

Behavior of ergatoid males in the ant, *Cardiocondyla nuda*

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Summary

Ergatoid males of the ant, *Cardiocondyla nuda*, attack and frequently kill young males during or shortly after eclosion. Smaller colonies therefore contain typically only one adult male, which may inseminate all alate queens which are reared in the colony over a few weeks. In larger colonies, several males may be present, however, fighting among adult males was not observed. We discuss the significance of male fighting behavior in ants.

Introduction

In the great majority of ant species, adult males are made for mating and little else. With a few exceptions, their main activities within the nest are self-grooming and receiving food, and outside the nest they disperse, locate females and mate. Other than scramble competition for female sexuals in mating aggregations, males do usually not compete aggressively and are not equipped for fighting (e. g., Hölldobler and Bartz, 1985; Hölldobler and Wilson, 1990).

In a small number of species, however, males are wingless and more or less closely resemble the typical ant workers. Ergatoid males (also “ergatomorphic males” or “ergataner”, Loiselle and Francoeur, 1988) are known from four phylogenetically distant genera: *Hypoponera*, *Cardiocondyla*, *Formicoxenus*, and *Technomyrmex*. Males of some parasitic species, e. g. *Anergates atratulus*, or *Plagiolepis xene*, are also wingless but else resemble female sexuals in morphology (gynaecaner or gynaecoid males; Wheeler, 1910; Passera, 1984). Such morphological modifications appear to be correlated with intranidal mating and at least in two genera also with fighting and the monopolization of mating within a nest. Ergatoid males of *Cardiocondyla wroughtonii* have long, sabershaped mandibles which they use to kill eclosing males and to attack adult rivals. Nests typically contain only one or a few ergatoid males, which inseminate all eclosing queens (Stuart et al., 1987; Kinomura

and Yamauchi, 1987). Fighting, leading to severe injuries and death, was observed also among ergatoid males of *Hypoponera punctatissima* (Hamilton, 1979).

Because of the workerlike morphology questions were raised whether ergatoid males can participate in social activities (e. g., Hölldobler and Wilson, 1990). Indeed, Santschi (1907) observed brood-carrying by ergatoid males of *Cardiocondyla nuda* var. *mauritanica*.

We here report observations on the behavioral repertoire of ergatoid males of *Cardiocondyla nuda*. Like *C. wroughtonii*, *C. nuda* is a cosmotropic tramp species. It differs from the former species in that all males are ergatoid, whereas in *C. wroughtonii* both winged and ergatoid males occur (Kugler, 1983).

Material and methods

Eleven colonies of *Cardiocondyla nuda* were collected by J.H. in April 1990 at Barranco de Las Angustias, La Palma, the westernmost of the Canary Islands. Colonies nested under stones in dry, sandy soil in an arid habitat with macchie vegetation. In the laboratory, ants were kept at room temperature in plastic boxes with a plaster floor. Colonies were fed three times a week with diluted honey and pieces of cockroaches or mealworms.

Some colonies were provided with glas tube nests or Buschinger's microscope slide nests (e.g., Buschinger, 1974), however, the ants frequently emigrated and settled in the open arena, under food dishes, pieces of dead cockroaches etc.

All males used in our experiments were offspring from one large, highly polygynous colony.

We observed the behavior of males for a total of approximately 25 hours in irregular session lasting 10 minutes to 2 hours between 7:30 and 20:30. In addition, the behavioral activity in a small colony fragment was videotaped for 24 hours.

Specimens were kindly determined by J. Kugler, Tel Aviv University.

Results

Composition of colonies

Colonies consisted of between approximately 20 and 200 individuals. At least six were highly polygynous, the other contained a single dealate queen each. Only in one nest an ergatoid male was observed shortly after collection. This colony grew rapidly over a period of two years and was repeatedly split into different subcolonies, which all produced males, alate queens, and workers.

In small nests (less than 50 workers) typically only one male was present, but larger nests contained up to twenty and more adult males. Many of these exhibited conspicuous injuries, such as missing appendages and indented heads (Fig. 1). In one nest we counted four male pupae, three callows, and five adult males: three of the adult males lacked one antenna and one male had both antennae cut off.

