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Queenright and queenless breeding systems within the genus *Pachycondyla* (Hymenoptera: Formicidae)

by

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The reproductive biologies of two species of *Pachycondyla* are contrasted. A nest of *P. wroughtoni* (Forel) that was excavated contained a mated dealate queen, but nests of *P. krugeri* Forel lacked any female sexuals. This queenless breeding system was investigated by examining the ovaries and spermathecae of a sample of workers from different nests. A significant proportion of the workers dissected had developing oocytes in their ovarioles, but only two workers had oocytes that were as large as the eggs laid in the nests. The remainder of the workers in the samples examined had undeveloped ovaries. The only individuals which had sperm in their spermathecae were the ones with mature oocytes. These are thought to be gamergates. This is the second report of the occurrence of both queenright and queenless breeding systems in a single genus.

INTRODUCTION

Modifications of the eusocial reproductive pattern are exhibited by a substantial number of ponerine ants. While winged or wingless (=ergatoid) queens occur in some species of this phylogenetically ancient subfamily, in others they have been replaced by mated laying workers (=gamergates, Peeters & Crewe 1984, 1985a & b). The nature of reproductive specialization in females has not previously been documented in *Pachycondyla*, which is a large paraphyletic genus in the sub-tribe Poneriti.

In this paper we contrast the reproductive systems of *P. wroughtoni* (Forel) and *P. krugeri* Forel. These two species were placed in different genera by Arnold (1915). However, Brown (pers. comm.) suggested that they should be placed in the same genus. He indicated that *P. wroughtoni* exhibited generalized external characters, and was thus more primitive than *P. krugeri*. This work was undertaken in order to extend our understanding of the reproductive division of labour in the ponerines.

MATERIALS AND METHODS

A nest of *Pachycondyla wroughtoni* was collected from forest litter in Knysna (southern Cape), in April 1982. The adult and brood numbers were not recorded. Two nests of *P. krugeri* were excavated in the following locations: (1) Mkuzi Game Reserve, northern Natal, in July 1983; (2) Hoedspruit, eastern Transvaal, in October 1984. Care

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was taken to collect every adult and most of the brood. In addition, a group of workers and brood was collected from Mkuzi during an above ground nest emigration in October 1981. A sample of the ants in each nest was dissected in order to examine ovaries and spermathecae. Eggs and large oocytes were measured with a micrometer eye-piece. Some of the cocoons were opened to study the developmental stage and sex of the pupae. One nest of *P. krugeri* was maintained in the laboratory for a few days, with live termites being supplied as a source of food. Oviposition was monitored.

RESULTS

Reproductive activity in *P. wroughtoni*

One dealate queen was found in the nest excavated. This individual had four ovarioles/ovary, each with a long string of developing oocytes. Mature oocytes were present at the BASE of most ovarioles. The spermatheca was conspicuous and packed with sperm. Dissection of a number of workers from this colony revealed that they had ovaries. These were completely undeveloped with no oogenesis. There also seemed to be four ovarioles in each ovary, but this was often difficult to determine (the individuals in this species are very small). The spermathecae were not easily found, since when empty they are generally inconspicuous. More workers would need to be dissected in order to establish the existence of queen inhibition on worker laying.

Reproductive activity in *P. krugeri*

There were relatively small numbers of adult workers in the various nests excavated (Table 1). Eggs, larvae and cocoons were found in each of the nests. The composition of the brood in July 1983 (26 eggs, only 4 larvae and 4 cocoons) suggests that there may be a certain seasonality in egg laying.

The cocoons collected (4 in July 1983, 10 in October 1984) were opened, and none contained male pupae. Adult males (2) were only found in the October 1984 nest (an additional nest excavated in September 1980 yielded no males). Flying males were collected in Mkuzi (at night) in March 1981 and October 1982, but the peak period of male activity is likely to be in summer.

Neither winged females nor ergatoids were found in any of the nests examined. Eggs were laid while a group of workers was kept in the laboratory, but the reproductive individuals could not be recognized by visual inspection. All the workers dissected had four ovarioles/ovary. A large proportion of these workers exhibited distinct ovarian activity, ie. there were opaque (yolky) oocytes in their ovaries. Such ants could be grouped into two categories (Table 1):

(a) With ovaries containing mature and immature oocytes. The former were measured and compared with eggs collected from the nests (October 1984 nest, mean egg length 1,57 mm, N=12), and they were found to be of the same size. Only two workers were placed in this category, and each of their ovarioles was packed with large oocytes as well as others of intermediate sizes. They were both inseminated.

(b) With ovaries containing immature oocytes only. Many of these ants had a number (1–3) of 'large' elongated oocytes in their ovarioles. However, these oocytes never reached the size of eggs, the longest having mean lengths of 0,94 mm (N=11, upper end of range was 1,03 mm). Two-thirds of these individuals were checked for insemination, and they all had empty spermathecae.

TABLE 1. Reproductive status (determined by ovarian and spermathecal dissection) of samples of *P. krugeri* workers collected from three different colonies. The two workers with mature oocytes were found to be inseminated, and were thus gamergates.

	Adult workers found in nests	Workers dissected	Workers with inactive ovaries	Workers with immature oocytes	Workers with mature oocytes	Workers checked for sperm
nest emigration						
October 1981	28*	15	12	2	1	2
July 1983	50	27	9	18	0	10
October 1984	67	55†	11	43	1	38

*This group of workers was collected above ground, and does not represent a whole colony.
†There were three callows in the nest that were not included in this total. These were not dissected, because earlier results showed this class of ants to have inactive ovaries.

