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Best wishes

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Worker reproduction in the ponerine ant *Ophthalmopone berthoudi*: an alternative form of eusocial organization

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Summary. Colonies of the ponerine *Ophthalmopone berthoudi* were collected throughout the year. The queen caste is absent. Dissection of large numbers of workers revealed that many of them (up to 100 in one nest) are inseminated and produce eggs. The ovaries are small and contain very few mature oocytes, indicating that there is a slow rate of egg-laying. Workers are produced throughout the year, and all are capable of becoming functional reproductives. However, only those that are sexually-attractive during the limited period of male activity become mated. Thus the percentages of mated laying workers (= gamergates) fluctuate seasonally (Fig. 2). Successive generations of gamergates do not overlap. Observation of nests in the field and in the laboratory indicated that gamergates were never active above ground. There is no aggression between them, and their numbers are not socially regulated. There are few interactions between gamergates and non-reproductive workers, and the former do not acquire more food during termite meals. The notion of parental oppression is undermined by the complete loss of the queen caste, while the nature of the breeding system of this ant leads to the prediction of low relatedness between nestmates.

Introduction

Formicid societies are characterized by a variety of interactions between queens and workers, e.g. trophallaxis, control over sexual brood production and ovarian activity of workers, regulation of queen numbers (e.g. Wilson 1971; Hölldobler and Wilson 1983; Fletcher and Blum 1981, 1983). Furthermore, the population-genetic theories used to explain the occurrence of worker sterility (Hamil-

ton 1972; Michener and Brothers 1974) have traditionally been framed in the context of a queen-based social organization. Yet a number of species in the subfamily Ponerinae do not have queens, and mated workers produce all the workers and males in the colony (Wheeler and Chapman 1922; Haskins 1970). This worker laying is distinct from that which gives rise to trophic eggs, males or in a few cases other workers through thelytokous parthenogenesis (Wilson 1971; Cagniant 1979; Itow et al. 1984). Ponerine worker reproduction is thus of particular significance, since the queen's supremacy as the diploid egg producer no longer holds. This eusocial alternative is a derived condition, but its viability suggests that there may be unexplored mechanisms involved in the "dynamics of established eusociality" (Crozier 1982).

Peeters and Crewe (1984) demonstrated that the egg-layers and the non-reproductive workers in the permanently queenless ponerine *Ophthalmopone berthoudi* have a common developmental history. Indeed, all species of *Ophthalmopone* appear to have this pattern of reproductive differentiation. We suggested that mated laying workers be called gamergates, in order to make a clear functional distinction between these reproductive individuals and ergatoids. In the Ponerinae, ergatoid queens are equivalent to winged queens. They belong to a distinct reproductive caste, but are wingless and have a worker-like thorax. A lack of clarity over this distinction has led to some confusion in the analysis of the breeding biology of some queenless species of *Rhytidoponera* (eg. *R. impressa* group; Ward 1981, 1983). The egg-layers are sometimes referred to and confused as "ergatoids", "reproductive females" or "gynes". It is now clear that these reproductives should more properly be called gamergates.

We focus on the control of worker reproduc-

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tion in *O. berthoudi,* and infer levels of genetic relatedness between nestmates from a detailed knowledge of the breeding structure of these colonies with gamergates.

Methods

The ants. Opthalmopone berthoudi Forel were collected from one locality in Mkuzi Game Reserve (north eastern Natal, South Africa). Thirty-four nests were excavated at various times of the year between July 1980 and July 1983. Most of these had been observed for a number of days prior to excavation. A colony in this species consists of a number of distinct nests, and there are regular transfers of brood and nestmates between these (Peeters 1984). Thus the terms "colony" and "nest" are used here with distinctly different meanings. The nest chambers were from 20–50 cm deep. Care was taken to collect every adult and most of the brood. Individuals from particular nests were kept together until killed for dissection.

