

Reproductive behaviour of *Plectroctena mandibularis* F. Smith (Hymenoptera: Formicidae), a ponerine ant with ergatoid queens

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Flight is the normal condition in insects, so instances of its loss invariably attract attention (Roff 1990). The queens of several species of the subfamily Ponerinae (Hymenoptera: Formicidae) are permanently wingless and worker-like (ergatoid) forms. The ability of normal queen ants to fly is important because it facilitates dispersal from the natal colony, reducing parent-offspring competition, reducing the potential for inbreeding, and increasing the likelihood of encountering more suitable habitat patches, and it enables some species to locate mates (Hölldobler & Bartz 1985). In ponerine ants the males generally fly to the queens (the female calling syndrome (Hölldobler & Bartz 1985)), but queens must first disperse from the natal colony. For this reason the occurrence of wingless, worker-like or ergatoid queens in several ant species has demanded explanation, and several hypotheses have been proposed (Maschwitz & Hänel 1985; Bolton 1986; Heinze 1989; Heinze & Buschinger 1989; Villet 1989, 1991; Tintaut & Heinze 1992). A shortage of biological information has, however, made it difficult to evaluate how realistic some of these hypotheses may be (Villet 1991).

The syntypes of *Plectroctena mandibularis* F. Smith are a male and an ergatoid queen (originally reported as a worker) taken *in copula* (Bolton 1974), but with no indication of where they were collected. Preliminary laboratory observations indicated that the ergatoid queens of *P. mandibularis* were able to found colonies on their own, and wild queens had been found apparently foraging alone (Villet 1991). This circumstantial evidence of mating and founding behaviour, however, required support as it is central to understanding how the ergatoid condition may have arisen in this species (Villet 1991). The present study reports on new observations on the reproductive biology of *P. mandibularis*, particularly the phenology of males, mating behaviour and colony founding, that may help in deciding between alternative explanations for the occurrence of ergatoid queens in this species.

Records of casual field observations of queens of

P. mandibularis were accumulated over several years. Observations were made in the Eastern Cape Province, South Africa, at Hogsback (32.35S 26.57E), Burntkraal (33.14S 26.29E) and Table Farm (33.15S 26.25E), the latter two both near Grahamstown. The spermathecae of some queens were dissected out, burst onto microscope slides, and examined with a phase-contrast microscope for the presence of sperm, that would indicate whether they had mated. The phenology of males was established from museum records and field observations.

The museum material examined extended over 90 years, from 1901, and covered most of the eastern half of South Africa. Four series of males were collected in January, two in February, twelve in March, two in April, and four in May. Males were present in three nests at Hogsback in March 1995, and in two nests at Burntkraal in March 1996. Neither males nor pupae were found in five nests excavated between July and December at Burntkraal.

Of the museum series, one was collected from Malaise traps in January, two in March and one in April. Males were observed flying at Table Farm in cool, overcast weather on 2 March 1996. They flew aimlessly at a height of about 400 mm in an area of grass and karoo vegetation 200–400 mm tall, interspersed with *Acacia karroo* Hayne trees. No queens were seen, but workers were active above ground.

In 1993 two queens were discovered on the outer edges of bushes about 250 mm tall at Burntkraal, and in April 1995 another was found on the top of a weedy roadside plant at Hogsback, about 180 mm from the ground in overcast weather. These queens hardly moved, and stood with their abdomens slightly curled under their bodies. They did not appear to be exposing any intersegmental glands. The Hogsback specimen was monitored for over an hour before observations were abandoned. No males were seen on these occasions. Dissection showed that all three queens lacked sperm in their spermathecae.

On 10 and 16 March 1996 two queens were found at Burntkraal, similarly perched in low

bushes. They were on the outer edge of the twigs, 240 and 190 mm above the ground. Their posture was similar to those in the previous observations. In each case a male was eventually observed approaching from downwind of the queen, casting across the breeze. This casting decreased in amplitude as the male approached the queen, and ceased when he was about 300 mm from her. He then landed in the bush, about 15 mm from the queen, and scrambled across the plant to her. When each male found the female, he climbed onto her back with his wings half raised, and orientated his head in the same direction as hers. He then extended his abdomen and curled it around the queen's so that he could run the tip down the side of her abdomen until their genitalia met. Once their genitalia were coupled, the male straightened his abdomen so that it lay along the female's dorsum. The queens were passive during all of these activities, but became active about a minute later, and copulation ended about a minute after this. Both sexes then groomed themselves briefly, and the males departed. Both the observed queens climbed down from the plants and walked away, but neither could be followed through the dense undergrowth.

