

# Queen Number and Sociality in Insects

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## Monogyny and polygyny in ponerine ants with or without queens

Christian Peeters

The Ponerinae is a phylogenetically primitive subfamily of ants. Bolton (1990a) considers it to be a monophyletic group, although it is morphologically very heterogeneous. Some genera exhibit primitive characters (i.e. similar to hypothesized wasp ancestors), while the morphology of others is considerably derived. Similarly, ponerine life histories and behaviour are a mixture of primitive and specialized traits. Four constituent tribes are currently recognized: Amblyoponini (7 extant genera), Ectatommini (9 genera), Platythyreini (2 genera), and Ponerini (27 genera) (Hölldobler and Wilson 1990). The tribe Cerapachyini (e.g. *Cerapachys* and *Sphinctomyrmex*) has been recently elevated to a subfamily (Cerapachyinae), which is now considered as part of a monophyletic lineage that includes the army ant subfamilies (Bolton 1990b). Ponerine ants flourish chiefly in tropical and subtropical regions, and are poorly represented in the temperate zones.

In this chapter, I present comparative data on the number of sexually reproducing individuals per colony in the Ponerinae, while paying special attention to their morphological characteristics. In ants two classes of female adults (queens and workers) exist which become differentiated during larval development. These physical castes represent morphological specialization for the performance of different roles. The evolution of increasingly complex societies has been possible through a progressive accentuation in queen-worker differences (Wheeler 1986), but this dimorphism is seldom very pronounced in the Ponerinae. An important characteristic of ponerine ants is the occurrence of two significant modifications to the normal pattern of ant reproduction. First, permanently wingless ('ergatoid') queens have replaced winged queens in many species. Second, in a few other species, the queen caste has completely disappeared, leaving some of the workers to reproduce instead. Both modifications have evolved repeatedly in different tribes and genera.

The replacement of queens by reproductive workers is possible in the Ponerinae because workers in most species have retained a spermatheca and are able to mate (Peeters 1991a). The study of queenless ants can provide useful insights into the nature of reproductive conflict within

colonies. Since the specialized reproductive caste has been eliminated, reproductive division of labour occurs among morphologically identical workers, thus maximizing the potential for conflict. In contrast, in species having either winged queens or ergatoid queens, caste membership dictates the reproductive options of each individual, and if workers are able to reproduce, they are generally restricted to producing males.

The analysis of interspecific data requires considerable care, and while the comparison of patterns of social phenomena resulting from convergent evolution is valid, comparison of patterns that are due to common ancestry should be avoided (e.g. Pagel and Harvey 1988). A common error in comparative studies is the failure to ensure that data values are independent. Species can rarely be treated as independent units because they usually share attributes as a result of common ancestry. In order to minimize this problem, I have carried out analyses at the generic and tribal levels.

Throughout this chapter, I restrict the term 'caste' to the description of groups of female adults distinguished by different phenotypes as a result of divergent larval development. Accordingly, 'queen' and 'worker' refer here to caste membership, and are not used to describe the partitioning of roles (i.e. reproductive or not) within a colony (Peeters and Crozier 1988). The term 'fission' here describes colony multiplication in which one or more reproductives (queens or gamergates), together with workers, separate permanently from the parental nest. No implication is made about the size of the colonial fragment which starts an independent existence. This differs from Hölldobler and Wilson (1990) who distinguish between 'fission', where the daughter colony is a large fragment of the parental colony, and 'budding' where small portions leave parental colonies. I believe that this distinction is operationally difficult to make, especially in the Ponerinae where few details are known of this process.

### Species with winged queens

The existence of queens with wings (which are shed following aerial dispersal from the natal nest) is the ancestral condition in ants. For example, they are found in such highly primitive genera as *Nothomyrmecia*, *Myrmecia*, and *Amblyopone*. In the Ponerinae, the extent of queen-worker dimorphism varies considerably, but it is generally less marked than in the other subfamilies. In *Amblyopone*, queens are hardly bigger than the workers, although their thorax has a distinct structure due to the wing musculature (Brown 1960). In other genera the divergence in size can be more marked (e.g. Brown 1958, 1976), and it reaches its maximum in *Brachyponera lutea*, in which queens are twice as large as workers. What are the effects of the relatively small morphological specialization of queens on colony reproduction and intra-colony interactions?

Table 11.1 Colony characteristics of various ponerine species having winged queens. Colony size is the number of adult workers, and is expressed (when sample size is large enough) as the mean  $\pm$  standard deviation.

Species	Colony size	Social structure	Colony reproduction	References
Tribe Amblyoponini				
<i>Amblyopone australis</i>	hundreds	M/P	haplo, fiss	Haskins and Haskins (1951)
<i>A. pallipes</i>	9-16 <sup>1</sup>	M/P	fiss	Traniello (1982)
<i>A. silvestrii</i>	18 $\pm$ 15 (N = 30)	M/P	haplo, pleo	Masuko (1987)
<i>Discothyrea sauteri</i>	44 $\pm$ 33 (N = 18)	M/P	fiss ?	K. Masuko (personal communication)
<i>Prionopelta amabiis</i>	282, 709	M	?	Hölldobler and Wilson (1986)
<i>Proceratium itoi</i>	92 $\pm$ 66 (N = 26)	M	haplo	K. Masuko (personal communication)
Tribe Ectatommini				
<i>Ectatomma permagnum</i>	38 $\pm$ 22 (N = 9)	M/P	?	Paiva and Brandão (1989)
<i>E. tuberculatum</i>	< 800	M	haplo	J.-P. Lachaud (personal communication)
<i>Rhytidoponera chalybaea</i> <sup>2</sup>	440 $\pm$ 171 (N = 21)	M	haplo	Ward (1981a, 1983a)
<i>R. purpurea</i>	803 (N = 10)	M	haplo	Ward (1981a, 1983b)
<i>Paraponera clavata</i>	708, 1329, 2326	M	haplo	Janzen and Carroll (1983), Breed and Harrison (1988)

Table 11.1 (continued)

Species	Colony size	Social structure	Colony reproduction	References
Tribe Ponerini				
<i>Brachyponera chinensis</i>	85 $\pm$ 46 (N = 10)	M/P	?	K. Masuko (personal communication)
<i>B. lutea</i>	> 3000 (N = 1) <sup>3</sup>	M	haplo	Haskins and Haskins (1950)
<i>B. senarensis</i> (04 ?)	1082 $\pm$ 55 (N = 14)	M/P	haplo, pleo	Dejean, and Lachaud (in press)
<i>Cryptopone sauteri</i>	112 $\pm$ 76 (N = 14)	M	haplo	K. Masuko (personal communication)
<i>Hypoponera excavata</i>	31 $\pm$ 23 (N = 32)	M	haplo	K. Masuko (personal communication)
<i>Odontomachus troglodytes</i>	up to 1300	M/P	haplo	Colombel (1971)
<i>Pachycondyla apicalis</i>	87 $\pm$ 75 (N = 85)	M	haplo	Fresneau and Valenzuela (in press)
<i>Paltothyreus tarsatus</i>	about 1000	M	haplo	Hölldobler <i>et al.</i> (submitted)
<i>Ponera scabra</i>	21 $\pm$ 14 (N = 39)	M/P	haplo, pleo	K. Masuko (personal communication)
<i>Trachymesopus pilosior</i>	4-11 (N = 6)	M	haplo?	K. Masuko (personal communication)

(M = monogyny; P = polygyny; haplo = haplometrosis; pleo = pleometrosis; fiss = colony fission.)  
All ants studied by K. Masuko were collected in Manazuru forest, Kanagawa Prefecture, Japan.