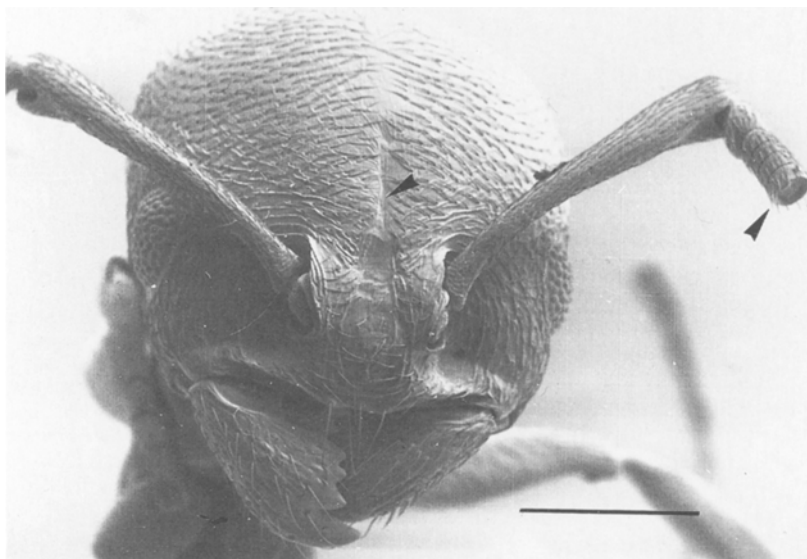


Figure 1. Head of an ergatoid male of the ant, *Cardiocondyla nuda*. In contrast to males of most ant species, males of *C. nuda* have strong mandibles and comparatively small eyes. The arrows indicate injuries due to attacks by other males shortly after eclosion: an indentation of the forehead and a rupture of the right antenna. The scale equals 0.2 mm

Occasionally we found isolated heads and bodies of males which were still showing vital signs.

Interactions between adult and callow males

Males were inactive for about a third of the observation time (Fig. 2). During most of the time they moved about the nest or tunnelled through the brood pile, rapidly antennating adult nestmates, pupae, and larvae. Presumably these were antennal inspections, which lasted a few seconds, after which the male moved on to the next individual. Prolonged interactions were observed less frequently: Males occasionally bit neck, thorax, or petiole of worker pupae or callows (3 observations), alate queens (3 obs.), or adult workers (4 obs.) with their mandibles, but all these attacks ceased within a few seconds. Males were considerably more aggressive when encountering eclosing males or male callows. Of eleven males which we observed during eclosion in the presence of adult males, ten were attacked by the latter and at least four were killed. When encountering a male callow, adult males promptly started to grip his neck, thorax, “waist” (between propodeum and petiole, petiole and postpetiole, or postpetiole and gaster) or extremities. Rather than pulling the attacked ant, as is often the case during fighting in other ant species, males seemed to tighten the mandibular grip as if they were attempting to crush the callow. Males repeatedly grasped different parts of the callow for several minutes, then left but occasionally

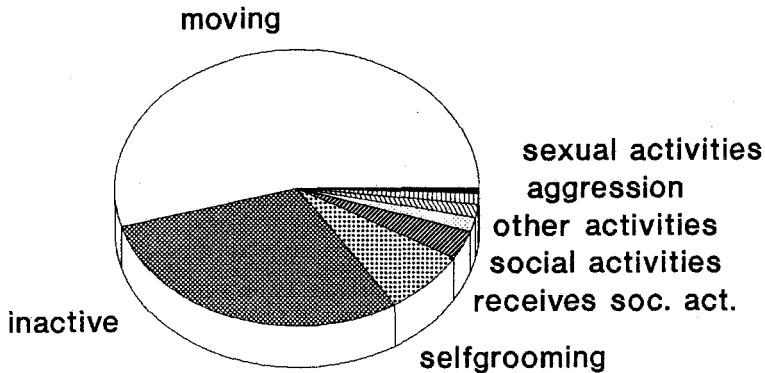


Figure 2. Time-budget of *C. nuda* males. The duration of behavioral acts of males was recorded in sessions of 15 minutes adding up to a total of five hours. These results were confirmed by additional observations over a total of appr. 12 hours, during which the frequency but not the duration of behavioral states were recorded

returned and attacked again. In at least three cases, two or three males attacked the same callow within twenty minutes. Workers, which assisted the male during eclosion, rarely interfered with attackers, but “indifferently” continued to pull off the exuvia or to groom the callow male. On two occasions we observed, however, a worker removing the attacked callow male from an aggressor.