Many medium-sized to large rocks were lifted at Burntkraal in April 1994 and 1995. Six lone queens were found in small chambers with 0, 14, 0, 5, 12 and 23 eggs, respectively, and 0, 4, 0, 0, 1 and 0 young larvae, respectively. There was a small, dismembered millipede, 1.7 mm in diameter, in one of the nests, but no other food was found in the remainder. The chambers were about 40–50 mm in diameter, with no sign of descending tunnels, and all appeared to have been sealed.

Besides its ergatoid queens, *P. mandibularis* has anomalous reproductive biology from two perspectives: their mating behaviour is more similar to that of winged ponerine queens than that of other ergatoid queens, and they raise new colonies in a manner not expected of ergatoid queens. The phenological pattern is less remarkable. Since the development time of *P. mandibularis* larvae was about three months in the laboratory (Villet 1991), the absence of males and cocoons in nests in winter implies that males are reared in early-to-mid summer. This corresponds with their modal appearance as museum records in March which, in turn, confirms that males of *P. mandibularis* are active above ground mainly during March. The production of queens is probably synchronized

with these events.

The mating behaviour of *P. mandibularis* matches the female calling syndrome (Hölldobler & Bartz 1985) that predominates in ponerine ants. It is particularly similar to that of the winged queens of another large ponerine, *Paltothyreus tarsatus* (Fabricius) (Villet *et al.* 1989). The manner in which males approach the queen by casting downwind suggests that a pheromone is involved in their attraction. The source of such a pheromone was not obvious from the posture of the queens, but there is a pygidial gland in *Plectroctena* Smith (Villet *et al.* 1984), and this gland is the source of mating attractants in *Rhytidoponera* Mayr (Hölldobler & Haskins 1977).

What makes this behaviour unusual, is that in other wingless ponerine reproductives (either ergatoid queens or mated workers), mating occurs within the nest or at its entrance (Wheeler & Chapman 1922; Ward 1981; Peeters & Higashi 1989). Males of several species then locate the nest by using the workers' pheromone trails (Maschwitz & Mühlenberg 1975; Longhurst & Howse 1979). Workers of *P. mandibularis* infrequently occur in small foraging bands, but they do not appear to have a trail pheromone that males could use to locate nests. The nests of *P. mandibularis* often occur in areas where the ground is covered with low-growing **forbes** and grasses that form a boundary layer in the atmosphere near the soil. Queens may have to climb out of this layer to disperse their pheromone. It will be impossible to determine whether the mating behaviour of *P. mandibularis* is a derived adaptation or an ancestral habit until more is known about the mating behaviour of related ponerines.

Queens of *P. mandibularis* are capable of founding colonies on their own in the laboratory (Villet 1991), and this study provides evidence that this also occurs under natural conditions. They are therefore haplometrotic, *i.e.* individual queens found their own colonies without assistance (Hölldobler & Bartz 1985).

The presence of a millipede in one of the nests containing lone queens indicates that foundation is semi-claustral, *i.e.* founding queens provision their brood by hunting. Although the nest chambers were sealed, a laboratory study showed that queens sealed the nests between hunting excursions (Villet 1991). Captive queens are also capable of killing and retrieving millipedes up to 4.5 mm in diameter.

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Millipedes, the main prey of *P. mandibularis* (Bolton 1974), breed in early summer in the Eastern Cape Province, so that by March there are sufficient small individuals (at least at the Burnt-kraal site), to provide a lone queen with a regular supply.

Several of the models explaining the origin of ergatoid queens rely on the presence of queens to assist workers during the foundation of new colonies (Maschwitz & Hänel 1985; Bolton 1986; Villet 1989, 1991; Tintaut & Heinze 1992). The manifestation of semiclaustral haplometrosis in *P. mandibularis* renders these models inapplicable in this case. In particular, this ant does not appear to specialize on prey that is dangerous or difficult to procure (Villet 1989). Neither is the habitat of this species patchy (Villet 1991), eliminating the need to avoid flight because of the risks of leaving suitable habitat patches (Heinze 1989; Heinze & Buschinger 1989). Models involving the energetic savings of producing wingless reproductive forms (Bolton 1986) are equivocal in ponerines. This is partly due the low cost differential between the castes and the high material costs of producing workers to assist the queens, and partly because of

the genetic and ecological costs of losing the ability to disperse over greater distances (Villet 1991). It is possible that ergatoid morphology arose as an adaptation in an ancestral species that conformed to one of the published models, and that *P. mandibularis* subsequently adapted to a broader niche. There is, however, insufficient information on the known biology of the genus to indicate that such ancestors did exist (Bolton 1974; Villet 1991).

There are several evolutionary pathways to the ergatoid condition, including one that requires further phylogenetic data before it can be clearly understood. The same applies to the mating behaviour of *P. mandibularis*, highlighting the need for phylogenetic studies on ants.

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