Determination of reproductive status. Cocoons collected throughout the year were opened, and pharate adults were sexed and examined for wing buds. The ovaries and spermathecae of adult workers were examined. Two classes of ants were recognized: (1) laying workers, those with developed ovaries containing oocytes made opaque by accumulating yolk; (2) nonreproductive workers, those with undeveloped ovaries. Certain homogeneous groups within the nests (eg. above-ground workers, as well as callow workers, distinguishable only by their soft exoskeletons) were always found to have undeveloped ovaries typical of non-reproductive individuals. Ants belonging to these categories, whose state of ovarial development could be predicted with certainty, were added to the dissected samples to make up the number of individuals examined (see Table 2); this procedure may slightly overestimate the proportion of non-reproductive workers in a nest, because not all the individuals in the other categories are dissected. The number of mature oocytes was recorded in most laying workers, and used as a measure of ovarian activity. The occurrence of sperm in the spermathecae of a sample of the workers in both functional classes was determined.

Morphometric measurements. The following body measurements were made using a micrometer: (1) head width and length, following Bolton 1974; (2) length of the first tergite of the gaster, the dorsal margin measured in profile from the anterior to the posterior edge; (3) height of the first segment of the gaster, the maximum height measured in profile from the dorsal to the ventral edge.

Behavioral observations. Male behavior was studied in the field. Most observations were made in the vicinity of colonies for which the location of the component nests was known, and in which all the above-ground workers were color-marked and had a behavioral record (Peeters 1984). A number of males were marked on the thorax with enamel paint.

Within-nest interactions were studied by maintaining some nests in the laboratory for a few weeks. Soil collected from the original nests was placed in the corners of arenas (0.3 × 0.6 m), and a sheet of red perspex was placed over shallow depressions made in this soil. The ants were released into the arenas, and moist conditions underneath the perspex prompted them to build inter-connected chambers. Live termites (*Trinervitermes* sp. workers) were provided as food. Various ants were marked using colors that could be distinguished through a red

filter. Some ants were dissected at the end of the observations to determine their reproductive status.

Results

Reproductive differentiation amongst the workers

Winged or ergatoid queens were absent from all colonies of *Ophthalmopone berthoudi;* this was confirmed by the examination of 431 cocoons containing pharate adults. There were, however, a number of egg-laying individuals in each nest, but these could not be recognized visually. As a consequence a large sample of workers needed to be dissected, yielding the following data. The developed ovaries of the laying workers had an unexpectedly simple appearance. There was, invariably, one pair of ovaries each having three ovarioles. The ovarioles were not much longer than the mature oocytes. Few ants had more than one mature oocyte in their ovaries, and three was the most that was found (Fig. 1). The majority of laying workers examined were found with only immature opaque oocytes, except at the end of the austral winter when most of them produced mature oocytes (Table 1). The rate of egg-laying appeared to be low (less than 1 egg/laying worker/day). The

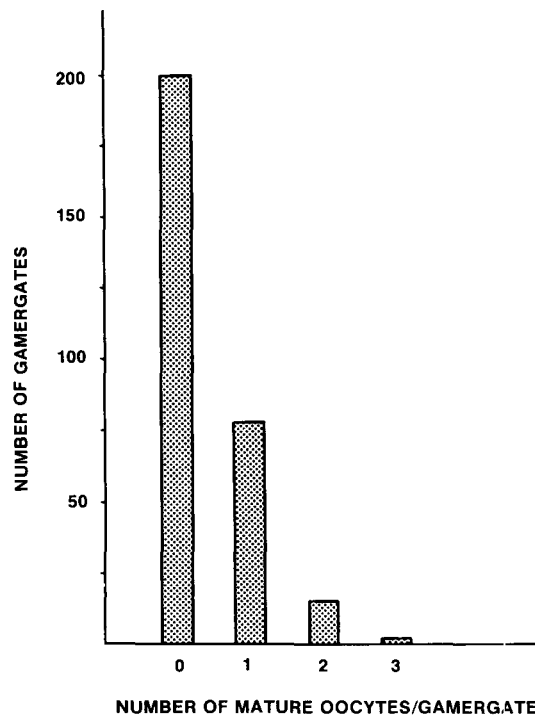**NUMBER OF MATURE OOCYTES/GAMERGATE**

Fig. 1. Frequency distribution of the number of mature oocytes found in the ovarioles of gamergates collected from five colonies (see Table 1). Note that the combined population of gamergates laid 254 eggs while awaiting dissection

eggs were found to be unusually large in relation to those in queenright ponerines. They were elongate with a mean length of 1.64 mm ± 0.08 SD (n = 50); the range was 1.5–2.0 mm. Egg width was constant and measured 0.8 mm. The spermathecae of 227 laying workers were examined (Table 2); all contained sperm.

