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Dominance Interactions Regulate Worker Mating in the Polygynous Ponerine Ant *Gnamptogenys menadensis*

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Abstract

In queenless ants, workers compete aggressively to be reproductives instead of sterile helpers. To limit the number of reproductives, either mating or egg-laying by mated workers can be regulated. In *Gnamptogenys menadensis*, all mated workers reproduce, and field data presented here indicate that mating is not random. We removed gamergates experimentally ($n = 16$ groups) to induce mating and gamergate replacement. Virgin workers engaged in agonistic interactions, allowing us to classify them into two groups: dominants performed antennal boxing and biting, while subordinates did not. However, a few subordinates cooperated to immobilize individual dominant workers. This effectively reduced the number of dominants because immobilized dominants became subordinates. Six to 12 wks after the removal of reproductives, between one and eight dominants per colony started to perform 'sexual calling' outside the nest entrance. Sixteen (out of 33) dominants mated with foreign males introduced in five experimental groups. None of the subordinate workers mated. The probability of mating is thus regulated by dominance interactions among workers and immobilizations initiated by infertile workers in this polygynous queenless ant.

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Introduction

Mating is rarely regulated in ants. Most species have winged queens and these disperse by flight before mating. Queens then copulate when they encounter males (Hölldobler & Wilson 1990). Every mated queen will attempt to found a

new colony, or in some species they are adopted in established colonies. Ant workers generally cannot mate, except in over 100 species belonging to the subfamily Ponerinae (Peeters 1993). In these ants, mated workers neither disperse individually nor create new colonies. Males do not mate in nuptial flights but search for foreign nests where they copulate with workers inside or close to entrances (Peeters 1991). Because all workers have a sperm reservoir, males encounter many potential sexual partners. However, mating is often restricted as a consequence of agonistic interactions. *Pachycondyla sublaevis* and *Dinoponera quadriceps* are two examples of monogynous queenless ants in which stereotyped aggression among a small subset of nestmates leads to the formation of a linear hierarchy, and only the top-ranking worker mates (Ito & Higashi 1991; Monnin & Peeters 1998). Similarly, in the genus *Diacamma*, only one worker mates in each colony, but there are no hierarchical relationships. Mutilation of newly emerged workers leads to irreversible neuro-anatomical modifications and the inability to mate (Peeters & Higashi 1989; Gronenberg & Peeters 1993).

In ants where multiple gamergates (i.e. mated reproductive workers) occur, two situations are found. In various species, many individuals can copulate in each colony without apparent regulation. In *Pachycondyla* (= *Ophthalmopone*) *berthoudi*, up to 63% of workers are inseminated in nests collected immediately after the period of male activity (Peeters & Crewe 1985), while an average of 89% of workers copulate in *P. tridentata* (Sommer et al. 1994). Instead of behavioral regulation, it appears that individual age is the only determinant of sexual activity; unrestricted mating is advantageous because males are only produced during a few weeks of the year. In *Harpegnathos saltator*, large numbers of young workers also mate, but only a few of these become gamergates (Peeters & Hölldobler 1995). In contrast, in other polygynous queenless species, only a few workers mate and they all lay eggs (Peeters 1993). In *Gnamptogenys striatula*, *Rhytidoponera confusa*, *R.* sp. 12 (tribe Ectatommini), *Amblyopone* sp. and *Leptogenys schwabi*, only a small proportion of workers copulate (Blatrix & Jaisson 2000; Ward 1983; Peeters 1987; Ito 1993; Davies et al. 1994), but it is not clear what factors limit mating.

