Ethology Ecology & Evolution 3: 145-152, 1991

Reproduction in ponerine ants without queens: monogyny and exceptionally small colonies in the Australian *Pachycondyla sublaevis*

C. PEETERS [1,3], S. HIGASHI [2] and F. ITO [2]

[1] *School of Biological Science, University of New South Wales, PO Box 1, Kensington NSW, 2033 Australia*

[2] *Graduate School of Environmental Science, Hokkaido University, Sapporo 060, Japan*

Received 19 April 1990, accepted 21 September 1990

Pachycondyla sublaevis may have the smallest colonies yet reported in ants (mean number of adults is 9 ± 2.5 SD per colony; $n = 12$). There are no queens in this ponerine species, and workers are able to mate and reproduce. Dissection of 102 workers from 12 colonies indicated that only one per colony is inseminated and has active ovaries. The mechanism regulating the incidence of mating is not known, although the single gamergate appears to inhibit ovarian activity in her nestmates.

KEY WORDS: ants, Ponerinae, *Pachycondyla*, reproduction, monogyny, queenlessness, gamergates.

INTRODUCTION

Reproductive division of labour is the essence of insect eusociality: only a minority of the adult females reproduce sexually, while others perform helper roles. In the vast majority of ants, these contrasting roles are performed by morphologically-differentiated queens and workers. However, in the primitive subfamily Ponerinae, workers generally have a spermatheca, and in various species they reproduce instead of the queens, which no longer exist. Some species always have only one gamergate

[3] Present address: Zoologisches Institut II der Universität, Röntgenring 10, D-8700 Würzburg, Germany.

(mated, egg-laying worker) per colony (WILDMAN & CREWE 1988, PEETERS & HIGASHI 1989, FUKUMOTO et al. 1989, WARE et al. 1990), while in others there are several to many (HASKINS & WHELDEN 1965, WARD 1983, PEETERS & CREWE 1985, PAMILO et al. 1985, PEETERS 1987).

About half of the Australian species of *Pachycondyla* belong to the *P. rufipes* group, which was formerly considered as the separate genus *Bothroponera* (W.L. BROWN pers. comm.). Little has been published about their ecology or behaviour. *P. sublaevis* and other species have a conspicuous defence mechanism whereby they emit a long thread of proteinaceous foam from the gaster tip (C. PEETERS unpublished data); this is identical to the behaviour described by MASCHWITZ et al. (1981). Queens have not been found in the Australian species of the *P. rufipes* group, whereas at least some south-east Asian species of the same group have winged queens (CHAPMAN & CAPCO 1951). This study aimed to establish some of the characteristics of reproductive division of labour in colonies of *P. sublaevis*, i.e. to determine which workers mate and lay eggs.

METHODS

Eleven nests of *P. sublaevis* were collected from two localities in far north Queensland during 1987 and 1989: Mount Garnet (west of Ravenshoe) (colony codes: ABUE, ABYX); Cape Cleveland Peninsula (50 km east of Townsville) (ABXF, ABXH). An additional nest (ABQN) was collected from Kapalga, Kakadu National Park, Northern Territory. Voucher specimens have been placed in the Australian National Insect Collection in Canberra, and in the Museum of Comparative Zoology at Harvard University.

These ground-dwelling ants occur in dry *Eucalyptus* woodland. Nests were usually found by following solitary foragers that were retrieving insect prey. During excavations, great care was taken to collect all adults and brood.

Adults were dissected in Ringer's solution in order to study their reproductive condition: spermathecae were checked for sperm, and ovaries were examined. Cocoons were opened to sex adults. Seven colonies were kept in the laboratory for several weeks, and oviposition was monitored by counting eggs at various time intervals.