The characteristically undeveloped ovaries of non-reproductive workers also consisted of three ovarioles in each ovary. Young workers confined inside the nests sometimes had small transparent oocytes (ie. without yolk) in their ovaries, but, with a few exceptions, this was distinct from the ovarian activity of laying workers. Thirty-five callow workers were dissected and all were found to have undeveloped ovaries. Similarly, the ovaries of 110 workers active above ground in the field were found to be undeveloped, with those of foragers showing definite resorption. All non-reproductive workers inspected (n = 322) possessed a spermatheca and a pair of accessory glands, but none were found to be inseminated. In this species, oogenesis is thus always associated with mating. Indeed, the haploid eggs which develop into males were laid exclusively by the inseminated laying workers, since no other individuals were found with mature oocytes.

A small sample of laying (n = 10) and non-reproductive (n = 29) workers were measured. While there was a marked uniformity in head size (neither head length, nor width was significantly different in size; two sample t-test), the gasters of laying workers were often significantly bigger (mean height of first segment: $t = 3.03$ $P < 0.01$; mean length: $t = 4.38$ $P < 0.001$; two-sample t-test). However, there were also laying workers with small gasters, as well as non-reproductive workers

with big gasters. Gaster size was thus not a diagnostic feature of reproductive status.

Dispersal and behavior of males

The winged males of this species were found inside excavated nests during January–April; this limited period of male production was confirmed by finding male pupae only during January to April. The number of males present above ground reached a peak in February–March.

Every day during a three-week observation period in January–February 1982, a few males (1–8) left from each of a number of nests under intensive observation. They climbed up low vegetation and flew off. Males were observed to walk into foreign nests, after investigating the entrance holes with their antennae. Males were never seen trying to copulate with workers outside nests as is the case in *Rhytidoponera* (Ward 1981), and it is inferred that it occurs underground.

Reproductive organization of nests

There can be a very large number of mated laying workers (= gamergates) in a nest (Table 2; eg. December 1981). Both the total numbers of gamergates and the proportion of gamergates in the adult population of nests varied considerably over the year and between nests. Gamergates were distributed in all the nests of a colony. When a few nests from one colony were collected at the same time, each contained different numbers of gamergates (Table 2; eg. December 1981, February 1982, March 1982). Nests collected in the same month of succeeding years showed large variations in their proportions of gamergates (eg. July 1981 and 1983,

Table 1. Ovarian activity (determined by the numbers of mature oocytes found in the ovarioles) in a sample of laying workers. The numbers of eggs laid in the laboratory are also included

	Time of the year when nests were excavated				
	December 1981	February 1982	March 1982	October 1982	April 1983
No. of laying workers dissected in detail	99	11	85	64	34
Proportion found with immature oocytes	76%	46%	93%	22%	76%
Proportion found with one mature oocyte	21%	27%	7%	67%	15%
Proportion found with more than one mature oocyte	3%	27%	0%	11%	9%
No. of eggs laid while waiting to be dissected[a]	41 (9 days)	69 (14 days)	37 (8 days)	28 (4 days)	79 (11 days)

[a] Other laying workers that were not dissected could have contributed to these numbers

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Table 2. Reproductive status of workers from a number of colonies. Sampled nests were excavated at different times of the year. The procedure for obtaining the number of ants examined is explained in the Methods. All laying workers examined $(n=227)$ were inseminated, and similarly, all non-reproductive workers $(n=322)$ had empty spermathecae

