

Male-male competition in ants (Hymenoptera: Formicidae)

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Abstract

Aspects of male mating behavior in ants have been largely ignored in research until recently. Mating in ants is usually a short episode at the beginning of their life, often in large, anonymous swarms; therefore it has been argued that the potential for male-male competition is limited. Despite of this, several earlier studies on mating in ants described that males heavily compete for female sexuals, indicating pre-copulatory male competition. In the last few years, more and more studies investigating post-copulatory competition have been conducted, and they revealed fascinating examples of male traits to gain fertilization advantages over other males. Ant species exhibiting intranidal mating have been researched thoroughly, providing new insights also into pre-copulatory conflicts. We review what is known so far on male-male competition in ants. Further studies may uncover additional unknown male competitive tactics and provide a better understanding of sexual selection in ant males, and we believe these studies offer an ideal system to compare male competition in social and non-social insects.

Key words: Male competition, male traits, mating, pre-copulatory, post-copulatory, fighting, review.

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Introduction

The mating biology of ants: While the fascinating cooperative behavior of social insects in general and ants in particular has been studied intensively for the last decades, mating biology has been largely neglected (e.g., BAER 2014). Research on conflict in ant societies has rather been focused on fitness optimizing strategies and reproductive conflict of female individuals than on competitive behavior between males (e.g., BOOMSMA & al. 2005).

This has several reasons. In most social Hymenoptera, mating is a short event early in life, with males serving only as "flying sperm missiles" (SHIK & al. 2013) and queens never remate after starting reproduction, resulting in a lifelong partner commitment (e.g., BOOMSMA & al. 2005). Exceptions have been discussed to occur in army ants (e.g., RAIGNIER & VAN BOVEN 1955, RETTENMEYER 1963, DENNY & al. 2004, but see KRONAUER & BOOMSMA 2007) and found recently in some species of *Cardiocondyla* ants, where virgin queens start reproducing by laying haploid eggs and mate only afterwards with their own sons (SCHMIDT & al. 2014; N. Moske, J. Heinze & A. Schrempf, unpubl.). This short time frame and the often inconspicuous mating make observation of nuptial flight in social Hymenoptera difficult. Even if researchers are in the right spot at the right time to witness a mating, it is often difficult to observe copulations in detail due to mating locations and the number of participating individuals.

The evolution of male traits in social insects in general has been reviewed by BOOMSMA & al. (2005) and male mating behavior of bees has been reviewed by PAXTON (2005). However, a review on male mating behavior, and

especially male-male competition, in ants does not exist so far.

HÖLLDOBLER & BARTZ (1985) distinguished between two main mating syndromes in ants: the "male aggregation" and the "female calling" syndrome. In case of the male aggregation syndrome, males take off in large aggregates and attract female sexuals chemically, which enter the mating swarm and mate with one or several males. These swarms can consist of thousands or even millions of individuals (e.g., "24 to 60 millions of ants were involved in this event" described by CARLTON & GOLDMAN 1984 for *Lasius alienus*), and individuals may fly and mate up to 250 m above ground or even higher (HÖLLDOBLER & WILSON 1990), making it complicated if not impossible to track individual behavior. Swarming is usually triggered by environmental cues to synchronize the timing of taking off for flight, often after rain, as it makes it easier for queens to dig in humid soil. In such swarms, males frequently outnumber female sexuals, and some authors describe that males struggle for access to female sexuals. For example, in WHEELER (1916), observations of W.W. Froggatt of mating in bulldog ants are described: "As soon as a male (and there were hundreds of males to every female) captured a female on a bush, other males surrounded the couple till there was a struggling mass of ants forming a ball as large as one's fist". BROWN (1955) described mating in *Notoncus ectatommoides*: "In a few seconds, the female was surrounded by a dense swarm of males in the form of a ball" (c.f. HÖLLDOBLER & WILSON 1990). Generally, species that exhibit the male aggregation syndrome are of-

ten characterized by large colony sizes and a seasonal production of large numbers of reproductives (HÖLLDOBLER & WILSON 1990, GRÜTER & KELLER 2016).

Obviously, such mating swarms are usually not inducible in the laboratory due to confined time, space and number of colonies. Furthermore, the exact conditions needed to elicit the swarming behavior may be difficult to simulate under laboratory conditions (but see e.g., breeding experiments with different *Formica* species by GÖSSWALD & SCHMIDT 1960).

In the case of the "female calling syndrome", usually fewer individuals are involved and copulations happen near or on the ground. Virgin queens disperse close to the nest and use pheromones to attract males searching for mating partners. Colonies of female calling species are often small at maturity and produce relatively few reproductives (HÖLLDOBLER & WILSON 1990, PEETERS & ITO 2001). This system has been described for several myrmicine, ponerine, and also formicine ants (HÖLLDOBLER & HASKINS 1977, HASKINS 1978, BUSCHINGER & ALLOWAY 1979, LENOIR & al. 1988, VILLET 1999).

However, variations of these two mating strategies and intermediate stages are manifold, and can impact e.g., dispersal distance from the nest, dispersing sex, aerial or ground mating and the number and sex ratio of participating individuals (HÖLLDOBLER & WILSON 1990, AYASSE & al. 2001, PEETERS & ITO 2001, PEETERS & MOLET 2009).

