

COLONY REPRODUCTION AND ARBOREAL LIFE IN THE
PONERINE ANT *GNAMPTOGENYS MENADENSIS*
(HYMENOPTERA: FORMICIDAE)

by

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ABSTRACT

Gnamptogenys menadensis is an Indonesian ponerine ant that is exclusively arboreal. Foragers hunt for prey and sweet secretions on the branches and leaves of shrubs and trees, but never walk on the ground. It nests in pre-existing tree cavities which are sealed with a lining of organic material. Several factors facilitate colony reproduction by fragmentation: available nest sites are plentiful, nest structure represents only a minor investment of labour, and nests cannot be enlarged, inducing nest emigration or polydomy as colonies grow in size. A mechanism of colony fragmentation is one of the preadaptations to enable the replacement of queens by worker reproductives. We found that the majority of colonies (95%) in the studied population (Sulawesi) are queenless, and reproduce through gamergates (mated workers laying reproductive eggs). Nevertheless, queens can occasionally be produced, and 5% of nests contained a single reproductive queen. Due to obligate arboreal life, alate queen production seems to remain an infrequent strategy in addition to budding, since only independent founding queens can colonise new patches of vegetation.

KEY WORDS: life history, gamergate, queen, nest emigration, budding, foraging, Ponerinae.

INTRODUCTION

All ants belonging to the subfamily Ponerinae are predators on arthropods, but other aspects of their ecological profile vary enormously. These mainly tropical ants nest in the ground or in rotting wood in the leaf litter stratum. Ponerine ants have conserved a great number of ancestral morphological traits (PEETERS, 1997). The queen-worker dimorphism is low, with little difference in the number of ovarioles between the two castes resulting in low queen fecundity and thus in small colony sizes (dozens to hundreds of

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workers). Solitary queen foundresses lack sufficient metabolic reserves to rear the first workers and need to forage outside their nest. In many species a special mode of colony reproduction has evolved: colony budding, in which a colony splits into two autonomous parts, each containing reproductives and workers (BOURKE & FRANKS, 1995). Although this modification can occur in species with alate queens, it is obligatory in species where alate queens have been replaced with either ergatoid (permanently wingless) queens or gamergates (mated workers laying reproductive eggs; PEETERS, 1991).

There has been little research on the biology of the widely distributed (in the Neotropical, Indo-Australian and Oriental region) genus *Gnamptogenys* (tribe Ectatommini). Limited ecological data are available mostly from taxonomic papers (BROWN, 1958, 1993; LATTKE, 1990, 1995). PRATT (1994) documented an age-based division of labour in two colonies of *G. horni*. Most *Gnamptogenys* have either alate or ergatoid queens, *G. menadensis* being the first documented species with gamergates. Nevertheless, alate queens are still produced infrequently, and both budding of workers and founding by queens seems to occur.

G. menadensis can be found throughout the Indo-australian region. Taxonomic records include West Malaysia (IMAI *et al.*, 1983); Central Sulawesi (SANTSCHI, 1935), Borneo (YAMANE, pers. comm.) and the Philippines (BROWN, 1958).

In the present contribution we investigate the ecology and behaviour of the arboreal species *Gnamptogenys menadensis*. Arboreal nesting is quite exceptional in ponerine ants (PEETERS, 1997). Although several species are known to forage in the vegetation near their ground nests (WEBER, 1946; YOUNG, 1977; DE VRIES, 1988; ROBBINS, 1991; PASSERA *et al.*, 1994), only four species, belonging to three different tribes, were found to be actually nesting in trees: *Platythyrea conradti* (LEVIEUX, 1976), *Pachycondyla luteola* (DAVIDSON & FISHER, 1991; VERHAAGH, 1994), *P. goeldii* (CORBARA & DEJEAN, 1996), and the South American *Gnamptogenys concinna* (LATTKE, 1990). All these species vary in colony size, degree of association with the plants, and mode of colony establishment, indicating that no single 'arboreal strategy' exists. However, all arboreal ponerine species have alate queens.

We argue that arboreal life in *G. menadensis* has consequences for their mode of colony reproduction, since it constrains colony budding to a single tree or patch of vegetation. Although budding has some advantages over solitary colony founding, alate queens remain necessary for colonisation of new trees in *G. menadensis*.