Date of excavation	No. of ants collected in the nest	No. of ants dissected	No. of ants examined	No. of laying workers found	% of laying workers in the sample examined	No. of ants checked for insemination	
						Laying workers	Non-reproductive workers
31.1.11982 (1 nest)	140	69	74	1[a]	1	–	26
27.1.1983 (1 nest)	222	42	64	1	2	–	5
11.2.1982 (5 nests, 1 colony)	72	70	71	1	1	1	34
	80	40	49	4	8	3	15
	168	99	108	2	2	2	28
	124	80	99	3	3	3	32
	27	23	23	1	5	1	13
23.3.1982 (2 nests, 1 colony)	119	74	78	46	59	32	10
	77	57	74	49	66	46	5
18.4.1983 (3 nests, 1 colony) (1 nest)	106	56	66	10	15	6	16
	29	25	–	1	4	1	8
	121	71	84	14	17	1	9
	74	28	–	9	32	9	4
16.7.1981 (1 nest)	247	122	–	11	9	11	57
15.7.1983 (1 nest)	262	43	49	15	30	13	2
27.10.1981 (2 nests, 2 colonies)	81	26	47	1[a]	2	–	9
	190	38	–	2	5	2	17
17.10.1982 (1 nest)	348	144	255	65	25	16	14
5.12.1981 (2 nests, 1 colony)	261	230	242	108	45	64	15
	50	36	39	17	44	16	3

[a] No laying worker was found, but there was at least one since eggs were laid in the isolated group of ants

October 1981 and 1982). Nonetheless, a seasonal fluctuation in gamergate frequency can be inferred from Fig. 2. Nests sampled in January–February contained very few or no gamergates and a large number of non-reproductive workers. In contrast, in March–April there were large numbers of gamergates in the nests and, significantly, these represented a large percentage of the individuals in the nests. This increase in the proportion of gamergates in nests can be related to the annual pattern of male activity. The increases suggested by nests with large numbers of gamergates at other times of the year (Fig. 2; July, December) result from comparing nests with different individual histories.

The pattern of worker mating was elucidated by excavating two nests in March 1982 (Table 3). The foragers and other above ground workers active in these nests had been marked, and dissection revealed that none of these individuals were inseminated or reproductively active (Table 3). In contrast, most of the workers confined inside the nests were inseminated, with the unmated ones being predominantly callow.

Interactions involving gamergates

Gamergates and non-reproductive workers exhibited differences in behavior, with the former never being active outside the nests, either in the field or in the laboratory. Unlike the non-reproductive workers which became active above ground as they aged, gamergates remained below ground for the rest of their lives, except when they were carried above ground from one nest to another within colony complexes $(n=10)$. This type of transfer occurred throughout the year.

Gamergates generally remained together in one part of the nest, and this reduced the frequency of interactions with other workers. There was a minimal degree of interaction within gamergate
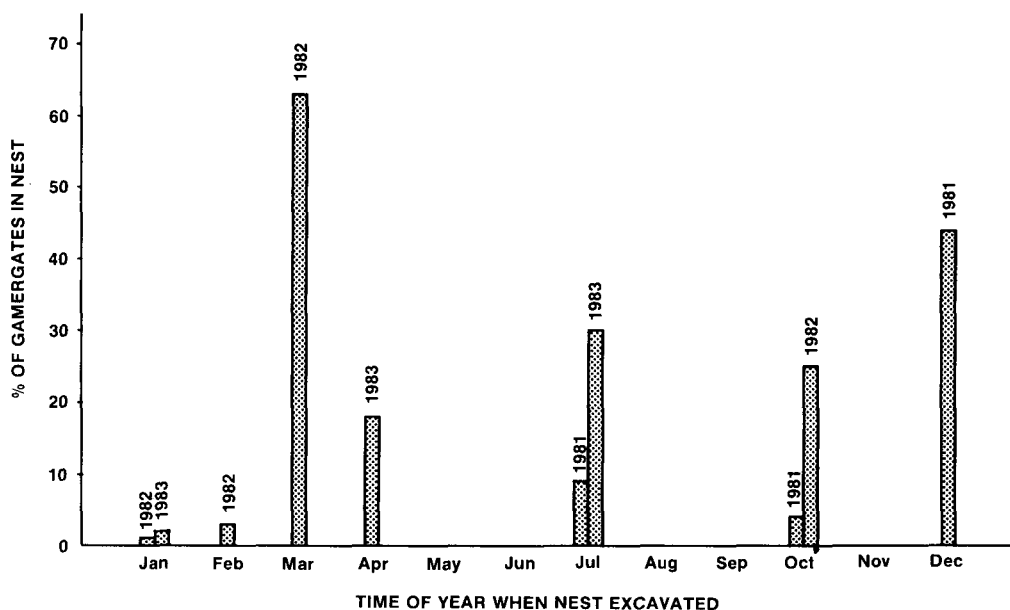
Fig. 2. Frequency distribution of the percentages of gamergates in various nests collected at different times of the year. When more than one nest was excavated on a particular date, the percentage of gamergates in the combined nest population is plotted

