Title
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Publication Date
2021

DOI
10.1007/978-3-030-28102-1_114

Peer reviewed

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If a female mates with multiple males resulting in the co-occurrence of ejaculates from multiple males within her sexual tract, sperm often have to compete with each other for limited storage space and/or a defined set of eggs. The resulting processes that bias the reproductive success and fitness toward more competitive males are known as sperm competition, which is a form of post-copulatory ▶ sexual selection. Sperm competition has been studied in a broad range of organisms and can be a key determinant of male reproductive success and fitness [17]. This is especially true for insects, in which polyandry seems to be the rule, rather than the exception. The importance of sperm competition in social insects has been studied in some detail, albeit more on a theoretical level rather than through extensive empirical work [4, 8, 9]. These contributions have concluded that the way of life of social insects is expected to restrict the evolution and phenotypic expression of sperm competition for a number of reasons.

The Rarity of Multiple Paternity in Social Insects

Single paternity is the ancestral mating system of social insects and remains widespread in present-day species. The discrepancy in female mating frequencies between social and nonsocial insects is expected from ▶ kin selection maximizing helper (worker) relatedness to increase inclusive fitness and therefore incentivize helping. As a consequence, sperm competition is by definition absent in all strictly monandrous social insects.

The Rarity of Partner Choice and/or Mating

Social insects only go through a single round of partner choice and commit to a partnership for life [3]. In the ants, social wasps, and social bees, individuals pair and copulate only during a very brief period of time early in a queen’s life, when they acquire and store a lifetime supply of sperm. Males die either during or shortly after copulation, and only their germ line survives as sperm inside a specialized storage organ of the queen known as the spermatheca. In contrast, termite males survive alongside their queens as kings and repeatedly copulate with them, but this

C. Starr (ed.), *Encyclopedia of Social Insects*,
https://doi.org/10.1007/978-3-319-90306-4_114-1

follows the same general principle of a lifetime partner commitment formed early in life and prior to egg laying [13]. The rarity of partner choice and/or mating therefore restricts the occurrence and possible impact of sperm competition in polyandrous queens.

Long-Term Sperm Storage

In the absence of repeated mating later in life, queens of ants, bees, and wasps store a lifetime supply of sperm, which can remain viable for up to several decades in some especially long-lived species of ants. This has several consequences. First, sperm competition is unlikely to play any significant role once conflicts among ejaculates over storage have been resolved, because healthy queens are effectively limited by the number of sperm they can store, rather than the number of eggs they can continuously produce. Second, because sperm cannot be replenished later in life, any sperm competition traits that would compromise the lifetime fecundity of queens or the sperm they store are not expected to evolve.

Absence of Intra-ejaculatory Sperm Competition

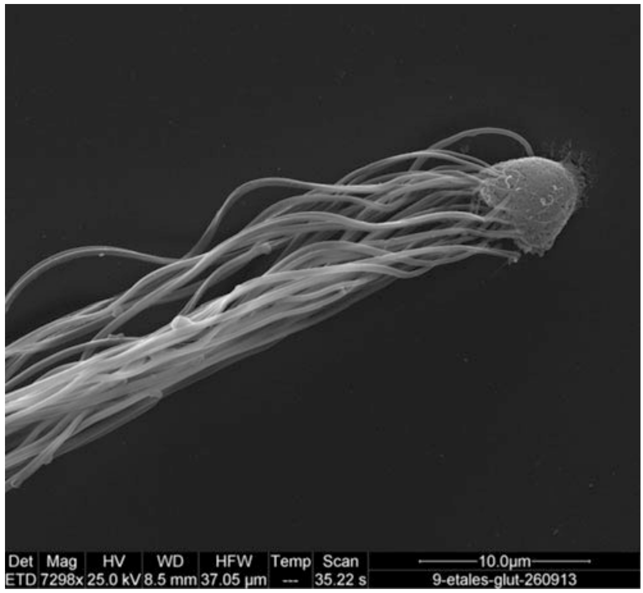
In the Hymenoptera, males are ▶ haploid, so that a given male's sperm is a genetically identical clone. Consequently, there is no basis for competition within a male's ejaculate, unlike among the sperm of a diploid male.

Sperm Competition in Social Insects

Despite these factors limiting the occurrence and phenotypic expression of sperm competition in social insects, polyandry has been documented in all major lineages, especially in species with large, long-lived societies such as ▶ army ants, ▶ leaf-cutting ants, and ▶ honey bees [4, 8, 9]. This has led to a number of studies to confirm the presence of sperm competition in these groups and attempts to quantify its impact on paternity distribution and nestmate relatedness. Evidence for sperm competition in social insects comes from a number of comparative studies of phenotypic expressions of specific traits found in other organisms. (1) Sperm viability is significantly higher in ejaculates of polyandrous compared to monandrous bees and ants, a predicted outcome of sperm competition selecting for maximal sperm quality and comparable to similar patterns in solitary insects [14]. (2) Sperm competition can result in males producing more sperm and/or larger ejaculates to outcompete their rivals. This is confirmed by a number of comparative studies in a wide range of animals [17] and is also the case in ▶ *Cataglyphis* desert ants, in which levels of sperm competition correlate with the number of sperm produced by males [1]. (3) Variation in sperm length is significantly lower in polyandrous compared to monandrous social insects, similar to what has been found in birds or mammals. The exact mechanisms of how sperm length relates to paternity success remain to be worked out, but sperm length influences storage success in ▶ bumble bees, although longer or shorter fractions of sperm within an ejaculate can become stored in the spermathaca, depending on male and queen genotypes [7].

