The occurrence of sexual reproduction among ant workers

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In less than 100 species of ponerine ants, queens no longer exist and have been replaced by mated egg-laying workers. Workers in other subfamilies can lay haploid eggs when queens are removed, but they never reproduce sexually. Ponerine workers are able to mate because they have a spermatheca in most species, foreign males are sexually active near their nests, and their pygidial gland secretions can assume a sexual meaning. Furthermore, ponerine queens are seldom very fecund, and one or several gamergates are able to approximate their egg production. Finally, opportunities for colony fragmentation occur consequent to their life history, and this is a necessary precondition because gamergates cannot start new colonies independently. Many of these characteristics are associated with the limited caste divergence exhibited in this phylogenetically primitive group. Although a few non-ponerine species exhibit some of these preconditions, gamergates have not been found outside the Ponerinae, which alone exhibit the combination of traits leading to queen elimination *and* worker mating.

KEY WORDS:—Ants – Ponerinae – reproduction – worker mating – dimorphism – males.

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INTRODUCTION

In ants, mating and diploid reproduction is typically the prerogative of the queens, which are morphologically specialized for colony foundation and efficient egglaying. Workers are morphologically adapted for helper behaviour, but they usually retain ovaries and in many species are also able to reproduce, either in the presence of the queen(s), or following her death (reviewed by Bourke, 1988; Choe, 1988). Workers generally produce males, which arise parthenogenetically from unfertilized eggs. Bourke (1988) suggested that worker reproduction greatly influenced the development of many characteristic colony

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traits, and remains a powerful influence on social cohesion, colony efficiency and sex investment ratios. However, he specifically excluded from his review species in which workers are capable of mating.

Worker reproduction takes on a special significance in the phylogenetically ancient subfamily Ponerinae, because in several species queens do not exist and have been permanently replaced by mated reproductive workers (= gamergates, 'married workers'). All the workers in a colony have identical ovaries and a spermatheca, but only the individuals who are able to mate during the annual period of male activity differentiate into gamergates. Mated workers are not active outside the nests, while the unmated workers perform all the helper roles. In some species only one gamergate occurs in each colony (Wildman & Crewe, 1988; Peeters & Higashi, 1989; Villet, Hart & Crewe, 1990), while in others there can be a variable number of gamergates per colony (Haskins & Whelden, 1965; Ward, 1983; Peeters & Crewe, 1985a; Peeters, 1987a). Queen loss in the latter species is accompanied by a low level of genetic relatedness between colony members (Crozier, Pamilo & Crozier, 1984).

TABLE 1. List of the species of ants from subfamily Ponerinae in which workers are known to exhibit sexual reproduction. In *Hypoponera eduardi*, mated egg-laying "major workers" were initially reported (Le Masne, 1956), but these are in fact ergatoid queens

Species	References	Notes
TRIBE ECTATOMMINI		
Rhytidoponera "metallica" group	Haskins & Whelden, 1965	2, 3
R. tasmaniensis, victoriae	Haskins & Whelden, 1965	1, 3
R. inornata	Haskins & Whelden, 1965	2, 3
R. confusa, chalybaea, impressa	Ward, 1981b, 1983	2, 4
R. enigmatica	Ward, 1983	2
Also, more than 40 large species, found in arid habitats of Australia (Brown, 1953, 1958). These include:		
R. violacea	Whelden, 1957	2
R. sp. 12 (near *mayri*)	Peeters, 1987a	2
Also, 18 species in New Caledonia	Ward, 1984	2
TRIBE PLATYTHYREINI		
Platythyrea schultzei	Peeters, 1987b	2
P. arnoldi	C. Peeters, unpublished	2
P. lamellosa	Villet, Hart & Crewe, 1990	2
TRIBE PONERINI		
Diacamma rugosum	Wheeler & Chapman, 1922	2
D. australe	Peeters & Higashi, 1989	2
Dinoponera gigantea	Haskins & Zahl, 1971	1
D. quadriceps	Dantas de Araujo, Fresneau & Lachaud, 1988	2
Hagensia marleyi	C. Peeters, unpublished	2
Leptogenys schwabi	M. Zini (personal communication)	2
Ophthalmopone berthoudi	Peeters & Crewe, 1985a	2
O. hottentota	Peeters & Crewe, 1985b	2
Pachycondyla krugeri	Peeters & Crewe, 1986b	2
P. porcata	C. Peeters, unpublished	2
P. sublaevis	Peeters, Higashi & Ito, 1991	2
Streblognathus aethiopicus	Ware, Compton & Robertson, 1990	2

[1]Occurrence of gamergates inferred from the production of new workers in the absence of queens.
[2]Occurrence of gamergates confirmed by dissection.
[3]Queens are occasionally produced but are not functional.
[4]Colonies have either one queen or several gamergates.

