Social organization of *Platythyrea lamellosa* (Roger) (Hymenoptera: Formicidae): I. Reproduction

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Colonies of *Platythyrea lamellosa* contained 18–276 workers, but no queens were found. Dissected workers had five to nine ovarioles per ovary, the two ovaries of an individual often differing. In each of the colonies examined, only one worker was inseminated, and it was the only individual that laid diploid reproductive eggs. Virgin workers showed partial development of their ovaries and oocytes, but these appeared to regress with age, and they never laid eggs. Mating was not a prerequisite for reproductive dominance, since a single, young, virgin worker assumed the role of the mated worker when the latter was removed from its colony. Adult males are present in the population for most of the year, but are especially common during summer.

Kolonies van *Platythyrea lamellosa* het 18–276 werkers bevat, maar geen koninginne is gevind nie. By ontleding is gevind dat werkers vyf tot nege eierstroke in elke eierstok het en dat die twee eierstokke van 'n individu dikwels verskil het. In elke kolonie wat ondersoek is, was net een werker bevrug, en sy was die enigste individu wat diploïde eiers gelê het. Onbevrugte werkers se eierstokke en oösiete was gedeeltelik ontwikkel maar regressie het blykbaar met ouderdom plaasgevind en hulle het nooit eiers gelê nie. Paring was nie 'n voorvereiste vir reproduktiewe dominansie nie, want 'n enkele, jong, onbevrugte werker het die rol van die bevrugte werker oorgeneem toe dié uit die kolonie verwyder is. Volwasse mannetjies het die hele jaar voorgekom, maar was veral gedurende die somer volop.

Although many species of ants in the subfamily Ponerinae are queenless, eusociality has been maintained because the role of reproduction has been assumed by inseminated workers (Peeters & Crewe 1985; Fukumoto, Abe & Taki 1989; Peeters & Higashi 1989; Villet 1989a). Initial studies of species with gamergate (= mated worker) reproductives revealed a number of similarities between species. Reproduction was found to be carried out by a number of mated workers which were not given preferential treatment by other workers; no dominance hierarchies or inhibition of laying were apparent; and only those workers that were inseminated reproduced (Ward 1983; Peeters 1987; Peeters & Crewe 1985). Subsequently, Wildman & Crewe (1988) described a gamergate breeding system in *Pachycondyla krugeri* which differed from those previously studied in that there was only one gamergate per colony. This study suggested that these mated workers inhibited reproduction by other workers. Similarly, in *Diacamma australe* and *D. rugosum* reproductive inhibition is achieved by the removal of the thoracic appendages of all newly eclosed individuals by the reproductive worker that alone retains them and is inseminated (Peeters & Higashi 1989; Fukumoto *et al.* 1989). The extent to which mated workers can mimic the attributes of a queen, as is the case in *P. krugeri* (Wildman & Crewe 1988) and *Streblognathus aethiopicus* (Ware, Compton & Robertson 1990), can be detemined only by thorough investigations of additional species.

The absence of a queen caste in *Platythyrea* sp. A and *P. schultzei* (Villet 1989a; 1991) indicated that this was a suitable genus for studies of reproduction by mated workers. The species selected for this investigation was *Platythyrea lamellosa*. The workers are black, 13 mm long and walk with their gasters curled downwards. They inhabit the drier regions of South Africa, Botswana, Zimbabwe and Zaire (Wheeler, Bequart, Bailey, Santschi & Mann 1922) and are often noted for the fine gravel gathered on the mounds about their nest entrances (Arnold 1915). A number of races and varieties have been named (Wheeler *et al.* 1922), but they are currently treated as redundant taxa (Brown 1975; Bolton pers. comm.). A queen caste has been reported from one of the varieties (Forel 1913).

Materials and Methods

Whole colonies, including foragers, were obtained from three localities: Quiet Waters Farm, Esigodini (20°17′S/28°55′E), Zimbabwe, Tosca (25°53′S/23°58′E), South Africa, and Dunstable Farm, 30 km west of Hoedspruit, (24°28′S/30°43′E), South Africa. Voucher specimens (Esigodini: SAM-HYMC000530; Tosca: SAM-HYMC001332) are deposited with the South African Museum, Cape Town. The external morphology of all colony members was examined for qualitative indications of caste, such as (traces of) ocelli or flight sclerites (Villet 1989b). The numbers of each caste, sex and brood stage were counted soon after collection.

Observation colonies were housed in the laboratory in modified, soil-filled, four-chambered Lubbock nests placed in wooden arenas covered with sheets of glass that prevented disturbances caused by air movements such as human breathing. Water was provided in a shallow dish, and an ample supply of small insects such as cockroaches, wax moth larvae and mealworm beetles was offered as food.

The reproductive organs of ants from 11 nests were dissected in Ringer's solution and stained with methylene blue. The number of ovarioles in each ovary was counted and the length of the longest one and the largest oocyte (if any) measured using a Wild M3 stereo microscope and an Olympus OSM optical micrometer. The presence and state of corpora lutea were noted. Spermathecae were crushed between a slide and coverslip and examined under a Leitz Labrolux 11 phase contrast microscope for spermatozoa.

