

Large colonies and striking sexual investment in the African stink ant, *Paltothyreus tarsatus* (subfamily Ponerinae)

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Most ponerine ants have colonies with up to a few hundreds of workers, but there has been sporadic evolution of species with more populous colonies. Forty two nests of *Paltothyreus tarsatus* were excavated from three distinct habitats in the Ivory Coast. Colonies were monogynous in Comoé (forest and savanna), but polygynous in Taï (rainforest). Mean colony size was 1576 ± 1543 workers, with the biggest colonies (exceeding 5000 adults) restricted to forest. Hundreds of sexuals occurred in many nests. Unlike males, young queens stay in the nests at least six months before the mating flight, presumably to accumulate fat reserves. This together with high absolute numbers of gynes and their large size relative to workers, amounts to a striking reproductive investment. We discuss this investment in the context of non-claustral independent colony foundation. Mating was observed in large male aggregations, unlike in South Africa where queens mate near the natal nests.

Key words: independent colony foundation, non-claustral, monogyny, reproduction, mating.

INTRODUCTION

Ponerine ants are remarkably diverse in morphology, reproductive behaviour and ecological profiles. Many species in this phylogenetically basal subfamily exhibit simple social traits: limited queen-worker dimorphism, colonies with a few dozens or hundreds of workers, and solitary foraging (Peeters 1997). Such traits are widespread in all lineages of Ponerinae, supporting the hypothesis that they represent plesiomorphic states (Schmidt 2009). Nonetheless, across different genera, a small number of species have evolved more advanced traits, such as polymorphic workers, bigger colonies and group hunting. One of the more atypical ponerine ant is *Paltothyreus tarsatus* Fabricius. This large ant (17–20 mm) is an epigeic hunter and scavenger and is widely distributed throughout Africa south of the Sahara (Arnold 1915; Wheeler 1922). Although the workers forage individually, they can recruit nestmates with chemical signals when retrieving bigger or more abundant prey items (Hölldobler 1984). The nests of *P. tarsatus* have multiple entrances, revealing an extensive system of shallow tunnels that lead to the foraging grounds (Hölldobler 1980, Braun *et al.*

1994). We collected over 40 complete colonies in savanna and forest habitats in the Ivory Coast, and compared nest structures, colonial demography and reproductive investment. We discuss modifications in colony size and strategies of colony foundation across the Ponerinae.

MATERIAL AND METHODS

We conducted field work at two localities (northern and coastal) in the Ivory Coast, West Africa. The southern part of Comoé National Park is a mosaic of savanna woodland and forest habitats. The savanna is compartmentalized by gallery forests running along permanent or temporary watercourses; in addition, forest islands are often found in the savanna (Adjanohoun 1963). Mean annual rainfall is 1076 mm; the dry winter season (<100 mm) lasts six months (October to March). Taï National Park (near the coast) consists mainly of rainforest. The dry season lasts four months (November to February); mean annual rainfall is 1657 mm (WorldClim 50-year climate data <http://bioval.jrc.ec.europa.eu/APAAT/>). We excavated a total of 42 *P. tarsatus* colonies from August

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1992 to April 1995 in Comoé (both in savanna and forests) and Taï. We aimed to collect all adults and brood in each colony. Excavations began at an active entrance, and we followed the shallow foraging galleries by gentle digging with a trowel. Once large concentrations of workers were found, vertical digging proceeded. In addition, incipient colonies were excavated soon after the mating season.

We dissected a total of 150 workers confined inside the nests to check whether they were able to produce eggs. We also determined the dry weight of 100 gynes and males from nine colonies sampled prior to dispersal.

RESULTS

Nest and colony structure

Paltothyreus tarsatus nests primarily in forest, but also in savanna. This broad range of habitat preferences is accompanied by differences in nest structure. The largest and most complex nests were found in gallery forests. In one colony we counted more than 300 chambers, connected together by short subterranean tunnels (5–10 cm deep, 2–10 cm in length). We also found deeper (50–70 cm below surface) tunnels up to 10 m long connecting separate aggregations of workers. Chambers (8 × 10 × 2 cm) could be as deep as 190 cm. Shallow subterranean tunnels extended in different directions, up to 60 m away. These foraging tunnels had exits to the surface at more or less regular intervals.

Nests located in savanna had considerably fewer chambers (<50), and did not exceed 90 cm in depth. Shallow foraging tunnels also occurred and some were even longer than 60 m. We did not find deeper underground tunnels connecting inhabited chambers in the savanna. In the rainforest, nests consisted of only about 20 chambers that were 30 cm below ground.

