Insemination Controls the Reproductive Division of Labour in a Ponerine Ant

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The control of oviposition in insect colonies is fundamental to the structure of their social systems. In most ant societies a distinct female caste performs the reproductive function, while the worker caste is sterile, or at the most produces trophic or unfertilized (male) eggs. Winged males and virgin queens are seasonally produced, and leave their nests on nuptial flights [1]. Thus a trend towards reproductive specialization and monogyny has accompanied the evolution of the division of labour. In contrast to this, we have found that colonies of the ponerine *Ophthalmopone berthoudi* reproduce by means of a large number of unspecialized egg-layers. Wheeler and Chapman [2] recognized two distinct evolutionary patterns in the ponerines, one leading to the development of wingless ergatoid (= worker-like) queens as in *Leptogenys*, and the other associated with the complete disappearance of the queen caste and its replacement with fertile workers [3]. It is the latter unusual reproductive pattern to which we wish to direct attention. Wheeler and Chapman [2] observed a normal male copulating with a worker in *Diacamma*, a genus in which there are no queens. The fertile workers may be called gamergates ("married workers") to distinguish them from ergatoids. Work on a number of species with gamergates [4, 5] has documented that in each colony there may be one or more fertile workers which supply the eggs that develop into workers and males. Many features of such a reproductive system are still unknown, e.g. how are gamergates differentiated, can all workers mate and if so, what is the proportion of gamergates in a colony?
Ophthalmopone berthoudi is an African species in which winged queens have never been found; it occurs in semi-arid regions and feeds on termites. Field observations in Mkuzi Game Reserve, South Africa, have shown that colonies consist of a number of distinct nests separated by various distances. Colony integration is maintained through the frequent transfer of adults and brood between the nests along non-chemical trails. Workers are produced for most of the year (with a hiatus in egg production before winter) and this results in a nest population with individuals of various ages.

Single nests and nest complexes of *O. berthoudi* were excavated at different times of the year, and a large sample of ants from each unit was dissected. This included a sample of 100 above-ground ants which were all found to be non-reproductive. Dissection of 350 cocoons containing pharate adults never yielded any winged females. In each nest there are various numbers of egg-laying workers, all of which are indistinguishable from sterile workers by simple visual inspection. These fertile workers were found to have 3 enlarged ovarioles per ovary, with short strings of developing oocytes and very seldom more than two large fully formed eggs per individual. The ovarian apparatus of sterile workers was the same as that of reproductive ones, but the 6 ovarioles were undeveloped. Thus there are no distinct female castes. Examination of spermathecae revealed that ants with active ovaries had been inseminated, while ants with undeveloped ovaries had not been inseminated (Table 1). These data demonstrate that insemination triggers ovarian activity. This is not simply a correlation between the occurrence of the two events, since the male data reported below indicate that the relationship is a causal one. Were ovarian activity to be responsible for changes in worker behaviour which lead to mating, we would expect to find unmated workers with developed ovaries. None have been found at any time of the year. Indeed we can state that the haploid eggs which develop into males are laid by inseminated gamergates. Insemination also produced a change in the chemical composition of the mandibular gland pheromone of these ants and in their behaviour. The mated ants remained inside their nests for the rest of their lives, except when they were carried from one nest to another. They are removed from the normal sequence of age polyethism exhibited by their non-reproductive sisters.

Males were only active above ground for a few weeks of the year (February to the beginning of March). Every day during this period a few males left their nests and flew off. They were seen to enter other nests and copulation occurred underground. Any ant that had not become active above ground prior to the period of male activity had a high probability of becoming inseminated and hence reproductive; this accounts for the large number of gamergates found in the nests sampled at this period (Table 1). Thus the sharp increase in the gamergate to worker ratio seen from February to March can be correlated with the pattern of male activity. During the rest of the year the proportion of gamergates usually decreased through the emergence of new non-mated ants. However, the wide variations over a one-year period seen

Table 1. Reproductive status of individuals from a number of colonies of *Ophthalmopone berthoudi* sampled at different times of the year (see text). All gamergates* examined were inseminated, and all workers had empty spermathecae

Date of excavation	No. of ants collected	No. of ants examined		% of ants checked for insemination		% of gamergates* in the sample examined
		gamergates*	workers	gamergates*	workers	
16. VII. 1981	247	11	111	100	51	9
5. XII. 1981	311	125	156	64	12	45
31. I. 1982	140	2	73	–	38	3
11. II. 1982	471	11	339	91	36	3
23. III. 1982	196	95	57	82	26	63
17. X. 1982	348	65	190	21	6	26