MATERIAL AND METHODS

During three field trips (January 1994, February 1995 and March 1996) we studied 58 colonies of the small (0.7 cm length) *Gnamptogenys menadensis* (MAYR) in 6 valleys of the Karaenta Nature Park, District Maros, South Sulawesi, Indonesia (park boundaries are situated at 119°46'54"E and 5°02'00"S; altitude \pm 265 m). Nests were located by checking cavities in branches in the lower 3.5 m of vegetation or by baiting foragers with live termites. When nests were located close to one another, we colour-marked foragers to check if nests belonged to a single colony. In some neighbouring valleys we could not locate any nest in the lower vegetation. Most observations were made between 08:30 h and 18:00 h, which is the larger part of the daylight period.

We collected all workers and brood of 37 colonies by wrapping branches in plastic and tape after which the branches were cut. In addition to counts from the field, sexuals emerging from cocoons collected in the field were recorded. Returning foragers were collected for at least half an hour after wrapping the nest, and in some cases, foragers clustering at the cut ends of branches were collected one day later. Most colonies were transported to Belgium and kept in plaster nests for further observations.

Standard measurements were taken at 50 \times magnification with 0.02 mm accuracy. Head width (HW), eyes not included, and pronotal width (PW) were measured and significance of differences between queens and workers were analysed using the Mann-Whitney *U* test.

RESULTS

Habitat description

Karaenta Park consists of limestone tower karst hills covered with secondary rain forest (WHITTEN *et al.*, 1987). The small valleys — a few hundreds m² each — are separated by high rock cliffs (up to 40 m) on which only limited vegetation is found. Valleys open into one another through gaps of only a few meters wide. The upper canopy, approximately 40 m high, is discontinuous. Therefore sunlight can penetrate to the forest floor, where the lower vegetation is abundant. The area receives an annual rainfall of about 3500 mm (WHITTEN *et al.*, 1987), with the peak of the rainy season in January (670 mm). These heavy rains cause a great deal of surface runoff on slopes, even in the dry season, when rainfall can be concentrated in only a few days. Valley floors consist of heavy moist clay which is only partially covered with a thin leaf litter layer because of the runoff. Most water is drained through holes in the limestone rocks, but on several occasions during the rainy season, we observed flooding on horizontal valley floors.

Colony composition

The mean size of the colonies was 113 ± 75 workers ($N = 37$), which seems average for the genus (LATTKE, 1990). Colonies contained large quantities of larvae and cocoons (table I), and quick colony growth is expected if food supply is sufficient.

Although complete colonies were collected, only two colonies (18 and 51; table I) were queenright, containing a single inseminated dealate queen. None of the workers or additional alate and dealate queens were mated, as determined by dissection of all colony members at the end of our observations. In all other nests one or several inseminated workers (gamergates) reproduced (B. GOBIN, unpublished). Gamergate colony 9 contained a single dealate queen which was virgin and had undeveloped ovaries, while in gamergate colonies 4, 10 and 13 alate queens emerged from cocoons collected in the field (table I). A few alate queens were produced in the laboratory in other gamergate nests. There is a small size dimorphism in *G. menadensis* (median queen HW = 1.06 mm ($N = 16$), median worker HW = 1.16 mm ($N = 27$), $U = 9.5$, $p < 0.001$; median queen PW = 1.07 mm ($N = 16$), median worker PW = 0.98 mm ($N = 27$), $U = 85.5$, $p < 0.005$). In laboratory conditions, queens that were unable to fly out remained in their natal nest, shed their wings and started performing nest maintenance and foraging. In the lab, several callow queens had abnormally inflated wings, which were then bitten off by workers. Dealate virgin queens were also found in nests in the field.

Male sexuals were found in all three sampling periods, so they seem to be present throughout at least a large part (January-April) of the rainy season. Unlike female alates, males were collected from many gamergate colonies (table I).

