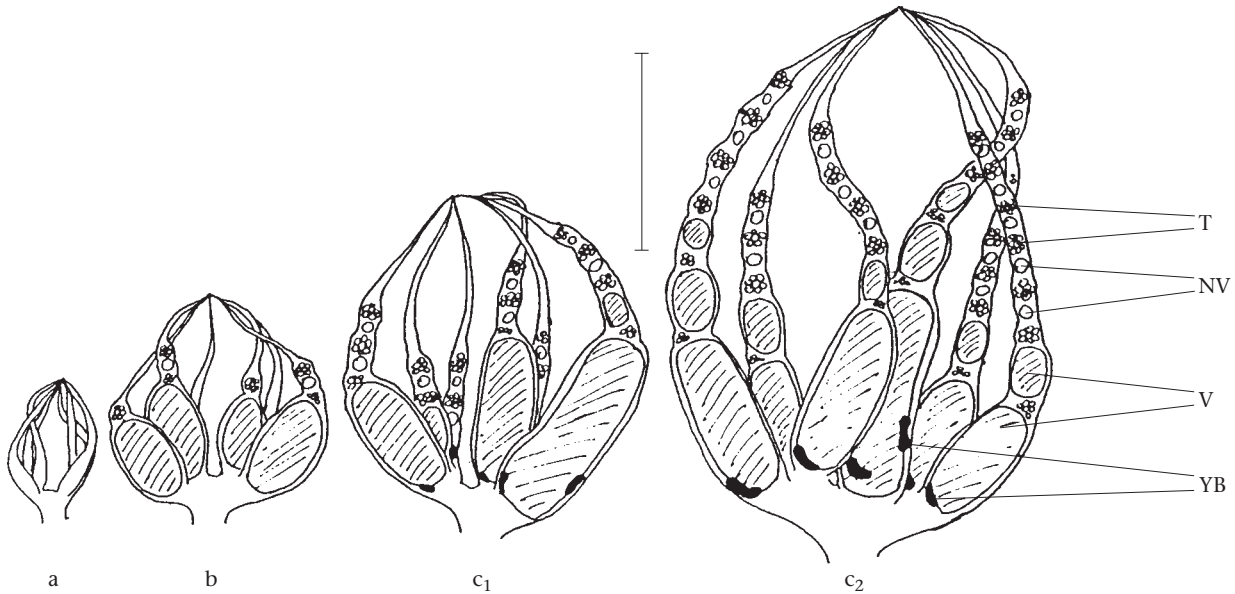
We investigated worker policing in *G. menadensis* by creating groups consisting exclusively of virgin workers. Colonies of this species are small ( $\bar{X} \pm SD = 113 \pm 75$  workers,  $N=37$ ; Gobin et al. 1998a), which allowed us to use experimental groups well within the normal size range. Behavioural observations of marked individuals and subsequent dissection of their ovaries revealed that sterile workers can distinguish between established gamergates and virgin workers that have switched to producing male eggs. In a polygynous society with related gamergates, workers could gain in inclusive fitness through such discrimination. This paper represents the first rigorous experimental evidence for the ability

of workers to recognize and police ovary-developed nestmates in a polygynous, outbred ant.

## METHODS

Colonies of *G. menadensis* were collected from Karaenta, south Sulawesi, Indonesia. In this population only a few colonies have queens (Gobin et al. 1998a). Ants were kept in plaster nests consisting of various chambers with a glass roof allowing observations, and connected to a foraging arena ( $7 \times 15$  cm) where live crickets and fruit flies were provided ad libitum. Laboratory conditions were  $25.5 \pm 2^\circ\text{C}$ ,  $75 \pm 15\%$  relative humidity and a 12:12 h light:dark cycle. All workers were identified with individual colour marks on the thorax and abdomen. We recognized gamergates by observing egg laying.

