



Seminal fluid mediates ejaculate competition in social insects

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Published in:
Science

DOI:
[10.1126/science.1184709](https://doi.org/10.1126/science.1184709)

Publication date:
2010

Document version
Early version, also known as pre-print

Citation for published version (APA):
Den Boer, S. P. A., Baer, B., & Boomsma, J. J. (2010). Seminal fluid mediates ejaculate competition in social insects. *Science*, 327(5972), 1506-1509. <https://doi.org/10.1126/science.1184709>

The implication of our results for dynamic combinatorial chemistry is that this technique need not be limited to exploring the thermodynamic minima of molecular networks; kinetic control can dominate, provided that the noncovalent interactions are sufficiently strong and/or numerous. Our results further show that it is possible to obtain kinetic products from an assembly process where all the individual steps (covalent disulfide exchange and noncovalent peptide-peptide interactions) are reversible. Such a transition from thermodynamically controlled self-assembly to kinetic control must have been an important step in the origin of life, as life is far from equilibrium (35). Finally, our approach represents a promising method for the discovery of self-synthesizing materials in general and noncovalent polymers in particular (36).

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Supporting Online Material

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Materials and Methods

Figs. S1 to S12

References

1 October 2009; accepted 10 February 2010

10.1126/science.1182767

Seminal Fluid Mediates Ejaculate Competition in Social Insects

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Queens of ants and bees normally obtain a lifetime supply of sperm on a single day of sexual activity, and sperm competition is expected to occur in lineages where queens receive sperm from multiple males. We compared singly mated (monandrous) and multiply mated (polyandrous) sister groups of ants and bees and show that seminal fluid of polyandrous species has a more positive effect on the survival of a male's own sperm than on other males' sperm. This difference was not observed in the monandrous species, suggesting that incapacitation of competing sperm may have independently evolved in both bees and ants. In *Atta* leafcutter ants, the negative effect of the seminal fluid of other males was negated by secretion from the queen sperm-storage organ, suggesting that queens may control ejaculate competition after sperm storage.

Much sexual selection in polyandrous species occurs after mating in the form of sperm competition and cryptic female choice (1–3). In most animals, males seek additional mates to increase the number of their offspring, and females may remate to gain direct or indirect benefits to promote offspring

quality [e.g., (1–5)]. The eusocial ants, bees, wasps, and termites, in which only relatively few individuals have the opportunity to mate, are exceptions, because they evolved from strictly monogamous ancestors (6, 7). Newly eclosed queens of ants, bees, and wasps are receptive for mating during a very brief period of time (a few hours to a few days) and never remate (7, 8). Whereas queens from basal lineages store only a single ejaculate, obligate multiple queen-mating has evolved secondarily in honeybees, vespine wasps, leafcutter ants, army ants, harvester ants, and a few minor taxa (6, 7, 9). Thus, opportunities for postcopulatory sexual conflict have repeatedly emerged and may have induced convergent adaptive responses.

The absence of remating implies that ejaculates from multiple males coexist within a queen's sperm storage organ (spermatheca) throughout her life (7, 10). This situation is likely to have undergone selection for prudent mutual exploitation among partners, similar to mutualisms characterized by lifetime commitment (11, 12). Ejaculate competition might occur shortly after multiple insemination, if it has no major negative effects on queen health and longevity (10, 13) and leaves sufficient high-quality sperm for her to realize her lifetime reproductive potential. However, selection is expected to act against antagonistic interactions between ejaculates after sperm storage, because a female's reproductive life span ultimately depends on her ability to fertilize eggs from this nonrenewable stock of sperm (14).

Queens of *Atta* leafcutter ants use few sperm to fertilize each egg, consistent with a correlation between lifetime reproductive success and sperm-storage limitations (15). This implies that selection on sperm viability should be strong and that both the male seminal fluid and queen spermathecal fluid are necessary for reproductive success. Male accessory gland (AG) secretion confers a positive effect on sperm survival, even in very small quantities, in leafcutter ants (16) and honeybees (17), and the spermathecal fluid of honeybee queens also positively influences the viability of stored sperm (17).

We used an *in vitro* sperm survival assay (16–18) to test the effects of own AG secretion, AG secretion of other males, and queen

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spermathecal fluid on sperm survival in two species of corbiculate bees and three species of fungus-growing ants. This assay (18) provides relative sperm survival data that can be directly compared within experiments, but does not allow accurate comparisons of absolute sperm survival percentages across species, because sperm and seminal fluid contributions may vary across natural ejaculates (19).