RESULTS

All the colonies collected were very small (mean number of workers 9 ± 2.5 SD; range 7-16; Table 1). Accordingly, little brood was found in most nests. Eggs were not found during the excavation of six colonies, but were later laid in three of these (Table 2). A few males were found in nests excavated in November, December and March, although they did not occur in all colonies then excavated (Table 1). A characteristic of the nests in this species is that the entrance shaft always continued 20-30 cm horizontally before proceeding down (Fig. 1). Up to six chambers were then connected by a single unbranched shaft, and the deepest chamber usually occurred at a depth of 60 cm. One chamber is often filled with refuse, e.g. empty cocoons and discarded prey remains.

A total of 102 workers, representing 94% of the ants collected, were dissected (Table 2), and of these all but five had their spermathecae examined. All workers had a pair of three ovarioles. One inseminated worker was found in each colony, except in

Table 1.
Demographic characteristics of the nests of *P. sublaevis* excavated in the field. Only completely-collected colonies are included.

Date collected (1987, 1989)	Colony code	Workers	Males	Eggs	Larvae	Cocoons
20.03.87	ABQN-1	7	0	3	0	0
15.12.87	ABUE-1	8	0	0	9	0
15.12.87	ABUE-2	9	3*	0	9	9
15.12.87	ABUE-3	9	0	3	6	0
09.03.89	ABXH-2	10	2*	0	1	3
09.03.89	ABXH-3	7	0	0	0	0
10.03.89	ABXF-2	8**	0	0	0	0
22.11.89	ABYX-2	8	0	5	7	5
22.11.89	ABYX-3	16	1	1	5	15
22.11.89	ABYX-4	9	2	5	12	1
24.11.89	ABYX-5	11	0	8	10	5
24.11.89	ABYX-6	7**	0	0	0	0

** No gamergate found (see Table 2); * a proportion of the cocoons also yielded males.

Table 2.
Reproductive status of workers belonging to the 12 nests listed in Table 1. All but 5 of the workers dissected were checked for sperm. «Active ovaries» consisted of enlarged ovarioles containing *yolky* oocytes of various sizes (and usually at least one was mature). Other workers dissected had ovaries that were either completely undeveloped, or contained only a few small partly-yolky or transparent oocytes.

Colony code	Workers found in nest	Workers dissected	Workers with active ovaries		Eggs laid in lab.
			mated	unmated	
ABQN-1	7	6	1	0	2
ABUE-1	8	8	1	0	3
ABUE-2	9	8	1	0	0**
ABUE-3	9	6	1	0	9
ABXH-2	10	8	1	1	2
ABXH-3	7	7	1	0	3
ABXF-2	8	8	0	1	0
ABYX-2	8	8	1	0	*
ABYX-3	16	16	1	0	*
ABYX-4	9	9	1	0	*
ABYX-5	11	11	1	0	*
ABYX-6	7	7	0	1	*

** However gamergate had 2 mature oocytes in her ovaries; * these ants were dissected immediately after excavation.

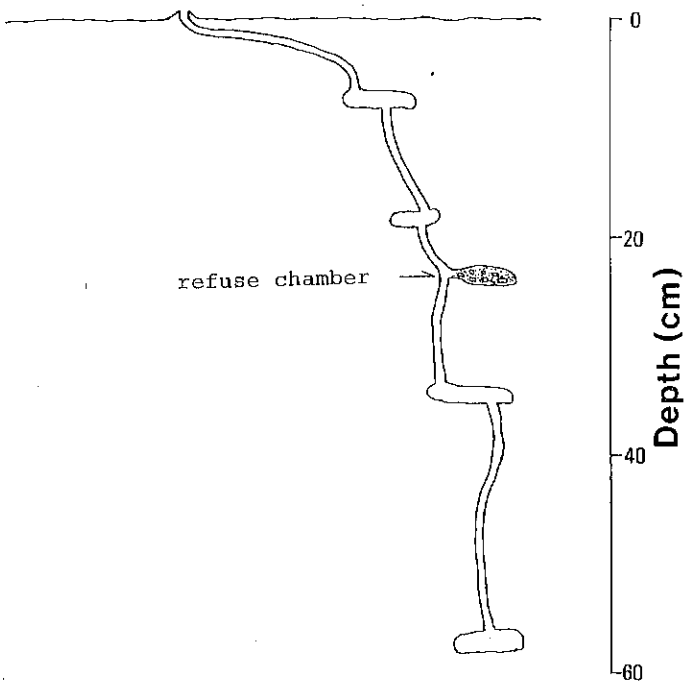

Fig. 1. — Architecture of nest ABYX-5, with chambers at different depths connected by a single unbranched shaft.

