

# Gamergates (mated egg-laying workers) and queens both reproduce in *Euponera sikorae* ants from Madagascar

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Most ponerine ants have flying queens that monopolise sexual reproduction, but in a minority of species, workers can also mate and lay fertilised eggs. Such 'gamergates' reproduce in addition to queens in some species but have replaced queens entirely in other species. The occurrence of a functional spermatheca in workers often appears associated with a slight difference in body size relative to winged queens, as is the case in *Euponera sikorae* (Forel) studied here. Eight colonies ( $19.9 \pm 8.7$  workers and 0–2 dealate queens) were collected in humid forests of Madagascar. A mated queen reproduced in most colonies, but ovarian dissections indicated that 1–3 workers were also inseminated, and one of these laid eggs if the original founding queen was missing or no longer fecund. Exoskeleton remains (including 29 heads) of a staphylinid beetle were found in one nest of *E. sikorae*, pointing to specialised predation. We review the occurrence of non-flying reproductives (gamergates and ergatoid queens) in *Odontomachus* genus-group.

**Key words:** monogyny, reproduction, mating, inbreeding, independent colony foundation.

## INTRODUCTION

Morphological specialisation of winged queens and wingless workers underlies the reproductive division of labour in ants. Queens can disperse by flight and start a new colony alone. Workers remain virgin and infertile, and generally lack a functional spermatheca. Yet in several unrelated taxa, workers can store sperm and mate like the queens. Both queens and 'gamergates' (mated, egg-laying workers) reproduce sexually in species belonging to subfamilies Ponerinae (e.g. *Harpegnathos saltator* Jerdon (Peeters *et al.* 2000); *Pseudoneoponera tridentata* (Smith) (Sommer *et al.* 1994), Ectatomminae (e.g. *Gnamptogenys menadensis* (Mayr) (Gobin *et al.* 1998); *Rhytidoponera confusa* Ward (Ward 1983) and Myrmicinae (*Metapone madagascariensis* Gregg (Hölldobler *et al.* 2002). In other species, queens have been lost and only gamergates reproduce, as with *Stigmatomma reclinatum* (Mayr) (subfamily Amblyoponinae) (Ito 1993a) or *Streblognathus peetersi* (Ponerinae) (Cuvillier-Hot *et al.* 2004). Body size divergence between queens and workers varies considerably across ant subfamilies, although species with slight dimorphism occur throughout (Peeters & Ito 2015). Among Ponerinae, the sexual ability of workers appears restricted to

genera that exhibit minimal size differences between queens and workers, although this is not always true, e.g. no gamergates in *Neoponera apicalis* Emery in which queens and workers are highly similar in body size (Dietemann & Peeters 2000).

We investigated colony reproductive structure and mating behaviour of *Euponera sikorae* Forel. This species is restricted to Madagascar where it has a widespread north–south distribution in humid habitats (Rakotonirina & Fisher 2013). Queens are almost the same size as workers and, after breaking off wings, can only be distinguished by differences in thorax segmentation (Fig. 1). Our results suggest that gamergates can reproduce after the death of the dealate founding queens in this species.

## MATERIAL AND METHODS

Eight colonies of *E. sikorae* were collected from various localities in the wet forests of eastern Madagascar: Midongy National Park (November 2006), Zahamena NP (February 2009), and Andohahela NP (Col de Tanantana, March 2015). Nests occurred in rotten wood lying on the ground, and great care was taken to find all of the adults and brood.

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**Fig. 1.** Comparison of winged (queens) and wingless (workers) female castes in *Euponera sikorae*. Arrows indicate the pronotum (first segment of thorax) that houses the neck muscles. Credits AntWeb.org: Erin Prado (queen CASENT0063893), April Nobile (worker CASENT0487847).

Some of the colonies were kept in observation nests for several weeks until dissection of the adults. Spermathecae were checked for presence of sperm, revealing previous copulation events. Presence of yolky oocytes and dark ‘yellow bodies’ in the ovaries provided information about current and past egg-laying activities, respectively. Only dealate queens were dissected in the 2006 and 2009 colonies, except in the case of BLF22426 which provided the first hints of gamergate reproduction. All 2015 colonies were completely dissected. In colony BLF36778, we video-recorded male behaviour and dominance interactions among workers,

but workers were not marked hence hierarchies were not studied.

