

MALE BIOLOGY IN THE QUEENLESS PONERINE ANT
OPHTHALMOPONE BERTHOUDI
(HYMENOPTERA: FORMICIDAE)

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INTRODUCTION

Various ponerine ants exhibit significant modifications in their pattern of male dispersal, and this is associated with changes in the queenright social structure. In some species the queen caste has become permanently wingless (= ergatoid queens), and in others it has been replaced by mated laying workers (= gamergates; Peeters and Crewe, 1984). Thus, male nuptial flights take on new characteristics since they have to locate flightless sexual partners. Data on male behavior are only available for a few of the ponerine species without a queen caste, but generally males disperse individually and orientate to foreign nests, around which mating then occurs. Brown (1953) observed low-flying males entering nests in two species of *Rhytidoponera*. Mating can occur outside the nest entrances (e.g. in *R. chalybaea*; Ward, 1981), or inside the nest (e.g. in *Diacamma rugosum*; Wheeler and Chapman, 1922).

Ophthalmopone berthoudi Forel is permanently queenless, and details of its reproductive system and polydomous organization appear elsewhere (Peeters and Crewe, 1985, MS). This paper deals with the pattern of male behavior in the field and the characteristics of male production in a breeding system made up exclusively of laying workers.

METHODS

Colonies of *Ophthalmopone berthoudi* were studied in one locality in Mkuzi Game Reserve (north-eastern Natal, South Africa), during 1981–1983. Observations were made throughout the year,

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but the ones specifically reported in this paper were made during the period of male activity (January–April). Male behavior was usually studied near colonies under intensive study (Peeters, 1984). In such colonies the location of all the nest entrances was known (colonies are polydomous), and all the workers active outside the nests had been color-marked with individual codes. In addition, a few males were marked on the thorax and then released. The presence of males was determined by observation of their activity outside nests and by examination of the contents of excavated nests.

RESULTS

Dates of male activity

Normal winged males are produced in this species and were found inside most nests excavated during January–April (Table 1). This limited period of male production was confirmed by finding male pupae during January–April only. A subjective impression is that the number of males present above ground reached a peak in February. Excavations also revealed that males are present in every nest of a colony. However, nests collected in the same month could contain different numbers of males (Table 1). During January and February, a few males were seen to be carried between the nests of a colony. This carrying did not follow any organized pattern, and occurred together with the recruitment of workers and brood. Many of the cocoons that were transferred between nests during that period contained male pupae (A sample of cocoons then found in the nests yielded 70 male pupae and 248 worker pupae).

The investment in male production does not appear exceptional in this queenless species; a colony (464 workers) with five nests excavated in February 1982 yielded 60 males (Table 1), and this is in addition to those that had already departed as well as pupae.

Dispersal behavior

Every day during a three-week observation period in January–February 1982, a few males (1–8) left from each of six nests under intensive observation. Departing males left the nests, often climbed up low vegetation and flew off. Once on the wing, they could no longer be followed. The time of departure (9H00 to 12H00) often coincided with the period when workers were no longer active on the surface because of high soil temperatures. Male exit times appeared not to be affected by cloudy or cooler weather.

Table 1. Size of the male population in nests excavated during January–April. Males were not present at other times of the year.

Date of excavation	Number of nests excavated	Number of males found in each nest (together with number of adult workers)
January 1981	4 #	5(145), 0(84), 6(142), 10(227)
January 1982	1	17(>140)
January 1983	3 #	3(116), 9(222), 6(121)
February 1982	5 +	7(20), 9(80), 19(168), 13(72), 12(124)
March 1982	2 +	0(119), 0(77)
April 1981	3 +	0(318), 0(75), 1(445)
April 1983	2 +	0(106), 2(121)

from 2 colonies

+ from same colony

Evidence that males remain in their natal nests until they are physiologically ready to mate was adduced from the following observations. An adult male that was painted while being carried between two nests, remained inside the second nest for nine days before it left and flew off. Dissection of males collected during excavations revealed that there was little or no sperm in the vasa deferentia and ejaculatory ducts of many of them.

After the initial dispersal flight, males alighted on the ground and appeared to search for nests haphazardly. They walked quickly with frequent changes of direction, and investigated little holes and depressions in the soil. They regularly climbed up short grass stems or low vegetation from which they flew off, often for only a short distance. This behavior was interspersed with ground searches. On a number of occasions, males were observed either landing very close to nest entrances, or walking straight towards occupied nests shortly after landing. Five marked males were observed outside one nest on two successive days, indicating that after locating a foreign nest,

Behavior around the entrances of foreign nests

During the period of their activity, males were observed waiting immobile outside nest entrances, either on the ground or on top of short grass stems. The working assumption was that such males did not originate from these nests, because they always flew away from their natal nests. Some nests frequently had many males in their vicinity, while other nearby nests seldom had any around them.

Males usually investigated entrance holes with their antennae and hesitantly walked in; some ran out immediately afterwards. Individual males were repeatedly evicted from nests by workers (in nests

under intensive study, these were often marked workers, i.e. active on the surface). Males were held by their legs, wings or antennae, and resisted fiercely; some managed to struggle free. After releasing the males in the vicinity of the nests (30 cm – 1 m away), the workers ran back into the entrance holes. The uninjured males cleaned their antennae and then immediately attempted to enter the nests again. On some occasions a number of workers cooperated in the eviction of foreign males, and some workers also chased males when they came across them outside the nests. Eviction did not always follow a male's entrance, and some marked males remained underground for at least 15 minutes.