Table 3. Reproductive status (determined by dissection) of workers from two nests excavated on 23.3.1982 (ie. after the mating season). All the ants that were active above ground prior to excavation had been marked, and thus the unmarked ants are those confined inside the nests. The marked ants could not all be dissected because many died soon after being brought to the laboratory

Total no. of ants found in nest	No. of above ground ants	No. of above ground ants dissected	Proportion of above ground ants with active ovaries	No. of unmarked ants dissected	Proportion of unmarked ants with active ovaries
77	24	7	0%	50	98%
119	13	7	0%	67	69%

groups (there were sometimes more than one). Their location within an observation nest often changed, and they were found occasionally in the vicinity of the brood, although they were seldom involved with brood care. A few instances of egg-laying were observed, where the individuals were by themselves and walked away after depositing a single egg on the soil. Ooophagy was never observed.

Trophallaxis does not occur between the inhabitants of a nest. Physical interactions between non-reproductive and breeding workers were often observed during termite feeds, especially when the supply of food to a nest was restricted. After food had been brought into the nest chambers by foragers, small aggregations of ants (3–6) fed around clumps of termite bodies that were held off the ground. Gamergates left their groups and attempted to gain access to these feeding aggregations. On many occasions they were clearly forced to re-treat by one or more of the individuals present. However such aggression was also exhibited towards non-reproductive workers trying to join one of the feeding groups. On a number of occasions, a few gamergates were feeding together and no mutual aggression was seen.

Discussion

Control of worker reproduction

On the basis of the external and internal morphology of adults, it is clear that there are no distinct worker and reproductive castes in *O. berthoudi*. The queen caste has been replaced by inseminated workers (= gamergates) which produce workers and males. All the workers in a colony have identical reproductive organs, but only mated ones lay eggs. Thus, insemination alone appears to control the reproductive differentiation amongst the col-

ony members. While we have no physiological evidence for insemination having a triggering effect on ovarian activity in the workers, the strict association between these two phenomena was true at all times of the year. Unmated workers with egg-producing ovaries, and mated workers with completely undeveloped ovaries, were never encountered. In many ant species insemination triggers egg-laying as well as influencing behavior. Buschinger and Winter (1978) found that only mated "ergatoid" reproductives of *Harpagoxenus sublaevis* lay eggs. In *Monomorium pharaonis*, mated and unmated queens differ in their ability to inhibit the development of larvae into sexuals (Berndt and Nitschmann 1979). In queenright colonies of *Rhytidoponera confusa* and *R. chalybaea*, unmated supernumerary queens have poorly developed ovaries (Ward 1983). In *Odontomachus affinis*, only mated females exercise effective control over worker oviposition. The unmated females in the nest do not lay eggs, and they take care of the brood as well as excavate and forage actively (Brandao 1983). A behavioral effect on the mated workers is also evident in *Ophthalmopone berthoudi*, since they are inhibited from following the normal pattern of age polyethism shown by sterile nestmates (Peeters 1984).

The maturation of oocytes is restricted to mated workers in *O. berthoudi*, and this is a very unusual situation in the Formicidae since the unmated workers should be under a strong selective pressure to produce males. Haploid egg production occurs in *Odontomachus troglodytes* (Colombel 1972a), and in orphaned colonies of *Rhytidoponera purpurea* (Haskins and Whelden 1965). In *R. confusa* and *R. chalybaea*, a few (8/139) reproductively active workers were not inseminated (Ward 1983). At those times of the year when few or no gamergates were present in our colonies, the unmated workers remained reproductively inactive, indicating that the ovarian activity of unmated workers in *O. berthoudi* is not inhibited by their breeding nestmates.