The smallest distance between the eyes (interocular width) of ants from four nests was measured with the same micrometer.

The effects of removing the mated worker from a colony were experimentally investigated. Members and brood of two whole colonies were subdivided to make five equal-sized sub-colonies. They were housed separately in the laboratory and fed liberally. Four weeks later all of the ants were dissected to examine their reproductive organs.

Results

In the field, ants from different wild nests readily responded to ants from other nearby nests by attacking them. Such qualitative trials indicated that each colony occupied a single nest. Colonies contained 18–276 members (Table 1), but no queen caste, alate or otherwise, was found in any of the nests.

The number of ovarioles in each ovary varied from five to nine, with a mean between six and seven, and 39% of the workers had left and right ovaries that differed. Workers appeared to undergo a cycle of ovarial development as they aged (Table 2). Ovariole length increased from a mean of 0,78 mm at eclosion to a maximum of 2,21 mm in ants tending cocoons, and then regressed to a mean of 0,90 mm in foraging ants. Oocytes were largest in young, sclerotized workers (maximum length = 0,36 mm) and absent in the oldest foragers. Small, mustard-yellow smudges, which were probably corpora lutea, were present near the bases of ovarioles in a third of the non-callow workers, including all of the ants with oocytes and some of the older foragers lacking oocytes.

Table 1 Composition of 25 *P. lamellosa* colonies. * = eggs present, but not counted; ? = workers not dissected

Date	Locality	Workers		Males	Eggs	Larvae	Cocoons
		Mated	Total				
01/87	Esigodini	?	256	12	*	42	165
01/87	Esigodini	?	250	28	*	28	66
01/87	Esigodini	?	225	33	*	39	12
01/87	Esigodini	?	218	15	*	52	117
01/87	Esigodini	1	203	24	*	43	98
01/87	Esigodini	0	87	0	*	40	95
01/87	Hoedspruit	1	62	1	*	29	33
01/87	Hoedspruit	1	46	1	*	14	20
04/87	Esigodini	?	276	3	*	14	58
04/87	Esigodini	?	169	0	*	12	12
04/87	Esigodini	?	167	2	*	18	45
04/87	Esigodini	?	158	5	*	23	16
04/87	Esigodini	?	98	0	*	10	9
06/88	Tosca	1	50	1	0	11	0
06/88	Tosca	1	38	5	0	18	6
06/88	Tosca	1	37	0	0	0	0
06/88	Tosca	1	18	0	0	0	0
09/87	Esigodini	1	110	1	*	18	24
09/87	Esigodini	0	84	0	*	15	13
09/87	Esigodini	1	63	0	*	16	1
09/87	Esigodini	0	20	0	*	31	0
10/88	Tosca	1	33	0	*	23	49
10/88	Tosca	1	42	0	*	17	56
10/88	Tosca	1	54	1	*	11	67
10/88	Tosca	1	104	1	*	26	39

Table 2 Ovarian characteristics of virgin workers of *Platythrea lamellosa* filling different roles

Worker category	Ovariole length (mm)			% Workers with oocytes	Mean oocyte length	% Workers with corpora lutea
	n	range	mean			
Callow	13	0,44–1,72	0,78	0	–	0
Tending larvae	10	0,49–1,92	1,28	50	0,31	20
Tending cocoons	18	0,39–2,21	1,09	50	0,28	33
Foragers	25	0,44–1,92	0,90	28	0,25	32

Table 3 Percentage of adults that were males in colonies collected at different times of year, and percentage of cocoons that were male

Month collected	Number of colonies	Males as % of adults		% of cocoons containing males
		mean	range	
January	7	6,9	(1,6–12,8)	12
April	5	1,1	(0–3,1)	3
June	4	3,4	(0–11,6)	0
September	4	0,2	(0–0,9)	0
October	4	0,7	(0–1,8)	0

No more than one worker in each nest was mated, and its ovaries were much longer, with more developed oocytes, than those of virgin workers. Its spermatheca was noticeably whiter than those of unmated workers, and engorged with live sperm. The ovarioles were elongated to a length of about 3 mm, and contained oocytes up to 0,94 mm long. The eggs in the nest measured 0,89 (*S.D.* = 0,03 mm; $n = 56$ from five nests). Well-defined, elongated, bright yellow corpora lutea were present, near the base of the ovarioles. The numbers of ovarioles and the density of tracheoles serving them were similar to the condition in virgin workers. The cuticle of mated workers was soft, like that of partially sclerotized callow workers. The mean interocular width of mated workers was not statistically different from that of the workers (*t* test for equal variances, $t = 2{,}5087$; $p = 0{,}0127$).