The ovaries of the remaining nestmates either only contained small transparent (ie. without yolk deposits) oocytes, or were completely undeveloped (and there was often definite resorption). Of the 11 such ants found in October 1984, 4 were active outside the nest and 3 were callows. One-sixth of the ants with inactive ovaries had their spermathecae checked, and all were empty.

DISCUSSION

While there is the conventional queenright system of reproductive differentiation in *P. wroughtoni*, the colonies of *P. krugeri* lack queens. All brood stages were found in each of the three nests of *P. krugeri* collected, and thus the progeny must be produced by some of the workers. Only mated workers had mature oocytes (ie. as large as eggs) in their ovaries (Table 1), and these seemed to be the only members of the colony capable of laying eggs. Many of the unmated young workers (age determined behaviourally as a function of polyethism: they were not active outside the nests) had yolky oocytes of various sizes in their ovaries, but these had never reached maturity in the samples dissected. Older workers that were active outside the nests had inactive ovaries in which resorption of oocytes had occurred. Consequently it appeared that unmated workers produced neither diploid individuals through thelytokous parthenogenesis, nor males. Haploid eggs must be laid (at the appropriate time of the year) by the gamergates.

Structural differences were not detected between the ovaries of gamergates and those of functionally sterile workers. There were no morphologically distinct castes in *P. krugeri*, but the ovaries in the two mated workers in addition to producing fully mature oocytes, had greater numbers of large elongate oocytes in the ovarioles than in the unmated workers. Reproductive differentiation among the workers appeared to be controlled by mating alone. The correlation of insemination with the ability to lay eggs has also been demonstrated in *Ophthalmopone berthoudi* Forel (Peeters and Crewe 1984, 1985a). In contrast to *P. krugeri*, the unmated workers of that species do not show any significant ovarian development. Similarly, in the *Rhytidoponera impressa* group, only a small number (8/139) of unmated workers with well developed ovaries were found (Ward 1983), while in *Rhytidoponera* sp. 12, Pamilo *et al.* (1985) reported that unmated workers from the lower regions of the nest have 'high levels' of ovarian activity. These authors measured ovarian activity in terms of the number of empty ovarioles, which

may give a different impression than a classification based on the size and number of oocytes in the ovarioles. It is not known whether the unmated workers of *Rhytidoponera* sp. 12 produce offspring. Pamilo *et al.* (1985) suggested that these oocytes may be destined to become trophic eggs. We think that if the immature oocytes were laid as trophic eggs in *P. krugeri*, they would be recognizable in the nest by their smaller size. However, all the eggs that were found were very similar in length (range 1,49–1,64 mm). Moreover, trophic eggs are not generally thought to be a feature of ponerine societies. The oogenesis seen in unmated workers may be a consequence of the relaxation of queen inhibition of ovarian activity in a society in which this cast has been lost. Other explanations for this phenomenon are possible, and it requires additional investigation.

The apparent occurrence of only one gamergate in both the October 1981 and 1984 colonies (Table 1) could be the result of sampling the workers to be dissected. No gamergates were found in the July 1983 nest, but there were eggs, larvae, worker pupae and callows. This indicates that the individual(s) that laid the fertilized eggs had either died recently or were not included in the sample dissected (only 54% of the nest population). Gamergate numbers can only be established by dissection of all individuals in the colony, and we suggest that there is normally more than one gamergate in each nest. This is based on evidence from other species with gamergate reproductives. While large numbers of mated workers have been found in the nests of *O. berthoudi* (e.g. up to 108 gamergates, representing 45% of a nest sample; Peeters and Crewe 1985a), this may not be typical of other queenless ponerines. There were 23 mated workers in a nest of *Rhytidoponera* sp. 12 (Pamilo *et al.* 1985), and a maximum of 15 in nests of the *R. impressa* complex (Ward 1983). Numbers of mated workers in colonies are influenced by the colonies individual past histories, and may thus vary within a population (Peeters and Crewe 1985a). There is no indication that the size of reproductive populations is regulated in each nest (either by the gamergates themselves, or by the other workers), and thus attempts at interspecific comparisons may be futile. However, the apparent loss by the unmated workers in queenless ponerines of their potential for producing males is enigmatic, because this ability exists in queenright species, eg. *Rhytidoponera purpurea* (Haskins & Whelden 1965).

If we assume that the loss of the queen caste is adaptive, its occurrence in only certain species of *Pachycondyla* may indicate the nature of some of the selection pressures involved. Thus we can try to link the absence of queens in *P. krugeri* with some aspects of its biology. It has been suggested (Peeters & Crewe, in prep.) that there is a relationship between extreme prey specialization, a simple foraging system, a seasonal food shortage, and queenlessness. *P. krugeri* has these characteristics since it feeds predominantly on termites, although it opportunistically takes other prey; foragers hunt alone and do not use trails on the substrate for recruitment (tandem running is used during nest emigrations only); and this species occurs in semi-arid habitats, where certain prey items may be difficult to find during the dry winters. In contrast, *P. wroughtoni* occurs in evergreen forests, a habitat without marked seasonal fluctuations in food availability. The details of the effects of ecological conditions on the alteration of eusocial states will have to be established by more extensive field studies of these two species.

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