Several kinds of aggressive behaviours occur in *G. menadensis*, but 'immobilization' (Fig. 1) is most relevant to the phenomenon of policing: one to eight workers bite the limbs and antennae of a nestmate worker, who is dragged to the foraging arena and held for several hours, or even several days when a succession of policing workers are involved. If workers escape from immobilization and re-enter the nest they are quickly immobilized again. Because of the prolonged nature of immobilization (usually more than 1 day) and the involvement of several workers, it is very easy to detect in short observation scans. Immobilization is very rare in nonmanipulated colonies, except when gamergates that stop laying eggs are the target. In the field, we observed immobilization near the nest entrance three times, but we lack data on ovary development. Immobilization is also involved in the early stages of dominance interactions leading to the establishment of reproductive egg layers in orphaned



**Figure 2.** Schematic drawings of various stages of ovarian development in *Gnamptogenys menadensis*. a: empty ovarioles; b: ovarioles of virgins laying trophic eggs; c<sub>1</sub>: ovarioles of virgins laying reproductive eggs; c<sub>2</sub>: ovarioles of gamergates. T: Trophocytes; NV: nonyolky oocytes; V: yolky oocytes; YB: yellow bodies; scale bar 1 mm.

worker groups (B. Gobin, J. Billen & C. Peeters, unpublished data). However, reproductive virgins are never immobilized and immobilization of other workers is rare once virgin egg layers are present.

Police workers must be able to discriminate between gamergates and virgin egg layers. We designed four manipulations of polygynous gamergate colonies to test various aspects of adult discrimination.

(1) Response of infertile virgin workers towards familiar egg-laying virgins upon introduction of a gamergate (two colonies). We separated 35 virgin workers from each colony until reproductive eggs were laid, after which both virgin groups were observed two to five times daily (10-min scans) for 1 week. Then a gamergate from the original colonies was introduced, followed by 12 10-min scans during the next 48 h. This allowed us to observe eventual policing behaviour by gamergate or workers. In the same 48-h period, an additional 4 h of general observation clarified if other aggressive interactions occurred. We used a Mann–Whitney *U* test to compare the number of immobilizations of egg layers per 10-min scan before and after gamergate introduction.

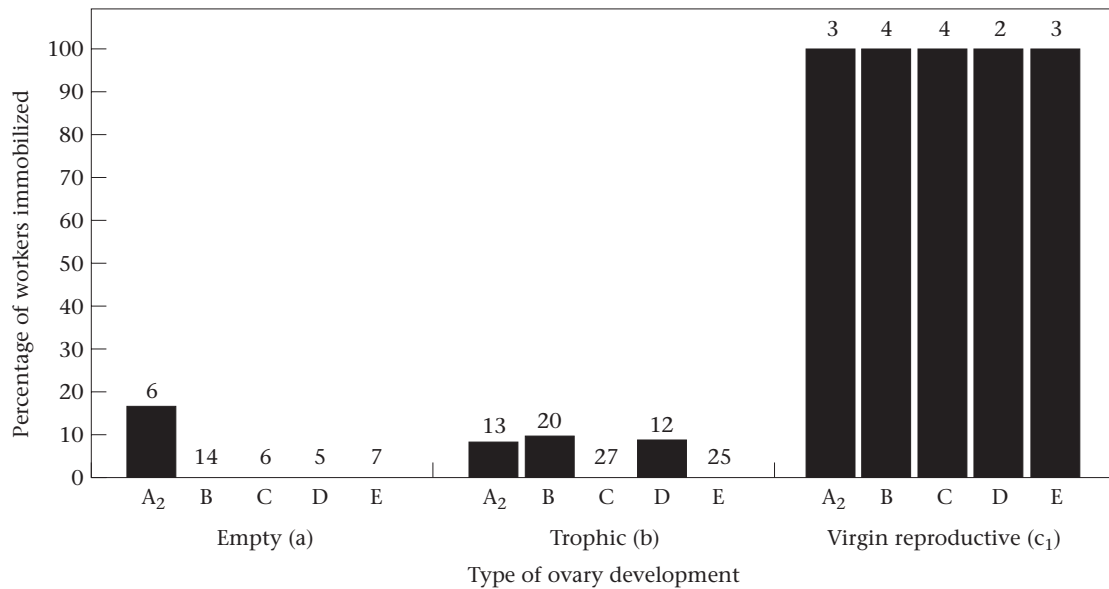
(2) To investigate whether policing behaviour is based on the recognition of cues related to egg laying, or previous familiarity with new egg layers, we separated six virgin worker groups from five colonies (groups A<sub>1</sub>, A<sub>2</sub>, D: 35 workers each; B, C, E: 45 workers) until reproductive eggs were laid (8–15 weeks). Then we observed both virgin worker groups and gamergate groups with two to five 10-min scans per day for 1 week. Subsequently, one to three gamergates and 15 workers were transferred from each mother colony to the respective virgin group, and observed immediately for 1 h. We then, recorded immobilization during eight 10-min scans in the next 36 h. The transferred workers had no previous experience with virgin egg layers and therefore had to rely on recognition