Sperm competition has also been studied in honey bees, whose queens are obligatory polyandrous, with the highest queen mating frequencies reported so far in social insects [2]. In the ▶ western honey bee *Apis mellifera*, queens can mate with 20 or more males to acquire 200 million sperm that become temporarily stored in a specialized part of their sexual tract known as the lateral oviducts. Because only 3–5% of these sperm eventually become stored in the spermatheca, exceptionally strong competition among ejaculates for storage is expected.

Another example is *Cataglyphis savignyi*, whose queens are also highly polyandrous and mate with up to 14 different males. In response to such strong competition, sperm seem to form bundles that are known to swim significantly faster compared to solitary sperm [16] (Fig. 1). Such team swimming of sperm that might have evolved in response to sperm competition could also be present in the ant ▶ *Lasius pallitarsis* [10]



Sperm Competition, Fig. 1 Team swimming of sperm in a polyandrous desert ant. Sperm bundles as found in ejaculates of *Cataglyphis savignyi*. Swimming of sperm in such bundles is significantly faster compared to solitary sperm and is therefore expected to have evolved in response to competition between ejaculates for sperm storage and paternity. (Photo by D. Monteyne and D. Perez-Morga)

and has more generally been reported for a substantial number of nonsocial insects.

Ejaculates not only contain sperm but also complex mixtures of glandular secretions, which are typically referred to as seminal fluid or seminal plasma. Their molecular composition and functioning have been studied in detail in some ants and bees [5] and provide solid evidence that these secretions also contain the molecular agents of sperm competition [11]. In honey bees and leafcutting ants, seminal fluid proteins are capable of recognizing and killing sperm of rival males, a phenomenon known as sperm incapacitation (Fig. 2). At the molecular level, sperm competition seems to be driven by the presence of several proteases in the seminal fluid of the leaf-cutter ant *Atta colombica*, as their degradation or inhibition coincides with the loss of seminal fluid to incapacitate rival sperm [12]. Because these molecules are under intense sexual selection, they evolved much faster in the polyandrous fungus-growing ants compared to monandrous species. Interestingly, *A. colombica* queens secret their own sets of proteases to the ejaculates present in their sexual tract that specifically target the hostile seminal fluid proteins and degrade them, thereby terminating sperm incapacitation among rival males. This example nicely illustrates the complexity of reproductive conflicts and the challenges to experimentally separate male-driven sperm competition from female cryptic choice. Seminal fluid components seem also able to reduce the level of sperm competition by manipulating female mating behavior. In the bumble bee *Bombus terrestris*, males transfer a mating plug to females that acts as an anti-aphrodisiac and reduces the queen's willingness to mate again [6]. In *A. mellifera*, seminal fluid components are able to trigger gene expression changes in the queen's brain that target her visual perception, which in turn alters her mating flight behavior. Queens exposed to seminal fluid leave their hives earlier and face a higher risk of failure not returning to their hives compared to queens not exposed to seminal fluid [15].

In conclusion, sperm competition is a widespread phenomenon in animals and a major determinant of male fitness, but it remains poorly investigated in social insects despite its potential implications for paternity and worker relatedness. Recent work has confirmed the presence of sperm competition in a few species of ants and bees. These studies developed the necessary theoretical and methodological approaches that can now also be used for the study of sperm competition in other species. Such future studies will be especially useful in understanding the importance and roles of sperm competition in species from several

Sperm Competition, Fig. 2 Queen of the leaf-cutter ant *Atta colombica*. Males of this species compete for limited sperm storage space in the queen's reproductive tract and maximize their storage success by reducing the viability of sperm in rival ejaculates. These males have been intensively studied to unravel the molecular basis of sperm competition, confirming that seminal fluid proteins transferred to the queen as part of the ejaculate are responsible for such sperm incapacitation. However, queens target hostile male proteins and inactivate them to avoid any negative impact on their lifetime fecundity

clades. Substantially more work will be required to analyze the molecular basis and mechanisms of sperm competition where it exists in social insects, such as the basis of discrimination between self and nonself that must be present on the proteomic level to reduce sperm viability in rival ejaculates. It is not too much to think that such new knowledge could in time inform the development of novel management tools for social insect pests.

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