<sup>1</sup> these may represent sub-units of a large unicolonial population.

<sup>2</sup> type A colonies, i.e. with a queen.

<sup>3</sup> Peeters unpublished.

The limited differentiation of ponerine queens is reflected in their pattern of colony foundation. In species where one or more queens start new colonies independently (Table 11.1), they are observed to leave the nest periodically in order to hunt for food (Haskins 1970). This contrasts with the independent colony-founding behaviour seen in most species of ants belonging to the more derived subfamilies. In these cases, queens isolate themselves underground and feed the first generation of larvae by metabolizing wing musculature and lipid reserves (e.g. Keller and Passera 1989). Ponerine queens do not have large wing muscles and they need to forage above ground to obtain additional nutrients. Furthermore, trophallaxis between adults and larvae is rare in this subfamily, thus the larvae must be fed with whole prey segments.

Ponerine queens and workers often have morphologically similar ovaries. In several species (e.g. *Pachycondyla obscuricornis*, *Mesoponera australis*, and *Amblyopone australis*), queens have only either 3 + 3 or 4 + 4 ovarioles, which is identical to the workers (Fresneau 1984; Peeters 1987a). This is associated with limited fecundity (e.g. 3 eggs/day in *P. apicalis*; Fresneau and Valenzuela, in press) and small colony sizes often recorded in this subfamily (Table 11.1). However in other ponerine species, the number of ovarioles in queens is higher. In *Rhytidoponera confusa*, queens have 6–8 ovarioles per ovary, while workers have 2–4 ovarioles; in *Paltothyreus tarsatus*, queens have 13–14 ovarioles per ovary, and workers have 6–7; in *Odontomachus cephalotes*, queens have 7 ovarioles per ovary, and workers 6–7 (Peeters 1987a). As queen-worker dimorphism increases there is a pronounced reduction of worker ovaries in some species. In *Prionopelta amabilis*, workers have only two ovarioles in total (Hölldobler and Wilson 1986), while they completely lack ovaries (and a spermatheca) in *Brachyponera lutea* (Peeters 1991a).

Table 11.1 outlines the occurrence of monogyny or polygyny in 21 ponerine species having winged queens. Many appear to be always monogynous, while in others both monogynous and polygynous colonies occur in the same populations. Polygyny may result either from co-operation between several queens during the foundation of new colonies (= pleometrosis), or from the addition of queens during colony ontogeny. From the evidence available, queen numbers in polygynous ponerine colonies are relatively low. There are no examples comparable to the highly polygynous colonies of various higher ants such as *Myrmica* (Elmes and Keller this volume), *Formica lugubris* (Rosengren *et al.* this volume), and *Iridomyrmex humilis* (Keller *et al.* 1989).

The presence of either one or several mated queens per colony must be considered in the context of colony reproduction. Haplometrosis (= colony foundation by a solitary queen) is typically exhibited in monogynous ponerine species (Table 11.1). In some cases, haplometrosis or pleometrosis may occur facultatively. In *Brachyponera senaarensis*, 5 out of 51

foundations observed were pleometrotic, and the remainder were haplometrotic (Dejean and Lachaud, in press). In *Amblyopone silvestrii*, 69 per cent of queenright colonies ( $N = 84$ ) were monogynous, and haplometrosis was recorded (Masuko 1987). However, a large proportion of those colonies having fewer than 10 workers were polygynous, suggesting that they were new colonies having originated by pleometrosis (Masuko 1987). In other species with several mated queens coexisting in a colony, fission occurs instead of independent colony foundation. For example, in *Amblyopone pallipes* queens have never been observed to found a colony alone, and groups of newly mated queens and workers fragment away from the parental colony (Traniello 1982). However, the majority of ponerine species which exhibit colony fission either have ergatoid queens, or lack queens (see following sections).

A range of colony sizes is exhibited by species having only one queen (Table 11.1). Although factors such as worker longevity must also be considered, this suggests that queen fecundity varies considerably among species, which is supported by data on ovarian specialization. The relationship between the degree of queen-worker dimorphism and the occurrence of either monogyny or polygyny remains to be examined; data on the morphological specialization of queens are seldom given in the literature. Little is known about queen longevity under natural conditions (but see Haskins and Haskins 1980), and it is a moot point that the greater longevity of queens in higher ants is a physiological consequence of increasing queen specialization.

As is common in other ant subfamilies (Bourke 1988), ponerine workers are able to produce males when removed from the queen's presence. Oviposition by orphaned workers has been documented in *Odontomachus affinis* (Brandão 1983, but no details), *O. troglodytes* (Colombel 1972), *Paltothyreus tarsatus* and *Rhytidoponera confusa* (Peeters unpublished), and *R. purpurea* (Haskins and Whelden 1965). In *Pachycondyla obscuricornis* and *P. apicalis*, workers oviposit in the presence of the queen (Fresneau 1984; Oliveira and Hölldobler 1990); these eggs are eaten by the queen in *P. apicalis*. In *Paraponera clavata*, a large proportion of the workers have active ovaries (Breed and Harrison 1988). In *Prionopelta amabilis*, many workers produce trophic eggs on which the queen appears to feed mostly or entirely (Hölldobler and Wilson 1986).

The relationship between insemination and oogenesis has been studied in detail in only a few ponerine queens. In *Odontomachus affinis*, unmated queens do not lay eggs and are unable to inhibit worker oviposition (Brandão 1983), but in *Pachycondyla obscuricornis* they oviposit (Fresneau 1984; Oliveira and Hölldobler 1991).

### Species with ergatoid queens

In many ponerine ants, queens never have wings (reviewed in Peeters 1991b; Villet 1989b). Ergatoid queens occur in species belonging to 12 genera in

4 tribes (the Cerapachyinae are excluded). In five genera of the tribe Ponerini, there are both species with winged queens and species with ergatoids. This suggests that, even within tribes, ergatoids have evolved independently multiple times. This adds strength to any evolutionary trend deduced from comparative data.