Brood care

Larvae eclose about two weeks after egg-laying, and are mature after another three weeks. As in most ponerine ants, trophallaxis is absent in *G. menadensis*, and workers feed larvae by placing pieces of prey or worker-laid trophic eggs near them. Larvae are able to crawl a few mm towards prey. When a larva is ready to spin, workers place it next to existing cocoons, which will be used as a scaffold for the silk threads. This is opposed to burying larvae with nest material, which is found in most other ponerine species (PEETERS, 1997). When the cocoon is nearly finished, workers tear it loose from the older cocoons. Callows eclose after three weeks of pupation with the help of several workers, who open the cocoon and drag out the callow which will remain nearly immobile for several hours.

TABLE I

Numbers of workers, brood and sexuals counted immediately after collection in 37 nests of *G. menadensis* (* = counted on arrival in Belgium); sexuals that eclosed from cocoons collected in the field are included. Numbers of foragers collected one day later near cut edges are indicated between brackets. Other symbols: al = alate; dl = dealate; p = present, but not counted; × = not counted. Colonies A-6 collected Jan. 1994; 8-19 collected Feb. 1995; 21-56 collected Mar. 1996.

Colony number	Total workers	Foragers	Eggs	Larvae	Cocoons	Males	Queens
A	12	0	2	0	0	0	0
1	63	7	50*	41*	19*	0	0
2	30	p	13*	14*	0	0	0
3	106	12	130	71	99	8	0
4	93	15	58	63	52	20	1al
5	18	p	38	16	8	0	0
6	93	7	48	55	44	0	0
8	112	36	93	55	62	3	0
9	100	8 (5)	122	109	105	0	1dl
10	96	15 (15)	63	50	52	10	2al
12	31	3 (6)	25	19	43	0	0
13	288	25	140	46	66	0	1al
15	43	p (13)	37	23	36	0	0
16	61	p (5)	42	25	62	0	0
18	107	13	36	43	66	2	2dl/7al
19	177	p (50)	100	16	69	0	0
21	188	31	142	133	63	0	0
23	68	4	29	41	21	0	0
25	80	14	33	24	1	0	0
28	124	31 (12)	74	78	73	16	0
29	105	25 (7)	67	32	37	0	0
30	106	25 (12)	43	71	36	1	0
32	38	2	29	27	8	0	0
33	82	11 (2)	100	67	39	0	0
34	170	10	63	70	17	4	0
35	28	18	11	6	8	0	0
38	82	10	124	54	41	0	0
42	140	6	123	88	80	9	0
44	296	28	246	140	141	0	0
46	193	5	111	63	101	0	0
47	120	17	113	60	19	4	0
48	344	37	289	138	96	7	0
49	76	9	7	30	3	0	0
50	122	×	375	134	176	0	0
51	168	23	99	121	11	0	2dl/1al
52	81	×	52	36	46	0	0
56	128	×	89	42	60	0	0

While grooming eggs and larvae, workers frequently rub these against the cluster of hairs on their abdominal tip. Workers and especially gamergates squeeze larger larvae, after which they will lick the larva's body and mandibles. We never actually observed droplets of regurgitated liquid. This behaviour resembles the haemolymph feeding by damaging the integument described in *Amblyopone silvestrii* (MASUKO, 1986). Haemolymph taps such as in *Leptanilla japonica* (MASUKO, 1989) are absent in *G. menadensis*.

When too little food was provided in the laboratory, this squeezing behaviour escalated in the killing and cannibalism of the larva, while pupae, pulled out of cocoons, and even recently emerged callows were also eaten. Reproductive eggs were rarely eaten. When nests were opened in the field, we regularly saw larvae feeding on remnants of pupae and other larvae, providing evidence of brood cannibalism under natural conditions. This is also suggested by the discrepancies in numbers of different brood stages found in the field (eggs, larvae and cocoons; table I).

Nest characteristics

The majority of colonies (51 out of 58) inhabited pre-existing cavities in various trees and shrubs, while 5 nests were located in cavities in limestone rocks and 2 in shafts of rotan palm leaves. For practical reasons, we could only investigate the lower part of the vegetation (up to 3.50 m). Nest cavities were an estimated 10 to 150 cm³, and colonies with few workers were generally living in the smallest cavities.