Similarly, species within a genus can differ in mating syndrome. In the genus *Formica*, the male aggregation syndrome has been described for some species (MARIKOVSKI 1961, TALBOT 1972, O'NEILL 1994, MORI & al. 2001), whereas other species exhibit female calling (for instance KANNOWSKI & JOHNSON 1969, HALVERSON & al. 1976, HENDERSON & JEANNE 1992, CHERIX & al. 1993). Moreover, the range of dispersal during flights can vary dramatically: from "several tens of meters" in *Cataglyphis cursor* males (LENOIR & al. 1988) or "a few hundred meters" for *Solenopsis invicta* gynes (GOODISMAN & al. 2000) to "up to ten miles" for *Solenopsis saevissima richteri* (MARKIN & al. 1971). However, data of most studies are calculated on genetic markers and do not distinguish between pre- and postmating dispersal. A recent study estimated dispersal distance based on queen range from the natal colony and suggested a median distance of 60 m for *Formica exsecta* gynes (VITIKAINEN & al. 2015).

The female calling syndrome with small numbers of sexuals mating close to their nest makes matings easier to observe and offers the opportunity to research male strategies and reproductive success. In addition, there are several detailed descriptions of mating in *Pogonomyrmex* harvester ants, in which mating is unique and shows "strong parallels to vertebrate lek systems" with male aggregations (HÖLLDOBLER 1976, DAVIDSON 1982). Mating takes place on the ground or on bushes and trees, and males strongly compete for queens (HÖLLDOBLER 1976).

In a much smaller number of species, mating takes place within the nest: this is for example the case for some social parasites (e.g., *Epimyrma* sp.: WINTER & BUSCHINGER 1983, BUSCHINGER & WINTER 1985, BUSCHINGER 1989; *Rhoptromyrmex* BOLTON 1986; *Plagiolepis xene*, TRONTTI & al. 2006), a few unicolonial species (e.g., *Monomorium pharaoni*: PEACOCK & al. 1950, *Lasius sakagami*: YAMAUCHI & al. 1981, *Linepithema humile*: KELLER

& PASSERA 1992) and in the genera *Hypoponera* (e.g., FOITZIK & al. 2002) and *Cardiocondyla* (e.g., HEINZE & HÖLLDOBLER 1993). In several of these, neither males nor female sexuals disperse before mating and thus mate with their nestmates, often resulting in high inbreeding levels (e.g., SCHREMPF & al. 2005b, LENOIR & al. 2007). Some species produce dispersing sexuals in addition to or alternating with dealate sexuals (e.g., in *Cardiocondyla* sp.: HEINZE & al. 2004; *Hypoconera* sp.: FOITZIK & al. 2010; *Plagiolepis xene*: KUTTER 1952, PASSERA 1964, TRONTTI & al. 2006). In other species, males still fly for mating with apterous female sexuals inside or in the surrounding of the colony (several doryline species, e.g., *Eciton* sp.: RETTENMEYER 1963, FRANKS & HÖLLDOBLER 1987, PEETERS 1991; *Harpagoxenus sublaevis*: BUSCHINGER 1979). Finally, there are even cases where both sexes are flightless: apterous queens together with apterous males have been described in *Hypoconera opacior* (FOITZIK & al. 2002), and short winged queens together with wingless males in *Cardiocondyla batesii* (SCHREMPF & HEINZE 2007). In case of apterous males, local mate competition will influence the sex ratio of the colony and result in a female bias, as for example shown in *Cardiocondyla obscurior* (CREMER & HEINZE 2002). Species with intranidal mating often also mate under laboratory conditions and thus make perfect subjects for studying mating in ants.

Male traits: As already mentioned above, the evolution of male traits in social insects including ants has been reviewed in detail by BOOMSMA & al. (2005). Similarly, there are two excellent reviews on the copulation biology of ants as well as on sexual selection in social insects by BAER (2011, 2014), and we thus describe the male phenotype briefly. As in all haplodiploid species, male ants arise from unfertilized eggs. In the social environment, males are probably the "least social" individuals, as they usually only stay within the colony for a short period of time before leaving to mate with female sexuals after which they die. Thereby, males are not engaging in social activities with "... their repertory almost always limited to grooming themselves and receiving food from the workers" (HÖLLDOBLER & WILSON 1990). Exceptions are found in *Hypoconera* sp., where ergatoid males engage in stomodeal trophallaxis (mouth-to-mouth transfer of food) with queens (HASHIMOTO & al. 1995) and in *Camponotus* sp., where stomodeal trophallaxis between males and other members of the colony has been observed (HÖLLDOBLER 1964, 1966 c.f. HÖLLDOBLER & WILSON 1990). With a few exceptions (e.g., *Cardiocondyla* sp., BOOMSMA & al. 2005), ant males are short-lived and their testes degenerate after eclosion, therefore they can often mate only once or a few times (up to 10 times, see BOOMSMA & al. 2005) during a short period of time (KELLER & PASSERA 1992).

The characteristics of male ants' traits and even male longevity depend on the mating syndrome of the species (SHIK & KASPARI 2009, SHIK & al. 2013). HÖLLDOBLER & WILSON (1990) already mentioned that males are often larger and "more robust" in case of female calling species, while they are smaller in species exhibiting the male aggregation syndrome. Usually, ant males have a bulky thorax and are winged. For orientation during mating flights, either in large swarms or in search of a calling female, most ant males have large compound eyes and ocelli while spe-

cies mating on the ground close to the nest may have smaller compound eyes (SHIK & al. 2013). In species mating in the nest, wingless male types have evolved, known from the genera *Cardiocondyla*, *Hypoconera* and *Formicoxenus* (see KINOMURA & YAMAUCHI 1987). These males resemble workers, usually possess small compound eyes and have reduced ocelli or completely lack them (e.g., in *Cardiocondyla*, see KUGLER 1983). Even in case males stay inside of the colony for a longer period, they do not seem to contribute to social life. Furthermore, in these wingless males, male behavior is usually limited to auto-grooming, receiving food from the workers and patrolling the nest in search of female sexuals or rival males (but see HEINZE & al. 1993 for males carrying brood).