of direct cues for possible policing behaviour. Groups A<sub>2</sub>–E were used for analysis of immobilization experienced by workers with different degrees of ovary development (Friedman test with Bonferroni–Dunn post hoc comparison). We introduced foreign males into group A<sub>1</sub> to allow egg layers to mate 1 week prior to the transfer. Although groups A<sub>1</sub> and A<sub>2</sub> originated from the same colony, we transferred different gamergates and workers in each group.

(3) Aggressive behaviour between workers from isolated groups could be due to a divergence in colony odour after weeks of separation. To control for this, another six colonies were divided in half, with gamergates in each group, and then merged again after 50 days.

(4) To investigate whether police workers recognize egg layers by physical contact or volatile pheromones, we isolated 30 virgin workers with a single mesh sheet (0.1 × 0.1 mm; no antennal contact possible) from their mother colonies (N=4) for up to 3 months. We used a Mann–Whitney *U* test to compare the number of aggressive interactions 1 week before and after separation (6 h of observation each).

After observations, all workers were killed by freezing and their ovaries were dissected. Three categories of ovarian development are clearly recognizable in this species (Gobin et al. 1998b; Fig. 2): (1) ovarioles empty; (2) ovarioles ( $\bar{X} \pm \text{SD} = 0.97 \pm 0.57$  mm in length; N=17) producing trophic eggs, with only one yolky oocyte per ovariole; and (3) elongate ovarioles producing reproductive eggs, with a succession of developing oocytes in each ovariole. Within the last category, gamergates always had longer ovaries ( $\bar{X} \pm \text{SD} = 3.85 \pm 1.96$  mm, N=13, i.e. up to two yolky and four nonyolky oocytes) than virgin egg layers ( $2.19 \pm 0.87$  mm, N=6). Yellow bodies (remains of nurse cells deposited at the base of the ovarioles whenever an egg is laid) were not visible in trophic egg layers.



**Figure 3.** Percentage of virgin workers that were immobilized for each type of ovary development (see Fig. 2) in five experimental groups (A<sub>2</sub>–E). Numbers above bars give sample sizes for each percentage. The effect of degree of ovary development on the percentage of workers that were immobilized is significant (Friedman test:  $\chi^2=0.844$ ,  $P<0.02$ ). Virgin reproductives were always immobilized and this differs significantly from both nonreproductive groups (Bonferroni–Dunn post hoc comparison:  $P<0.0001$ ). There is no significant difference in immobilization of workers with empty ovaries or type b ovaries (Bonferroni–Dunn: NS).

We checked whether spermathecae were filled with sperm. Dissection results and behavioural data were combined for analysis.

## RESULTS

Dominant egg layers were never immobilized in virgin worker groups. However, reintroduction of a single gamergate in two groups led to the immobilization of egg-laying workers (six and nine times; Mann–Whitney  $U$  test:  $U=162$ ,  $N_1=18$ ,  $N_2=12$ ;  $U=189$ ,  $N_1=21$ ,  $N_2=12$ ;  $P<0.05$  in both groups). Within a few minutes, many workers approached the gamergate and antennated her. The gamergate was never aggressive towards any workers. During the next day, we observed increasingly frequent attempts to immobilize egg-laying workers, and these were eventually dragged out of the nest. Dissections revealed that all immobilized workers ( $N=3$ ) had elongate ovaries (category c<sub>1</sub> in Fig. 2). Immobilization behaviour was performed only by workers with ovaries in categories a or b, and these workers were never immobilized.