The differentiation of workers into gamergates occurs during the limited period of male activity. Workers with bigger gasters are not more likely to become mated, and this size characteristic may in fact result from ovarian development. Not all workers are sexually attractive when foreign males visit the nests. Only workers below a certain age, ie. those confined inside the nests, can become mated (Table 3). This may be explained by the release of a suitable pheromonal signal from the pygidial gland of workers in this age group. This gland occurs in non-reproductive workers of all

ages as well as in the gamergates of *O. berthoudi* (Villet et al. 1984). The discovery of a sex attractant, produced by the pygidial glands in workers of the queenless *Rhytidoponera metallica* (Hölldobler and Haskins 1977), would lend support to this possibility. In contrast, Ward (1983) suggested that the inhibition of sexual calling behavior in most workers results from subtle dominance interactions. There is no evidence for this in *O. berthoudi*.

Structure of the breeding system

There appears to be little overlap of successive yearly generations of gamergates. The low gamergate numbers present in nests in January and February (Fig. 2) suggest that these individuals are the survivors of the previous year's mating activity. The decline in their numbers at this time of the year could be attributed to a particular age cohort of individuals coming to the end of their adult life span (the workers which became mated were all of roughly equivalent age, and thus they should die contemporaneously). Non-reproductive workers probably have even shorter lives, because once they leave the shelter of the underground nests, their mortality increases drastically (Peeters 1984). The relatively short life-span of gamergates is a further reflection of their worker origin. In queenright ponerines, the queens greatly outlive their own workers, eg. in *Odontomachus* and *Rhytidoponera* (Haskins and Haskins 1980). They also live substantially longer than *O. berthoudi* gamergates.

Many workers mate during February–March, resulting in a temporarily high ratio of gamergates to non-reproductive workers in the nests. The generations of workers that emerge at times other than during the mating season cannot become inseminated and remain sterile. Thus, while the numbers of gamergates remain constant, those of non-reproductive workers increase, and the ratio of gamergates to workers gradually decreases until the next period of male activity. Since we could not monitor the gamergate population in a single nest over time, different nests were sampled in order to detect seasonal fluctuations in the percentages of gamergates. The yearly pattern obtained (Fig. 2) suggests that large increases in gamergate numbers are a result of the restricted period of male activity. However, fluctuations in gamergate numbers in the nests are also affected by various biological factors inherent in the life history of the species, eg. the number of foreign males that locate a particular nest. The success with which males find nests varies

along a continuum from those nests that are completely overlooked, to those that receive large numbers of males (Peeters, in preparation). Hence, workers of mating age will remain sterile if their nests recruit too few (or none in the extreme case) males to achieve complete insemination of the receptive fraction of the worker population. The number of gamergates in a nest is also directly related to the number of sexually-attractive workers present during the mating season. Such factors may account for the large gamergate population found in the nests excavated in December 1981 (Table 2).

The existence of marked variations in the numbers and percentages of gamergates in different colonies (Table 3) may reflect a lack of social regulation. There is no consistent relationship between the numbers of non-reproductive workers and gamergates. The ratio between these two classes of workers fluctuates during the year with the foundation of new nests and the occurrence of colony fission. No interactions among the breeding workers appear to regulate their numbers in the nests. This sharply contrasts with queenright ponerines for which the number of reproductives is under social control (eg. in the polygynous *Odontomachus troglodytes*, Colombel 1972b).

The seasonal production of males is an evolutionary legacy of queenright ancestors. Since the queens have disappeared, the males are restricted to mating with a sample of the workers, whose emergence coincides with theirs. The limited period of male activity has the effect of ensuring that non-reproductive workers are present for most of the year.

Social interactions within the nests

There is only one caste in the nests of *O. berthoudi*, and the interactions between individuals are not very elaborate. While breeding and non-reproductive workers behave differently, the former have evidently not re-evolved queen attributes. The low laying rate means that oviposition is performed by a succession of different individuals, and one gamergate probably contributes only a small number of eggs during its adult life span of under a year. Thus cooperative breeding by many gamergates is necessary for colony survival. However, since there is no queen caste, this is not a true polygynous system. Large numbers of gamergates can coexist inside a nest, and there is no aggression between them. Dominance hierarchies were not detected. The reproductive output of cohabiting breeding workers does not decline with an increase

in their numbers in the nest (Tables 1 and 2). Indeed, there were no systematic differences in the number of mature oocytes found in the ovaries of gamergates belonging to reproductive populations of different sizes (Table 1). Rather, trophic restrictions at the level of the colony may affect the number of eggs laid. Some gamergates seem to be better egg-layers than others, and those with mostly immature oocytes may lay eggs inconsistently or not at all.