Among the higher eusocial Hymenoptera (in which queens and workers differ morphologically, i.e. bumble bees, stingless bees, honey bees, vespine wasps and ants), it is only in the ants that the queens have occasionally disappeared and workers reproduce sexually. The lower eusocial Hymenoptera (polistine wasps, polybiine wasps and halictine bees) are excluded from consideration (as in Bourke, 1988) because reproductive and helper roles are performed by morphologically undifferentiated female adults. Throughout this article I use 'worker', 'queen' and 'caste' in a strict morphological sense (Peeters & Crozier, 1988).

Sexual reproduction by workers is found in fewer than 100 ant species (Table 1), and all of these belong to the subfamily Ponerinae. Why do workers not reproduce sexually in other ants? In order to explain this restricted occurrence, we need to examine *both* (1) the morphological and social attributes which enable workers to replace queens; (2) the ecological circumstances in which queen reproduction is non-adaptive. A companion paper (Peeters & Crewe, in prep.) examines the latter, i.e. why workers perform the reproductive function better than queens under certain conditions. In this article I concentrate on the former consideration, i.e. the morphological competence of ponerine workers for sexual reproduction, and other preconditions which must exist to enable the transition from queen to worker reproduction. To this end I present comparative evidence on the biology of species with and without queens.

MORPHOLOGICAL COMPETENCE OF WORKERS

An ever-increasing dimorphism between queens and workers has made possible the elaboration of social organization in ants (Wheeler, 1986). Although workers are morphologically specialized for the performance of helper roles, they have seldom lost the ability to produce and lay eggs (examples of ant workers without ovaries are given in Bourke, 1988: 299). However, workers in most species have lost their spermatheca or the ability to mate (Brian, 1979). Nevertheless, the extent of caste divergence varies widely between ant groups, and primitive species are exceptional in that most workers have retained a spermatheca. In the course of ovarian dissections in 20 genera of ponerine ants, I documented the lack of a spermatheca in the workers of only four genera, i.e. *Sphinctomyrmex* c.f. *steinheili* (Buschinger, Peeters & Crozier, 1989), *Cerapachys* c.f. *heros*, *Brachyponera lutea* and *Onychomyrmex hedleyi* (Peeters, unpublished data). Furthermore, Le Masne (1956) also reported the absence of a spermatheca in *Hypoponera eduardi*. The loss of a spermatheca in ponerine workers seems to be a general consequence of the increasing dimorphism between the castes. In *Brachyponera lutea*, which is distinguished by the most pronounced difference in size between queens and workers in the Ponerinae, workers lack ovaries entirely.

DIFFERENCES IN FECUNDITY BETWEEN THE CASTES

Colonies of higher ants often reach a large size, partly because inseminated queens are able to sustain a high rate of egg production. Indeed, the ovarian specialization of the queen caste can be very pronounced, while workers

generally have only a few ovarioles. Such highly fecund queens could not be replaced by gamergates because the latter cannot produce eggs sufficiently quickly. However in the Ponerinae, it is characteristic of many queens that they have only 6–8 ovarioles and a correspondingly lower fecundity (Fresneau, 1984; Peeters, 1987b). Their egg-laying rate is also limited by the lack of trophallaxis among nestmates (Wilson, 1971; Hölldobler, 1985; Masuko, 1986). Since ponerine workers do not regurgitate liquid nourishment to the queen, she has to feed herself on the prey that is retrieved to the nests. Many ponerine queens may not be able to lay more than 10 eggs per day, although the ergatoid queens of some species (e.g. *Leptogenys* c.f. *mutabilis*, *Megaponera foetens*) are considerably more fecund (Maschwitz *et al.*, 1989; Peeters, 1991).