In *Gnamptogenys menadensis* (tribe Ectatommini), a few gamergates (mean 5; range 1–14) reproduce in colonies from Sulawesi (Indonesia). Gobin et al. (1998a) found only two queenright colonies out of 37, and in these none of the workers were mated. Many virgin workers have active ovaries in all colonies, but they only lay unviable trophic eggs that are morphologically distinct (Gobin et al. 1998b). However, when virgin workers are separated from established reproductives, several individuals become dominant and switch to producing male eggs after 6–12 wks. Re-introduction of the established reproductives leads to these new egg-layers being immobilized and sometimes killed by infertile workers, which suggests that virgins are normally infertile as a consequence of mutual policing (Gobin et al. 1999). It is thus essential to distinguish between two types of agonistic interactions: (i) dominance by reproductives; and (ii) worker policing. In this study we describe how dominance interactions (antennal boxing and biting) by reproductives, and policing (immobilization) by subordinates regulate worker

mating in *G. menadensis*, a species with multiple gamergates. It is important to understand the mechanisms regulating mating in queenless ants, because workers are either reproductives or sterile helpers. Particularly in polygynous queenless ants, an excess of reproductives would lead to a breakdown in the division of labour. Regulation of mating is one of the possible behavioral means preventing this.

Material and Methods

Colonies of *G. menadensis* were collected in Jan. 1994, Feb. 1995 and Mar. 1996 in south Sulawesi (Indonesia). This period corresponds to the latter half of the rainy season (Oct. to Mar.). Colonies contained 113 ± 75 workers ($n = 37$) and males were present during each sampling month (for details on colony composition see Gobin et al. 1998a). Colonies were housed in plaster nests (about 9×6 cm) covered with glass roofs and connected to a 20×15 cm foraging arena. We maintained constant climatic conditions of $25 \pm 2^\circ\text{C}$, $75 \pm 15\%$ relative humidity and a 12 : 12 h day : night cycle.

All workers were individually marked with paint to allow investigation of oviposition and behavioral interactions in colonies with a queen ($n = 2$, 50 h) or gamergates ($n = 18$, 230 h and additional ad libitum scans). Gamergates were identified when they laid eggs: gamergates lay only elongate reproductive eggs, virgins lay round trophic eggs (Gobin et al. 1998b). Virgin worker groups ($n = 16$) were created by isolating 20–50 workers in a separate nest-box and their behavior was observed for 300 h. Two of these groups were observed for 6 and 10 wks after the start of egg-laying to check the stability of the group of virgin egg-layers. To provide details on the dynamics of dominance interactions, a group of 25–45 workers was observed during three consecutive periods in four colonies: (i) in the presence of gamergates (10 h); (ii) during the first 5 wks of separation from the gamergate (10 h); and (iii) when they had started laying reproductive eggs, after 7–11 wks (10 h).

We distinguished three main types of agonistic interactions in *G. menadensis*.

1 Antennal boxing, in which a worker repeatedly hits its antennae against any body part of another worker. When two workers direct antennal boxing towards each other simultaneously we called this reciprocal antennal boxing.

2 Biting, in which a worker bites a limb of another worker and briskly drags it through the nest for a distance of a few mm up to 9 cm. This behavior is generally accompanied by antennal boxing from the biting worker towards the passive worker.

3 Immobilization, in which a single or up to eight workers hold another worker by its limbs (Gobin et al. 1999). Generally, the immobilized worker will then be pulled outside the nest. Immobilization can last for several hours. When performed sequentially by several workers, it can last for days and usually results in the death of the immobilized worker. In virgin worker groups, this behavior is always directed from subordinate workers towards dominants. In colonies with gamergates, it is directed from virgin workers to virgin nest-mates with increased

ovary development. This behavior is more difficult to quantify due to the prolonged nature of the interaction (Gobin et al. 1999).

When workers perform frequent antennal boxing (> 3 times/h) or biting, we call them dominant. Workers that are infrequently boxing (≤ 0.5 times/h) but are targets of attacks from dominants are called subordinates. When attacked, subordinates can avoid the attacks or behave submissively (pulling antennae backwards or assume a pupal posture), or show no response. Antennal boxing has frequently been described as ritualized aggression (e.g. Heinze et al. 1994; Bourke & Franks 1995). Is antennal boxing a form of dominance, or merely a way to gather information from the opponent? Ants can get information by simply touching other individuals with their antenna, without the need for rapidly hitting them. It is possible to construct a hierarchy on the basis of the pattern of antennal boxing, and only the top-ranking members of the hierarchy reproduce. This strict correlation between behavioral interactions (antennal boxing) and reproductive success (egg-laying) leads us to categorize antennal boxing as dominance behavior.