Flightlessness in ergatoid queens is not associated with a reduction in reproductive specialization; there are species in which colonies can be exceptionally large (see Table 11.2), and high reproductive output by ergatoid queens is frequently associated with an increase in the number of ovarioles or a decrease in egg size (e.g. Peeters 1991b; Villet 1990a). There are also species in which ergatoid queens do not have more ovarioles than the workers, but this condition is also exhibited in ponerines having winged queens.

Along with a modification in external morphology, the evolution of ergatoid queens is accompanied by various social characteristics. Monogyny is apparently the rule. No instance of polygyny has been reported either for the species listed in Table 11.2 or in anecdotal reports in the literature (e.g. *Leptogenys diminuta*; Wilson 1958). (Note that in *Sphinctomyrmex* c.f. *steinheili* of the subfamily Cerapachyinae, several mated ergatoid queens occur together (Buschinger *et al.* 1990).) The monogynous condition in ergatoid species contrasts with the occurrence of either monogyny or polygyny in species having winged queens. Thus monogyny appears to

**Table 11.2** Colony sizes in various ponerine species with ergatoid queens. All colonies collected were monogynous. Independent colony foundation has never been observed; colony fission is very likely to occur but has seldom been documented.

Species	Colony size	References
<i>Leptogenys</i> sp.1 (= <i>distinguenda</i> )	> 30000 ( $N = 5$ )	Maschwitz <i>et al.</i> (1989)
<i>L. longensis</i>	$37 \pm 13$ ( $N = 4$ )	Peeters (unpublished)
* <i>L. mjobergi</i>	22, 28, 44	Peeters (unpublished)
* <i>L. nitida</i>	$126 \pm 60$ ( $N = 9$ )	M. Zini (personal communication)
<i>Megaponera foetens</i>	$583 \pm 174$ ( $N = 16$ ) $1475$ ( $N = 16$ )	Longhurst and Howse (1979) Lepage (1981)
<i>Onychomyrmex hedleyi</i> <sup>1</sup>	$543 \pm 184$ ( $N = 4$ ) $734 \pm 219$ ( $N = 10$ )	Peeters (1991b) S. Higashi (personal communication)
<i>Plectroctena mandibularis</i>	110, 172, 275	Peeters and Crewe (1988)
<i>Simopelta oculata</i>	> 360 ( $N = 1$ )	Gotwald and Brown (1966)

<sup>1</sup> *Onychomyrmex* belongs to tribe Amblyoponini; all others belong to tribe Ponerini.

\* *L. chinensis*

Maschwitz & Schönagge 1983

be an obligate feature of societies with ergatoids, although nothing is known about the physiological or behavioural mechanisms involved in this rigid social regulation. Parallels with the biology of army ants (also exhibiting wingless queens and monogyny; e.g. Franks and Hölldobler 1987) are intriguing. While few ponerine species have been investigated systematically, it appears that, as in army ants, very few new ergatoid queens are produced annually in each colony. It is not known whether they are produced every year, because there are few published details on the collection of sexual cocoons. It seems that ergatoid queens never establish new colonies independently from workers. They mate near or inside the nests (reviewed in Peeters 1991a), and thus, during a short period, more than one inseminated queen may occur in a colony; this may trigger colony fission (as in army ants).

The ability of ergatoid queens to inhibit worker oviposition has been documented only in *Plectroctena mandibularis* and *P. conjugata*, in which orphaned workers produce males (Peeters and Crewe 1988). In *Megaponera foetens*, some workers with developing oocytes occur together with the queen, but it is not known whether they oviposit (Crewe *et al.* 1984; Villet 1990b).

### Species without queens

Queens are absent in several unrelated ponerine genera belonging to three of the four tribes (Peeters 1991a; see also Table 11.1). Instead, some workers mate and reproduce in each colony, while the others remain infertile and function as labourers. In a few genera (e.g. *Rhytidoponera* and *Pachycondyla*), some species have queens and others have none, suggesting that the disappearance of the queen caste is a derived condition. In addition, a few species exist in which both queens and gamergates reproduce. Since workers of other ant subfamilies generally lack a spermatheca or cannot mate, the evolutionary replacement of queens by mated reproductive workers is restricted to this subfamily.

Although worker mating was first observed by Wheeler and Chapman (1922), the pattern of reproductive division of labour in species without queens only became understood after workers in a colony were shown to be morphologically identical, i.e. they all have a spermatheca and can reproduce. The morphologically indistinguishable egg-layers were initially considered to be developmentally distinct from the sterile workers. Sometimes, they were mistaken for ergatoid queens, due to the latter's external resemblance to workers in various ponerine species. Queenless species of *Rhytidoponera* were the first to be studied in detail; Haskins (1970) recognized that a proportion of the workers take the place of colony reproductive vacated by the queen, and later it was reported that all workers have functional spermathecae. Peeters and Crewe (1985a) showed that,

in *Ophthalmopone berthoudi*, the reproductive organs of mated, ovipositing members of the worker caste are structurally similar to those of infertile individuals, and subsequent work on other genera has confirmed this for all queenless species.

The term 'gamergate' (= married workers), suggested by W.L. Brown, jun., is used to describe workers who take part in *sexual* reproduction (Peeters and Crewe 1984). This functional term emphasizes the existence of mated reproductive individuals which do not belong to the queen caste. A recent study on *Harpegnathos saltator* has shown that some of the workers mate, but are inhibited from producing eggs; such individuals are not gamergates (Peeters, unpublished). The terms 'monogynous' and 'polygynous' are appropriate to describe the number of gamergates in a colony. Indeed, the coexistence of several gamergates has the same sociobiological implications as the presence of several reproductive queens.

While the first queenless ponerine species investigated were polygynous, subsequent studies have showed that in other genera there is always only one gamergate per colony. Here I want to review the pattern of ovarian activity in different species, and consider the mechanisms of regulation among nestmates. I also compare the social and ecological characteristics of species having either one or multiple gamergates per colony.

#### *Methodological approach to the study of queenless ants*

Investigation of reproductive division of labour in species without queens is often difficult because, unlike queens, gamergates cannot be recognized by simple visual inspection. The sole exception is in some *Diacamma* species where the gamergate retains a pair of tiny bladder-like appendages on the thorax (these are removed in all the other workers after they emerge from the cocoons). Although ponerine workers are characteristically monomorphic, they can exhibit size variation in some species. In these, gamergates and unmated workers do not differ in size (Peeters and Crewe 1985a; Villet *et al.* 1990; Villet 1991; Ware *et al.* 1990). Furthermore, although slight differences in the softness and pigmentation of the cuticle of gamergates have been found in some species (e.g. *Ophthalmopone berthoudi*, *Platythyrea lamellosa*, and *Rhytidoponera* sp.12; Peeters and Crewe 1985a; Villet *et al.* 1990; Peeters 1987b), these cannot be used reliably as diagnostic features. Thus it is often essential to dissect the ovaries and spermatheca in order to determine reproductive status. Such destructive sampling hinders attempts to correlate reproductive activity and behavioural profile.