If and how male competition can arise depends on several factors – e.g., mating system, mating site or colony structure. While swarm mating bears few chances for competition before and during mating and flying ability might be the only factor for queens to assess male quality, mating in confined spaces – in territories, leks, on the ground close to the nest or in the nest give the opportunity to monopolize female sexuals or to gain fitness by being more "attractive" to them. Only in case females mate multiply, i.e. under polyandry, competition after copulation might occur and result in the evolution of postcopulatory male traits to gain fertilization (see below). If queens mate with several males, males might try to prevent rivals from mating as multiple insemination can reduce a male's fitness by lowering its contribution to the queen's offspring (ALLARD & al. 2002). Especially in polygynous colonies, where competition between queens occur, queens may have greater interest in influencing the number and timing of male production (e.g., local mate competition, CREMER & HEINZE 2002, DE MENTEN & al. 2005, FOITZIK & al. 2010) and workers might influence male mating success (SUNAMURA & al. 2011, HELFT & al. 2015) or worker and male interests may be conflicting (BOURKE & FRANKS 1995, SCHREMPF & al. 2007).

In many solitary species, male-male competition may have detrimental effects on the females, for instance if males try to force females into investing more resources into offspring they sire even if this reduces the female's lifespan (e.g., JOHNSTONE & KELLER 2000). In social insects however, sperm storage results in a lifelong partner commitment and queens have to establish sufficiently large colonies consisting of sterile workers before they can start to produce sexual offspring. Thus, reducing a female's lifespan will also entail a reduction in male fitness (BOURKE & FRANKS 1995, SCHREMPF & al. 2005a). Even if intersexual conflict seems to be reduced or even reversed to cooperation in social insects, male competition may be contrary to the females' interests. Due to haplodiploidy, males only profit from female sexual offspring, thus their interest lay in influencing the queens towards a more female-biased offspring. Contrary, queens share their alleles with both their male and female offspring and are expected to profit from a less biased sex-ratio (BOOMSMA 1996). If sperm from one male is sufficient to establish a colony and raise sexual offspring, it would still be in the interest of males to monopolize paternity e.g., by sperm competition. For the queens, however, sperm competition may be beneficial in terms of selection for the fittest sperm, but in the long term, they will profit from having as much

sexual offspring as possible. Thus, queens are expected to eventually terminate male-male competition, e.g., by stopping or relaxing sperm competition (DEN BOER & al. 2010). Studies on paternity skew suggest queen influence on the use of sperm resources: a meta-analysis revealed that in species with low paternity frequencies, paternity skew is higher than expected (JAFEE & al. 2012), sometimes even resulting in monandrous offspring in spite of multiple queen mating (BOOMSMA & RATNIEKS 1996, BOOMSMA & SUNDSTRÖM 1998, BOOMSMA & VAN DER HAVE 1998).

In this review, we summarize data on male-male competition in ants. Studies on pre-copulatory competition reach back as far as to the beginning of the 20th century, while post-copulatory competition has been addressed only more recently.

In the following, we distinguish between male-male competition before and during mating, and post-copulatory male competition. While direct fighting as observed e.g., in *Cardiocondyla* species is probably the most conspicuous form of competition, many more aspects and strategies of male-male competition can be found in ants.

Pre-copulatory male competition

Interference with other males during mating: Direct competition between ant males has been found for species mating on the ground or in the nest. In several ant species interference of males with their rivals during copulation has been observed. In *Linepithema humilis* (= *Iridomyrmex humile*), a unicolonial ant species with intranidal mating and a heavily male biased sex ratio, mating pairs are frequently disturbed by other males. While no successful displacement of mating males has been observed, the presence of rival male reduces the amount of sperm stored by female sexuals during mating (KELLER & PASSEIRA 1992). In *Formica aquilonia*, latency to the first mating is larger in situation with a male-biased sex ratio, indicating some interaction of males during the pre-copulatory phase (FORTELIUS 2005). O'NEILL (1994) observed males of the species *Formica subpolita* trying to mount a female sexual that was already mating, however, he concludes that males may not aim to remove a rival but simply attempt to mount and copulate themselves. In *Pogonomyrmex*, several males try to gain access to a female sexual and intervene with other males' mating attempts but usually are not able to remove the other male either (see below). Thus it may be difficult to differentiate between targeted attempts to remove a rival male and normal scrambling for mating attempts by males not realizing the queen is already mating.

The influence of male size: Lengthy flight periods restrict male ants in terms of size and mass, forcing them to optimize flight abilities. However, if mating takes place on the ground, these restrictions are relaxed and higher variability in male size can be found (DAVIDSON 1982).

In the lek-mating *Pogonomyrmex* ants, groups of males compete for female sexuals, but male-male fighting has not been described so far (HÖLLDOBLER 1976, WIERNASZ & al. 1995). *Pogonomyrmex* males struggle for access to female sexuals which they grasp and hold firmly with their strong mandibles. HÖLLDOBLER (1976) proposes that strong mandibles are selected for as males might be pulled or pushed away by competitors. Female sexuals resist mating

for a while after landing on the mating site and thus might select the "strongest" male. In fact, *Pogonomyrmex* males show a continuous variation in size and several studies have found larger males to be generally more successful in mating (*P. occidentalis*: see ABELL & al. 1999, WIERNASZ & al. 1995, 2001, 2004; *P. desertorum* and *P. barbatus*: see DAVIDSON 1982). In addition, it has been shown that the first male copulating with a female sexual invests the most time in the copulation, probably discharging all his sperm. Longer copulations might be adaptive for males to prevent queens from remating; sometimes males even leave parts of their copulatory organs inside the female genital tract (NAGEL & RETTENMEYER 1973, FUKUMOTO 1989). Queens mate multiply, but the second or third male spends less time copulating, "probably due to the fact that those males may not have a chance to unload all their sperm and may therefore be more inclined to give up their first female", leaving the chance to remate with another female sexual (HÖLLDOBLER 1976).

