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<https://escholarship.org/uc/item/7nx8g0xc>

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Publication Date

2021

DOI

10.1007/978-3-030-28102-1_104

Peer reviewed

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Sexual Selection in Social Insects



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As defined by Charles Darwin, sexual selection is “the advantage which certain individuals have over other individuals of the same sex and species solely in respect of reproduction.” It is, then, a special case of natural selection driven by conflicts among individuals over reproductive decisions. Furthermore, as originally set forth by Darwin, we distinguish between *intra-sexual selection*, which is driven by individuals of the same sex (typically males) to compete with each other, and *intersexual selection* that is driven by conflicts between opposite-sex individuals over reproductive decisions.

There is ample of evidence that sexual selection can be a remarkably strong evolutionary force. It can occur prior to mating (Table 1), for example, as male-male competition for access to females and/or eggs or female choice to discriminate against unwanted males (Table 1). However, sexual selection can continue to operate beyond mate choice and copulation. Such post-copulatory sexual selection can impact reproductive success and fitness either as ► **sperm competition**, in

which rival ejaculates compete for access to storage sites and eggs, or as cryptic female choice, in which a female manipulates ejaculates of males in her own interest. The latter process is cryptic in the sense that it typically occurs inside the female’s reproductive tract in the physical absence of males and is therefore inaccessible to males to further influence their paternity success.

Although sexual selection has been extensively investigated in many species and over a broad range of taxonomic groups, it remains substantially understudied in social insects. This is surprising, given that sexual selection can have substantial impact on offspring relatedness, which has received intense attention as a key component of inclusive fitness and ► **kin selection**. Several reviews have developed a theoretical framework of how sexual selection operates in social insects and summarized available knowledge in bees [3], ants [4, 5], and termites [6]. The following paragraphs provide a brief summary synthesis of these contributions.

The colony organization of social insects has fundamental effects on their reproductive biology and therefore on the way sexual selection operates. In most insect societies, there is only one or very few reproductive females (queens), and mate choice only occurs during a very brief period early in their adult lives. In a termite colony, there is typically a single reproductive pair, which mates repeatedly over the life of the colony, while in all social wasps, social bees and ants

Sexual Selection in Social Insects, Table 1 An overview of different levels of sexual selection with some examples from social insects. For a more complete overview, see tables in [1, 2]

	Pre-copulatory	Post-copulatory
Intra-sexual selection	<p><i>Male-male competition</i> <i>Cardiocondyla</i> ant males kill rivals Bumblebee males establish and defend territories Scramble competition for copulations in harvester ants</p> <p><i>Female-female competition</i> Virgin honey bee queens kill their sisters prior to mating</p>	<p><i>Sperm competition</i> Male bees and ants use seminal fluid components to kill sperm of rival males</p>
Inter-sexual selection	<p><i>Mate choice</i> Bumblebee queens refuse to mate with some males and can kill persistent males Ant males monopolize females by copulating with queens prior to hatching and mate guarding them</p>	<p><i>Cryptic female choice</i> <i>Atta</i> queen secretions terminate hostile interactions between competing male ejaculates <i>Female remating</i> Males transfer mating plugs or seminal fluid proteins to reduce female remating</p>

mating appears limited to the period of mate choice, the males dying shortly afterward. In these latter groups (as in solitary wasps and bees), sperm is stored in a specialized organ, the spermatheca, for the life of the queen (Fig. 1).

Consequently, any sexually selected traits harming queens or compromising their lifetime fecundity are not expected to be favored in social insects and have not been reported. Mating has even been found to have beneficial effects on *Cardiocondyla* ant queens by prolonging their lifespan. Paternity analyses show that the queens of many social insects store and/or use sperm from a single male. If this results from queens only accepting to mate with a single male, they are

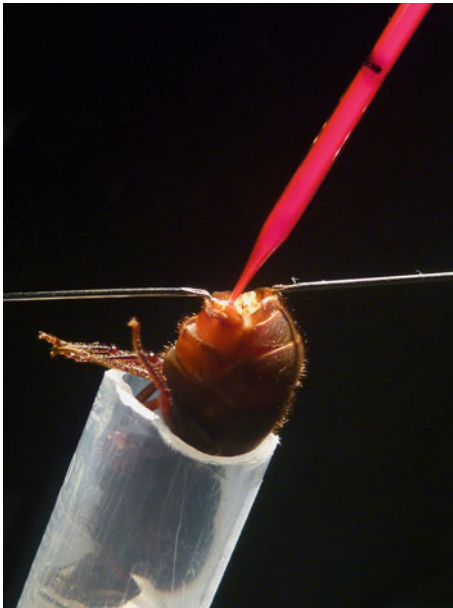
monandrous, and there is no post-copulatory sexual selection.