Gamergates are never active outside the nest, even as they age, and thus they do not follow the normal pattern of age polyethism exhibited by other workers. Gamergates can be identified behaviourally if they are

observed to lay eggs (although virgin workers may also lay eggs in some species). However, oviposition can be a rare event, because gamergates frequently have a low fecundity. Besides oviposition, other behavioural differences may exist between gamergates and infertile workers, e.g. activity in the nest, or patterns of physical interactions among nestmates. In *R. confusa*, gamergates always behave timidly during colony disturbance, but all timid workers are not gamergates (Ward 1983a). In *Platythyrea schultzei*, the single gamergate is the only worker that carries eggs in her mandibles (Villet 1991), but in other species, behavioural markers become clear only after quantitative ethological study (see Villet 1990d; Ware *et al.* 1990).

Since the determination of reproductive activity usually relies on ovarian dissections rather than direct observation of oviposition, it is necessary to gain an adequate understanding of the pattern of oogenesis in each species. As noted by Peeters and Crewe (1986b) and Peeters (1987b), the presence of yolky oocytes in the ovaries is not necessarily indicative of oviposition. Descriptions of oogenesis and ovarian development in the literature are sometimes incomplete and the terminology is used inconsistently by different authors. This makes interspecific comparisons difficult. In an attempt to standardize descriptions, I list briefly some important features (Fig. 11.1): (i) number of ovarioles, and length (e.g. relative to eggs); (ii) occurrence of yolky (i.e. filled with white opaque material) and non-yolky oocytes; (iii) number of mature oocytes (i.e. basal oocytes which are as long or longer than an egg, with a distinct chorion), and number of smaller yolky oocytes; (iv) presence or absence of yellow bodies (= corpora lutea) at the base of individual ovarioles—these inclusions originate from degenerating nurse cells, and they usually indicate active oviposition. However, they may also result from oocyte resorption (Billen 1985), and thus their occurrence in virgin workers does not necessarily indicate that eggs were laid. Variations in colour intensity and size of the yellow bodies appear to reflect the frequency of egg-laying; they are dark and large in gamergates.

To study reproductive differentiation in queenless ants, it is necessary to determine, for each colony, which workers are inseminated, and which workers are capable of laying eggs. With these data, we can then determine (i) what is the pattern of worker mating; (ii) how the pattern of ovarian development differs between mated and unmated workers, i.e. the effects of insemination. These two distinct considerations are central to the control of reproductive division of labour, and will be discussed separately using comparative data.

#### *Regulation of mating: polygynous species*

Little is known about the factors which lead some workers to mate, and not others. No laboratory study has investigated the relationship between

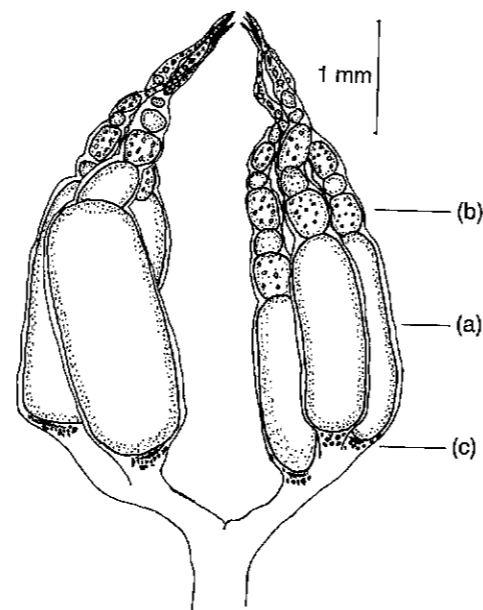


Fig. 11.1 Characteristics of the active ovaries of a gamergate in *Pachycondyla sublaevis*. Large yolky oocytes (a) (including a mature one) occur at the bases of the six ovarioles, followed by developing oocytes alternating with nurse cells (b). Yellow bodies (c) are situated basally in each ovariole. Note the large size of the mature oocyte relative to total ovariole length. (From Peeters *et al.* (1991)).

behavioural profile and the likelihood of mating in species with multiple gamergates. Since colony sampling is destructive, the number of mated workers in a particular nest cannot be monitored over the year. Thus breeding structure must be pieced together using dissection data from many nests collected in the field at different times of the year (Table 11.3).

The largest number of gamergates in a nest has been reported in *Ophthalmopone berthoudi*: 108 out of 242 adult workers (Peeters and Crewe 1985a). Males of this species are active above ground between January and April, and they visit foreign nests where they copulate with workers underground (Peeters and Crewe 1986a). This is inferred from the large proportion of inseminated workers found in nests excavated after the period of male activity. In two nests containing 77 and 119 workers, all the workers active outside the nests were marked prior to excavation. None were found later to be inseminated. In contrast, most of the workers (98 per cent and 69 per cent respectively) confined inside the nests had been inseminated. The unmated intranidal workers were predominantly callows (Peeters and Crewe 1985a). Thus it appears that only workers that are past the callow stage, but not yet active above ground, can mate. It is possible that only workers

Table 11.3 Colony characteristics of various species without queens. Average colony sizes of several species were calculated from published collection data ( $N$  = number of colonies).

Species	Workers per colony	Gamergates per colony	References
<b>Monogynous species</b>			
<i>Diacamma australe</i>	139 ± 61 ( $N$ = 10)	1	Peeters and Higashi (1989)
<i>D. rugosum</i>	118 ± 88 ( $N$ = 21)	1	Abe and Uezu (1977), Fukumoto <i>et al.</i> (1989)
<i>Pachycondyla sublaevis</i>	9 ± 3 ( $N$ = 12)	1	Peeters <i>et al.</i> (1991)
<i>P. krugeri</i>	52 ± 20 ( $N$ = 14)	1	Peeters and Crewe (1986b); Wildman and Crewe (1988)
<i>Platyhyrea lamellosa</i> <sup>a</sup>	115 ± 83 ( $N$ = 25)	1	Villet <i>et al.</i> (1990)
<i>P. schultzei</i> <sup>a</sup>	21 ± 10 ( $N$ = 7)	1	Villet (1991)
<i>Streblognathus aethiopicus</i>	27 ± 13 ( $N$ = 12)	1	Ware <i>et al.</i> (1990)
<b>Polygynous species</b>			
<i>Dinoponera quadriceps</i>	66 ± 26 ( $N$ = 10)	14/10/1	Dantas de Araujo <i>et al.</i> (1990)
<i>Leptogenys schwabi</i>	68 ± 29 ( $N$ = 20)	6 ± 4	M. Zini (personal communication)
<i>Ophthalmopone berthoudi</i>	186 ± 151 ( $N$ = 34) <sup>b</sup>	19 ± 29	Peeters and Crewe (1985a)
<i>Rhytidoponera confusa</i> <sup>a</sup>	164 ± 208 ( $N$ = 64)	4 ± 3,5 <sup>c</sup>	Ward (1983a)
<i>R. sp. 12</i> (near <i>mayri</i> ) <sup>a</sup>	415 ± 165 ( $N$ = 3)	23 & 21	Pamilo <i>et al.</i> (1985); Peeters (1987b)

<sup>a</sup> *Platyhyrea* belongs to tribe Platyhyreini, *Rhytidoponera* belongs to Ectatommini, and all others belong to Ponerini.