Gamergates generally have a low fecundity because their ovaries are unspecialized. In various species studied, they lay between one and two eggs per day (Peeters & Crewe, 1985a; Peeters, 1987a; Wildman & Crewe, 1988). Indeed, even when there are many gamergates, the colonies of queenless ants are invariably small (less than 500; Peeters, 1990). However, gamergates with a low egg-laying rate are able to take over the oviposition role of ponerine queens having a fecundity which is not dramatically higher than theirs.

PONERINE MALES LOCATE NESTS, NOT SEXUAL PARTNERS

Ponerine ants without a queen caste have normal winged males, and outbreeding occurs. Workers mate inside their natal nests or near the entrances, and thus males must be able to locate foreign nests (see Peeters & Crewe, 1986a). This male behaviour is essential for the ground-borne workers to become inseminated, and its evolutionary origin can be traced to the dispersal patterns exhibited in various ponerine species with winged and ergatoid queens (Fig. 1).

In many ants, males and virgin queens from different colonies find each other and mate during mass nuptial flights which occur away from the nests ('male-aggregation syndrome'; Hölldobler & Bartz, 1985). This behaviour is appropriate when both male and female sexuals are winged, but it is almost never observed in ponerine species. In *Amblyopone pallipes*, the virgin queens disperse singly or in small groups over short distances, and alight on the ground or low vegetation (Haskins, 1978). They then adopt a stereotyped 'calling' posture while releasing sex attractants, and flying males soon appear and mate with them ('female calling syndrome'; Hölldobler & Bartz, 1985). Similarly, the sexuals in *Odontomachus assiniensis* (Ledoux, 1952) and *Paltothyreus tarsatus* (Villet, Crewe & Robertson, 1989) fly away from their nests singly. The only ponerine ant in which mating is known to take place in large groups is *Ponera pennsylvanica* (Haskins, 1970), and this appears to be a derived condition (Fig. 1). Thus, while conspecific sexuals in *P. pennsylvanica* and many higher ants locate each other by orienting to the mating swarms, in the other ponerines mentioned above the males fly around searching for individual virgin queens. Their chances of success are enhanced because, as in higher ants, both sexes are active above ground simultaneously, presumably because they all respond to the same environmental cues for dispersal.

A deviation from this pattern is found in ponerine ants with ergatoid queens. Such queens never have wings and have evolved from winged queens (Haskins,
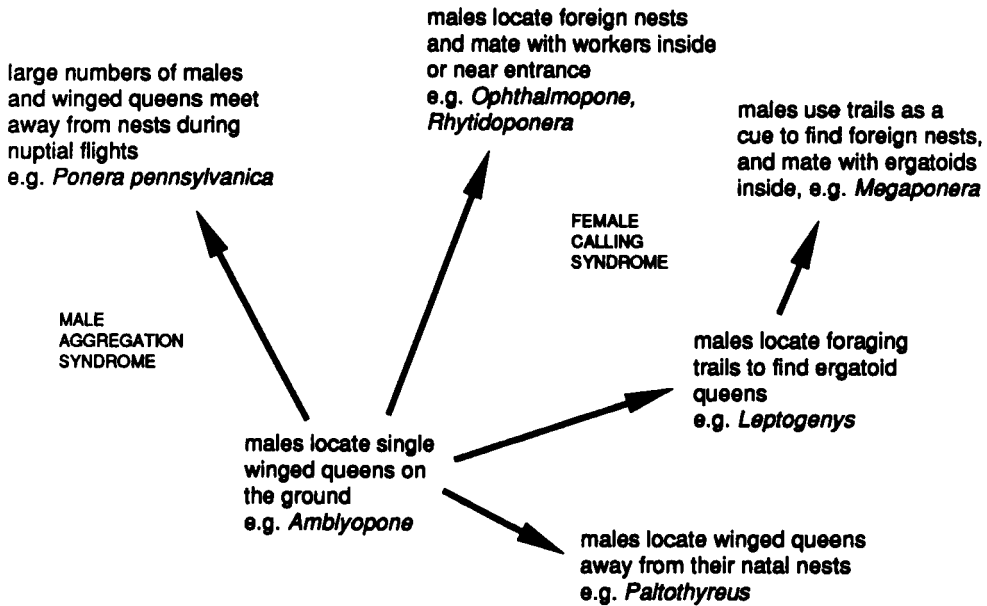
Figure 1. The range of male behaviours exhibited in ponerine ants. The ancestral pattern, as seen in the most primitive genus *Amblyopone*, has been modified in various ways, e.g. to locate wingless sexual partners (either ergatoid queens or workers).