## RESULTS

### Reproductive structure of colonies

The eight colonies consisted of  $19.9 \pm 8.7$  workers (mean  $\pm$  standard deviation), together with 0–2 dealate queens (Table 1). Males were found in most colonies collected in February–March, often together with winged gynes. All stages of brood were present, including up to 27 cocoons in one nest.

**Table 1.** Demography and reproductive structure of eight colonies of *E. sikorae* collected in eastern Madagascar at different times of the year: BLF14894 from Midongy (November 2006), BLF22098-22426 from Zahamena (February 2009), BLF36778-36846 from Andohahela (March 2015).

BLF codes	Dealate queens [mated]	Workers [mated]	Cocoons	Larvae (med-large)	Eggs	Winged gynes	Males
14894	1 [1]	20 *	0	28	>23	0	0
22098	1 *	20 *	20	2	–	0	0
22308	1 [1]	30 *	23	9	>1	17	8
22424	1 *	12 *	27	Few	–	10	15
22426	1 [0]	22 [2]	22	>4	–	5	4
36778	2 [0]	15 [3]	21	0	3	0	2
36811	1 [1]	33 [2]	11	16	2	0	1
36846	0	7 [1]	0	0	–	0	0

\*Not dissected.

Both queens and workers had six ovarioles (Fig. 2). Some dealate queens were unmated, but others were inseminated and ovipositing (Table 1). There was only one gamergate in each of four colonies that were completely dissected, and also 1–2 inseminated workers with undeveloped ovaries. Fertile queens and gamergates never occurred together, as detailed below:

BLF22426: two mated workers, one of which was a gamergate (dark yellow bodies in its ovaries,

indicating a long egg-laying activity). No mated queen.

BLF36811: one mated queen with dark yellow bodies but very little oogenesis, and two mated workers, one of which had slightly developed ovaries characteristic of a recently differentiated gamergate (Fig. 2; 28 workers and 1 dealate queen dissected). We interpret this to be a transition between an old queen and a new gamergate.

BLF36778 : two virgin dealate queens, and three



**Fig. 2.** Comparison of ovaries from a young gamergate (small developing oocytes, pale 'yellow bodies' [white arrowheads] [pale yellow online] ) and an old mated queen (oogenesis has stopped, but dark 'yellow bodies' [black arrowheads] [dark yellow online] indicate many eggs laid before; arrow shows spermatheca) coexisting in colony BLF36811. Note the size difference, which is linked to both caste and past reproductive activity.



**Fig. 3.** Ovaries from an old gamergate (ovaries lacking yolky oocytes and thus no longer active, but dark 'yellow bodies' (white arrowheads) [dark yellow online] indicate many eggs were laid previously) in colony BLF36778.

mated workers, one of which was an old gamergate with dark yellow bodies but no yolky oocytes (Fig. 3). The other mated workers lacked yellow bodies; one of these had previously engaged in dominance interactions (10 workers and two dealate queens dissected).

BLF36846: one old gamergate in a group of seven workers. This may have resulted from the accidental fragmentation of a bigger colony.

Our dissection results thus suggest monogyny, involving either a dealate queen or a gamergate. This hints that the presence of a resident egg layer inhibits another mated individual from starting oogenesis.

### Intra-nidal mating attempts

A resident male in colony BLF36778 attempted to copulate with his sister workers. Courting was surprisingly forceful and persistent, although it was observed on one afternoon only. The behavioural sequence was as follows: (i) male stands in front of target worker with stiff antennae held laterally, forelegs off the ground and shaking sideways; (ii) worker usually reacts by biting head of male, who then freezes for 10 s before trying again; (iii) a proportion of courting attempts were followed by the male mounting the worker from the back,

with his genitalia out. However, copulation never followed.

One worker engaged in an aggressive interaction with another worker, after which the male courted her, suggesting that the male was interested only in dominant workers. Later, the male courted, in quick succession, two workers that had been interacting agonistically. Our observations are suggestive of sib-mating although we lack definite proof.

### Specialised predation on staphylinid beetles

Colony BLF36811 nested in a rotten branch lying on the ground. A large number of exoskeleton pieces were embedded in wood dust close to the inhabited chambers. Microscope examination revealed that these cuticle segments all corresponded to the same beetle species. A whole dead adult staphylinid was found elsewhere in this nest, and the cuticle pieces matched this beetle (especially the short elytra and heads). We counted 29 head capsules in this midden of prey remains. Highly specialised predation on staphylinids has been reported in *Myopias darioi* Probst & Boudinot and a few other ponerine ants (Probst *et al.* 2015, and references therein). We need additional field observations on prey preferences in *E. sikorae* before we can conclude about specialised predation.