Records of prey carried by foragers as well as prey remains outside nest entrances show more than 90 % arthropods, especially termites (*Macrotermes bellicosus* and *M. subhyalinus*) and millipedes, but also ants (mainly *Camponotus* sp.) and beetles. We also recorded earthworms as prey remains, and these may be hunted in the subterranean tunnels where they were often present during our excavations.

Mean colony size was 1576 ± 1543 workers ($n = 42$), and three colonies yielded more than 5000 workers (Table 1). Colony P33 was first

excavated in March 1995 when we collected 7161 workers, 3 dealate queens, 823 gynes and many brood. Two months later we discovered in the exact same spot an additional network of galleries, yielding 5361 workers, two dealate queens and more brood.

We found a huge quantity of brood, exceeding 1000 eggs and several thousands of larvae in some colonies (Table 1). Five colonies had more than 1000 cocoons. We assume that the few colonies having one dealate queen and only a few hundred workers, were young.

In the rainforest (Taï), colonies were smaller (Table 1) but several (up to nine) dealate queens were present in all colonies. Colonies in Comoé were strictly monogynous, except the two largest colonies from the forest (P32 and P33) which had six and five dealate queens, respectively. None of the queens were dissected, hence we cannot say whether these were all mated and ovipositing. It appears that habitat has an influence on queen number.

Dissection of 150 younger workers revealed no developing oocytes and no yellow bodies in the ovaries (consisting of six ovarioles). This suggests that the queens lay all the eggs.

Production of sexuals and mating activity

Queen cocoons were already found at the end of April (Table 1); since the mating season occurs end of March–beginning April (see below), this indicates that the production of the next generation of gynes begins at the end of the mating season. Adult gynes were present in many nests excavated in August and later in the year, thus they stay at least six months before dispersing. In contrast, the first male cocoons were found in November, and adult males emerged in December–January, closer to the start of the mating season (Table 1). Our observation that gynes are produced six months earlier than males is strong evidence that gynes accumulate fat reserves in their natal colonies, as occurs in many other ants. Gynes were 3–4 times heavier than males (dry weights), which is due to large sexual dimorphism as well as metabolic reserves. Ant males have no need for reserves since they die soon after mating.

Some of the bigger colonies (>1000 workers) reared hundreds of winged gynes, with a maximum of 823 (Table 1). Sexuals were also present in a few small colonies (<500 workers). Conversely, there were no sexuals in some bigger colonies. In

Table 1. Demographic data for 42 colonies collected at different months of the year in Comoé (F: forest, S: savanna) and Taï (rainforest). Five colonies (indicated by asterisks) were collected without a dealate queen.

Colony	Date	Habitat	Workers	Gynes	Males	Gyne pupae	Male pupae	Worker pupae	Larvae	Eggs
P6	Feb93	F	1552	0	0	0	0	94	1376	208
P7	Feb93	F	1191	466	696	0	0	444	129	945
P8	Feb93	F	1522	408	131	0	25	141	2016	139
P17	Feb94	F	3830	175	1141	0	354	817	3013	405
P18	Feb94	F	2405	96	174	0	10	112	1019	258
P19	Feb94	F	2391	67	58	0	2	377	2009	448
P20	Feb94	F	1049	133	242	0	0	28	1942	871
P33a	Mar95	F	7161	823	4930	0	648	1166	5945	1442
P34	Mar95	S	959	25	161	0	0	49	2445	673
P35	Mar95	S	1132	0	283	0	61	118	1853	601
P9 *	Apr93	F	2444	0	0	362	0	756	2789	177
P36	Apr95	Taï	735	0	0	0	45	139	1007	303
P37	Apr95	Taï	436	0	14	0	31	96	604	148
P38	Apr95	Taï	518	0	19	0	133	57	713	120
P39	Apr95	Taï	1036	0	36	0	23	231	2818	575
P40	Apr95	Taï	742	0	13	0	13	108	851	467
P41	Apr95	Taï	219	31	20	0	3	24	200	108
P10*	May93	F	692	0	0	72	0	508	915	163
P21	May94	S	555	0	0	4	0	106	633	29
P22	May94	S	102	0	0	0	0	27	76	25
P23	May94	S	1166	0	0	0	0	262	1358	108
P24	May94	S	422	0	0	1	0	145	218	47
P25*	May94	F	1243	0	0	4	0	518	178	0
P26	May94	S	335	0	0	0	0	178	54	42
P27	May94	S	1744	0	0	0	0	165	1122	88
P28*	May94	F	929	1	11	0	0	317	749	0
P33b	May95	F	5361	0	0	788	0	2167	10152	301
P1	Aug92	F	385	0	0	0	0	499	458	218
P2	Aug92	F	157	0	0	0	0	120	7	35
P3	Aug92	F	247	59	0	20	0	48	91	19
P4	Aug92	F	688	73	5	97	0	667	241	0
P5	Aug92	F	377	36	0	6	0	24	164	0
P11	Sep93	F	2874	638	0	0	0	30	4058	859
P12	Sep93	F	2216	365	0	0	0	37	3210	223
P13	Sep93	F	2333	74	0	0	5	100	1705	93
P29	Oct94	S	253	0	0	0	0	34	362	134
P14	Nov93	F	3081	769	1	0	22	169	3261	1250
P15	Nov93	F	2270	734	0	0	13	148	2564	220
P16	Nov93	F	2530	240	0	0	23	367	3904	315
P30*	Nov94	S	686	117	0	76	0	718	0	0
P31	Nov94	S	942	0	0	0	0	337	1920	205
P32	Nov94	F	5285	0	0	0	0	2492	4827	1273