1970; Peeters, 1991). They occur in 15 ponerine genera, but details of mating behaviour are known only from a few species. In *Leptogenys ocellifera* and *L. chinensis*, males leave on a dispersal flight, then land and search on the ground. They locate and run along the durable recruitment trails laid by workers, and it has been suggested that ergatoid queens mate on these trails (Maschwitz & Muhlenberg, 1975; Maschwitz & Schönegge, 1983). It is not known whether the ergatoids release sex attractants. Again, the exits of male and female sexuals from their natal nests are synchronized in time, and this facilitates their attempts at finding each other. A further step in this evolutionary sequence occurs in *Megaponera foetens*, where males use the foraging trails laid by the workers to find foreign nests (Longhurst & Howse, 1979). The virgin ergatoid queens are inseminated inside the nests, and thus the male strategy relies on locating conspecific nests, and not individuals. This change in male behaviour (Fig. 1) has significant consequences, because it brings foreign males in contact with young workers. However, workers never mate when queens exist (see below).

In species with gamergates, males must search for receptive workers inside the nests, although the latter may also be active outside the entrances. It is not clear which orientation cues are used by the males to locate foreign nests, because almost all queenless ponerines studied cannot lay chemical trails (Peeters & Crewe, in prep.). Males copulate underground in *Diacamma rugosum* (Wheeler & Chapman, 1922) and in *Ophthalmopone berthoudi* (Peeters & Crewe, 1986a). Males have been observed flying into the nests of *Rhytidoponera tasmaniensis* and *R. mayri* (Brown, 1953), while successful worker-male matings have been reported outside nest entrances in *R. metallica* (Hölldobler & Haskins, 1977) and

R. chalybaea (Ward, 1981b). In the latter, males also entered nests and may have mated with workers within these. The manner in which receptive workers are able to perceive that males are active outside the nests has not been determined. In *R. chalybaea* (where colonies have either a queen or gamergates), the virgin queens and the males leave the nests together, and this stimulates the exit of large numbers of workers which mill around the entrances (Ward, 1981b).

In summary, we can detect a number of evolutionary changes in the behaviour of ponerine males (Fig. 1) which are associated with the loss of the flying ability by their sexual partners. The switch to worker mating appears to have been possible because, in many ponerine species with queens, mating takes place on the ground near the natal nests. The latter may be associated with the low colony density which is characteristic of many ponerine species. There is a need to investigate the pattern of male behaviour in other ponerine species with winged queens, ergatoid queens, or gamergates, in order to accumulate details about how the nests and sexual partners are located, and where mating occurs.

PONERINE WORKERS CAN ATTRACT MALES

How do males recognize workers as suitable sexual partners? Generally in ants, queens attract males by releasing sex pheromones, but this is not well documented in the Ponerinae. In *Amblyopone pallipes*, virgin queens leave the parent colony and adopt a 'calling' posture—they rest motionless with gaster arched and sting extruded (Haskins, 1978). In *Rhytidoponera metallica*, a species with gamergates, workers exhibit an identical 'calling' behaviour during which pheromones are released from the pygidial gland, and this attracts males (Hölldobler & Haskins, 1977). It has not been determined whether the queens of *Amblyopone pallipes* also use the pygidial gland to produce sex attractants.

Hölldobler & Haskins (1977) postulated that the primary function of the pygidial gland in ponerine workers is not the secretion of sex pheromones, because the workers of many species with a queen caste also have this abdominal gland (e.g. Hölldobler & Engel, 1978; Jessen, Maschwitz & Hahn, 1979; Villet, Peeters & Crewe, 1984; Hölldobler, 1984; Jessen & Maschwitz, 1983). The pygidial gland is then used either to release air-borne tandem running pheromones or to lay recruitment trails on the substrate (e.g. Maschwitz & Schönegge, 1977; Hölldobler & Traniello, 1980a, b). Thus, the same exocrine gland is used for two different purposes by the workers of different ponerine species: to recruit fellow workers during foraging or nest emigration, or to attract males.