In all nests (except colony A), the cavity was sealed from the outside with a lining of organic material, consisting of a mixture of cocoon strips, diverse arthropod parts (presumably remnants of prey), decaying and occasionally fresh plant material. By building walls of this same material, larger cavities can sometimes be divided into a number of chambers, thus enlarging the useful surface area. PRATT (1994) described a wall-papering behaviour in *G. horni*, in which certain nest areas were lined with old cocoons to protect brood from excessive moisture. Within the lining we found nests of the small formicine ant *Paratrechina* sp. ($N = 6$), the myrmicine *Strumigenys godeffroyi* ($N = 1$), as well as several small arthropods, diatomea and algae.

Foraging

G. menadensis workers forage exclusively on the leaves and branches of trees and shrubs. In the rock nests, foragers also preferred walking on vegetation growing over the rocks. Where there is contact between neighbouring shrubs, workers will forage up to 10 m from the nests, sometimes over as many as 5 contiguous plants. A large proportion of the workforce

forages (table I). *G. menadensis* is a generalist predator, with prey sizes generally under 5 mm, and maximal 25 mm. Foragers can actively search for prey, stalk it by standing motionless on a leaf surface, or scavenge on dead arthropods. Prey localisation, capture and retrieval are generally performed by individual workers, but short-lasting cooperation of nearby nestmates is sometimes obtained, presumably through the release of an olfactory signal. When a prey is caught and stung, workers will quickly return to the nest, following a fixed route, sometimes tapping their sting onto the branch surface. Rubbing off the surface of branches or displacing contact points between branches clearly disorientated foragers, suggesting that a trail pheromone is deposited on the substrate. Trails seem to enhance foraging to certain areas on shrubs. A trail pheromone could also provide orientation clues when workers are homing to the nest. Foraging is not limited to any particular time of day, although many foragers either returned to the nest or hid into small cavities whenever heavy rain started. Around several of the observed nest sites and near exploited sugar sources, workers of the formicine ant *Polyrhachis rufipes* often interacted with *G. menadensis* foragers (B. GOBIN, unpublished).

We observed foragers biting flowering buds and licking at the sap exuding from the newly created wounds. When workers fed on sap from a freshly unfolded rotan leaf situated about 1.5 m from the nest, all workers leaving the nest foraged to this leaf. Several callows left the nest, to lick at the wounds inflicted by other workers. Since trophallaxis does not exist in this species, foraging is the only way in which callows can obtain plant secretions.

Nest emigration

Whenever nests were situated close to each other, we marked foragers with paint and observed them for 30-60 min. Nests were considered part of a polydomous colony when we observed movement of workers between the two nests during this period. We found 7 polydomous colonies in the field, with two ($N = 6$) or three subnests on the same tree or shrub, and distances between nests ranging from 0.25 m to 2 m. In two of these we observed transport of callows between nests. In neighbouring colonies 38 and 39, connected over 6m of rotanpalm leaves, we marked 40 and 35 workers respectively, and observed these for 17 h during 3 days. There was a considerable overlap in foraging area but contacts between alien workers were rare and never resulted in aggression. Nearly all foragers carrying prey returned to their own nest ($N = 40$), while only 3 entered the other nest. Four days later, workers could no longer reach each other's nests because of the presence of a new colony of *Polyrhachis rufipes* in the connecting

palm tree. This observation suggests that subnests in polydomous colonies can eventually become independent. When colony 38 was collected and released near colony 39, workers immediately started transporting brood and adults towards it. After a short period of aggression all brood and workers entered nest 39.

We recorded one nest emigration in the field, when a slightly disturbed nest of *G. menadensis* became completely evacuated two days later. During two consecutive field trips, half of the located nests were empty the next year, while many new nests were discovered in previously unoccupied cavities. Nest moving was also easily induced by disturbing colonies in the laboratory. *G. menadensis* never enlarges the nesting cavity by excavating wood. Thus the fixed cavity size limits nest growth, and might induce nest moving. The likelihood of nest moving is also linked to the low investment represented by this simple nest structure (HANSELL, 1984). In all valleys we found an abundance of vacant nest sites. We presume that the small colony A (table I) had only recently occupied its cavity, since no sign of building activity was present.