Mating experiments were conducted as soon as workers started sexual calling. They stood motionless in the foraging arena with the abdomen lifted in the air for up to 20 min. Only the abdomen tip moved rhythmically, thus exposing the intersegmental membranes between the 5th and 6th, as well as between the 6th and 7th abdominal segments. Meanwhile, the dominant frequently rubbed its hind legs on the gaster. Males used for mating experiments were removed from the nest chamber and allowed to fly. Only males that readily flew when dropped from 50 cm height were selected and isolated overnight. Between two and five males were introduced daily into five virgin worker groups. Fifteen males were introduced into two virgin groups in which egg laying or sexual calling had not yet started. To check for mating in the presence of gamergates we introduced 10 males during 1 wk into two colonies containing gamergates and young workers. After the observation periods, the ovaries and spermatheca of all workers in these groups were dissected to check for oogenesis and the presence of yellow bodies and sperm.

Results

Our field data suggest that mating is not a function of the mere presence or absence of males. Indeed, the percentage of mated workers in *G. menadensis* colonies did not increase significantly in our three sampling periods (ANOVA on arcsine transformed data $F_2 = 1.05$; $p = 0.37$, Table 1), which were each 1 mo further into the period of male activity. Furthermore, the introduction of foreign males in two laboratory colonies with identified gamergates and many young workers did not result in additional mating. We never observed workers in a typical sexual calling posture in gamergate- or queen-right colonies ($n = 18$, $n = 2$, respectively). Furthermore, males never attempted to mate with their own nest-mates in eight colonies with identified gamergates, indicating that inbreeding is absent.

Table 1: Colony size, number of workers and gamergates, and proportion of gamergates present in 21 colonies of *G. menadensis*, collected in three sampling periods. Colony codes correspond to those in Gobin et al. (1998a)

	Colony	Workers	Gamergates	Percentage
Jan. 94	A	12	1	8%
	2	30	4	13%
	3	106	3	3%
	4	93	1	1%
	5	18	3	16%
	6	93	13	14%
Mean		59	4	9%
SD		43	4	6%
Feb. 95	9	100	4	4%
	10	96	2	2%
	12	31	3	7%
	15	43	2	5%
	16	61	5	8%
	19	177	14	8%
Mean		85	5	6%
SD		53	5	2%
Mar. 96	23	68	1	1%
	25	80	6	8%
	28	124	2	2%
	33	82	9	11%
	44	296	5	2%
	46	193	9	5%
	47	120	3	3%
	50	122	13	11%
	52	81	5	6%
Mean		130	6	5%
SD		73	4	4%

Dynamics of Dominance

In colonies with gamergates or a queen, dominance interactions among workers were rare (no biting; acts of antennal boxing per worker per hour: median 0.13, quartiles 0.09 and 0.16; 50 h on four colonies, Fig. 1). This low frequency of antagonism involved $75 \pm 11\%$ ($x \pm SD$) of the workers (see Fig. 2A), so no clear hierarchical relationships could be determined. Gamergates were often engaged in reciprocal antennal boxing with other gamergates (median times per gamergate per hour: 3.4, quartiles 3.35 and 4.9, $n = 10$ colonies). In spite of this, all gamergates laid reproductive eggs. Dissections confirmed this because they have multiple yolky oocytes in each ovariole, with elongate mature basal oocytes and dark yellow bodies. While gamergates infrequently boxed infertile workers (times per gamergate per hour: median 0.30, quartiles 0.16 and 0.49, $n = 10$