## DISCUSSION

Several colonies of *E. sikorae* had a dealate queen that was mated and laying eggs, so initially there was no inkling of sexual reproduction by workers. However, diploid offspring were produced in one colony lacking a dealate queen, and dominance interactions involving some workers were consistent with the existence of gamergates (e.g. Cuvillier-Hot *et al.* 2004). Dissection of three complete colonies indicated the occurrence of a few inseminated workers, although they did not all oviposit. It appears that each colony has only one mated egg layer, either a dealate queen or a gamergate. Other ponerine species with a single gamergate mostly lack queens (Monnin & Peeters 2008). Several ants are known in which secondary reproductives function to extend the lifespan of a colony after the death of the original foundress (Peeters & Molet 2010). Flight is not required, and neither is the ability to start a colony independently, hence gamergates can be secondary reproductives because they are cheaper to manufacture relative to queens. In *E. sikorae* and various other ponerines, queens and workers have the same number of ovarioles, thus they differ in dispersal ability only, not fecundity.

The intra-nidal mating attempts suggest that gamergates are inseminated by brothers. This is consistent with the pattern in termites where secondary reproductives inbreed to maximise a founding queen's genetic fitness (Myles 1988). Sib mating was also documented in the ant *Harpegnathos saltator* where the dealate founding queen is replaced by gamergates: young males copulate with sister workers before presumably flying off to search for foreign queens that wait outside entrances of their natal nests (Peeters *et al.* 2000). We lack field observations of mating behaviour in *E. sikorae*, but we expect queens to mate on the ground close to natal nests as in several other Ponerinae (Peeters 1991; Peeters & Molet 2010).

In most Ponerinae, colonies are started by a solitary queen in a non-claustral manner, *i.e.* she regularly hunts outside the nest in order to feed the first generation of workers (Peeters 1997). We did not observe founding behaviour in *E. sikorae*, but the large size of the queen's pronotum (*i.e.* dorsum of first thoracic segment, Fig. 1) indicates the presence of large, worker-like neck muscles necessary to hunt and carry prey (Keller *et al.* 2014). The insect thorax shows a trade-off between the size of

the muscles that power the head and the wing muscles attached to the second segment (mesonotum). In Ponerinae, flying queens have a pronotum similar in size to workers', and this characteristic is associated with foraging during colony foundation (Keller *et al.* 2014). Field observations in the closely-related *Mesoponera cafferria* Smith indicated that colony founding is indeed non-claustral (Villet 1990b).

Schmidt & Shattuck (2014) revised the subfamily Ponerinae based on a molecular phylogeny and a reappraisal of morphological diversity. Nineteen genera resulting from the split of *Pachycondyla* are now spread across four major monophyletic clades, and this allows comparative analyses, *e.g.* modifications in reproductive structure. Gamergates appear to be more prevalent in some clades than others. *Euponera* belongs to the *Odontomachus* genus-group (Schmidt & Shattuck 2014), a lineage including seven other genera in which gamergates are known (*Bothroponera*, *Hagensia*, *Leptogenys*, *Mesoponera*, *Ophthalmopone*, *Pseudoneoponera* and *Streblognathus*; Table 2). Several species in this clade lack queens altogether, while many others lack gamergates. Queens together with gamergates (AQ+G) is a mixed strategy that evolved repeatedly and convergently in *Odontomachus* genus-group. Gamergate reproduction can evolve in a proportion of ponerine genera because workers generally retain an incomplete spermatheca, *i.e.* all the structures are present except various organelles needed for long-term conservation of sperm (Gobin *et al.* 2008). It is likely that genes for these organelles (already expressed in queens) can be expressed in workers whenever gamergate reproduction is selected for.

The retention of sexual ability by various ponerine workers allows the replacement of flying queens. However, in lineages where workers have completely lost the spermatheca, ergatoid (*i.e.* permanently wingless) queens evolved instead (reviewed in Peeters 2012). In *Odontomachus* genus-group, the winged queens of some species have been replaced by ergatoid queens, *e.g.* in *Anochetus*, *Megaponera*, and especially *Leptogenys* (>300 species) (Table 2). *Euponera fossigera* Mayr has small colonies (up to 50 workers) with a single ergatoid queen (Villet 1994). Similarly, *E. zoro* Rakotonirina & Fisher is reported to have ergatoid queens, although more details are required (Rakotonirina & Fisher 2013).