All attacked callows suffered at least temporarily from injuries, such as distorted legs or bent antennae. In two callows the head started to cave in while attackers had gripped their thoraces. In one callow, hemolymph leaked from a crack in the cuticle of the thorax where the attacker had bit the ant, while the head visibly indented. The fluid was licked by a worker, who later began to cut the still living callow to pieces and fed it to larvae. The frequent incidences of separated, but still living body parts suggests that males are capable of severing head or gaster from the rest of the body with their mandibles.

In one case, interactions between an eclosing and adult males were surprisingly different: after briefly antennating the callow, at least two different adult males backed off (5 obs.). The callow remained unattacked and started to move around and antennate nestmates two hours after eclosion.

Interactions among adult males

Though most larger nests contained several males, interactions between adult males were rare. They generally appeared to ignore each other even when moving about the brood pile in close proximity. Occasionally males backed away from each other. On two occasions, a male opened his mandibles and advanced towards an approaching male, which then instantly moved away. We once observed fighting between adult males, which were both engaged in attacking a callow. One male gripped the head of the other male for 20 seconds, then let go and continued to bite the callow. In two

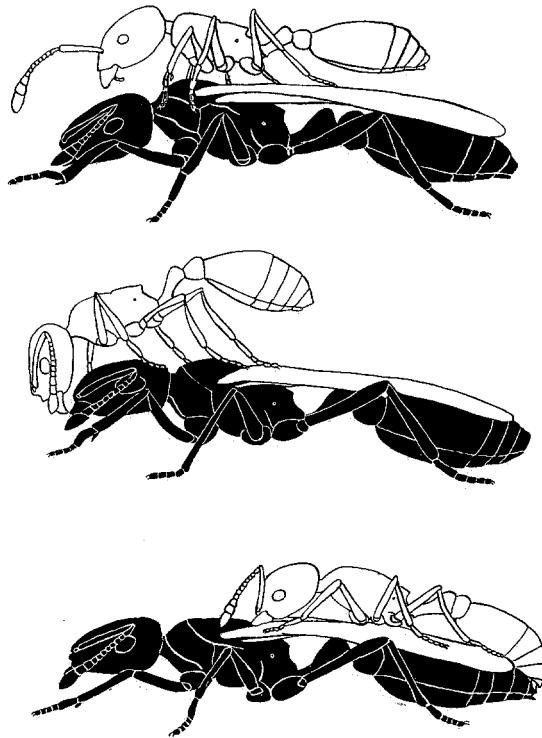


Figure 3. Mating behavior of the ant *Cardiocondyla nuda*. After hammering with his mandibles on the alate queen's head, the male slides backwards and seeks to insert his genitalia into the queen's genital opening

instances males groomed head, thorax and gaster of other males, once intensely and once for about five seconds.

Mating behavior

Male sexual activities were observed during most of the observation period (between 10:08 and 18:40). Shortly after eclosion males began to patrol the nest, antennating brood and adults, and copulation attempts were observed on the first day of their adult life. Alate queens were courted less than two hours after they had eclosed. Males rapidly antennated the head of a queen, climbed onto her thorax and hammered their mandibles onto the queen's forehead and mandibles (Fig. 3). Single pecking bouts lasted approximately two to three seconds and consisted of five to ten individual knocks; they were interrupted by pauses of two seconds. Between periods of hammering, males – two thirds the size of queens – repeatedly slid backwards on top of the queen, trying to insert their extruded genitalia into the alate queen's genital opening. In most cases, queens did not cooperate, instead they bent the gaster forwards, making it impossible for the males to copulate. Unsuccessful copulation attempts lasted ten seconds to five minutes.

Unfortunately we never succeeded to witness a complete copulation in these colonies. Nevertheless, dissections proved that even not yet completely pigmented callow queens which had eclosed in the presence of males were already inseminated, days or even weeks before they shed their wings. We therefore isolated ten female pupae in a group consisting exclusively of workers and larvae and added a male of unknown age five days after the first queen had eclosed. The male successfully mated with a first alate queen within twenty minutes and with a second queen five minutes later. After 15 seconds of pecking the male moved backwards and immediately managed to insert his genitalia (Fig. 3). In contrast to other ant species, the male did not tilt backwards during the copulations, which lasted for five and eight seconds, respectively, but held his head near the queen's postpetiole. Between copulations, the male groomed himself, then launched an unsuccessful second mating attempt towards the first queen, which, however, resisted by bending the gaster forward.