Examination of the five equal-sized sub-colonies after four weeks, showed that all but one ant in each sub-colony had poorly developed oocytes and ovarioles which were less than 1,5 mm long. Two of the ants with well-developed ovarioles were mated, and were certainly the reproductives of the parental nests. The three other ants were unmated, and their ovarioles were at least 2,1 mm long and contained developing oocytes. These ants were sclerotized and fully pigmented, indicating that they were at least two weeks old, but unmarked, showing that they were no older than seven weeks.

Sexing of the pupae from cocoons (Table 3) indicated that

12% of them were males in January and 3% in April. At the three other times of the year when colonies were sampled, no males were found in cocoons. In addition, the largest number of adult males was encountered in colonies collected in January. Males are produced in these colonies from at least December to April, with adult males being present in the colonies predominantly during the summer months.

Discussion

A queen caste was clearly absent in the colonies excavated for the present study, and the reproductive role appears to be undertaken by a single mated worker in each nest. In this respect the social organization of this species is similar to that of *Pachycondyla (= Bothroponera,) krugeri* (Wildman & Crewe 1988), *Diacamma rugosum* (Fukumoto *et al.* 1989), *D. australe* (Peeters & Higashi 1989), *Dinoponera quadriceps* (Dantas de Araujo, Fresneau & Lachaud 1988), *Platythyrea schultzei* (Villet 1991), *P. sp. A* (Villet 1989a) and *Streblognathus aethiopicus* (Ware *et al.* 1990). The colonies in which no mated workers were found were excavated from hard, rocky soils veined with schists and were probably not dug out completely. Two of these three nests were unusually small compared to others collected from the same site in the same month (Table 1), supporting this interpretation. Alternatively, they might be fragments of colonies that had undergone fission, and that the mated workers accompanied other colony fragments.

At odds with the findings of this study is Forel's (1913) description of a queen under the taxon *Platythyrea lamellosa longinoda* var. *rhodesiana*, which is now regarded as a synonym of *P. lamellosa* (Brown 1975). The specimen differed from workers in being larger (14 mm as against 12–13 mm), and in having broader and more pronounced epinotal teeth than workers. Forel also noted 'Les ailes manquent' (wings missing), which Arnold (1915) translated as 'Deälated'. If Forel intended to describe a queen that never had wings, rather than one that had shed its wings, as Arnold's translation implies, the specimen might be an ergatoid, or worker-like, queen. However, no evidence of such queens was found in this study: reproductively active colony members were not larger than their nestmates (Figure 1), and they lacked any distinctive features. Furthermore, epinotal structure is a variable character in this species (Arnold 1915), and apart from the slight difference in epinotal structure, there are no characters (Villet 1989b) that might indicate that Forel's specimen is an ergatoid queen. It is probably only an isolated specimen of a geographically variant worker, accorded the taxonomic status of a queen owing to a lack of comparative material, and because of its large size, rather than from any knowledge of its reproductive abilities.

The results of the two manipulation experiments suggest that reproductive status in *P. lamellosa* is regulated by ovarian development. In the experimental sub-colonies lacking a mated worker, a single ant underwent extensive ovarian development, while its nestmates showed only slight development. Only one worker in each fragment had developed ovaries containing mature oocytes; the remaining ants showed levels of ovarian activity and development typical of virgin workers in intact colonies. Similar events, sometimes involving two or three young virgin workers, followed the removal of mated workers from colonies of *Platythyrea schultzei* (Villet 1991), *Streblognathus aethiopicus* (Ware *et al.* 1990) and *Pachycondyla krugeri* (Wildman & Crewe 1988). It appears that a young worker which was undergoing ovarial development when the mated worker was removed out-competes its nestmates in some way which results in its ovaries producing reproductive eggs. This simultaneously confers control over the colony's reproduction. Pheromones are probably involved, since no significant interactions between workers (Villet 1990) were seen during the experiments.

Oviposition by virgin workers in the presence of a mated worker has been completely suppressed in *P. lamellosa*, although ovarial activity follows a cycle of development normal in ponerines and other ants (e.g. Billen 1982; Fresneau 1984; Peeters 1987). The mustard-coloured tissue in the ovaries of unmated workers did not resemble the corpora lutea in the ovaries of the mated worker, which were larger and a brighter yellow. The corpora lutea of virgin workers may be the remains of resorbed oocytes, since there was no evidence that workers laid eggs, trophic or otherwise. Similar structures were described following oocyte resorption in workers of *Formica sanguinea* (Billen 1982). Thus the presence of corpora lutea in the ovarioles does not always imply oviposition, but there might be qualitative differences between these bodies in mated and unmated workers which can be correlated with the fate of the oocytes.

From the limited data available, male production peaks during the summer months of January–April. This pattern of male production is similar to that of *Ophthalmopone berthoudi* (Peeters & Crewe 1985). In both species there is a seasonal pulse of male production with males being present in colonies for large periods of the year.

The significance of this seasonality in male production in queenless species is obscure, but may be related to the foundation of new colonies by fission. If colonies split owing to vigorous growth in summer, only one daughter colony will contain a mated worker. Young virgins in the other fragments may become reproductively dominant, and receptive to male courtship. This model is largely speculative owing to the scarcity of apposite evidence.

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