An advantage of large body size is also found in *Hypoponera opacior*, where larger males mated more often in comparison to smaller males and hence gained a clear advantage over smaller males (KURECK & al. 2013).

Male size variability in some *Myrmica* and *Formica* species is bimodal instead of the continuous variation in most other ant species: they produce a larger class of males in addition to a smaller class. FORTELIUS & al. (1987) describe rather different tactics of the two male size classes in *Formica exsecta*: Large males (macraners) are poor fliers and mate close to the ground near nests, whereas small males (micraners) are dispersers and fly high. Similarly, large and small males are produced in *Myrmica ruginodis* (see ELMES 1991), but their dispersal strategy seems to be independent of male size (WOLF & SEPPA 2016). However, in both cases the production of these male forms seems to be related to the colony of origin: In *M. ruginodis*, queen and worker size often correlated with male size (colonies producing macrogynes produce larger males and vice versa), and larger males have a distinct advantage in terms of matings (ELMES 1991). In *F. exsecta*, the production of macraners and micraners may be determined by colony characteristics like size, queen number, polydomy, lifecycle or resource availability, however, results are not fully consistent between studies. Nevertheless, no mating advantage was found for macraners in this species (FORTELIUS & al. 1987, BROWN & KELLER 2000, VAINIO & al. 2004). The production of macraner and micraner males may thus rather be seen under the aspect of fitness advantages on the colony level.

Depending on the conditions, larger sized males might not always be at an advantage. In *Cardiocondyla obscurior*, the outcome of fights depends on male age and thus other male traits may be of lesser importance (CREMER & al. 2012). In a recent study on *Cardiocondyla venustula*, no mating advantage was found for larger males in spite of a large variability in male size within colonies (JACOBS & HEINZE, in press). The agility necessary for fighting in small confined spaces may reduce the large-male advantage often described for fighting (e.g., PAXTON 2005) or influence of workers may reduce the importance of male strength itself (YAMAUCHI & KAWASE 1992). In their studies on body size and sperm content in *Atta colombica*, FJERDINGSTAD & BOOMSMA (1997) and STÜRUP & al.



Fig. 1: Males of the winged and the wingless morph of *Cardiocondyla obscurior* (Picture: J. Giehr).

(2011) found high inter-colonial variability in body fresh mass, but other traits, including sperm content, did not vary. From their data, they conclude, that there might be a tradeoff between size and flying abilities. Similarly, O'NEILL (1994) did not observe an advantage for larger males during mating swarms of *Formica subpolita* and males did not interfere with other males' matings contrary to the observations made in *Pogonomyrmex* (see HÖLLDOBLER 1976). This seems to be in accordance with PAXTON (2005), who suggests that large male mating advantage should be weaker in high male densities with scramble competition, a condition that is met in large mating swarms.

Male fighting (vs. hide and seek): The strongest form of male competition culminates in fighting between the opponents, sometimes even resulting in death. In several *Cardiocondyla* as well as some *Hypoponera* species, wingless males kill rival males, usually pupae or freshly eclosed callows (*H. punctatissima*: see HAMILTON 1979; *H. bondroiti*: see YAMAUCHI & al. 1996; *C. mauretana*, *C. minutior*, *C. emeryi*, *C. kagutsuchi*, *C. tjibodana*: see HEINZE & al. 1993, HEINZE & al. 1998). Both genera have evolved ergatoid (worker-like) male morphs in addition to or completely without the existence of winged males (Fig. 1). In addition to the already described worker like morphology (see above), they usually also have a paler coloration in comparison to their nestmates. Thus, mating predominantly takes place in the nest without the need for males to search for female sexuals outside of the colony, and this mating in the confined space of the nest might be one condition favoring direct male competition (BOOMSMA & al. 2005). Adaptations to this caused a unique feature of wingless males in the genus *Cardiocondyla*: in contrast to all other social hymenopteran males, their testes do not degenerate, but produce sperm throughout their life, allowing them to mate with all virgin queens that they can monopolize inside of the nest. Going hand in hand with this, wingless males can live for up to one year (YAMAUCHI & al. 2006), in contrast to the comparatively short average lifespan of winged *Cardiocondyla* males (mean lifespan *C. obscurior*: 12.25 ± 5.75 days from SCHREMPF & al. 2007) and winged ant males in general (BOOMSMA & al. 2005). Similarly, queens of *Cardiocondyla* have a relatively short lifespan (*C. obscurior*: max. 56 weeks, SCHREMPF & al. 2005a; *C. batesii* (corrected for hibernation): max. 112 weeks, SCHREMPF & HEINZE 2007). As in most of these species older males usually kill their freshly eclosing ri-



Fig. 2: Wingless *Cardiocondyla obscurior* males in fight (Picture: J. Giehr).

vals, the males eclosing first might gain an advantage in comparison to males eclosing later, whereas the size of the males is probably irrelevant (JACOBS & HEINZE in press; A. Schrempf, unpubl.).