<sup>b</sup> colonies are polydomous; these data refer to individual nests.

<sup>c</sup> pooled results from 12 *confusa* and 21 *chalybaea* colonies.

*Dinoponera australis*

13 ± 6 ( $N$  = 37)

1

Peira and Brandão

*Amalysopone*

of an appropriate age attract foreign males. The evidence obtained in *O. berthoudi*, for example, suggests that all workers which are of an appropriate age during the annual period of male activity can mate. The limiting factor appears to be the number of foreign males which locate successfully a particular nest. The numbers of gamergates remain constant between mating seasons (except for mortality), but as new workers eclose, the proportion of gamergates in each colony decreases gradually. The proportion of gamergates in 18 nests collected at other times of the year was often low (less or equal to 5 per cent of worker population in 9 nests). In fact, there was considerable variation among nests, even those collected at the same time of the year. There was no consistent relationship between number of gamergates and number of infertile workers. However, a distinct seasonal pattern is obscured by differences in the histories of individual nests, e.g. the number of young workers present during the mating season, and the number of foreign males which visit.

*Rhytidoponera confusa* is another species with multiple gamergates which has been studied in detail. A large number of nests were collected (Ward 1983a), but only in autumn or winter, and thus no data are available after the mating season. The number of gamergates per colony was not correlated with colony size. It is striking that few gamergates were found in the colonies of *R. confusa*, compared to *O. berthoudi*, despite their similar colony sizes (Table 11.3). Ward (1983a) speculated that subtle dominance interactions (observations of 'antennal boxing') may result in the inhibition of sexual calling behaviour in most workers, but he provided no data to support this. It seems unlikely that age structuring in the colonies is sufficient to limit the numbers of workers that mate, because a considerable number of workers are produced along with queens and males each year (Ward 1981b, 1983a).

#### *Regulation of mating: monogynous species*

As in polygynous species, workers in colonies with a single gamergate eclose throughout the year. Thus, there should be a number of sexually attractive workers in the nests during the period of male activity. Yet only one mated worker is present in each nest (Table 11.3). The limited evidence available suggests that only one worker is sexually attractive when males visit each colony, probably as a result of competitive interactions.

The Australian *Pachycondyla sublaevis* has exceptionally small colonies (Table 11.3). Study of one laboratory colony revealed the existence of a dominance order (Ito and Higashi 1991) in which the gamergate was engaged in infrequent ritualized attacks directed at one or two subordinate workers. After removal of the gamergate, the frequency of attacks among the remaining workers doubled and the second-ranked worker became dominant. When dissected later, only this worker had well-developed ovaries. When a foreign male was introduced into another colony, he attempted

to copulate only with the dominant worker. This implies that only the dominant worker is sexually attractive, perhaps as a consequence of having active ovaries (Ito and Higashi 1991).

In *Streblognathus aethiopicus*, ovarian activity and sexual behaviour in workers is apparently inhibited by the presence of a gamergate (Ware *et al.* 1990). After one colony was divided in two, four workers in the group without the gamergate were observed in a sexual-calling posture outside the laboratory nest. When all workers were later dissected, only these four workers had developed ovaries (they had not mated). All the workers in the group with a gamergate had undeveloped ovaries. However, no dominance interactions were observed among nestmates.

A novel mechanism for controlling sexual attractiveness has been discovered in *Diacamma australe* (Peeters and Higashi 1989) and *D. rugosum* (Fukumoto *et al.* 1989). The single gamergate in each colony is the only worker which retains the 'gemmae' (tiny bladder-like thoracic appendages which are unique to this genus). All workers have gemmae at eclosion, but these are soon pulled off by the gamergate. After experimental removal of the gamergate, one of the newly emerged workers (often the first one) behaves aggressively and proceeds to mutilate the other callow workers. When foreign males were introduced in laboratory colonies, they copulated only with the worker having gemmae. These gemmae are filled with exocrine cells, but the involvement of gemmae secretions in male attraction is unclear (Peeters and Billen 1991). Thus, gamergates in these two *Diacamma* species inhibit permanently the sexual activity of nestmates through one aggressive act: mutilation of the gemmae.

#### *Regulation of ovarian activity*

In the absence of physiological studies on the endocrine control of oogenesis in ponerine ants, our knowledge of the regulatory mechanisms involved is based on a comparison of the characteristics of ovarian activity in mated and unmated workers. Furthermore, the occurrence of inhibition has to be investigated by experimental manipulation of colonies, e.g. creating groups without gamergates. This is easy in monogynous species: even if the gamergate cannot be identified visually, the division of field-collected colonies into two always results in the formation of one orphaned group of workers. In contrast, it is seldom possible to remove all the gamergates from an experimental group in polygynous species. When dissecting the workers of a particular colony, it is important to kill them simultaneously and freeze them until needed. If ants are kept alive in their colonial group until dissected, individuals who may have been inhibited previously will begin to exhibit oogenesis.