ABXF-2 and ABYX-6 (see below). Mated workers all had enlarged active ovaries with conspicuous yellow bodies (which accumulate when eggs are laid), and are thus the gamergates. However three of these lacked yolky oocytes at the time of dissection, although they had previously laid eggs in the laboratory. The eggs are extremely large (2.7 × 0.9 mm), and only a maximum of one or two mature basal oocytes were present in the ovaries of individual gamergates. Individual ovarioles seldom contained more than one large yolky oocyte, together with nurse cells and non-yolky oocytes (Fig. 2).

Most unmated workers had completely undeveloped ovaries, although a few had several ovarioles swollen at the bases and containing small non-yolky oocytes. Undeveloped ovarioles were considerably shorter than ovarioles containing yolky oocytes. Three unmated workers had more active ovaries (Table 2), and these are detailed below.

Colonies ABXF-2 and ABYX-6 were unusual because there was no brood, and the nests were shallow (in ABYX-6, a single chamber occurred at a depth of 18 cm). No gamergate was found, but in each colony one virgin worker had enlarged ovarioles containing partly-yolky oocytes and nurse cells. All other workers had undeveloped ovarioles. There was a mound of freshly-excavated soil outside the entrance of nest ABXF-2, and continuous digging activity, which suggested that the ants had recently moved there.

Colony ABXH-2 had a gamergate, but one unmated nestmate had ovaries with

one mature oocyte and two smaller yolky oocytes (and extremely faint yellow bodies). Another two nestmates exhibited more limited oogenesis. The gamergate lacked any yolky oocytes in her ovaries, although the presence of many yellow bodies indicated that she had actively oviposited in the past.

Colony ABUE-3 was experimentally-divided in two groups (3 and 4 workers), and oviposition monitored for a month. Eggs were only laid in the group in which the gamergate was later dissected, although one worker in the other group exhibited distinct oogenesis in all ovarioles, with two small yolky oocytes in one ovary.

DISCUSSION

Excluding social parasites, the colonies of *P. sublaevis* are possibly among the smallest of all ants (see table 3-2 in HÖLLDOBLER & WILSON 1990). Ponerine ants without queens characteristically have colonies consisting of 50-200 workers (table 1 of PEETERS 1990), and thus those of *P. sublaevis* are even smaller. Two other ponerine species with queens have comparable colony sizes: *Hypoponera coeca* in Africa have an average of 20 workers (LÉVIEUX 1967), and *Amblyopone pallipes* in North America have 9-15 workers (although these may represent sub-units of a large subterranean population; TRANIELLO 1982).

Queens have never been found in *P. sublaevis*, and instead some of the workers reproduce sexually. This is also the case in two closely-related species (C. PEETERS unpublished data). There is always only one inseminated worker in each colony, and she is also the only individual with active ovaries (and conspicuous yellow bodies). The mechanisms regulating the presence of only one gamergate in each colony are unknown, but there may be two components: (1) control of the incidence of mating; (2) control of ovarian activity. Although other monogynous queenless species have been studied, a mechanism of reproductive dominance has only been detailed in *Diacamma australe* and *D. rugosum*, in which mating is conditional on the retention of a pair of unique bladder-like appendages on the thorax (PEETERS & HIGASHI 1989, FUKUMOTO et al. 1989, PEETERS & BILLEN 1991).