Several different male tactics have evolved in ants from the genus *Cardiocondyla* and male appearance varies with these tactics (e.g., HEINZE & HÖLLDOBLER 1993, HEINZE & al. 2005). Fighting seems to be ancestral in the genus and species can be divided into a clade producing males with saber-shaped mandibles and a second clade producing males with shear-shaped mandibles. Winged males have been lost in many of the species in both clades (in the *C. argyrotricha* group, *C. mauritanica*, *C. venustula* and the Palearctic group) (OETTLER & al. 2010). Males with saber-shaped mandibles kill callow and adult nestmate males. Pupae or callows are easily killed by puncturing the soft cuticle, but males are usually not able to crush the sclerotised cuticle of an adult rival. Hence, they grasp their opponent and transfer secretions of their hindgut on its cuticle inducing worker aggression (described for *C. obscurior*, *C. wroughtonii*, *C. sp.*: see KINOMURA & YAMAUCHI 1987, STUART & al. 1987, YAMAUCHI & KAWASE 1992; Fig. 2). Males may transfer secretions on each other reciprocally, sometimes even resulting in the death of both males. In these species, colonies thus generally do not contain more than one male at a time, allowing the "winner" male to monopolize all his eclosing sisters. Older males have a clear advantage over young males with a not fully sclerotised cuticle, but this benefit disappears in case the rival has grown older than one day (CREMER & al. 2012). In *Cardiocondyla* species with shear-shaped mandibles, killing of pupae or callows by crushing the soft cuticle is the prevailing male strategy. Especially in larger colonies, some freshly eclosed males manage to hide inside a colony and thus avoid being killed during the first days of their life. As adult male fighting seems to be unusual in this clade, two or three adult males may sometimes be found together in one colony (*C. mauritanica*, *C. emeryi*, *C. kagutsuchi*, and *C. minutior*: see HEINZE & al. 1998). However, in some of those species males also occasionally fight against and kill adult rivals, and in at least two species, the transfer of hindgut secretions has been observed (*C. venustula*: see FROHSCHAMMER & HEINZE 2009 and *C. cf. kagutsuchi*: M. Suefui & J. Heinze, unpubl.).

Given the increased chance to survive fighting once the cuticle has hardened, it is in the interest of freshly eclosing males of both clades to hide under the brood pile and stay undetected from an older male, which on the other hand patrols the colony to detect rivals as soon as possible. In accordance with this, it has been shown that under polygynous conditions, the timing of male production is premature, as queens probably try to increase the chances of their own son to eclose early, survive and reproduce (YAMAUCHI & al. 2006, SUEFUJI & al. 2008). Interestingly, males of the palearctic clade of *Cardiocondyla* characterized by derived monogyny are mutually peaceful and do not engage in fights at all (SCHREMPF & al. 2005b, SCHREMPF & HEINZE 2007).

Similar to male fighting in the genus *Cardiocondyla*, wingless males in *Hypoponera punctatissima* and *H. bondroiti* have been observed fighting with other adult males (HAMILTON 1979, YAMAUCHI & al. 1996). *Hypoponera punctatissima* males fight for access to the chamber in which female sexuals are reared and can inflict injuries upon their opponents. Some of them might die from their injuries (HAMILTON 1979). In *H. bondroiti*, dimorphic ergatoid males (major and minor) can be found in one nest. While majors attack each other until one of the males is driven out of the nest, they do not attack minor males, but mount them in some cases. YAMAUCHI & al. (1996) suggest that the minor males mimic queens and thus are not recognized by majors, similar to winged males in *Cardiocondyla* (see below). Between minors, fighting or mounting has been observed in rare cases. Both male morphs mated with virgin females. In this case, both direct competition (majors) and avoidance of competition (minors) occur within one colony. However, the study by YAMAUCHI & al. (1996) provides no detailed data on the reproductive success of the respective strategies.

Another form of male killing might have arisen in *Hypoponera opacior*: It has been shown that males embrace other males in their cocoon by inserting their genitalia into the rear end of the pupal cocoon. In this way, more than 70% of such embraced males are killed (KURECK & al. 2011), and hence it might be an adaptive strategy of males to kill competitors. Similar to the above, early emerging males might gain an advantage, as males that emerge earlier are able to mate more often (KURECK & al. 2013).

As an alternative tactic to fighting, males of some of the above mentioned species evolved a strategy to succeed by escaping direct competition: they try to hide from fighter males by mimicking female sexuals. This has been suggested for minor males of *Hypoponera bondroiti* (see YAMAUCHI & al. 1996) and chemically shown for winged males in *Cardiocondyla obscurior* (see CREMER & al. 2002). These males are not recognized by the wingless males and hence stay concealed in the colony and "sneak" copulations inside the nest before dispersing. Interestingly, the males react quite flexibly to the availability of mating partners and opponents inside of the colony and leave the nest earlier in case that future mating opportunities are low (CREMER & al. 2011, YOSHIZAWA & al. 2011).

Territoriality: Wingless males of the species *Cardiocondyla venustula* have evolved a strategy hitherto not known for ants: they establish territories (FROHSCHAMMER & HEINZE 2009). The colonies of *C. venustula* live in subterranean nests with several small chambers. Male and

female sexuals are produced in relatively high numbers during short periods of the year. Freshly eclosing male pupae are usually killed in this species similar to other *Cardiocondyla* species; however, males often do not manage to kill all emerging rivals, probably due to nest structure and number of eclosing males. Unlike in other species like *C. mauritanica* or *C. emeryi*, adult fighting is common and males also occasionally transfer secretions on each other. Some males defend small nest chambers and thereby create a territory, in which they kill eclosing males and mate with virgin females. This seems to be more efficient than patrolling the whole nest. Other males are usually pushed away from these territories by mandible threatening and biting. However, not all males behave in this way, and it remains to be investigated which factors inside of the nest influence the strategies of the different males (JACOBS & HEINZE in press).