When 6 collected colonies were released by attaching the container to a branch, some workers immediately left while tapping the substrate at high intensity with their sting. In all cases some workers located a new nest site and started strong recruitment of nestmates within 30 minutes after release. Workers carried brood but also callows and other workers over their heads while holding them by their mandibles as in *Rhytidoponera metallica* (MÖGLICH & HÖLLDOBLER, 1974). Carried workers always assumed a pupal posture. About 1 hour after the recruitment started, workers did no longer reinforce the trail. Two to three hours after release no brood and only few workers remained in the containers. In *G. horni* a similar nest emigration with trail recruitment occurs (PRATT, 1994).

DISCUSSION

Due to low queen specialisation in ponerine ants, founding queens lack sufficient reserves to rear their first brood, and therefore need to forage until the first workers emerge and take over (semi-claustral foundation). This constraint on independent foundation might lead to increased post-dispersal mortality due to predation and competition (PEETERS, 1997). Nevertheless, this ancestral strategy is adaptive under certain ecological conditions, since most *Gnamptogenys* have alate queens (BROWN, 1958; LATTKE, 1990, 1995).

Colony fragmentation as a means of colony reproduction has the advantage that the new nest starts off with an established work force, able to

defend territories and compete for food sources. In those *Gnamptogenys* species having ergatoid queens as reproductives (BROWN, 1958), fragmentation must exist as the mechanism for starting new colonies (PEETERS, 1993). In *Gnamptogenys menadensis*, all factors facilitating colony reproduction by fragmentation are present: nests are energetically cheap due to low building investment (HANSELL, 1984; PEETERS & HÖLLDOBLER, 1995), nests have fixed sizes and cannot be enlarged while many long-lived possible nest sites are available, thus inducing nest emigration (WARD, 1981; PEETERS, 1997). Nest moving in *G. menadensis* might result in temporary or even longer lasting polydomy, which in itself enhances the possibility of fragmentation.

The existence of a mechanism for colony fragmentation is one of the biological characteristics necessary to enable the complete replacement of queens by worker reproductives in ants (PEETERS, 1991). Additionally, *G. menadensis* workers have a functional spermatheca and there is only a limited difference in fecundity between queens and gamergates (B. GOBIN, unpublished). These factors enable gamergates to take over the egg-laying role of the queen. We found gamergate reproduction in 95% of colonies in the studied population. Because of the observed polygyny in gamergate nests, and the presumably haphazard fragmentation of colonies, colony budding seems to be the general mode of colony establishment in *G. menadensis*. Since colony budding with worker reproduction exists in this species, we might expect a loss of the queen caste, as is the case in other ponerine species. However, alate queens can still be produced (table I) and two colonies (5%) were queenright. Both queenright colonies were monogynous, suggesting that these were actually founded by these queens. In another ectatommine ant, *Rhytidoponera metallica*, alate queens are occasionally produced. Queenright colonies are never found in the field, but WARD (1986) collected two inseminated alate queens and these started colonies in the laboratory. Ward interprets occasional queen production as an alternate, long range dispersal strategy in response to changes in environmental conditions. In *Harpegnathos saltator*, alate queens are necessary to start new colonies since budding is not possible due to the elaborate nest structure designed to survive floods (PEETERS & HÖLLDOBLER, 1995). When the short-lived queens die, highly related gamergates will take over reproduction, thus ensuring continued use of the expensive nest.

In *G. menadensis*, because of their completely arboreal life (nesting and foraging), dispersal by budding is limited to interconnecting patches of vegetation and even the smallest gap cannot be crossed. Daughter colonies will remain close to the mother colony, and compete with it for resources (local resource competition; BOURKE & FRANKS, 1995). Although gene flow occurs through alate males, alate queens are needed to colonise new trees or patches of new habitat. Furthermore, due to the small difference in size

between queen and workers, queens seem relatively cheap to produce compared to species with a distinct size dimorphism. Their ability to perform tasks within the colony reduces the investment in queens even further. Even if success rates of independent founding by queens are low, a strong advantage can be obtained if a queen can colonise a new patch. Therefore it is adaptive to continue producing queens at a low frequency (*e.g.*, when food is plentiful). In this way, occasional queen production in *G. menadensis* remains an alternative mode of reproduction, necessary to colonise new patches of vegetation. After colonisation, the patch can be further exploited by gamergate reproduction and budding.

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