In *P. sublaevis*, in all but one (ABXH-2) of the colonies with a gamergate, unmated workers all had undeveloped ovaries (Table 2). In contrast, in the colonies without a gamergate, there was one unmated worker with active ovaries (although no oviposition occurred). These data suggest that the single gamergate inhibits the ovarian activity of her unmated nestmates. In colony ABXH-2, an unmated worker with active ovaries cohabited

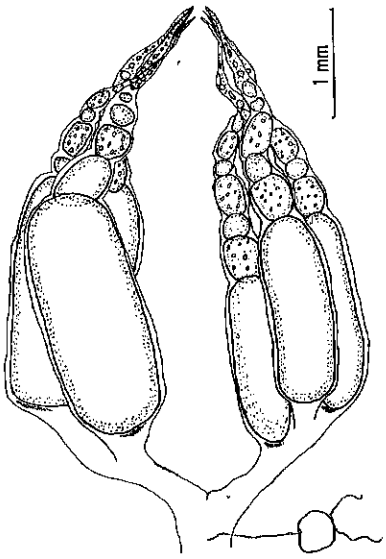

Fig. 2. — Characteristics of the active ovaries of the gamergate collected in colony ABYX-4. Large yolky oocytes occur at the base of the ovarioles, followed by alternating developing oocytes and nurse cells.

with the gamergate, but the latter seemed not to be laying eggs any longer, and thus inhibitory ability may decrease with a drop in fecundity. Casual laboratory observations failed to reveal any aggressive interactions between workers in the nests, and thus a volatile primer pheromone may be involved.

The colonies collected in this study were remarkably constant in size, with the exception of ABYX-3 (Table 1). This indicates that budding becomes likely once a colony exceeds a certain size. Budding may provide the opportunity for the differentiation of a new gamergate, because workers are then no longer inhibited (this also occurs following the natural death of a gamergate). Thus in newly-budded groups of workers lacking a gamergate such as ABXF-2 and ABYX-6, one unmated worker had developed ovaries. This individual may consequently become sexually-attractive when foreign males visit the nests, and mate to the exclusion of others. In *Streblognathus aethiopicus*, when a group of workers had been isolated without the gamergate, a few individuals with active ovaries positioned themselves outside the nest and «called» for males (WARE et al. 1990).

In *P. sublaevis*, gamergates laid an average of 0.5 eggs/day, and this low fecundity seems a direct consequence of the small number of ovarioles and the very large size of eggs. There is also fragmentary evidence that gamergates do not lay eggs continuously. Indeed, several colonies collected in the field did not yield any eggs (Table 1), and there were no mature oocytes in some of the gamergates dissected. The occurrence of a cyclical pattern of oviposition appears to be a further cause of the tiny size of colonies. Gamergate fecundity varies between ponerine species, and indeed monogynous colonies exhibit a marked range of sizes (PEETERS 1990). For example, in *Diacamma australe*, which is also monogynous, colonies have 139 ± 61 SD workers (PEETERS & HIGASHI 1989).

The eggs of *P. sublaevis* are exceptionally large. To our knowledge they are the largest recorded in ants. We would expect that selection on females to maximize fecundity would reduce egg size to the minimum viable size, irrespective of adult body size (WIKLUND et al. 1987). Workers in *P. sublaevis* are large (14 mm in length), but it is not possible to establish whether the eggs are scaled to body size since comparative data on the relationship between egg weight and adult worker weight in the Ponerinae are lacking. Consequently it is not clear whether the gamergate's ability to achieve high fecundity is constrained as a result of either adaptive adjustment of egg size or nonadaptive allometry (WIKLUND et al. 1987).

It is counter-intuitive that there should exist in ants a positive correlation between egg size and offspring fitness, as larvae hatch in a social environment where workers care and feed them. However, since ponerine workers cannot feed the larvae by trophallaxis, and the latter must feed on pieces of prey, larger first instar larvae may be more viable. Nonetheless there exist many ponerine ants with small eggs. We speculate that the large size of eggs is not the result of selection, but further studies should consider whether it is adaptive in *P. sublaevis* to produce larger first instar larvae as a protection against a fluctuating trophic flow into the nest, i.e. bigger first instar larvae would survive better during a temporary food shortage. It seems clear that the limited fecundity of gamergates in *P. sublaevis*, together with the strict monogyny observed, are the principal proximate causes for their exceptionally small colonies.