DISCUSSION

In *Ophthalmopone berthoudi* copulation was never observed above ground, and it is inferred that it occurs exclusively inside foreign conspecific nests. This is an unusual situation in ants, who usually mate some distance from the nests. However, copulation can take place in the immediate vicinity of nests in queenright and queenless ponerines, and in socially parasitic myrmicines (e.g. *Harpagoxenus*; Buschinger and Alloway, 1979). In *Rhytidoponera chalybaea*, in which colonies have either a queen or gamergates, large numbers of workers and males mill around nest entrances, and males make repeated attempts to mate with workers (Ward, 1981). However, males also enter nests and may mate with workers there. In the queenless *R. metallica*, workers attract males by the release of a pygidial gland pheromone; this distinct behavior ('sexual calling') occurs outside the nest entrances (Hölldobler and Haskins, 1977). The pygidial gland has been found in *O. berthoudi* (Villet et al., 1984), and we speculate that if young workers release this sex pheromone, they only do so inside the nests and hence encounter males underground. Sexual calling was never observed in the field or in the laboratory.

Direct data are not available on the activities of males inside foreign nests, and the occurrence of mating is inferred from the large proportion of inseminated workers in nests excavated after the period of male activity (Peeters and Crewe, 1985). The existence of many gamergates in some nests (up to 108) strongly suggests that males copulate more than once; otherwise, such nests would need to be visited by larger numbers of males than we observed entering any

nest. The substantial variations in the percentages of gamergates present in different nests at any one time of the year (Peeters and Crewe, 1985) suggest that the number of male visits to a particular nest is irregular. Some nests may be located more often than others, and consequently varying numbers of young workers become mated. In polydomous colonies such as these, gamergates can be transferred between nests and, hence, a colony should survive from year to year as long as one of its nests is visited by males.

The exit of males from their natal nests is not coordinated, and they disperse over a period of a few weeks. This is different to the situation in queenright species where the emergence of all the male and female reproductives is synchronized in time (e.g. in *Camponotus herculeanus*, through the release of a mandibular gland pheromone by the males; see Hölldobler and Bartz, 1985). Dispersal is then often associated with the initiation of new nests, which must occur during optimal environmental conditions (e.g. after rain). In contrast, copulation in *O. berthoudi* is not followed by independent colony foundation by the mated workers, because colonies reproduce by fission (Peeters, 1984). Thus it is no longer selectively advantageous for males to disperse simultaneously in response to a specific environmental cue. However, males continue to be produced only during a short period of the year. Unmated workers show no ovarian activity in *O. berthoudi*, and haploid eggs are laid exclusively by gamergates (Peeters and Crewe, 1985). Egg fertilization is thus a voluntary act by the mated workers, and males are produced following the first summer rains. Sperm exhaustion is unlikely since individual gamergates lay relatively few eggs during their lifetime. It is not known whether all the gamergates in a nest produce haploid eggs; the inter-nest transfer of male adults and pupae would make this hard to determine.

The importance of chemical attractants during nest location remains unclear. In *Leptogenys ocellifera*, a ponerine with ergatoid queens, dispersing males search for the chemical trails that lead from the nests into the surroundings (Maschwitz and Mühlenberg, 1975), and males of *Megaponera foetens* follow trails laid by workers during raids on termite nests (Longhurst and Howse, 1979). This is impossible in *O. berthoudi* because continuous trails are not laid. There is evidence that discrete scent marks are deposited on the substrate by inexperienced foragers (Peeters and Crewe, MS), but this may be of no use to males. It is conceivable that the pygidial

gland secretions also work as a long-distance attractant. In addition to signalling sexual receptiveness to the males inside the nests, these volatile secretions (which are produced by many workers) may diffuse out of the nests and be perceived by searching males.

Males of *O. berthoudi* need to enter foreign nests in order to find sexual partners. The colony units have distinct identities (Peeters, 1984), and alien males are recognized as different by workers, which then attempt to remove them from the nest; similar hostility is also displayed in *R. chalybaea* (Ward, 1981). This aggression contrasts with the acceptance of alien males by workers in ponerine species with ergatoid queens, e.g. males in *Leptogenys* and *Megaponera* were not attacked following their entry into foreign colonies (Wheeler, 1900; Longhurst and Howse, 1979). In the queenless *Dinoponera gigantea*, Overal (1980) observed a male being carried into a nest by a forager. Carrying of males in *O. berthoudi* was always between the nests of a single polydomous colony and is thus not equivalent to the observations made by Overal. Access by males to foreign nests may be facilitated by the fact that the older workers that perform activities on the surface and are responsible for the evictions, are usually not active during the daily peaks of male activity. The younger workers confined inside the nests are those likely to become mated (Peeters and Crewe, 1985), and these probably do not behave aggressively towards foreign males.

If the queenright ancestors of this species exhibited the typical formicid pattern of reproduction, then male and female reproductives would have been produced seasonally. With the change to worker reproduction, the sexually-attractive workers do not disperse from their nests prior to mating, and mating is no longer coupled with colony foundation, hence the times of male activity no longer need to be synchronized with female activity periods or with appropriate environmental conditions for colony foundation. This relaxation of the selective pressures on the timing of male dispersal has resulted in an extended mating period. Nonetheless, male activity remains seasonal. This has no adaptive significance in *O. berthoudi*, because young workers that can be mated occur throughout the year. However it has the effect of ensuring that an adequate number of infertile workers are present in the colonies.

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