Queens are unknown in most species of *Euponera*

**Table 2.** Species in *Odontomachus* genus group for which reproductive phenotypes are known: AQ (alate queen), EQ (ergatoid queen), G (gamergate), AQ+G (alate queen and gamergate). Most *Leptogenys* species have EQ (e.g. Lattke 2011). Other genera have AQ only (G unknown): *Brachyponera*, *Buniapone*, *Odontoponera*, *Paltothyreus* and *Phrynoponera* (Schmidt & Shattuck 2014).

Genus	Species		Reference
<i>Anochetus</i>	<i>goodmani</i>	EQ	Fisher & Smith 2008
	<i>kempfi</i>	EQ	Torres <i>et al.</i> 2000
<i>Bothroponera sulcata</i> -group	<i>kenyensis</i>	G	C. Peeters unpubl.
	<i>kruegeri</i>	G	Wildman & Crewe 1988
	<i>soror</i>	AQ	Haskins 1941
	<i>tesseronoda</i>	G	Ito 2010
<i>Bothroponera pumicosa</i> -group	<i>cavernosa</i>	G	H. Robertson unpubl.
	<i>comorensis</i>	AQ	C. Peeters unpubl.
<i>Euponera</i>	<i>fossigera</i>	EQ	Villet 1994
	<i>sharpi</i>	AQ	F. Ito unpubl.
	<i>sikorae</i>	AQ+G	This study
	<i>wroughtonii</i>	AQ	Peeters & Crewe 1986
<i>Hagensia</i>	<i>havigandi</i>	G	Villet 1992
	<i>saldanhae</i>	G	H. Robertson & C. Peeters unpubl.
<i>Leptogenys</i>	<i>peuqueti</i>	G	Ito 1997
	<i>schwabi</i>	G	Davies <i>et al.</i> 1994
	<i>unistimulosa</i>	G	Lattke 2011
<i>Megaponera</i>	<i>analis</i>	EQ	Villet 1990a
<i>Mesoponera</i>	<i>australis</i>	AQ	C. Peeters unpubl.
	<i>cafraria</i>	AQ	Villet 1990b
	sp.M4 Gombak	AQ+G	F. Ito unpubl.
<i>Myopias</i>	<i>concava</i>	AQ+EQ	Willey & Brown 1983
<i>Odontomachus</i>	<i>coquereli</i>	EQ	Molet <i>et al.</i> 2007
	<i>pararixosus</i>	EQ	Terayama & Ito 2014
<i>Ophthalmopone</i>	<i>berthoudi</i>	G	Peeters & Crewe 1985a
	<i>hottentota</i>	G	Peeters & Crewe 1985b
<i>Pseudoneoponera</i>	<i>insularis</i>	AQ+G	Ito 1993b
	<i>intermedia</i>	G	C. Peeters unpubl.
	<i>oculata</i>	G	C. Peeters unpubl.
	<i>porcata</i>	G	C. Peeters unpubl.
	<i>sublaevis</i>	G	Peeters <i>et al.</i> 1991
<i>Streblognathus</i>	<i>tridentata</i>	AQ+G	Sommer <i>et al.</i> 1994
	<i>aethiopicus</i>	G	Ware <i>et al.</i> 1990
	<i>peetersi</i>	G	Cuvillier-Hot <i>et al.</i> 2004

(Rakotonirina & Fisher 2013), and it is possible that the winged caste has been permanently replaced by gamergates (or ergatoid queens) in several species. In Ponerinae showing little difference in body size between workers and winged queens, the occurrence of gamergates may be more widespread than is currently known, and needs to be checked with ovarian dissections.

## ACKNOWLEDGEMENTS

The fieldwork and laboratory processing of specimens could not have been completed without the assistance of F. Esteves and the Malagasy Arthropod Team (B. Rajemison, J.-C. Rakotonirina, J.-J. Rafanomezantsoa, C. Ranaivo, H. Rasoazanamavo, N. Rasoamanana, C. Randrianandrasana, and M. Ramamonjisoa). A. Sébastien dissected a

fragment of colony BLF22426. We also thank Ministère de l'Environnement et des Forêts and Madagascar National Parks for authorisation to

collect and export ants. CP is funded by the French National Research Agency (ANTEVO ANR-12-JSV7-0003-01).

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