the majority of nests sampled, males were more numerous than gynes, with a maximum of 4930 males (P33a).

During three successive years (1993 to 1995), nuptial flights occurred after the second heavy rainfall (>5 mm) that ended the dry season. Early in the morning, aggregations of hundreds of males were observed above an exceptionally tall

(25 m) tree. About two hours later, hundreds of gynes flew to this aggregation. Mating occurred on the wing. Clusters of copulating pairs dropped to the ground near the base of this tree, surrounded by up to 10 competing males. However the copulating pairs separated and queens flew away from the male aggregations, hence a second mating was unlikely.

Dealate queens were observed foraging above ground during several weeks after the nuptial flight, hence colony foundation is non-claustral. Only two of 60 incipient colonies that we excavated were pleometrotic, with two queens.

DISCUSSION

Paltothyreus tarsatus is arguably the most ecologically dominant ponerine ant in Africa, based on the extent of its geographical range and its local abundance. It occurs in a broad variety of habitats, which is unusual for ponerine species that are usually restricted to narrow ecological niches (Peeters 1997). The large hunters lack prey specificity, and they scavenge as well. Colonies are populous, and the nests are decentralized to allow harvesting food throughout a large home range while reducing predation on foragers. The subterranean tunnels lead foragers away from the nest centre; once on the surface, they do not roam more than 3–5 m from an exit. They use canopy orientation during their excursions away from the tunnel exits (Hölldobler 1980). There can be chambers close to the exits in which up to 30 foragers inhabit, and these can be quickly recruited to larger (*e.g.* millipedes) or more abundant (*e.g.* termites) prey using pheromones from the abdominal sternal glands (Hölldobler 1984).

Colonies of *P. tarsatus* are much bigger than previously thought, which is related to either the completeness of our excavations or geographical differences (Braun *et al.* 1994 studied this species in Kenya). Colony size is easily underestimated in *P. tarsatus*: given numerous underground connections between different chambers of one nest, brood and workers can be evacuated as the ants perceive vibrations caused by human digging. *P. tarsatus* has large colonies relative to other monogynous ponerine ants (reviewed in Peeters 1993). In *Odontomachus opaciventris*, three large monogynous colonies (about 5000, 8000 and 10 000 workers; 600 cocoons in the latter) nested in chambers distributed throughout large fallen logs, as well as in the shallow soil underneath (De la Mora *et al.* 2008). In *Leptogenys distinguenda*, colonies can yield more than 30 000 workers (Maschwitz *et al.* 1989). Tens of thousands of workers occur in various swarm raiding species of the *L. processionalis*-group (Witte & Maschwitz 2000). Only a few other species scattered throughout subfamily Ponerinae have thousands of workers

per colony, *e.g.* *Brachyponera lutea* (Haskins & Haskins 1950; Dejean & Lachaud 1994), *Centromyrmex bequaerti* (Dejean & Féneron 1996), *Megaponera analis* (Hölldobler *et al.* 1994), *Neoponera luteola* (Verhaagh 1994). Large colony size in these monogynous species is associated with a high number of ovarioles in queens. To explain populous colonies in *Paltothyreus*, we do not simply invoke increased queen fertility. Instead we suggest that the excavation of shallow foraging tunnels causes a significant increase in foraging success, including reduced mortality. Such underground construction is unknown in other ponerine ants, and this behavioural innovation may have allowed a substantial increase in colony productivity.