Dissection and behavioural data obtained from 11 queenless species reveal that the mated workers monopolize reproduction. Nonetheless, in some species, one or a few virgin workers are able to oviposit in colonies



without gamergates. This indicates that insemination is not a prerequisite for oviposition, and that the ovarian activity of virgin workers is inhibited by the gamergates. The pattern of oogenesis in the ovaries of unmated workers varies markedly among species (Table 11.4). In some, unmated workers normally have undeveloped ovaries, but once the gamergate is removed, a few workers exhibit ovarian activity (and may eventually lay eggs). In orphaned colonies of *Pachycondyla sublaevis*, *Dinoponera*, and *Streblognathus*, only one or two virgin workers produce mature oocytes. These individuals are likely to mate when foreign males visit the nests. In contrast, in *Diacamma australe* and *D. rugosum*, removal of the gamergate is followed (after one to two weeks) by oviposition involving a large proportion of workers. However, in *D. rugosum*, this unrestricted oviposition is short-lived (Peeters and Tsuji 1993). In small orphaned groups of workers without cocoons, a dominance order is soon established, based on agonistic interactions among those workers having active ovaries. The dominant worker proceeds to eat the eggs laid by her nestmates, and after a few weeks the ovaries of all individuals, except the dominant worker, become resorbed again. Since this dominant worker lacks gemmae, she cannot mate. However, having groups of orphaned workers without female cocoons is an artificial situation, and as new workers emerge in field colonies without a gamergate, one of them will keep her gemmae (Fukumoto *et al.* 1989; Peeters and Higashi 1989). In *D. rugosum*, this unmutated virgin worker is able to inhibit the ovarian activity of the mutilated workers (Peeters, unpublished). She begins to lay eggs, and will mate once an opportunity arises. In *Ophthalmopone berthoudi*, unmated workers were always found to have undeveloped ovaries, which led Peeters and Crewe (1984) to conclude that insemination is the trigger for oogenesis in this species. However, since groups of virgin workers were never isolated from gamergates, the possibility of inhibition was not investigated. Nevertheless, in several nests that contained only one gamergate, virgin workers did not have active ovaries (Peeters and Crewe 1985a).

There are also species in which a large proportion of virgin workers have developed ovaries while coexisting with one or more gamergate(s) (Table 11.4). In *Rhytidoponera* sp. 12, a majority of the unmated workers have ovaries containing many medium and large yolky oocytes (Pamilo *et al.* 1985; Peeters 1987b). However, workers active outside the nests have undeveloped ovaries. Peeters (1987b) indicated that there were consistent differences in the pattern of oocyte development between mated and virgin workers. In the latter, oocytes develop abnormally and never mature; this interpretation is confirmed by the absence of yellow bodies in their ovaries. Thus only mated workers lay eggs, and oocytes do not accumulate in their ovaries. In *Pachycondyla krugeri*, many unmated workers have yolky oocytes, but these never grow to more than half the

reproductive

Table 11.4 Characteristics of oogenesis in the ovaries of unmated workers from experimental groups with or without a gamergate.

Monogynous species	Gamergate(s) present	Gamergate(s) removed	References
<i>Diacamma australe</i>	Undeveloped ovaries	Many lay eggs	Peeters and Higashi (1989)
<i>D. rugosum</i>	Undeveloped ovaries, except 1 individual	Many lay eggs	Fukumoto <i>et al.</i> (1989)
<i>Pachycondyla krugeri</i>	Immature yolky oocytes in 59-92% ants	Only 1-2 lay eggs	Peeters and Crewe (1986b); Wildman and Crewe (1988)
<i>P. sublaevis</i>	Undeveloped, or no yolky oocytes	Mature oocytes in 1 individual	Peeters <i>et al.</i> (1991)
<i>Platythyrea lamellosa</i>	Immature yolky oocytes	Mature oocytes in 1 individual	Villet <i>et al.</i> (1990)
<i>P. schultzei</i>	Undeveloped ovaries	Mature oocytes in 1 individual	Villet (1991)
<i>Streblognathus aethiopicus</i>	Undeveloped ovaries	Mature oocytes in a few individuals	Ware <i>et al.</i> (1990)
<b>Polygynous species</b>			
<i>Dinoponera quadriceps</i>	Mature oocytes in 1 individual in some nests	?	Dantas de Araujo <i>et al.</i> (1990)
<i>Ophthalmopone berthoudi</i>	Undeveloped ovaries	?	Peeters and Crewe (1985a)
<i>Rhytidoponera confusa</i> <sup>1</sup>	Mature yolky oocytes in 8/139 individuals	?	Ward (1983a)
<i>R. sp. 12</i> (near <i>mayri</i> )	Immature yolky oocytes in 82%	?	Pamilo <i>et al.</i> (1985); Peeters (1987b)

<sup>1</sup> type B colonies, i.e. with gamergates.

size of an egg (Peeters and Crewe 1986b; Wildman and Crewe 1988). In colonies divided in half, eggs were laid in the groups without a gamergate, but only one or two workers had active ovaries (Wildman and Crewe 1988). In *Platythyrea lamellosa*, sclerotized workers confined inside nests with a gamergate produce immature oocytes (Villet *et al.* 1990). In contrast, all virgin workers of *P. schultzei* have undeveloped ovaries in the presence of the gamergate (Villet 1991).

The finding that virgin workers are able to oviposit in various species indicates that oogenesis is not conditional on insemination. Thus reproductive division of labour is based both on the regulation of mating and on inhibition of ovarian activity. Gamergates in some species have been found to be unable to inhibit the oviposition of one or more unmated nestmates (e.g. in *Pachycondyla sublaevis* and *Streblognathus aethiopicus*; Peeters *et al.* 1991; Ware *et al.* 1990). These gamergates lacked mature oocytes in their ovaries, and were presumably old. Furthermore, in *Diacamma rugosum* and *Dinoponera quadricaps*, one virgin worker laid eggs in some colonies with gamergates (Taki 1991; Dantas de Araujo *et al.* 1990); the gamergate in these colonies may no longer have been ovipositing. These data suggest that inhibition ability may correlate with fecundity.

#### Cohabitation between gamergates

In species where several gamergates coexist in one colony, how do they interact? Do they have similar fecundity? In *Rhytidoponera* sp. 12 and *O. berthoudi*, the gamergates occur together in the same parts of the nest, and there are no obvious antagonistic interactions. However, more detailed data are not available due to the difficulty in identifying gamergates prior to dissection. In *R. confusa*, gamergates and infertile workers engaged in short bouts of reciprocal antennation, sometimes followed by retreat, but the existence of dominance orders was not investigated (Ward 1983a). All gamergates had well-developed ovaries, and data on genotypic pattern confirmed that several laid eggs (Ward 1983a). In contrast, the ovarian development of mated workers in *O. berthoudi* varied markedly. Out of 293 dissected mated workers, only 94 had one or more (sometimes two, rarely three) mature oocytes in their ovaries (Peeters and Crewe 1985a). It is yet unclear whether the other individuals were non-reproductive mated workers or whether they lacked mature oocytes because they did oviposit recently. This could not be verified since the presence of yellow bodies was not recorded. At any rate, there was a strong seasonal component to the proportion of gamergates having only immature oocytes (decrease from 93 per cent in March (end of mating season), to 22 per cent in October; Peeters and Crewe 1985a). Assessing fecundity on the basis of the number of mature oocytes found during dissection is difficult because in several queenless ponerines only few mature oocytes can be accommodated simultaneously in the ovaries (there are only six or eight ovarioles, and eggs are long

relative to these; Fig. 11.1). Thus dissection of ovaries before or after an oviposition event may provide different estimates of an individual's fecundity.