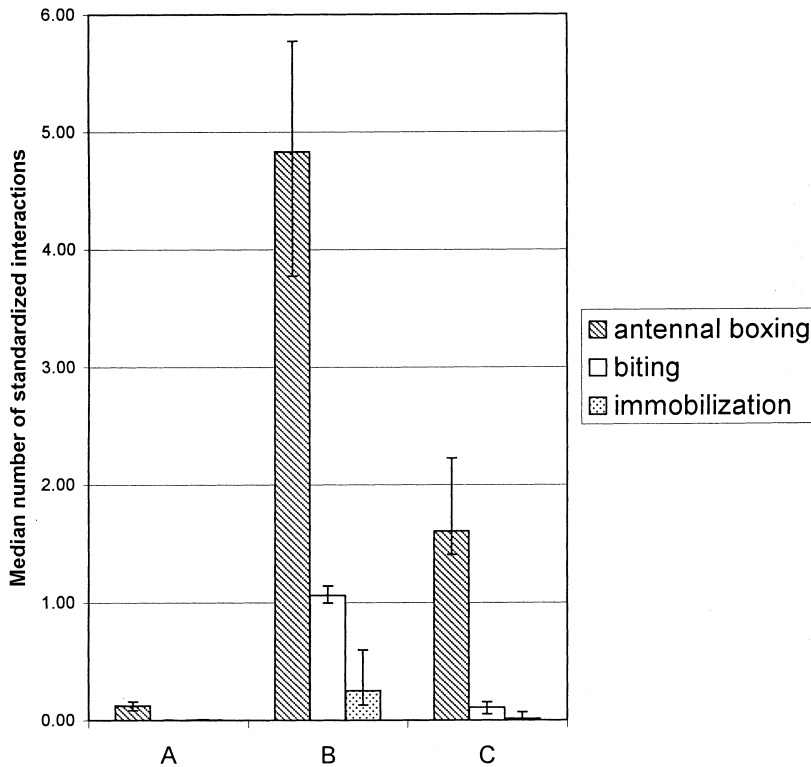


Fig. 1: Agonistic interactions observed in four colonies, each during three consecutive periods (10 h per colony in each period). Agonistic interactions were standardized for each colony by division through number of workers and hours of observation. (A) Gamergates present; (B) virgin worker groups during the first 5 wks of separation; (C) dominants have started laying reproductive eggs. Median values and upper and lower quartiles are given for antennal boxing, bite and drag, and successful immobilization, and each type of behavior was analyzed for differences between periods with Friedman ANOVA. For the three periods, there was a significant difference in antennal boxing ($\chi^2_2 = 8$, $p < 0.05$) and biting ($\chi^2_2 = 7.6$, $p < 0.05$), but not for immobilization ($\chi^2_2 = 5.1$, $p = 0.08$)

colonies), workers never boxed gamergates in unmanipulated colonies. Only after gamergates ceased to lay eggs ($n = 7$, revealed by their resorbed ovaries), did workers immobilize them, and this always led to their death. In both queenright colonies, the queen showed dominance towards virgin workers (2.29 and 6.21 acts of antennal boxing per hour), while workers rarely boxed among themselves (0.02 and 0.49 times per hour). Again, when the queen of one colony stopped laying eggs, workers immobilized her until she died.

When groups of virgin workers were experimentally separated from the gamergates, antennal boxing and biting increased significantly (Fig. 1: Tukey HSD post-hoc comparison for period A and B: $p < 0.05$). Widespread antagonism was already evident after 12 h and lasted between 3 and 5 wks after orphaning, during which up to $35 \pm 9\%$ of the workers performed 60–80% of