Ponerine queens in some species may also use pygidial gland secretions to attract males. In several species males are active in or near foreign nests, and thus they come in contact with workers who also release a pygidial gland signal. Assuming that males respond to the pygidial gland secretions of queens, they will thus be attracted to 'calling' workers and will mate with them. In *Rhytidoponera confusa*, both gamergates and mated queens occur although never in the same colony (Ward, 1983), which suggests that workers are inhibited from mating when a queen is present.

OPPORTUNITIES FOR COLONY FRAGMENTATION

The limited behavioural repertoire and low fecundity of gamergates preclude them from starting new colonies independently, and instead colonies reproduce by budding, i.e. a parental colony can divide into two fragments, each containing mated and unmated workers (e.g. *Ophthalmopone berthoudi*; Peeters & Crewe, 1985a). Colony budding is a different process from colony fission (Franks & Hölldobler, 1987), and the latter is obligatory in species with ergatoid queens (Haskins & Haskins, 1955; Bolton, 1986). Colony budding in queenless species appears to be associated with the frequent above ground movement of workers and brood. For example, budding can occur accidentally during nest emigration in *Diacamma rugosum* (Fukumoto & Abe, 1983), *Rhytidoponera* sp. 12 (Peeters, 1988), and *R. impressa*-group (Ward, 1981a).

Thus opportunities for colony fragmentation need to be a feature of the life history of the queenright ancestors of species without queens, and these may be afforded through nomadism, frequent nest emigration or polydomy (i.e. one colony inhabiting several distinct nests). In addition, some ponerine species with multiple dealate queens also exhibit colony budding (Traniello, 1982).

DISCUSSION

Mated workers reproduce instead of the mated queens in several species of ponerine ants. The phenomenon of sexual reproduction by members of the worker caste has only been reported in this subfamily. The myrmicine *Pristomyrmex pungens* is the only non-ponerine ant in which the queen caste never exists; however, workers do not mate but reproduce parthenogenetically (Itow *et al.*, 1984; Tsuji, 1988). Unmated workers also produce diploid eggs in *Cataglyphis cursor*, but this is a temporary event which occurs after the death of a queen (Lenoir & Cagniant, 1986; Lenoir, Quérard & Berton, 1987). In several leptothoracine genera, there exists an exceptional pattern of female polymorphism, because a proportion of nest inhabitants consist of a variety of forms intermediate between queens and workers (intercastes, or 'intermorphs', e.g. Francoeur, Loiselle & Buschinger, 1985). Few alate queens are produced, and intercastes sometimes have a spermatheca and can become inseminated. Workers lack a spermatheca in most species, e.g. *Harpagoxenus sublaevis*, *Formicoxenus chamberlini* (Buschinger & Winter, 1978, Buschinger & Francoeur, 1983), but in *F. provancheri* a proportion of the workers have a spermatheca and have been observed to 'call' (Buschinger, Francoeur & Fischer, 1980). Mated workers have been found, but it is arguable that this situation is not analogous to that in ponerine species with gamergates. Indeed, the worker caste in *Formicoxenus* is not uniform since not all workers have a spermatheca, and those possessing one have more ovarioles (2×3) than those without (2×2). Furthermore, mated workers can occur together with mated queens or intercastes, and they can then be inhibited from laying eggs. In contrast, in ponerine ants with sexually reproducing workers, queens have completely disappeared. It is only in *Rhytidoponera confusa* that functional queens and

TABLE 2. Occurrence outside the ponerine ants of the various biological characteristics which enable workers to reproduce sexually

Characteristics	Occurrence outside the Ponerinae
(1) Do workers have a spermatheca?	Generally absent, except in *Myrmecia*, and a proportion of workers in *Formicoxenus*
(2) Limited difference in fecundity between queens and workers?	True in some *Myrmecia*, Pseudomyrmecinae, various leptothoracines (often social parasites). But queens are very fecund in other Myrmicinae, and many Formicinae and Dorylinae
(3) Do males locate nests?	No mass nuptial flight in several *Myrmecia* spp. In Dorylinae, males find nomadic colonies with wingless queens. Mating occurs outside or inside nest in socially-parasitic Myrmicinae
(4) Can workers attract males?	Unknown at present since it has been assumed that workers never mate. In *Formicoxenus provancheri*, some workers call
(5) Do mechanisms of colony fragmentation exist?	Throughout the ants. Exclusive mode of colony reproduction in Dorylinae. In some social parasites, fission occurs as well as independent foundation

Sources: Wilson, 1971; Francoeur, Loiselle & Buschinger, 1985; A. Buschinger, personal communication.

gamergates exist conspecifically, albeit in distinct colonies (Ward, 1983). In some other species of *Rhytidoponera* having gamergates, queens are occasionally produced, but they are rarely mated and they are not functional (Haskins & Whelden, 1965; Ward 1986; Table 1).