Because mate choice and copulation are rare events in the lives of social insects, they can be rather challenging to study, especially in species that mate on the wing or will not mate under laboratory conditions. More recently developed techniques such as artificial insemination (Fig. 2) and molecular tools from systems biology [7] offer very promising new ways to unravel the sophisticated processes and conflicts that determine paternity and fitness of social insect males and queens.

Present knowledge of sexual selection in social insects rests on a limited number of ant and bee species in which it has been studied in detail. Despite these limitations, there is solid empirical evidence that all levels of sexual selection as outlined in Table 1 are manifested in social insects. Male-male competition for access to females can be intense, especially in those species with highly male-biased sex ratios, such as ► [honey bees](#), in which thousands to tens of thousands of males compete to mate with one or a few virgin queens. In ► [harvester ants](#) males form a dense ball around a virgin queen, forcefully competing with each other for contact with access to her genital opening. Some ► [bumblebee](#) males establish territories, which they mark with ► [pheromones](#) and defend against other males. ► *Cardiocondyla* ants provide a fascinating example of pre-copulatory sexual selection [8], in which male-male competition has resulted in the evolution of two distinctly different male morphs (Fig. 3). Winged males, which resemble the typical male phenotype found in many ants, leave the colony to disperse on the wing in search of virgin queens. The second male morph is wingless and possesses a pair of pointy mandibles; they remain in the maternal colonies and monopolize access to emerging virgin queens by patrolling the nest and killing emerging rival males. Because these wingless males are present in the colony for longer periods of time, they are currently the only documented cases in ants, social wasps, or social bees where continuous spermatogenesis re-evolved in adult life. Winged *Cardiocondyla* males seem to have responded to the threat of being killed by



Sexual Selection in Social Insects, Fig. 1 An *Atta colombica* fungus-growing ant queen has just started a new colony in a Panamanian rainforest. These queens have driven fecundity to record extremes, as they only mate during a single nuptial flight early in life, during which they can acquire over 400 million sperms [10]. They are afterward able to store sperms for several decades in a special organ known as spermatheca and only use 1–3 sperms per egg fertilization [11], which is key to maintain a population of several million workers in mature colonies.



Sexual Selection in Social Insects, Fig. 2 Artificial insemination (AI) was initially developed for honey bees and has since been used for breeding purposes. AI was eventually adopted for the use in other social insects such as in leafcutter ants [12], as seen here, and is a valuable tool to study the mating biology and reproductive conflicts in social insects



Sexual Selection in Social Insects, Fig. 3 Pre-copulatory sexual selection has been intensively studied in *Cardiocondyla* ants. These ants produce two different male morphs, a winged one (top) leaving the colony to search for mates and a wingless male morph (bottom) patrolling colonies and killing rival males with their pointy mandibles. (Photos provided by Jürgen Heinze)

wingless males by altering their ► [cuticular hydrocarbon](#) profiles to mimic those of females.

Pre-copulatory intra-sexual selection can also occur as female-female competition, for example, in honey bees, in which colonies produce an excess of virgin queens that fight to the death after their emergence, so that typically only one remains to participate in nuptial flights and mating before taking over of the colony from their mother. Intersexual selection is present as a mate choice in bumble bees, in which queens resist mating attempts of some males and sometimes even kill them if they persist. In *Hypoponera* ants, males are able to monopolize queens by patrolling colonies for queen pupae and mating with them while they are still in their cocoons [9].

In polyandrous social insects such as honey bees and ► [leafcutter ants](#), post-copulatory sexual selection takes the form of sperm competition, in which males transfer seminal fluid proteins to queens as part of their ejaculate [1]. These proteins reduce the viability of rival sperm, yet queens are able to suppress such male-male interactions through proteins in their own glandular secretions as a form of cryptic female choice.

Finally, males have a number of traits to avoid remating by queens with additional males. As one tactic, they can remain firmly attached to females in copula as a form of mate guarding, even if females dismember their thoraxes and heads, for example, in ► [Dinoponera quadricaps](#) [4]. Ant and bee males also transfer mating plugs to queens, which have been found to contain molecules acting as anti-aphrodisiacs and reducing the willingness of queens to accept further copulations. In honey bees, proteins in the seminal fluid have multiple effects on queens. Apart from killing the sperm of rival males, they trigger significant changes in gene expression in the queen's brain to reduce her visual perception and alter her nuptial flight behavior.

In conclusion, sexual selection is an important force in social insects that has resulted in a number of rather extravagant traits and body forms. Inclusive fitness theory can be used to make accurate predictions about the way reproductive conflicts operate and have evolved in social insects. This offers exciting opportunities for future work, especially to unravel the molecular basis of these sexual conflicts, which – in combination with studies of further species – will allow an understanding of the evolutionary history of these traits and their potential effects during early social evolution. A key effect of sexual selection is to reduce genetic diversity among offspring of a given colony. A broader understanding of the key underlying reproductive traits could therefore be of

interest in a number of research fields, such as conservation biology and the management of honey bees or other social insects of economic importance.

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