Observations of gamergates in the laboratory indicated that they were not given preferential treatment by the other ants during termite meals. Energetic constraints place an upper limit on the rate of egg production of breeding workers, because they have to feed themselves by acquiring termites from the stocks that are brought inside the nest. There may well be individual variability in the ability to obtain sufficient food. Workers are usually crowded around termites when they feed, and it is then difficult for additional nestmates to push their way in.

The modified form of eusociality found in this species is not maintained by an inhibitory effect of the gamergates on the other workers (Peeters and Crewe 1984). Thus parental manipulation (Michener and Brothers 1974; Alexander 1974) cannot adequately explain the functional sterility of a class of nestmates. The notion of parental oppression is further undermined by the complete loss of the queen caste, which has ocurred repeatedly and independently in the Ponerinae.

Ecological correlates of worker breeding

The seasonal rise in gamergate numbers that coincides with male activity results in a temporary reduction in the numbers of foragers. Once those older workers which did not mate have died, there may be a scarcity of younger non-reproductive workers to replace them (the gamergates do not take part in above ground activities as they age), until such time as those which were callow during the mating season or which eclosed subsequently reach the age at which they leave the confines of the nest. A reduced number of foragers during these few weeks of the year would result in a decreased flow of resources into the nests and this in turn may affect the egg-laying rate of gamergates as well as brood mortality. Larvae perish or may be used as food by the adults, and this is reflected in an increased larval mortality during the winter months (Peeters 1984).

Worker reproduction offers an obvious ergonomic advantage, since there is no energy wastage

through the production of excess female reproductives. However, in evolutionary terms, worker breeding may be merely an ad hoc response to the loss of the queen caste (Peeters and Crewe, in preparation).

Multiple breeding workers and genetic relatedness

The effectiveness of kin selection (Hamilton 1972) as an explanation for the presence of a non-reproductive group of individuals is dependent on the degree of relatedness between colony members. An understanding of the structure of the breeding system in *O. berthoudi* leads to the prediction of low relatedness between nestmates. A large number of gamergates and a substantial number of males take part in sexual reproduction. There is no overlap between successive generations of gamergates so that the relatedness of the egg-layers in a colony ranges from sisters to cousins. As a result, the degree of relatedness among the progeny is probably low. This is in spite of the likelihood that gamergates are singly-inseminated and that individual males mate with a number of workers within a nest. Both these factors would raise the relatedness between nestmates to a limited extent. There is no indication that inbreeding occurs in this species. Male sexual behavior is normally triggered only once they have left their natal nests, and they should not copulate with their nestmates. Furthermore the initial flight takes them away from the other nests of their colony. The frequent transfer of brood and adults between the nests of a colony (Peeters 1984) also leads to a decrease in the number of sisters in a nest. This has significant consequences when a new colony buds off from an existing one. We suggest that the reproductive division of labor in *O. berthoudi* cannot be accounted for by arguments such as the genetic ones used in the kin selection hypothesis.

Electrophoretically-detectable genetic variation has been studied in other ponerines, and low levels of relatedness between nestmates have often been found (see references in Crozier et al. 1984). Ward (1983) estimated pedigree relatedness in both queenright and queenless colonies of *Rhytidoponera confusa* and *R. chalybaea*. He found that within-nest relatedness in the former was more than twice as high as in the latter. In the most primitive living ant *Nothomyrmecia macrops*, Ward and Taylor (1981) found a low level of kinship among workers from the same nest. Since this queenright species has monogynous colonies, such results strongly suggest the possibility of additional reproduction by mated workers, although Hölldobler

and Taylor (1983) did not find any inseminated workers in the sample they dissected. More importantly, these data from ponerine societies emphasise that high kinship between colony members is not one of their notable characteristics. Thus in any explanation of the origin of eusociality in these organisms, other factors such as nestmate recognition may be crucial for the development of the social integrity of an ant society (Peeters and Crewe, in preparation).

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