In *Dinoponera quadricaps*, 9 out of 18 gamergates were found without mature oocytes in their ovaries, which was interpreted as an age effect (Dantas de Araujo *et al.* 1990). It was claimed that young, recently mated workers do not yet have completely developed ovaries, although the possibility of inhibition was not investigated experimentally. Several gamergates, all belonging to the same age cohort (as revealed by the degree of mandibular wear), can coexist in a colony (even in the same chambers) and exhibit well-developed ovaries with mature oocytes.

Future studies need to investigate whether dominance orders exist among the gamergates in polygynous species, and if so, whether they result in differential reproductive output.

#### Characteristics of reproductive inhibition

Evidence has been presented that various workers (mated or not) are able to regulate the ovarian activity of their nestmates. In some species, this takes the form of dominance orders based on aggressive interactions. This was demonstrated in *Pachycondyla sublaevis* (Ito and Higashi 1991), and among orphaned *Diacamma rugosum* workers without gemmae (Peeters and Tsuji 1993). Hormonal changes which affect oogenesis probably result from the ritualized attacks or direct aggression (including biting) experienced by individuals of subordinate status.

In several other monogynous species, the ovarian activity of nestmates is regulated without dominance orders. Physical interactions involving the gamergate or other nestmates have never been observed in *Pachycondyla krugeri* (Wildman and Crewe 1988), *Platythyrea lamellosa* (Villet *et al.* 1990), *P. schultzei* (Villet 1991), or *Streblognathus aethiopicus* (Ware *et al.* 1990). It seems clear that the gamergate signals her presence by chemical means, or there may be production of inhibitory pheromones. In *Diacamma australe*, gamergates never behaved aggressively towards their nestmates lacking gemmae, but in recently orphaned colonies containing an unmutated worker which had not yet mated, this future gamergate frequently harassed other workers (violent jerking, biting of limbs and antennae) (Peeters and Higashi 1989). In both cases suppression of ovarian development in other workers was achieved. Thus in *D. australe*, insemination appears to cause a switch from physical to pheromonal inhibition. (Since trophallaxis does not occur among ponerine adults (see Hölldobler 1985; Masuko 1986), the putative pheromones are likely to be transmitted by contact chemoreception or by airborne perception.)

The presumed ability of gamergates to produce inhibitory pheromones parallels the situation in Cape honeybees where, in orphaned colonies, some laying workers are able to elicit retinue behaviour and inhibit the rearing of new queens (Crewe and Velthuis 1980). These dominant workers

(who never mate) influence reproduction of nestmates by producing mandibular gland substances which are similar to the queen's. Indeed, the proportion of the various pheromonal components changes with the social position of workers in orphaned groups (Crewe and Velthuis 1980).

The existence of dominance orders probably represents the ancestral situation in ant (and other hymenopteran) societies. Nevertheless, pheromonal regulation occurs widely in ants, and hence in the queenless ponerines it is reasonable to expect both to occur. The presence or absence of antagonistic interactions among workers may be related to existing physiological and exocrine traits at the evolutionary time when the queen caste disappeared. Dominance interactions among workers exist in a few species with queens (sometimes together with pheromonal queen inhibition). In *Pachycondyla apicalis*, they serve to regulate the production of male eggs by workers (Oliveira and Hölldobler 1990). The queen did not attack the dominant workers, but she often ate their eggs. After queen removal, worker oviposition increased, and the dominant worker then ate the eggs laid by subordinates (Oliveira and Hölldobler 1990). In queenless species, reproductive competition among workers functions secondarily to regulate mating as well.

#### Is gamergate number adaptive?

The presence of multiple queens in a colony has generally been assumed to be adaptive, either with reference to particular ecological circumstances (Hölldobler and Wilson 1977, 1990), or to kin-selection considerations (Nonacs 1988). Similar selective advantages are probably associated with the presence of multiple gamergates. Comparative evidence suggests that an adaptive shift from polygyny to monogyny (or vice versa) can occur easily. Indeed, some genera exist in which there are both species with one gamergate per colony, and species with multiple gamergates (Table 11.5). However, possible responses to local selection pressures may be affected by phylogenetic constraints, i.e. the evolutionary potential for changes in queen (or gamergate) number may vary from lineage to lineage (Ross and Carpenter 1991). For example, in all the queenless species of *Rhytidoponera* that have been studied (Table 11.5), multiple gamergates are found in the colonies (occasionally, individual colonies are found with only one gamergate).

Assuming that extant species with queens are representative of the ancestral stocks from which queenless species evolved, do they have one or several mated queens in their colonies? Comparative data, although fragmentary, indicate that related species with queens are monogynous (Table 11.5). The unique cases of *R. confusa* and *R. chalybaea* are particularly interesting because, in each species, reproduction is performed either by mated queens or by gamergates. Colonies in which queens occur are strictly monogynous, while colonies without queens contain several

Table 11.5 Number of functional reproductives per colony in various congeneric species with or without queens. A dash (-) indicates that either queens, or gamergates, do not occur.

Species	Queens	Gamergates	References
<i>Diacamma australe</i>	-	one	Peeters and Higashi (1989)
<i>D. rugosum</i>	-	one	Fukumoto <i>et al.</i> (1989)
<i>Dinoponera australis</i>	-	one	R. Paiva (personal communication)
<i>D. quadriciceps</i>	-	several <del>one</del>	Dantas de Araujo <i>et al.</i> (1990)
<i>Ophihalmopone berthoudi</i>	-	several	Peeters and Crewe (1985a)
<i>O. hottentota</i>	-	several	Peeters and Crewe (1985b)
<i>Pachycondyla apicalis</i>	one	-	Oliveira and Hölldobler (1990)
<i>P. krugeri</i>	-	one	Wildman and Crewe (1988)
<i>P. nigrita</i>	-	several	F. Ito (personal communication)
<i>P. obscuricornis</i>	one	-	Fresneau (1984)
<i>P. porcata</i>	-	one	Peeters (unpublished)
<i>P. sublaevis</i>	-	one	Peeters <i>et al.</i> (1991)
<i>Platythyrea arnoldi</i> <sup>1</sup>	one?	several	Peeters (unpublished), Villet (1990c)
<i>P. cf. cribrinodis</i>	-	one	Villet (1990c)
<i>P. lamellosa</i>	-	one	Villet <i>et al.</i> (1990)
<i>P. schultzei</i>	-	one	Villet (1991)
<i>Rhytidoponera confusa</i> <sup>2</sup>	one	several	Ward (1983a)
<i>R. sp. 12 (near mayri)</i>	-	several	Peeters (1987b)
<i>R. purpurea</i>	one	-	Ward (1983b)
other queenless spp.	-	several	Haskins and Whelden (1965)

<sup>1</sup> queen and gamergates reproduce in the same colonies.

