Male Polymorphism in the Ant Species 
Cardiocondyla minutor (Hymenoptera: Formicidae)

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Received: 1998-08-10


Males [MM] of the myrmicine ant species Cardiocondyla minutor (Forel 1899) may be either winged and similar to normal ant MM in morphology and behavior, or aggressive, wingless and workerlike in external appearance ('ergatoid'). Compared to other ant MM, spermatogenesis appears to be prolonged in both male morphs, though the testes had completely degenerated in winged MM 20d after eclosion. A comparative investigation supports the hypothesis that only ergatoid MM are produced in those Cardiocondyla species that have on average large colony sizes, whereas both male morphs co-occur in species with small colony size.

Key words: Cardiocondyla minutor (Forel 1899) - Myrmicinae - male polymorphism - alternative reproductive tactics


Männchen der Myrmicinae-Species Cardiocondyla minutor (Forel 1899) sind entweder geflügelt und ähneln in Morphologie und Verhalten den MM anderer Arten, oder aber sie sind aggressiv, flügelloser und in ihrem Aussehen arbeiterinnenähnlich ('ergatoid'). Verglichen mit anderen Ameisen-MM ist der Zeitraum der Spermatogenese bei beiden Morphen verlängert, wenngleich die Hoden bei geflügelten MM 20 Tage nach dem Schlüpfen degeneriert waren. Ein Vergleich verschiedener Cardiocondyla-Species unterstützt die Hypothese, wonach ergaoid MM bei Arten mit im Durchschnitt größeren Kolonien auftreten, beide MM-Morphen aber bei Arten mit kleinerer Koloniegröße.

Schlüsselbegriffe: Cardiocondyla minutor (Forel 1899) - Myrmicinae - Männchen-Polymorphismus - Alternative reproduktive Taktiken

0171-8177/99-0023-0251 $ 2.00
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1 Introduction

Male polymorphism is a widespread phenomenon among animals. In species such as ants, diversity includes males that are endowed with wings and others that are wingless, depending on whether or not they will mate with females. Although in most cases winged males (MM) are rare, they can be so in many species. The MM can be either those that develop after having been reared as adults with wings (adult winged MM), or those that have not been reared from larvae (virgin). The MM of C. ewingi, C. nigrum, and C. rugatoni have been described in detail (Gross 1999). Winged males are known to occur in many species, such as in the genus Cardiogona (Gross 1999). In ants, the term "polymorphism" is used to refer to the different types of males that may coexist within a species. The type of polymorphism can vary depending on the species, with some species showing more than one type of male (e.g., Cardiogona). In general, male polymorphism is thought to be an evolutionary adaptation that allows species to adapt to different environments and conditions. It is important to note that male polymorphism is not restricted to ants, but is also found in other insect species, such as bees and wasps.
As it appears that the survival rate of ergatoid MM depends on colony size - in very large colonies, several ergatoid MM may eventually co-occur [HEINZE et al 1993] - both models suggest that species with male polymorphism should on average have smaller colonies than species with only ergatoid MM.

Here, a new case of male polymorphism is described for C minutor (Forel 1899), and data are presented on colony sizes in various species of the genus Cardiocondyla.

2 Material and methods

Cardiocondyla minutor is a widely distributed tramp species in the Pacific islands and the neotropical region [B BOLTON, pers comm]. It was originally described from Hawaii as a variety of the cosmotropical C nuda (FOREL 1899) and later synonymized with the latter [WILSON & TAYLOR 1967]. Recently, however, C minutor was elevated to species rank [HEINZE 1997]. In addition to morphological differences in the worker caste, which were already reported by FOREL [1899] and WHEELER [1922] and summarized by SMITH [1944], such as smaller size and more acute epinotal spines, C minutor most notably differs from C nuda in the presence of winged MM.

A total of nine colonies of C minutor were collected in April 1995 and March 1998 from their nests under stones on a gravel road on the area of CEPLAC, Itabuna, Brazil. In the laboratory, the colonies were housed in plastic boxes with a plaster floor as previously described [HEINZE et al 1998]. Ergatoid and winged MM were regularly reared in two colonies from 1995 in the laboratory over more than two years. All measurements were made using a Wild M8 binocular microscope with an ocular micrometer at 100x magnification.

For histology, winged MM were fixed in alchololic Bouin solution, embedded in Durcupan (Fluka) and serially sectioned at approx 1μm with glass knives and a Reichert microtome. Sagittal sections were stained with toluidine blue solution (0.1% toluidine blue in 0.1% sodium borate).