Enforced copulations: In *Hypoponera opacior* and *H. nubatama*, males do not wait until the eclosion of virgin queen pupae; instead, they mate with queens which are still inside of their cocoon to ensure mating. Males of this species do not fight against each other. Yet, by prolonging their copulation for up to 40 h and thereby acting as a "living" mating plug (see below, YAMAUCHI & al. 2001), they can prevent other males from mating. Obviously, female sexuals cannot choose their mating partner when they are in the cocoon, however, several of the queens have been observed to mate a second time after eclosion from the cocoon (FOITZIK & al. 2002). It remains to be investigated whether they selectively use the sperm of a preferred male by cryptic female choice.

In both species, two or more males may scramble for access to a cocoon, but only one is copulating with the female as long as she is in the cocoon, and no fighting between adult males has been observed (FOITZIK & al. 2002). However, as described above, males embrace nestmate male pupae which afterwards die in a number of cases (35.3% in YAMAUCHI & al. 2001, 73% within two days in KUR-ECK & al. 2011).

The role of workers: Beside direct competition between the males, the interference of workers might contribute to the resulting mating pair. Naturally, this is only possible for species mating inside or close to the nest with workers in direct proximity.

Even though in *Cardiocondyla* workers are utilized by males to kill their rivals (see above, e.g., KINOMURA & YAMAUCHI 1987), they rather seem to be "tools" of the males, as they normally kill the "marked" male (and do not "choose" to kill e.g., a "less related" male from a different colony; A. Schrempf, unpubl.), and sometimes even kill both males as an outcome of aggressive behavior. So far, there is no evidence of *Cardiocondyla* workers deliberately interfering with a given male's mating success.

In *Cataglyphis cursor*, males aggregate in front of alien nests and try to mate with gynes from these nests. While there may be aggression between males (LENOIR & al. 1988), CRONIN & al. (2011) observed workers to be highly aggressive towards males, yet, the aggressiveness varied between colonies and no clear difference in behavior towards a specific male was found. However, workers seem to treat males differently depending on their relative weight: while heavier males mate more often than lighter males in the absence of workers, this effect ceases when workers are

present. Thus, workers may be able to influence male mating success (HELFT & al. 2015).

In *Linepithema humile*, workers have been observed to heavily attack males from other but not from their own supercolonies, and thus they influence mate choice of the queens. This reproductive interference by workers leads to a reduced gene flow between supercolonies (SUNAMURA & al. 2011). In army ants (e.g., from the genus *Eciton*), queens are flightless and never leave their colony, hence males have to enter the colonies to mate and workers can influence which male inseminates the future queen during colony reproduction (FRANKS & HÖLDOBLER 1987), even though mating frequency of queens is extremely high (KRONAUER & al. 2004, 2006).

In the ponerine species *Megaponera foetens*, males use trails laid by the workers to locate and enter the nests of alien colonies, thus workers at least influence the recruitment of males. In several other (queenless) ponerine species (e.g., *Ophthalmopone*, *Rhytidoponera*), workers possess spermathecae and are therefore able to mate and produce offspring after mating with foreign males inside the nest (PEETERS 1991).

Competition in male larvae: A recent study by SCHULTNER & al. (2013) suggested that males compete already during the larval stage. They show that in *Formica aquilonia*, larvae cannibalize eggs, and that male larvae do this more frequently than female larvae (three times more often). By doing so, males do not only enhance their own survival probability but might at the same time also remove possible competitors later in life. So far, it is unclear whether males prefer male instead of female eggs. Mating in polygynous *Formica aquilonia* can be near or even inside of the nest and males might have to compete for access to female sexuals with other males. Males are able to mate with several female sexuals, which also mate multiply. Even though they do not directly attack each other, they compete in securing mating quickly before another male gains access, and increasing male bias decreases mate number in males (FORTELIUS 2005).

Post-copulatory male competition

Mate guarding and mating plugs: Mating plugs produced by the accessory glands are used by males in several insect species to inhibit or at least reduce remating of queens (e.g., GILLOTT 2003). In social Hymenoptera, the existence of mating plugs has largely been neglected; however, studies in bumble bees have revealed the function of lipids as mating plugs (e.g., BAER & al. 2000, SAUTER & al. 2001) and several investigations in ants also suggest the existence of mating plugs.

In *Hypoponera*, males mate longer in presence of competing males, suggesting that they act as "living" mating plugs (YAMAUCHI & al. 2001, KURECK & al. 2011). In other species, substances from the accessory glands may serve as mating plugs. In *Diacamma*, *Monomorium* and *Carebara*, accessory gland compounds have been found to form a "sperm plug" or spermatophore (ROBERTSON 1995, ALLARD & al. 2002, 2006). In *Carebara*, the mating plugs are of a rather temporary nature. Thus, they may influence remating with subsequent males but do not inhibit remating itself. However, they might serve to prevent sperm leakage out of the vagina, ensuring the maximal number of sperm possible is transferred to the spermatheca (RO-

BERTSON 1995). In *Monomorium*, spermatophores also do not inhibit remating, thus they might only be used to transport sperm to the spermatheca or influence, but not prevent further matings (ALLARD & al. 2006). In *Solenopsis invicta*, fatty acid compounds of the accessory gland fluid are similar to those that have been proven to prevent remating in bumble bees, thus possibly having the same function in ants (MIKHEYEV 2003). Generally, it might not be easy to distinguish whether these compounds only function for sperm transfer or whether they serve as mating plugs and inhibit remating. Indeed, different components from the accessory glands may serve different purposes and DEN BOER & al. (2015) found that mating plug functions are more pronounced in the rather monandrous species whereas sperm transfer, sperm survival and sperm competition are more important functions in highly polyandrous species. In line with this, a study by BAER & BOOMSMA (2004) suggests that males invest less into accessory glands but more into accessory testes (sperm number) when they are no longer able to influence paternity (in polyandrous species).