Gamergates and companion sterile workers reintroduced into virgin worker groups ( $N=5$ ) never showed immobilization behaviour during the week prior to their transfer. Upon first encounters, workers from the gamergate groups started biting and immobilising specific workers from the virgin groups. Additional workers joined in and helped to drag immobilized workers to the foraging arenas. Immobilization continued during the next few days ( $\bar{X} \pm \text{SD}=21 \pm 5$ ) times for eight 10-min scans; Mann–Whitney  $U$  test:  $P<0.05$  for all five colonies) and often resulted in damaged antennae or death (50%). In a few instances, a previously attacked worker escaped and walked freely in the arena, but was soon immobilized

again. Dissections confirmed that all workers with elongate (c) ovarioles had been immobilized ( $N=16$ ). Only one out of 38 workers with empty ovarioles (a) and four out of 97 workers with ovaries (b) had been immobilized (Fig. 3). Gamergates and workers were transferred in an identical way to group A<sub>1</sub>, in which egg layers had recently mated although their ovary development was still similar to that of virgin reproductives. This did not prevent their immobilization and these new gamergates were similarly removed from the nest. We conclude that workers can distinguish between gamergates and virgins laying reproductive eggs. Furthermore, only the latter were immobilized if together with a gamergate. The main physiological difference between gamergates and virgin egg layers is their degree of ovary development. Workers of the virgin groups sometimes immobilized gamergates for a short time. However, these attacks were performed by single individuals only and soon abandoned. None of the gamergates suffered any damage from them.

Reuniting gamergate groups from the same colonies did not result in immobilization of gamergates. Only two out of 39 previously identified gamergates were attacked and immobilized, and both of these lacked yolky oocytes in their ovaries, indicating that they had recently stopped ovipositing. There was no aggression between workers of either group, which shows that possible divergence in colony odour had no effect on our experimental results.

When groups of virgin workers were separated from the remainder of their colonies with a single mesh sheet allowing the transfer of airborne odours ( $N=4$ ), this resulted in a significant increase in aggression (from a  $\bar{X} \pm \text{SD}$  of  $0.13 \pm 0.05$  to  $3.94 \pm 0.92$  times/worker per h; Mann–Whitney  $U$  test:  $U=16$ ,  $N_1=N_2=4$ ,  $P<0.05$ ), similar to that in virgin groups that were completely separated.

In all groups, two to four dominants started to lay reproductive eggs after 1–3 months, suggesting that direct physical contact with gamergates is needed for reproductive regulation.

## DISCUSSION

Our behavioural observations and detailed data on ovarian activity indicate that, in the ponerine ant *G. menadensis*, sterile workers play an important role in the regulation of their nestmates' oogenesis. Some virgin workers start to produce reproductive eggs when gamergates were temporarily removed, but these virgin egg layers were attacked and immobilized as soon as the presence of gamergates was detected again. Thus workers with increased ovarian activity are recognized on the basis of some external characteristics. Olfactory cues seem to be involved since prior behavioural interactions are not required. In honeybees, orphaned workers with newly developed ovaries are similarly attacked by nestmates, and recognition was suggested to involve some olfactory concomitants of ovarian activity (Visscher & Dukas 1995). In the queenless ant *Dinoponera australis*, egg layers and sterile workers have different blends of cuticular long-chain hydrocarbons (Monnin et al. 1998). We did not study cuticular hydrocarbons in *G. menadensis*, but they seem good candidates for a chemical signal associated with ovarian activity, since long-chain hydrocarbons have low volatility. Indeed, our mesh experiments showed that information about the presence of gamergates is not volatile and might be transmitted by antennal contact.

Attacks and immobilization inflicted severe damage to all victims, of which 50% died during the observation period. We think this is due to the extreme nature of our experiment, since in natural conditions virgin workers can probably never increase their oogenesis to a level sufficient to produce reproductive eggs, and thus antagonism would never be so strong. Immobilization is also an important behaviour in the establishment of a dominance hierarchy in virgin worker groups, before the start of reproductive egg laying (B. Gobin et al. unpublished data). In these, immobilization resulted in loss of dominant status and reduced ovarian activity, but not death. In nonmanipulated colonies, virgin workers were also immobilized occasionally. Policing behaviour has recently been found in the polygynous *Harpegnathos saltator* (J. Liebig, C. Peeters & B. Hölldobler, unpublished data) as well as in the monogynous and monandrous *Diacamma* sp. and *Dinoponera quadriceps* (Monnin & Peeters 1999; Kikuta & Tsuji, in press), suggesting that it is an important phenomenon in ants. Policing behaviour can also take the form of oophagy in *Apis* and *Diacamma* (Ratnieks & Visscher 1989; Kikuta & Tsuji, in press), but we never observed the destruction of reproductive eggs in *G. menadensis*.