* gamergates = fertile workers

in the percentage of fertile workers per nest or colony (see December nest; Table 1) show that the numbers are not regulated. They are a result of the number of male visits, the number of young ants present inside the nests during the mating period, the foundation of new nests and the occurrence of colony fission. This situation is unlike that found in most other polygynous ants [6]. Gamergates of the previous year have largely disappeared (see January and February nests; Table 1) by the time the next set of males becomes active, and are then replaced by a new cohort of inseminated workers.

Careful observations of laboratory colonies housed in perspex-covered nests have failed to reveal any evidence of aggressive interactions between marked gamergates and workers, or among gamergates themselves. This indicates that there are no dominance hierarchies among the reproductives, and no resulting inhibition of laying or oophagy. Circumstantial evidence indicates that all fertile workers lay eggs at a slow rate (a maximum of 3–4 eggs/week), and thus their cooperative breeding is necessary for colony maintenance.

Our results afford an insight into a unique formicid reproductive system, one where the functional differentiation into fertile and sterile workers can be accounted for by mechanistic arguments other than the genetic ones used in the kin selection and parental manipulation hypotheses. The complete loss of the queen caste undermines the notion of parental manipulation [7, 8] and its use as an explanation for the present reproductive differentiation in *O. berthoudi*. As there is a large number of fertile workers and a substantial number of males taking part in sexual reproduction, the average genetic relatedness of members of a colony will be very low. This finding again raises the question of the adequacy of kin selection as an explanation for the origin of insect societies [9, 10].

In this and other ponerine species, there has been an evolutionary loss of the female reproductive caste and, as a result, the egg-laying function has been assumed by a number of the workers. Originally, the ancestral reproductive castes would have been produced seasonally; however, since the queens have disappeared, the male re-productives are now restricted to mating with a sample of the workers, whose emergence coincides with theirs. The reproductive division of labour among these workers results from insemination of young workers, and is not the consequence of a conflict over reproductive fitness [11] between members of a colony. Mating of males with particular workers occurs by chance and hence cannot be affected by directional selection. This may account for the lack of specialization in the ovaries of the gamergates of *O. berthoudi* and suggests why queens have not been re-evolved [12].

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Ein neues Sinnesorgan bei *Gammarus*

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Mit einem Rasterelektronenmikroskop der Firma Cambridge (MK II) und mit histologischen Schnitten von 7 µm Dicke (Einbettungsmittel Paraffin, Bouinfixierung, Azanfärbung) wurden morphologische Untersuchungen an *Gammarus roeselii* Gervais 1835 (Crustacea, Amphipoda) vorgenommen. Dabei wurden Sensillen entdeckt, die bisher in der Literatur über Crustaceen nicht beschrieben sind.

Die Sensillen verteilen sich in größerem Abstand über alle Glieder der beiden Antennenpaare, über die Propoden der Gnathopoden, über alle Glieder der fünf Pereiopodenpaare, das Telson, die dritten Uropoden und über die Schilder von Mesosom, Metasom und Urosom (ob sie auf dem Kopf vorhanden sind, ist unsicher). An den Pereiopoden, den Schwimmbeinen und damit „Motoren" der Gammariden [1] treten sie am häufigsten auf. Sie befinden sich auf allen Gliedern außer dem Dactylus; ihre Anzahl nimmt von der Basis bis zum Propodus kontinuierlich ab.

Das Sensillum besteht aus einem sich aus der Cuticula wölbenden Becher, der ringsum von einem schmalen Spalt umgeben ist (Fig. 1 a), und einem Schaft, der manchmal zweigeteilt zu sein scheint (Fig. 1 b). Der Becher liegt in der Mitte einer besonders reich mit Microtricha besetzten Epidermiszelle, die etwas vertieft scheint.

Er kann auch abgeflacht sein; dieses Phänomen tritt in zunehmendem Maße von der Basis zum Propoden auf. Auf den zweiten Antennen, den dritten Uropoden und dem Telson finden sich nur abgeflachte Becher (Fig. 1 b).

Im histologischen Längsschnitt kann man deutlich den Haarschaft, den Becher, den Dendriten und die zwei Hüllzellen, die diesen umhüllen, erkennen (Fig. 2).