Males of other species even go further and perform extreme forms of mate guarding, staying attached to the queen leaving their genitals inside the female genital tract even after their death and thus acting as mating plugs themselves. In *Diacamma* sp., a ponerine ant, males stay attached to the female sexual for as long as 20 - 24 h. Shortly after the start of the mating, the female sexual returns to the nest. In the nest, the male is finally killed by the workers, leaving his genital inside of the female sexual (FUKUMOTO 1989, ALLARD & al. 2002). It has been shown that in *Diacamma pallidum*, sperm is transferred in the form of a spermatophore already 15 minutes after copulation. The extremely prolonged copulation may be an effective prevention of remating (*Diacamma* females mate only once) but the mating inside the nest might also allow worker influence on mating (ALLARD & al. 2007). Males of the species *Dinoponera quadricaps* also exhibit suicidal mating: the male mates with a gamergate near her nest, and attached to the female, the male is dragged into the nest where the gamergate cuts off the end of the male's abdomen, leaving parts of his genitalia in her reproductive tract (MONNIN & PEETERS 1998). Generally, suicidal mating seems to be restricted to the monogynous species providing only very rare mating opportunities for additional males. In species with multiple gamergates, where the sex-ratio is thus more female-biased, males can mate multiply (MONNIN & PEETERS 1998, ALLARD & al. 2007). In army ants with a highly male-biased sex-ratio, males shed their wings before mating on the ground and stay in copula for a prolonged time (GOTWALD 1995). As described above, *Pogonomyrmex* males in some cases leave their genital organs stuck to the female's mating tract, which however does not seem to inhibit remating completely (HÖLLDOBLER 1976).

Sperm competition: Whenever queens mate multiply, sperm competition between the sperm of males in the female sexual tract might occur. After an initial monandrous phase during the evolution of eusociality, multiple mating in ants has evolved several times (HÖLLDOBLER & WILSON 1990), and even if mate numbers are generally low (STRASSMANN 2001), there are also a few highly polyandrous clades (e.g., seed harvester ants, leafcutter ants, army ants, species of *Cardiocondyla*, *Plagiolepis* and *Catagly-*

phis; see PAGE & METCALF 1982, BOOMSMA & al. 1999, MURAKAMI & al. 2000, KRONAUER & al. 2004, 2007, SCHREMPF & al. 2005a, TRONTTI & al. 2007, LENOIR & al. 2007, SCHREMPF 2014). A comprehensive review on polyandry in ants has recently been published by BAER (2016). Colonies have to invest into their sterile worker force before they start with the production of sexuals, and the lifelong commitment of the queens and the males makes it necessary that sperm survives inside of the queen throughout her entire lifespan (BOOMSMA & al. 2005, BAER 2011, 2014). Even if a male might benefit from outcompeting the sperm of rival males in case he is able to transfer sufficient sperm for the complete lifespan of the queen, intense competition between the ejaculate of several males within the spermatheca is not expected after the mating period and the storage of the sperm (BOOMSMA & al. 2005, DEN BOER & al. 2010, BAER 2014). This does not mean, however, that males do not try to increase their own fitness and indeed, an elegant study by DEN BOER & al. (2010) confirmed that in highly polyandrous ants (and bees), males manipulate the sperm of opponents with their seminal fluid protein. Sperm survival in *Atta colombica* and *Acromyrmex echinatio* queens was significantly reduced when mixed with alien seminal fluids in comparison to sperm in monandrous species (*Trachymyrmex* cf. *zeteki*). Importantly, they were also able to show that at least in *Atta*, the spermathecal fluids of the queen inhibit this negative effect. Hence, while males might be able to outcompete some sperm during the sperm storage process, they are probably unable to harm the sperm in the spermatheca after storage (DEN BOER & al. 2010).

The important role of queens for sperm storage has already been suggested by SUNDSTRÖM & BOOMSMA (2000) and queens might for example reduce the effect of sperm clumping. Their study suggested that in *Formica truncorum*, it is in the interest of all males to achieve sperm clumping, as this will bias the worker controlled sex ratio towards female offspring because cohorts of highly related individuals would be produced at a time. However, they also suggest that queens oppose this male strategy by probably actively mixing the sperm, resulting in a "compromise between complete sperm clumping (the joint interests of the males mated to a queen) and complete sperm mixing (the queen's interests), where some queens are more successful than others in mixing sperm and, thus, having more male-biased sexual broods". Thus, even if sperm clumping is aimed at by males, it may be concealed by mixing by the queen. Several studies have confirmed random sperm use by the queen (KRONAUER & al. 2006, HOLMAN & al. 2011), and a recent detailed study on sperm use in *Acromyrmex echinatio* over time also confirmed that sperm is equally mixed and used randomly from the spermatheca (STÜRUP & al. 2014).

Sperm competition is not only expected to select for male traits against alien sperm, but certainly also for the enhancement of their own sperm fertilization probability. One older and three recent studies independently describe the formation of sperm bundles in adult ant males, in which queens are polyandrous (*Crematogaster victima*: see BOOMSMA & al. 1999, OLIVEIRA & al. 2014; *Lasius pallitarsis*: see BURNETT & HEINZE 2014; *Cataglyphis savignyi*: see PEARCY & al. 2014). While sperm bundles are well known

in the testes of premature males due to the development of sperm in cyst cells, sperm cells usually disorganize after maturation in the seminal vesicles (e.g., MOREIRA & al. 2004).