the antennal boxing ($n = 16$; see Fig. 2B). The same individuals performing antennal boxing also performed biting (Pearson's product moment correlation $r = 0.82 \pm 0.1$, 27 ± 8 workers, $n = 6$ colonies). At this point, subordinates started to attempt to immobilize all highly agonistic workers (0.11 ± 0.6 attempts per worker per hour, $n = 6$ colonies). Typically, a worker approaches a dominant worker, grooms it, and then tries to immobilize it. In response, the dominant worker immediately performs antennal boxing or bites the subordinate for more than 1 min, during which the subordinate assumes a pupal posture. Between two and six workers were successfully immobilized in each worker group. There was no significant difference in successful immobilizations (Fig. 1), although this might be due to low sample size and the prolonged nature of immobilization, therefore recorded as one event per observation bout. We observed the process of immobilization of 15 dominant workers in detail. During immobilization attempts they refrained from attacking subordinates and rather moved away from them. Up to eight subordinates then quickly succeeded in immobilizing the previously dominant worker and removed them from the nest, where they were held for 1–3 days. When immobilized workers could finally re-enter the nest, they stopped performing antennal boxing nor biting. Such former dominants were therefore classified as subordinates. Nine immobilized workers died.

Only dominant workers that could successfully avoid being immobilized remained dominant. After 6–12 wks the occurrence of antennal boxing and biting in virgin worker groups diminished significantly (Tukey HSD post-hoc comparison of periods B and C, $p < 0.05$), while immobilization became rare (Fig. 1). Dominants directed $61\% \pm 13\%$ ($n = 37$ from six colonies) of their antennal boxing towards other dominants (different from expectation with $27.2 \pm 8\%$ dominants, $\chi^2 = 325.6$, $df = 5$, $p < 0.05$). Dominant workers were between three and 18 wks old at the time of orphaning, even when younger individuals were present. The 16 virgin worker groups included 2–9 callows, and only in two groups did one callow become dominant. Callows born in virgin groups quickly became subordinates. Six young alate and dealate queens (1–6 wks of age) all became subordinates in four virgin worker groups.

Once the dominants became differentiated, all of them started to lay gradually more elongate eggs. Two weeks later, these eggs were morphologically indistinguishable from gamergate eggs. Although subordinates occasionally continued to attempt immobilizing dominants after this change, they were never successful. Dominants dissected at this stage ($n = 37$) had elongate mature oocytes or yellow bodies in their ovaries, confirming that all laid eggs. Subordinates ($n = 236$ dissected) had either empty ovarioles, or ovarioles with a single round basal oocyte associated with trophic egg laying (details in Gobin et al. 1998b). The group of virgin egg-layers remained dominant for at least 6 and 10 wks of subsequent observation after the start of egg-laying ($n = 2$ colonies). When virgin egg-layers were removed from such virgin worker groups ($n = 3$), an increase in dominance interactions was again observed, leading to a new group of dominants that eventually laid reproductive eggs.

Mating Behavior

As soon as dominants started laying reproductive eggs, they began performing sexual calling behavior outside. Twenty-six dominants (in 16 worker groups) were observed to perform sexual calling, two of these on multiple occasions separated by several days. Nest-mate males present in virgin groups ($n = 6$) with egg-laying dominants showed no interest in them, and mating with nest-mates never occurred.

We introduced foreign males into the arena of five virgin worker groups in which dominants had started to lay elongate eggs. Mating was directly observed three times. A male approached a dominant worker and climbed on top of it. The male then extruded its genitalia and actively searched for contact with the worker's gaster tip. The dominant worker lifted its abdomen and allowed the male to copulate. Intromission lasted about 30 s, after which the male retracted its genitalia and moved away. When males had short contact with dominants, but failed to mount them (five observations), they searched for the dominants excitedly and often mounted foragers or even other males. Non-dominant workers always turned their abdomen tip away, so mating could not take place. Subsequent dissections confirmed that 16 out of 32 of the dominants had mated (Table 2), while subordinates (including former dominants) never mated. Foreign males were often attacked and immobilized in the arena by foragers. This might account for the fact that not every dominant worker showing sexual calling had mated. On the other hand, probably due to the limited observation period (5–10 h in 5–10 days), 10 workers that mated were not observed in sexual calling behavior. The introduction of 15 foreign males into two virgin groups before egg-laying dominants had established did not result in any matings.