Likewise, males mounted and pecked physogastric dealate queens (2 obs.), workers (20 obs.), worker callows and pupae (4 obs.), and male callows (2 obs.), and frequently mounted in the wrong direction, i. e. pecking the gaster rather than the head. In several cases unwilling queens released whitish, milky drops from the tip of the gaster. Based on dissections we assume that this material originates from the rectum; the substance seems to impair the male's activities. The fluid was licked up by workers and also by the males themselves. Queens, workers, and males occasionally produced similar droplets when they were seized with forceps at the petiole or thorax. However, during an attack, for example, by an introduced *Solenopsis* worker, the queens and workers employed their sting and smeared clear secretions onto the cuticle of the opponent.

Other activities of males

Males only rarely engaged in social activities. They were groomed and fed by workers and also alate and dealate queens. Males occasionally groomed workers, queens, or males (3, 1 and 2 observations, resp.), but grooming typically lasted only for a few seconds. In one case it appeared that a male fed a worker, however, male regurgitation could not be verified during later observations. One male was seen carrying pupae, but other brood care activities did not occur.

In an artificially composed group consisting of 16 adult males, five male pupae and 19 larvae, males more frequently groomed each other and they also licked larvae, although in a rather brief and inefficient way. Though at least once a male picked up and carried a larvae, the brood remained scattered throughout the nest instead of being gathered in a brood pile as would be the case in the presence of workers. The males frequently faced each other slowly antennating each other's heads. All larvae and most males had died within eight days.

Origin of males and colony growth

A series of experiments gave information on the origin and the production of males in colonies. In five groups of appr. 50–100 workers isolated with brood, no eggs were

laid. According to dissection results, workers apparently lack functional ovaries, though we cannot completely exclude the presence of degenerate reproductive organs. Five groups of workers and brood quickly grew into complete colonies: from the brood, males and alate queens eclosed and eggs and new brood appeared within four or five weeks.

Twelve young queens, which eclosed in the presence of males and were then isolated with 30 to 50 workers and brood, started to lay eggs within a few days. Males were already reared from their first brood, but new alate queens appeared only after 10 to 14 weeks, when colonies had reached a size of approximately two hundred workers.

In contrast to larger queenright colony fragments, which grew rapidly, six queens accompanied by smaller groups of workers (20 workers, 10 larvae) failed to rear a substantial number of brood within seven weeks and finally declined, though eggs were laid. These data suggest that as in *C. wroughtonii* (Stuart, 1990), new colonies are unlikely to arise from solitary queens, but instead are founded by fractioning of large colonies. Budding was indeed frequently observed in our laboratory set-ups. Dispersal flights by winged queens after intranidal mating, as described by Yamauchi and Kinomura (in press), did not occur in our colonies, in fact, we did not witness any flight activity at all.

Ten virgin queens which were isolated in groups of approximately 50 workers and brood shed their wings less readily than mated queens; most of them, however, were dealated after two weeks. Though we attempted to remove all males eclosing from the added brood, in eight experiments, a few male pupae were missed and the queen was eventually inseminated. However, in two cases we succeeded in keeping the queen unmated. Their eggs developed into ergatoid males within eight weeks.

The ovaries of queens consist of 6 ovarioles, and queens are capable of laying two or three eggs per day.

Discussion

Several hypothesis have been proposed to explain the scattered occurrence of morphologically aberrant males throughout the Hymenoptera (e.g., Kukuk and Schwarz, 1988). Our observations suggest that competition for the chances of insemination has shaped the morphology of ergatoid males in the ant *Cardiocondyla nuda*. By eliminating eclosing rivals, males apparently increase the number of alate queens they can mate with.