ACKNOWLEDGMENTS

We thank Bill Brown and Bob Taylor for identifying the ants, as well as Alan Andersen, Bill Brown, Ross Crozier and Penny Kukuk for comments on this manuscript. C. Peeters is grateful to Jay Evans for his enthusiastic help during nest excavations near Townsville, and to Alan Andersen for organizing accommodation at the CSIRO research station in Kakadu National Park. This work was supported by an Australian Research Council grant to R.H. Crozier, and by the Japan Ministry of Education, Science and Culture.

REFERENCES

CHAPMAN J.W. & CAPCO S.R. 1951. Check list of the ants (Hymenoptera: Formicidae) of Asia. *Monographs of the Institute of Science and Technology, Manila* 1: 1-327.

FUKUMOTO Y., ABE T. & TAKI A. 1989. A novel form of colony organization in the «queenless» ant *Diacamma rugosum*. *Physiological Ecology Japan* 26: 55-61.

HASKINS C.P. & WHELDEN R.M. 1965. «Queenlessness», worker sibship and colony vs population in the formicid genus *Rhytidoponera*. *Psyche* 72: 87-112.

HÖLLDOBLER B. & WILSON E.O. 1990. The ants. *Cambridge: Harvard University Press.*

LÉVIEUX J. 1967. Recherches écologiques dans la savane de Lamto (Côte d'Ivoire): données préliminaires sur le peuplement en fourmis terricoles. *La Terre et la Vie* 3: 278-296.

MASCHWITZ U., JESSEN K. & MASCHWITZ E. 1981. Foaming in *Pachycondyla*: a new defence mechanism in ants. *Behavioral Ecology and Sociobiology* 9: 79-81.

PAMILO P., CROZIER R.H. & FRASER J. 1985. Inter-nest interactions, nest autonomy, and reproductive specialization in an Australian arid-zone ant, *Rhytidoponera* sp. 12. *Psyche* 92: 217-236.

PEETERS C. 1987. The reproductive division of labour in the queenless ponerine ant *Rhytidoponera* sp. 12. *Insectes Sociaux* 34: 75-86.

PEETERS C. 1990. La reproduction chez les fourmis ponérines. *Actes des Colloques Insectes Sociaux* 6: 195-202.

PEETERS C. & BILLEN J. 1991. A novel exocrine gland inside the thoracic appendages («gemmae») of the queenless ant *Diacamma australe*. *Experientia* 47 (in press).

PEETERS C. & CREWE R. 1985. Worker reproduction in the ponerine ant *Ophthalmopone berthoudi* — an alternative form of eusocial organization. *Behavioral Ecology and Sociobiology* 18: 29-37.

PEETERS C. & HIGASHI S. 1989. Reproductive dominance controlled by mutilation in the queenless ant *Diacamma australe*. *Naturwissenschaften* 76: 177-180.

TRANIELLO J.F. 1982. Population structure and social organization in the primitive ant *Amblyopone pallipes* (Hymenoptera: Formicidae). *Psyche* 89: 65-80.

WARD P.S. 1983. Genetic relatedness and colony organization in a species complex of ponerine ants I. Phenotypic and genotypic composition of colonies. *Behavioral Ecology and Sociobiology* 12: 285-299.

WARE A.B., COMPTON S.G. & ROBERTSON H.G. 1990. Gamergate reproduction in the ant *Streblognathus aethiopicus* Smith (Hymenoptera: Formicidae: Ponerinae). *Insectes Sociaux* 37: 189-199.

WIKLUND C., KARLSSON B. & FORSBERG J. 1987. Adaptive versus constraint explanations for egg-to-body size relationships in two butterfly families. *American Naturalist* 130: 828-838.

WILDMAN M.H. & CREWE R.M. 1988. Gamergate number and control over reproduction in *Pachycondyla krugeri* (Hymenoptera: Formicidae). *Insectes Sociaux* 35: 217-225.