Discussion

Our results show that behavioral interactions in orphaned worker groups lead to the formation of two distinct classes of individuals: dominants and subordinates. We base this distinction on the fact that dominants perform antennal boxing frequently, aiming half of this antennal boxing towards each other. This arbitrary distinction appears to have high predictive power because all workers classified as dominant showed increased ovary development and started producing elongate reproductive eggs (see Gobin et al. 1998b). Membership of either class thus has physiological consequences. Only the dominant workers performed sexual calling behavior and, when foreign males were introduced in five groups, 16 dominants mated.

The regulation of reproduction in orphaned colonies of *G. menadensis* differs from other queenless species because many workers are initially highly agonistic and it takes a long time (up to 3 months) before a group of egg-laying dominants is established. Haploid egg laying starts within a few weeks after orphaning in other ponerine ants (e.g. Oliveira & Hölldobler 1990; Ito & Higashi 1991; Peeters & Tsuji 1993). In the monogynous *Dinoponera quadriceps* and *Pachycondyla*

Table 2: Behavioral and dissection data of five virgin worker groups in which foreign males were introduced. Observation period, male introduction and dissection are given in days since the separation of the virgin worker group. The number of antennal boxing observed is given for each dominant. Data on subordinate workers are lumped together. In colonies II and III, immobilized workers (lumped as 'immobilized') were boxing on the first 2 d of observation, but this ceased entirely after successful immobilization and they are thus considered subordinates

I: Observation on days 71–75, hours observed 6, males on days 75–97, number of males 14, dissected on day 125					
Individual	Antennal boxing	Egg type	Sexual calling	Insemination	Yellow bodies
YYGG	282	R	+	0	+
BBYY	219	R	+	0	+
RRBB	213	R	+	+	+
WWWW	139	R	+	0	+
BBOrOr	119	R	–	–	–
RRGG	52	R	–	+	+
WWOOrOr	36	R	–	+	+
22 workers	≤ 1	8T	–	0	0
II: Observation on days 83–93, hours observed 10, males on days 93–98, number of males 8, dissected on day 100					
Individual	Antennal boxing	Egg type	Sexual calling	Insemination	Yellow bodies
RPOrB	181	–	–	0	0
GGBB	167	R	+	+	+
GGGG	125	R	–	0	+
YRRY	57	R	+	0	+
PRBOr	38	R	–	+	+
5 immobilized	8–13	–	–	0	0
32 workers	≤ 3	4T	–	0	0
III: Observation on days 60–69, hours observed 7, males on days 69–72, number of males 17, dissected on day 101					
Individual	Antennal boxing	Egg type	Sexual calling	Insemination	Yellow bodies
YYGG	198	–	–	0	0
RRRR	146	–	+	+	+
OrOrPP	140	–	–	0	0
YYOrOr	85	R	–	+	+
WOOO	85	–	–	0	0
WWYO	42	–	+	+	+
WWRR	32	–	–	0	0
POOO	24	R	–	+	+
2 immobilized	8–9	–	–	0	0
29 workers	≤ 3	11T	–	0	0

Table 2: (Continued)

IV: Observation on days 35–41, hours observed 5, males on days 41–42, number of males 1, dissected on day 43					
Individual	Antennal boxing	Egg type	Sexual calling	Insemination	Yellow bodies
YBOY	107	R	+	+	+
RRGB	46	–	+	0	+
GWBR	33	–	+	0	0
BBRB	30	–	+	0	+
GRRW	22	–	+	0	0
13 workers	≤ 2	2T	–	0	0
V: Observation on days 68–74, hours observed 6, males on days 75–90, number of males 28, dissected on day 95					
Individual	Antennal boxing	Egg type	Sexual calling	Insemination	Yellow bodies
OrWWOr	130	–	–	+	+
PGPOr	122	R	–	+	+
WRBB	98	–	+	+	+
WYYY	70	–	–	0	+
BRBB	66	R	–	+	+
WOPP	65	–	–	0	+
PPRR	37	–	–	+	+
PBY Y	33	–	–	+	+
26 workers	≤ 3	5T	–	0	0