For comparison, material of C emeryi from Barbados [HEINZE & TRENKLE 1997], C nuda from Barranco de Las Angustias, La Palma, Canary Islands [HEINZE et al 1993], and C wroghtontii from a coconut plantation at Lemos Maia Exp Station, Una / Bahia, Brazil, was examined.

3 Results

3.1 Description of the male morphs of C minutor

The ergatoid male (Measurements from 7 MM, in mm): Thorax length [TL] 0.49-0.55; thorax width [TW] 0.25-0.27, head width [HW] 0.35-0.43, length of scapus [SL] 0.26-0.29, eye diameter [ED] 0.09-0.11, length of petiolus [PL] 0.18-0.22, height of petiolus in lateral view [PH] 0.13-0.18, width of petiolus in dorsal view [PW] 0.12-0.17, length of postpetiolus [PLP] 0.12-0.20, length of hind femur [LHF] 0.28-0.32, length of hind tibia [LHT] 0.25-0.27. Coloration (in 2 of 7 investigated individuals, one antennae each had 12 segments). Mandibula with 4–5 teeth. (Fig 1), scutellum visible as a separate sclerite in some specimens, but absent in others. Petiolus approx 2/3 as wide as postpetiolus.

The winged male (Measurements from 10 winged MM, in mm): TL 0.65-0.73; TW 0.33-0.35; HW 0.37-0.41, SL 0.37-0.39, ED 0.12-0.15, PL 0.27-0.31, PH 0.13-0.16, PW 0.11-0.16, pre apexa 1.52-1.60, length of postala 1.12-1.18 mm. Coloration dark reddish brown to reddish oval, convex eyes, ocelli present; antennae typically with 13 segments (of 12 individuals investigated in this respect, one had 2 antennae with 11 segments each, and another had 2 antennae with 12 segments each); clypeus without indentation and longitudinal carinae. Mandibula with 4–5 teeth, the apical tooth much larger than the others. Alitruncus with well differentiated sclerites, but without Mayrian forrows. Propodeum with 2 spines. Wing venation reduced, but in contrast to winged MM of C emeryi [KUGLER 1983] the cubital cell is posteriorly closed. Petiolus approx 2/3 as wide as postpetiolus.

Fig 1: Thorax (in dorsal view) of males of the ant species Cardiocondyla minutor (Forel 1899) from Brazil [Formicidae: Myrmicinacae]. Left of a winged male (the wings were removed for better visability of the thorax structure), right of an ergatoid male (in addition to the lack of wing remnants, ergatoid MM differing from winged ones also in coloration, a much simpler thorax structure, the shape and size of the caput etc). The bar on the left equals 0.2 mm.

Diagnosis: C minutor ergatoid MM differ from those of C wroghtontii (and C paguanda) in that they do not have elongated mandibulae. In dorsal view, the petiolus does not have a distinct, broad node, hence in this respect C minutor ergatoid MM are similar to those of C emeryi and C nuda, but differ from those of C elegans and others. C minutor ergatoid MM differ from those of C emeryi in that their pronotal shoulders are not strongly angular and the absence of ocelli. The antennae of ergatoid MM of C nuda are 12-segmented, but 11-segmented in most investigated ergatoid MM of C minutor. The winged MM of C minutor differ from those of C nigra, C emeryi, and C wroghtontii in coloration, which is yellowish in the latter 3 species.
Deposition of specimens: Both male morphs, workers, and queens have been sent to the Museum of Comparative Zoology, Cambridge, Mass / USA, and the British Museum of Natural History, London.

Histoxy: Four winged MM of different ages were investigated histologically to determine the development of their testes. In the two 14d old MM, testes with spermatogenic tissue were well developed and no sperm cells were present in the seminal vessels. Testes had degenerated in MM 20d and 25d after eclosion, and the seminal vesicles were filled with sperm.

As expected, dissection showed that the testes were well developed and the seminal vesicles were filled in an ergatoid M at least seven weeks old, suggesting that spermatogenesis continues in ergatoid MM for an even more strongly extended period after eclosion.