Sperm of haploid insect males is clonal and hence, there is no conflict between individual sperm within an ejaculate, making the evolution of cooperation between sperm cells to enhance a male's fertilization ability in case of intense sperm competition likely. While it is still not clear in *Lasius pallitarsis*, whether sperm bundles are just the result of incomplete decomposition of cyst cells after maturation or whether sperm bundles are the result of sperm competition to increase mobility (BURNETT & HEINZE 2014), PEARCY & al. (2014) were able to show for *Cataglyphis savignyi* that sperm swimming speed in bundles is indeed faster in comparison to single sperm. As it is a well-known fact that sperm velocity transfers into fertilization success (BIRKHEAD & al. 1999, GASPARINI & al. 2010), it is very likely that sperm bundles in all of these species are formed to increase the fertilization success of individual ant males. On the species level, clear adaptations to the level of sperm competition have been found in males from *Cataglyphis* species. Males from species experiencing higher sperm competition have a higher sperm production and thus ejaculate size compared to those from species with less competition. Sperm length and male size also varied with competitive situations; however, this effect was much weaker (BAER & BOOMSMA 2004, ARON & al. 2016).

During postcopulatory selection, queens are involved as a third party via cryptic female choice (CFC). While it has been shown that queens disable negative effects of seminal fluids on rival sperm (DEN BOER & al. 2010), queens might have no influence on sperm displacement. However, with or without active sperm choice of females it might be that sperm of superior males is differently used for insemination. Moreover, one might argue that sperm of high quality males survives longer and hence is the only one to be able to fertilize eggs at the end of the queens' life (at the time where often sexuals are produced). Yet, more studies are needed to understand the dynamics of male-male competition and cryptic female choice in social insects and to investigate whether CFC might select for higher quality sperm in males.

Conclusion and future perspectives

With an increasing number of studies that have been published in recent years, it has become evident that competition between ant males is more common than previously assumed. Indeed, competition might already take place at the larval stage (SCHULTNER & al. 2013). More studies are needed to investigate whether egg eating actually represents a form of selective killing of rivals and whether this phenomenon is unique to *Formica* ants or whether it is a general trait in species where larvae are able to move and feed by themselves.

After eclosion, ant males might differ in quality with regard to mature sperm number, size and viability. Even though the testes of ant males degenerate before or shortly after maturation (HÖLLDOBLER & BARTZ 1985), males might nevertheless produce more sperm in a given period of time and / or higher quality sperm when reared in an environment that predicts future sperm competition conditions. For example, it has been shown in flatworms that

sperm is produced faster under sperm competition conditions (GIANNAKARA & al. 2016). It remains to be investigated whether also ant males "react" to the level of sperm competition on an intraspecific level, e.g., in *Hypoconera* or *Cardiocondyla*, depending on the number of competitors inside the colony. Under the assumption that only healthy, well-fed larvae can produce optimal sperm cells, competition between larvae, e.g., in begging for food, might occur and needs further investigation. Under such conditions, workers might be able to support larvae differently depending on relatedness (in case they are able to discriminate kin, see e.g., NEHRING & al. 2011, HELANTERÄ & al. 2013; but see BARONI-URBANI 1991 and SCHULTNER & al. 2013).

Theory predicts that sperm competition selects for an optimal sperm phenotype (PARKER 1993), and a species comparison by FITZPATRICK & BAER (2011) indeed confirmed that variance in sperm length is lower in social insect males that experience sperm competition.

In solitary insects, it has also been shown that males are able to adjust ejaculate size and viability directly to the level of sperm competition (THOMAS & SIMMONS 2007, MARTIN & HOSKEN 2002). The above-mentioned studies by BAER & BOOMSMA (2004) and ARON & al. (2016) show that at least concerning between species comparison, adaptation to competition can be found in attine fungus growing and *Cataglyphis* ants. Again, further studies are needed to investigate, whether males adjust their sperm number and viability to competition on an intraspecific level – on condition that sperm number is sufficient for the offspring production of the female mating partner.

Studies on post-copulatory traits in polyandrous species as conducted by Baer and colleagues can help to assess the magnitude of male manipulations after and during the storage process, respectively, and might reveal, in addition, previously undetected male traits to manipulate their reproductive success. For example, similar to solitary insects, sperm displacement might be a strategy of males mating subsequently (again only provided that a single male can transfer sufficient sperm for the offspring that a queen produces during her complete lifespan).

It is similarly conceivable that queens might sometimes reject sperm of males, which transfer "low" quality sperm, but studies on cryptic female choice are rare. This could be investigated in the future e.g., by offspring analysis of queens that are allowed to mate with known males whose ejaculate quality has been manipulated. Species with intranidal mating and the possibility to perform matings in the laboratory will be valuable model systems for future research. A very recent study in *Drosophila* revealed that females are even able to counter-act to mechanisms of chemical mate-guarding (LATURNEY & BILLETER 2016). In several ant species, females change their "bouquet" after mating and become unattractive for males. It remains to be investigated whether similar antagonistic co-evolution of males and females on the "chemical level" is existent in ants. Advances in proteomics will allow deeper insights into molecular pathways of sexual selection. As an example, the comparison of seminal fluids and spermathecal fluids of additional species may be used to detect general patterns in sperm competition and / or cryptic female choice in social insects and to compare them with solitary insects where life history is different.

Ants exhibit an enormous variety of mating systems, thus it will be crucial to include as many different study species as possible in further studies to compare levels of sexual conflict and sexual selection. Insights into intra- and interspecific differences of male-male competition and their evolutionary background may contribute to a better understanding of the evolution of sexual selection in social insects and beyond. The availability of more and more ant genomes will provide the opportunity to analyse these evolutionary processes on the genomic and / or proteomic level.

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