The occurrence of sexually-reproducing workers in a few ponerine ants is associated with five biological characteristics (Table 2). It is necessary to determine whether these characteristics are prerequisites for the replacement of queens by gamergates, or whether they are its consequences. The limited morphological divergence between queens and workers is linked with the primitive phylogenetic position of this subfamily. Thus, in the Ponerinae, workers are more similar to queens than in the other subfamilies. In many species they retain a functional spermatheca, and when mated, they can attain an egg-laying rate which is not dramatically lower than that of the queens they replace. This limited difference between the castes is the ancestral condition, and is thus not a consequence of worker reproduction. Furthermore, the existence of opportunities for workers to encounter foreign males, together with processes of colony multiplication which do not rely on a single foundress, can be shown to be necessary preconditions for the emergence of mated workers as the functional reproductives. As seen in Table 2, the five characteristics identified in this paper are not unique to the Ponerinae. In various leptothoracine species (subfamily Myrmicinae), queens and workers can sometimes have the same number of ovarioles (e.g. *Harpagoxenus sublaevis*; Buschinger & Winter, 1978), and the small colony sizes reflect the low queen fecundity. Females 'call' close to their natal nests and attract foreign flying males (although foreign males are never tolerated inside the nests (A. Buschinger, personal communication), and mating inside the nests is associated with inbreeding). There is strong comparative evidence that these traits in leptothoracines are derived. However, since workers lack a spermatheca in almost all species, gamergate breeding is not an evolutionary option. In contrast, many ponerine ants exhibit all five characteristics in combination.

While gamergates are exclusive to the Ponerinae, why do they only occur in a minority of species? I argue that (1) the replacement of queens by gamergates is not possible in those ponerine species which exhibit a marked queen-worker dimorphism; queens then have very many ovarioles while workers may lack a spermatheca; (2) where the substitution of queens is possible, it is not necessarily selected for. Indeed, queenless species occur in several unrelated taxa, and it appears that the queen caste disappeared only when ecological conditions dictated it (Peeters & Crewe, in prep.). Thus there are many species of ponerine ants having queens in which workers may be able to mate and reproduce, yet they do not. This reveals that there exist effective mechanisms of queen control. Bourke (1988), reviewing the instances of worker (haploid) reproduction in the higher eusocial Hymenoptera, suggested that queen control of worker fertility can be explained as a response to the threat to queen fitness posed by worker reproduction. An even more intense queen-worker conflict occurs in many species of primitive ants, since their workers have the potential to usurp the queen's reproductive role entirely.

Sexual reproduction by workers is a derived condition in ants. Indeed, in *Nothomyrmecia macrops*, *Myrmecia* and *Amblyopone*, which are the most primitive genera of living ants, queens reproduce instead of workers (Hölldobler & Taylor, 1983; Clark, 1951; Traniello, 1982). Nonetheless, workers in these ancient groups have seldom lost the morphological competence to reproduce sexually, and in some evolutionary lineages, selective pressures led them to mate and replace queens. Why do gamergates not occur in *Myrmecia*? Some species indeed exhibit various of the prerequisites for gamergate breeding. Thus, although large mating flights occur in several species, in others with ergatoid queens, new sexuals disperse independently (Haskins & Haskins, 1950, 1955). Queens sometimes have a limited fecundity, and workers have retained a spermatheca (e.g. *M. gulosa*, Crosland, Crozier & Jefferson, 1988). More details of the life history of myrmeciines will be needed to understand why gamergates do not occur.

It is important to emphasize that, although various biological characteristics combine to make diploid worker reproduction viable in many Ponerinae, the pattern of queen loss cannot be accounted for by the occurrence of these characteristics alone. Independent colony foundation by dealate queens was selected against in various species because queens must forage outside the nest while rearing the first workers, and because reproductive investment is limited (Peeters & Crewe, in prep.). Selection favouring worker diploid reproduction may have existed in various non-ponerine ants, but in such species workers cannot mate.

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