As was already described for *Cardiocondyla wroughtonii*, males attack and kill eclosing males with their mandibles. In contrast to *C. wroughtonii* males, which possess saber-shaped mandibles, the mandibles of *C. nuda* males are similar to those of workers, although they appear to be more sclerotized. *C. nuda* males are able to destroy male callows by crushing the soft cuticle of the thorax or by severing head or gaster from the rest of the body. In larger colonies, however, some young males have a chance to eclose undetected or survive attacks with only minor injuries, and therefore several adult males were occasionally found within a single nest. In such

situations, adult males of *C. nuda* usually ignored each other. In contrast, Kinomura and Yamauchi (1987) and Stuart et al. (1987) reported deadly fighting between adult rivals in *C. wroughtonii*, which lasted for hours. During these fights, but also when attacking callows, males of *C. wroughtonii* used their forelegs to beat the opponent and to spread secretions from the gaster tip over his cuticle. These secretions appeared to induce worker aggression (Stuart et al., 1987; Yamauchi and Kawase, 1992). Beating with the forelegs was never observed in *C. nuda*. When seized with forceps, males and females of *C. nuda* occasionally released whitish fluid, probably contents of the hindgut, but this was never observed during male-male interactions.

In some cases, adult *C. wroughtonii* males tolerated each other and colonies with multiple males are known from nature (Lupo and Galil, 1985). Stuart et al. (1987) suggested that different degrees of relatedness might underlie the observed variation in male-male compatibility. In *C. wroughtonii*, in addition to ergatoid males, winged males occur which are thought to disperse for mating in addition to intranidal mating (Kinomura and Yamauchi, 1987; Stuart et al., 1987). In contrast, in *C. nuda*, as well as in several other species (Kugler, 1983) winged males have never been found. Furthermore, we never observed flight activity in young *C. nuda* queens, although they have fully developed wings. Therefore, dispersal capability and gene exchange between populations, such as that at Barranco de Las Angustias, might be highly inbred. Inbreeding could affect male behaviors: Losses in direct fitness due to a lower number of potential mates might then be compensated by increased inclusive fitness. Fighting among adult males is highly risky for both opponents (Stuart et al., 1987), but to attack callows is quite safe. In this sense it might always pay to attack even closely related, vulnerable male callows. In the future, it will be necessary to supplement our observations on mutual tolerance of adult males with material from other, larger populations.

In ants, as in the majority of insects, spermatogenesis is completed and testes have atrophied by the time males reach sexual maturity (e. g., Hölldobler, 1966; De Wilde and de Loof, 1973; Davey, 1985; Hölldobler and Bartz, 1985). Sperm supply and the number of potential inseminations are thus limited and most ant males are thought to be capable only of few matings. The published record is appr. 10 copulations in *Harpagoxenus sublaevis* (Winter and Buschinger, 1986). Fighting among males and female defense polygyny, on the other hand, "make sense" in evolutionary terms only if males are capable of inseminating numerous alate queens. According to Kinomura and Yamauchi (1987) ergatoid males of *C. wroughtonii* mated nine times in 12 hours, and winged males 113 times (!), however, sperm transfer was not demonstrated and "mating" may have been mating attempts. *C. nuda* males frequently tried to mate with freshly eclosed alate queens as well as with inseminated queens but rarely succeeded. Similarly, Stuart et al. (1987) reported that copulations in *C. wroughtonii* were rare. On the other hand, the two observed copulations in *C. nuda* were inconspicuous, short, and occurred immediately after a male had been introduced to isolated alate queens. Furthermore, queens which had eclosed in the presence of males were inseminated within a couple of days. Both observations suggest that matings occur shortly after the queens eclose. The readiness of *C. nuda* queens to mate a first time and the general rejection of males by older alate queens might indicate that multiple inseminations are rare. More detailed observations are needed to clarify this

aspect, because multiple matings by alate queens were observed in *C. wroughtonii* (Kinomura and Yamauchi, 1987).

Our recent observations leave no doubt that *C. nuda* males can inseminate a surprisingly large number of queens during their life span. In contrast to other ants, spermatogenesis continues after eclosion in *C. nuda* and adult males possess active testes throughout their life span (Heinze and Hölldobler, unpubl.).

As already described by Santschi (1907) for males of *C. nuda* var. *mauritanica*, *C. nuda* males occasionally picked up and carried brood. We observed a similar behavior by an alate male of *C. emeryi* when the colony was suddenly exposed to light (unpublished). Male brood carrying is especially remarkable, as similar behaviors are not known from other ant males, including the males of *Camponotus ligniperda* and *C. herculeanus*, which show a considerable amount of social behavior at the beginning of their adult life (Hölldobler, 1966).

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