Colony size: Because of the small size of Cardiocondyla it is often extraordinarily difficult to locate their nests [CREIGHTON & SNELLING 1974: report on an unsuccessful search], especially in those species where nest chambers may reach down in the soil to a depth of 1.3-1.5m [MARKOVSKI & YAKUSKIN 1974: C elegans], [A TINAT & J HEINZE, unpublished: C nigra]. Exact data on colony composition especially of ground-nesting species are therefore difficult to obtain and published colony sizes are probably too low. On the other hand, in laboratory culture, colonies may quickly reach unnaturally large sizes due to the restriction of budding in artificial nests. Hence, worker numbers given for laboratory colonies of C wroghtonii [STUART et al 1987: 376 ± SD 200 workers] are astonishingly large compared to data from field colonies collected in Brazil and Okinawa (Tab 1). In fact, many of the laboratory colonies studied by STUART et al [1987] were derived from a single colony found in Florida, consisting of a queen and less than 20 workers [STUART, pers comm].

Tab 1 gives an overview on what is currently known about Cardiocondyla colony sizes in species with polymorphic MM and species with only ergatoid MM. Worker numbers per colony overlap between the two groups, but average colony size appears to be considerably smaller in species with polymorphic MM. For the statistical analysis of differences in colony size I used only one data point per species, excluding the smaller or less accurate data sets (C emeryi, C wroghtonii from Brazil and Florida, C nuda from Texas and La Palma). Mean colony size of species with ergatoid MM was significantly larger than mean colony size of species with polymorphic MM (Mann-Whitney U-test, n1 = 5, n2 = 3, U = 0, p = 0.025).

4 Discussion

Cardiocondyla minutor exhibits a striking male polymorphism which is similar to that in C emeryi, C wroghtonii and C nigra. Both male morphs can easily be distinguished from the described MM of other Cardiocondyla species by morphological traits among ergatoid MM, and in both male morphs the number of antennal segments differed between individuals. It is therefore likely that a new and more detailed morphological examination will become necessary with the investigation of MM from other populations could be provided here and in previous comparative analyses [KUGLER 1983].

As in other Cardiocondyla, ergatoid MM of C minutor are highly aggressive and do not fight. Both male morphs are capable of inseminating nestmate queens, but disperse several days after eclosion [HEINZE et al 1998].

According to dissections, the testes of ergatoid MM of C minutor do not degenerate shortly after eclosion, but instead spermatogenesis probably continues throughout their whole lives as in ergatoid MM of other Cardiocondyla species [HEINZE & HOLLODOBER 1993, HEINZE et al 1998]. Surprisingly, the testes were still well developed functional in 14 days old winged MM, though no sperm was found in their seminal vesicles. Testes had degenerated and all sperm had been transferred into the seminal vesicles by day 20 after eclosion. This stands in contrast to previous observations that in winged MM of C wroghtonii and C emeryi the testes degenerate within a week or so after eclosion [HEINZE & HOLLODOBER 1993, HEINZE et al 1998]. The winged MM of C minutor available for histological analyses eclosed in the absence of virgin queens and therefore did not have a chance to mate in the maternal nest. It was suggested that the presence of virgin queens probably affects the timing of dispersal in winged MM in C emeryi [HEINZE et al 1998] and one might speculate whether a more general influence of the availability of virgin queens on the maturation of MM could explain the observed prolonged spermatogenesis in winged MM of C minutor. More data are needed to clarify whether the timing of reproduction depends on the availability of virgin queens.

HAMILTON [1979] observed that in fig wasps, species with large broods tend to have wingless MM, whereas species with small broods have both winged and wingless MM. Strong evidence in support of this proposed correlation between brood size and male morph was recently found in a comparative analysis using data from 114 species of fig wasps [COOK et al 1997]. A model developed by TSUI et al [1994] similarly predicts that average colony size influences male morph. Average colony sizes indeed appear to be larger in Cardiocondyla species with ergatoid MM than in species with polymorphic MM. Though very small colonies of Cardiocondyla have been observed to produce very large broods, [MARKOVSKI & YAKUSKIN 1974: young alate queens may by far outnumber all other adults per colony], brood size in general is presumably positively correlated with colony size. Hence, the pattern described for fig wasps appears to hold also for Cardiocondyla. It must be noted, however, that as yet nothing is known on the phylogeny of Cardiocondyla species, and therefore it is unclear whether different species represent independent data points.

5 References


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Acknowledgements: I thank Dr Jacques H C Delabie and Jose Inacio Lacerda Moura for the permission to collect ants on the territories of CEPLAC at Itabuna and Una, respectively. The investigations were supported by DFG (He 1623/7). Thanks are due to S Karpeles for her technical assistance in histology.

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