Policing behaviour preventing worker production of males is expected to evolve under conditions of reduced relatedness (high mating frequencies or multiple related queens; Woyciechowski & Lomnicki 1987; Ratnieks 1988; Pamilo 1991), or when the costs of worker reproduction

or benefits of policing to colony efficiency are high (Nonacs 1992; Frank 1996). In *G. menadensis*, workers are able not only to produce males but also to mate and produce female offspring, which generalizes the conditions favouring policing. Additional research on the relatedness structure and relevant costs and benefits is needed to determine the ultimate causes of policing behaviour in this species.

The regular production of trophic eggs in *G. menadensis* provides an opportunity to explore whether chemical signals can give detailed information about different levels of ovarian activity. Many workers in a colony lay trophic eggs (Gobin et al. 1998b), yet they are not immobilized. This is expected, since trophic eggs play no part in reproductive competition. Only when workers start to develop their ovaries and produce reproductive eggs does policing behaviour become relevant. Once dominant virgins have switched to laying reproductive eggs, their ovaries remain less active than those of gamergates, and they lay only a mean  $\pm$  SD of  $0.77 \pm 0.35$  eggs/day. Ovarian activity reaches a maximum 4–5 weeks after mating, and gamergates lay  $1.42 \pm 0.95$  eggs/day (Gobin et al. 1998b).

The ability of police workers to discriminate between these two types of egg layers is necessarily based on accurate information about ovarian physiology. We suggest that sterile workers are intolerant when confronted with two levels of signal, and they attack the weaker. The stronger signal is likely to be emitted by one's mother, and there is no need to invoke individual recognition. The 'mistakes' made by workers of the virgin worker groups when they immobilized gamergates for short periods is a consequence of their tendency to immobilize any worker with increased ovarian activity during dominance fights. All subordinates continually attempt to immobilize dominants but they do not succeed because of the dominant's aggressive behaviour (B. Gobin et al., unpublished data). The immobilization of old gamergates soon after a decrease in their fecundity is further evidence for the ability of workers to assess the level of ovary development. In experiments designed to elucidate whether colony odour originates from the queen, workers from groups of *Aphaenogaster cockerelli* and *Rhytidoponera confusa* with queens attacked reintroduced nestmates with developed ovaries more than those with empty ovaries (Hölldobler & Carlin 1989; Crosland 1990). In *Solenopsis invicta*, workers can discriminate queen fecundity and eliminate the least productive queens (Fletcher & Blum 1983; Willer & Fletcher 1986; see also Keller & Ross 1998). In *D. quadriceps*, the biosynthesis of different blends of cuticular hydrocarbons is thought to be controlled by hormonal titres in the haemolymph which also regulate oogenesis (Monnin et al. 1998). Such a fertility signal is intimately linked with ovarian physiology, and can thus provide reliable information. Indeed, honesty was hypothesized to depend on the correlation between fecundity and pheromonal output (Keller & Nonacs 1993).

The worker policing hypothesis assumes that there is no single worker that can dominate reproduction (Ratnieks 1988), which is the case in some ants with small

colonies (Heinze et al. 1994; see also Bourke 1999). Our study confirms that a mechanism for worker policing is nevertheless possible in a species with small colonies. Since we studied policing behaviour in colonies with gamergate reproductives, the interference of a caste-specific signal can be ruled out. In contrast to the morphologically distinct queens, gamergates differ from workers in ovarian physiology only. This is strong support that an honest fertility signal is the basis for a variety of behavioural interactions that have evolved to resolve reproductive conflicts in social insects.

### Acknowledgments

We are grateful to Andrew Bourke, Fuminori Ito, Laurent Keller, Kazuki Tsuji and an anonymous referee for their constructive comments on the manuscript. This work was supported by IWT research grant no. 942047 to B.G. and TOURNESOL exchange program no. T.95071 and largely written at Kagawa University (JSPS fellowship T98-167).