Entries are as follows: (+) present; (0) absent; (R) reproductive eggs laid; (T) trophic eggs laid, preceded by number of workers where lumped; (–) not observed.

sublaevis, the interference of subordinates with high-ranked workers speeds up the establishment of the top dominant worker and it lasts only a few days (Monnin & Peeters 1999; Higashi et al. 1994). In *G. menadensis*, immobilization of dominants does not speed up the formation of the dominant group, but effectively reduces the number of dominant workers. Workers can reliably assess the degree of ovary development of their nest-mates and will attack virgin egg-layers in the presence of queen or gamergates (policing behavior). The cues detected are non-volatile concomitants of ovary development (Gobin et al. 1999) and are presumably responsible for the discrimination of nest-mates during dominance interactions: dominants and subordinates recognize each other with information about their ovarian physiology. Nevertheless, dominants need to remain highly agonistic to avoid immobilization and maintain their status even after they switch to reproductive egg laying. Only several weeks after mating, new gamergates have reached their maximum ovary development (Gobin et al. 1998b) and are no longer agonistic towards virgin workers. Frequent dominance interactions continue between gamergates, but they show only a minor skew in reproductive egg laying (Gobin, unpubl. data).

Dominant workers leave the nest to perform sexual calling behavior, which is identical to sexual calling in *Rhytidoponera* species (Hölldobler & Haskins

1977; Ward 1981). No mating occurred when foreign males were introduced into two colonies with known gamergates. Additionally, no mating occurred when males were introduced into two colonies where egg-laying had not yet started. Although our sample sizes are very low, we argue that being behaviorally dominant is a precondition for mating, because we never observed sexual calling behavior in the presence of gamergates, nor in virgin groups before a group of dominants was visible. The receptivity of a worker determines the possibility for males to mate with her (Hölldobler & Haskins 1977; Monnin & Peeters 1998; Ito 1999). The behavioral regulation of mating is confirmed by our field data, because there was no increase in the average number of gamergates during the period of the year when males are active. In other species with multiple gamergates, mating is not restricted to dominant workers, and the proportion of mated workers increases markedly during the period of male activity (Peeters & Crewe 1985; Davies et al. 1994; Sommer et al. 1994; Peeters & Hölldobler 1995).

The exact rank of a dominant with respect to other dominants is of no biological relevance in *G. menadensis*, because all dominants can mate (Table 2). This is different from the linear hierarchy documented in monogynous queenless ants in which only the top-ranking worker can mate (Higashi et al. 1994; Monnin & Peeters 1999). The occurrence of several dominant workers is in accordance with the polygynous character of gamergate colonies in *G. menadensis*. The mating pattern of *G. menadensis* differs from that of the two South American species *G. moelleri* and *G. striatula*, in which several workers inbreed or mate with foreign males within the nest (Gobin unpubl. data, Blatrix & Jaisson 2000). So far, we know little about the natural process of gamergate replacement and mating in ponerine ants. A field study on a Malaysian population of *G. menadensis* suggests that gamergates are only replaced after they all die. This strategy seems possible because males are available throughout the year (Gobin & Ito, unpubl. data).

G. menadensis virgin workers' eggs are morphologically indistinguishable from those laid by gamergates. Although an egg-pile was formed in all virgin worker groups with established dominants, only two males were reared. However, once allowed to mate, worker larvae are readily reared to adulthood (Gobin et al. 1998b). In our experimental groups, the start of reproductive egg laying coincided with the start of sexual calling behavior. *G. menadensis* workers thus compete for mating rather than male production. Only workers that belong to the dominant group will mate and reproduce sexually, thus becoming the new gamergates.

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