In the Ivory Coast, the mating behaviour of *P. tarsatus* follows the 'male-aggregation' syndrome which is uncommon in Ponerinae (Peeters & Ito 2001). In contrast, Villet *et al.* (1989) described a 'female-calling' syndrome for *P. tarsatus* in South Africa. In late September (*i.e.* the end of dry season at the southern end of Africa), gynes emerged from a nest entrance, climbed low vegetation nearby, and adopted a resting posture; after some time males flew in and mated. Female-calling resembles the sexual behaviour of solitary wasps and may be ancestral in ants (Hölldobler & Bartz 1985). Male-aggregations seem possible only in ponerine species with big colonies and numerous sexuals produced concurrently. The intraspecific variation documented in *P. tarsatus* suggests that a transition from female-calling to male-aggregation is possible upon an increase in the number of sexuals in the population.

After mating, ant foundresses are alone for several weeks while they raise the first generation of workers. Foundations are especially hazardous in the Ponerinae because queens must hunt outside the nests and produce workers that are similar in size to themselves (no nanitics) (reviewed in Peeters 1997). This is unlike formicoid subfamilies in which foundresses are claustral: they can rely on histolysis of their big flight muscles and other metabolic reserves. In *P. tarsatus*, non-claustral foundation has been observed in South Africa (Villet *et al.* 1989) and in the Ivory Coast (this study). Founding queens presumably have low success rates due to predation while foraging as well as parasitism of unguarded brood. Field data on the success rate of colony founding in non-claustral species are scarce, and prolonged obser-

variations can interfere with queen performance itself. However the annual number of gynes produced by colonies gives indirect evidence about high rates of mortality.

Reproductive investment is a product of the absolute number of sexuals (mostly the gynes) and their cost *per capita*, this cost having two components: pre- and post-adult emergence. We did not quantify the storage of metabolic reserves (*i.e.* post-emergence costs) in *P. tarsatus*, but the degree of size dimorphism allows a reliable assessment of pre-emergence costs. The ratio of thorax volume between queens and workers is 4.7 in *P. tarsatus*, compared to 1.4 and 1.8 in *Neoponera apicalis* and *Harpegnathos saltator*, respectively (M. Molet, pers. comm., measurements based on photographs in www.antweb.org). Compared to other Ponerinae, the gynes of *P. tarsatus* are indeed much bigger than workers, although their flight thorax is not as greatly enlarged as in formicoid species. Together with the metabolic reserves accumulated during their long residency in the nest (in *Solenopsis invicta*, gynes can triple their weight before dispersal (Tschinkel 2006), big flight muscles means that non-claustral foundresses can leave their underground nest less frequently, and this likely increases success rate. Across the ants, queens exhibit quantity or quality trade-offs: produce many cheap gynes, or few expensive gynes (Peeters & Molet 2010a). Is it not a paradox that *Paltothyreus* gynes are numerous and expensive? No matter how specialized the queens are for independent colony foundation, they experience high mortality during aerial dispersal, especially in species exhibiting the male-aggregation syndrome. A majority of gynes die within hours of leaving the natal nest, destroyed by predators in flight and on the ground (in

Mkuzi, C. Peeters observed a large raptor standing next to a *P. tarsatus* nest while eating departing sexuals; unpubl. data). Hence, many gynes must be produced annually to compensate for mortality during both dispersal and foundation itself. The relationship between colony size and gyne investment has seldom been studied in the subfamily Ponerinae. Comparisons across species are valid only if colonies were collected at the right moment before the dispersal flight: after gynes have finished accumulating reserves, but before any have flown off. In *Harpegnathos saltator*, such colonies (60 ± 34 workers; $n = 22$) yielded 17 ± 17 gynes (two colonies had 58 and 61 gynes) (Peeters *et al.* 2000). For comparison, *P. tarsatus* colonies containing gynes had 307 ± 278 (maximum 823).

The relatively large colonies of *P. tarsatus*, an unusual trait among Ponerinae, underlies an ecological dominance in Africa. Peeters & Molet (2010b) argued, in the case of *Amblyopone australis*, that basal ants can evolve advanced social traits although this is not often selected for. In *Paltothyreus*, the existence of queens better specialized for independent colony foundation supports the generality of this evolutionary potential, and the ability to produce expensive queens in sufficient numbers appears linked to bigger colonies and increased foraging success.

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