### References

- Bourke, A. F. G.** 1999. Colony size, social complexity and reproductive conflict in social insects. *Journal of Evolutionary Biology*, **12**, 245–257.
- Crosland, M.** 1990. The influence of the queen, colony size and worker ovarian development on nestmate recognition in the ant *Rhytidoponera confusa*. *Animal Behaviour*, **39**, 413–425.
- Fletcher, D. J. C. & Blum, M. S.** 1983. Regulation of queen number by workers in colonies of social insects. *Science*, **219**, 312–315.
- Frank, S. A.** 1996. Policing and group cohesion when resources vary. *Animal Behaviour*, **52**, 1163–1169.
- Gobin, B., Peeters, C. & Billen, J.** 1998a. Colony reproduction and arboreal life in the ponerine ant *Gnamptogenys menadensis* (Hymenoptera: Formicidae). *Netherlands Journal of Zoology*, **48**, 53–63.
- Gobin, B., Peeters, C. & Billen, J.** 1998b. Production of trophic eggs by virgin workers in the ponerine ant *Gnamptogenys menadensis*. *Physiological Entomology*, **23**, 329–336.
- Heinze, J., Hölldobler, B. & Peeters, C.** 1994. Conflict and cooperation in ant societies. *Naturwissenschaften*, **81**, 489–497.
- Hölldobler, B. & Carlin, N. F.** 1989. Colony founding, queen control and worker reproduction in the ant *Aphaenogaster* (= *Novomessor*) *cockerelli* (Hymenoptera: Formicidae). *Psyche*, **96**, 131–151.
- Keller, L. & Nonacs, P.** 1993. The role of queen pheromones in social insects: queen control or queen signal? *Animal Behaviour*, **45**, 787–794.
- Keller, L. & Ross, K. G.** 1998. Selfish genes: a green beard in the red fire ant. *Nature*, **384**, 573–575.
- Kikuta, N. & Tsuji, K.** In press. Queen and worker policing in the monogynous and monoandrous ant, *Diacamma* sp. *Behavioral Ecology and Sociobiology*.
- Monnin, T. & Peeters, C.** 1999. Dominance hierarchy and reproductive conflicts among subordinates in a monogynous queenless ant. *Behavioral Ecology*, **10**, 323–332.
- Monnin, T., Malosse, C. & Peeters, C.** 1998. Solid phase microextraction and cuticular hydrocarbon differences related to reproductive activity in the queenless ant *Dinoponera quadricaps*. *Journal of Chemical Ecology*, **24**, 473–490.
- Nonacs, P.** 1992. Male parentage and sexual deception in the social Hymenoptera. In: *Evolution and Diversity of Sex Ratio in Insects and Mites* (Ed. by D. L. Wrench & M. A. Ebbert), pp. 384–401. New York: Chapman & Hall.
- Pamilo, P.** 1991. Evolution of colony characteristics in social insects. II. Number of reproductive individuals. *American Naturalist*, **138**, 412–433.
- Peeters, C.** 1993. Monogyny and polygyny in ponerine ants with or without queens. In: *Queen Number and Sociality in Insects* (Ed. by L. Keller), pp. 234–261. Oxford: Oxford University Press.
- Ratnieks, F. L. W.** 1988. Reproductive harmony via mutual policing by workers in eusocial Hymenoptera. *American Naturalist*, **132**, 217–236.
- Ratnieks, F. L. W. & Visscher, P. K.** 1989. Worker policing in the honeybee. *Nature*, **342**, 796–797.
- Visscher, P. K. & Dukas, R.** 1995. Honey bees recognize development of nestmates' ovaries. *Animal Behaviour*, **49**, 542–544.
- Walín, L., Sundström, L., Seppa, P. & Rosengren, R.** 1998. Worker reproduction in ants: a genetic analysis. *Heredity*, **81**, 604–612.
- Willer, D. E. & Fletcher, D. J. C.** 1986. Differences in inhibitory capability among queens of the ant *Solenopsis invicta*. *Physiological Entomology*, **11**, 475–482.
- Woyciechowski, M. & Lomnicki, A.** 1987. Multiple mating of queens and the sterility of workers among eusocial Hymenoptera. *Journal of Theoretical Biology*, **128**, 317–327.