<sup>2</sup> colony dimorphism: either queens or gamergates reproduce.

*P. villosa*  
several queens

gamergates (Ward 1983a). It is possible that colonies cannot grow sufficiently with only one gamergate per colony, given that the fecundity of gamergates (two to four eggs/day) is less than that of queens (nine eggs/day) (Peeters, unpublished).

In species with polydomous colonies (i.e. occupying several distinct nests), polygyny clearly seems to have adaptive benefits. In *Ophthalmopone berthoudi*, there are two to seven nests per colony, and gamergates occur in each (Peeters and Crewe 1985a, 1987). Although workers and brood are normally transferred between nests, in the event of one nest becoming isolated from the others, it will remain viable. Except for *O. berthoudi*, other queenless species with a polydomous organization have not been found. Little is known about the importance of ecological characteristics such as temporal stability of nesting sites or habitat as a whole, two factors suggested by Hölldobler and Wilson (1977) to favour polygyny.

#### Social correlates of gamergate number

Interspecific comparison of monogynous and polygynous colonies reveals the following relationships.

#### Colony size

Colonies having a single gamergate range in mean size from 9 to 139 workers (Table 11.3). This reflects partly interspecific differences in gamergate fecundity. Workers of different species can have different numbers of ovarioles, or produce eggs of different sizes, both of which can affect fecundity. Gamergates of *Diacamma australe* can lay 5 eggs/day, as a consequence of having 12–18 ovarioles and relatively small eggs ( $1.4 \times 0.4$  mm) (Peeters, unpublished). In contrast, gamergates in *Pachycondyla sublaevis* appear to lay one egg every two to three days, which is associated with having only 6 ovarioles and laying much larger eggs ( $2.7 \times 0.9$  mm) (Peeters *et al.* 1991). Colonies with multiple gamergates appear generally larger (Table 11.3), but attempts to correlate colony size and gamergate number are confounded by interspecific differences in fecundity.

#### Genetic relatedness among nestmates

Low relatedness among nestmates is expected when several gamergates reproduce in a colony, and this has been confirmed electrophoretically for *Rhytidoponera* sp. 12 ( $r = 0.16$ ; Crozier *et al.* 1984) and *R. confusa* (gamergate colonies:  $r = 0.30 \pm 0.13$ ; Ward 1983a). The large expected differences in intra-colony relatedness between monogynous and polygynous queenless species raise the question of whether there are concomitant changes in other colony characteristics. Ward (1981a, 1983a) predicted that in *R. confusa*, altruistic behaviour and colony cohesion would be less developed in colonies with lower levels of relatedness, due to a reduction in the efficacy of colony-level selection. Indeed, Ward showed that worker

aggressiveness and size of individuals differ between queen- and gamergate-colonies. This is by no means conclusive as other interpretations are possible (e.g. colony size, influence of the queen during larval development).

#### Colony identity

Nestmate recognition has been documented in two species having multiple gamergates. In *Rhytidoponera* sp. 12, low intra-nest relatedness should lead to considerable variability in worker-produced odour cues (Peeters 1988). Nonetheless, older workers attack foreign conspecific workers, and intra-colony hostility was never observed. Crosland (1990) also showed that variation in relatedness has no influence on the recognition ability of *R. confusa* workers. No differences in worker aggressiveness towards aliens were exhibited between colonies having either a single queen or several gamergates. Nestmate recognition has not been studied in monogynous species without queens, although casual observations confirm its occurrence (e.g. *Diacamma australe*; Peeters, unpublished).

#### Colony reproduction

The creation of new colonies occurs necessarily through the fission of existing ones in all queenless ponerine ants (Peeters 1991a). Gamergates have never been observed to start new colonies independently; they mate inside or near their nest, and there is no solitary dispersal away from the natal nest.

Whether a species has one or several gamergates per colony influences the characteristics of colony fission. In monogynous species, colony fragmentation provides opportunities for the differentiation of a new gamergate. Once released from the inhibition of the existing gamergate, one or more workers can exhibit ovarian activity and/or become sexually attractive. However, depending on the time of the year when fragmentation occurs, males may not be active above ground. Therefore, colony fission is not always immediately followed by mating, and a temporary period of male production may occur. In polygynous species, it is likely that when a colony divides, the gamergates are distributed in each group, and viable daughter colonies are immediately formed.

Crozier (1979) suggested that fission in *Rhytidoponera* might occur when intra-colony relatedness drops below a critical level, but this has never been investigated empirically. It is not known whether colony fragmentation occurs accidentally (e.g. during nest emigration) or through a specific organized process. In monogynous species, fragmentation may follow the recent appearance of more than one mated worker in a colony.

#### Concluding remarks

Concurrent with the evolutionary disappearance of queens in some species, reproductive division of labour has evolved among workers. The

proximate mechanisms leading to either monogyny or polygyny differ between species with or without queens. When queens exist, they usually disperse and mate with foreign males away from the natal nests. Many inseminated queens are later eliminated, either during independent foundation, or later in a colony's ontogeny (often as a result of worker aggression). In some species, dominance interactions among inseminated queens regulate oviposition.

Dominance interactions also play an important role in species without queens with regard to which workers mate and reproduce. Most or all the workers of a certain age during the period of male activity are apparently able to mate. However, in most species studied, workers engaged in aggressive interactions and only the dominant worker(s) mate. One exception is *Ophthalmopone berthoudi* where some colonies contain many mated workers. Dominance interactions among mated workers may also affect reproductive status as demonstrated in *Harpegnathos saltator* where some mated workers are inhibited from reproducing as a consequence of physical attacks from the gamergates.

### Summary

As in many other ant subfamilies, ponerine species can be either monogynous or polygynous. The factors associated with this pattern are reviewed, with particular emphasis on the morphological characteristics of reproductives. In various species, queens have lost the ability to fly, or they have been replaced by workers.

The occurrence of winged queens represents the ancestral condition. Although the extent of queen-worker dimorphism varies considerably within the subfamily, the queens of many species exhibit little morphological specialization. Consequently, they cannot found new colonies without foraging outside the nest. Monogyny is the predominant type of colony organization; polygynous species also exist, but large numbers of functional queens never occur together.

In the large group of ponerine ants having ergatoid queens, colonies are always monogynous, and independent foundation does not occur. Ergatoid queens have become very fecund in some species, and relatively large numbers of workers can be present in each colony.

In some ponerine species, queens are unknown, and mated workers reproduce. Control over mating and reproduction often takes the form of aggressive interactions among workers, although pheromonal regulation can also occur. In monogynous queenless species, only one worker is able to lay eggs and mate as a result of dominance orders. In polygynous species, the factors regulating the number of workers that mate remain poorly understood. There is generally little or no aggressive interactions among reproducing workers in polygynous colonies.

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