Our choice of species exploited the sharp evolutionary transition shown by both the corbiculate bees and the fungus-growing ants from exclusive single mating of queens, i.e., storing sperm from a single ejaculate (*Bombus terrestris* bumblebees and *Trachymyrmex cf. zeteki* ants), to multiple mating, i.e., queens storing sperm from multiple males with which they mate in quick succession (*Apis mellifera* honeybees and *Atta colombica* and *Acromyrmex echinator* leafcutter ants) (6, 20). We found that providing sperm with AG secretion from the same male significantly increased sperm survival in all five species (Fig. 1), indicating that sperm is consistently protected by the quantities of AG secretion that we used in our assays. The absolute sperm survival values are almost certainly underestimates for sperm viability in natural ejaculates, because the Hayes saline buffer used does not nourish sperm, so that higher AG concentrations may be needed to reach the close to 100% *in vitro* sperm survival that can be achieved with this assay (16).

We next investigated whether the AG secretion of other conspecific males would be equally effective in enhancing sperm survival (18). We expected that AG secretions might be at least partially hostile to other males' sperm in the polyandrous species, but that no such effects should occur in their monandrous sister groups where ejaculates never interact *in vivo*. We used generalized estimating equations, nesting species within mating systems and using individuals as repeated measures (18), to compare the effects of AG secretions from a focal male, brothers of the focal male, and unrelated males on sperm survival. We found significant effects of mating system (polyandrous versus monandrous, $\chi^2 = 22.33$, $df = 1$, $P < 0.001$) and treatment (AG origin, $\chi^2 = 19.17$, $df = 2$, $P < 0.001$). The overall mating system difference may not be biologically meaningful because the absolute sperm survival percentages across species (nested within mating system) are not directly comparable. However, a significant interaction between mating system and treatment ($\chi^2 = 18.62$, $df = 2$, $P < 0.001$) indicated that sperm exposed to alien seminal fluid showed reduced levels of sperm survival in polyandrous species, but not in monandrous species (Fig. 2). This was confirmed by a rerun of the analysis for the monandrous species separately, where no significant effect of treatment could be detected ($\chi^2 = 2.13$, $df = 2$, $P = 0.346$ for *Bombus* and $\chi^2 = 0.02$, $df = 1$, $P = 0.883$ for *Trachymyrmex*). The origin of nonself

Fig. 1. Positive effects of male AG secretion on sperm survival across three species of fungus-growing ants (*Trachymyrmex cf. zeteki*, *Acromyrmex echinator*, *Atta colombica*), a bumblebee (*Bombus terrestris*), and a honeybee (*Apis mellifera*). The upper five charts show the absolute sperm viability values in the control treatments with Hayes saline (left) and the AG supplementations (right) that produced the AG/control survival ratios in the lower panel. The data for *A. colombica* and *A. mellifera* are from previous studies (15, 16), whereas those for the other three species were collected in the present study. The slope of the regression in the lower panel ($y = 0.824x + 0.784$; $r^2 = 0.876$; $P = 0.019$) is not significantly different from 1 (i.e., approximately parallel to the diagonal; 95% confidence interval slope: 0.254–1.395). The intercept of the regression is significantly different from 1 (zero after log-transformation: $t_3 = 7.196$; $P = 0.006$), indicating that the AG treatment had a consistently positive effect relative to control exposure to Hayes saline. The inset shows the male AGs and accessory testes (ATs) of a representative species (*B. terrestris*) as they were dissected. All bars are SEM.

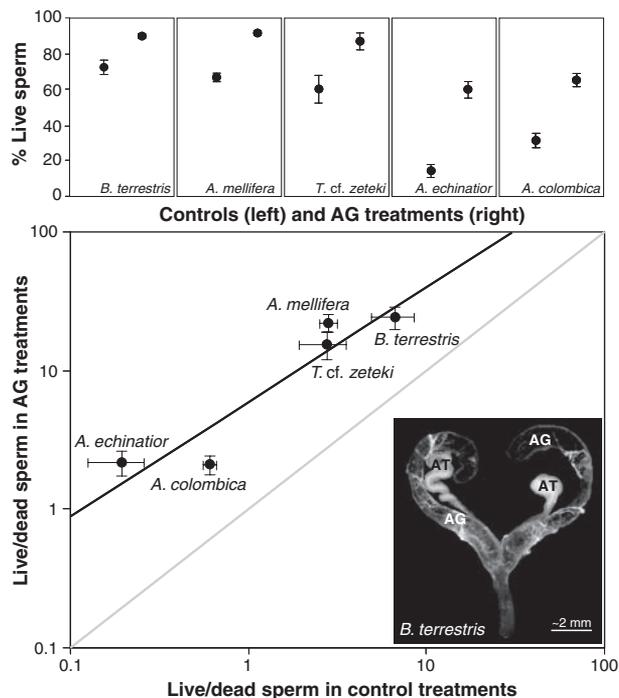
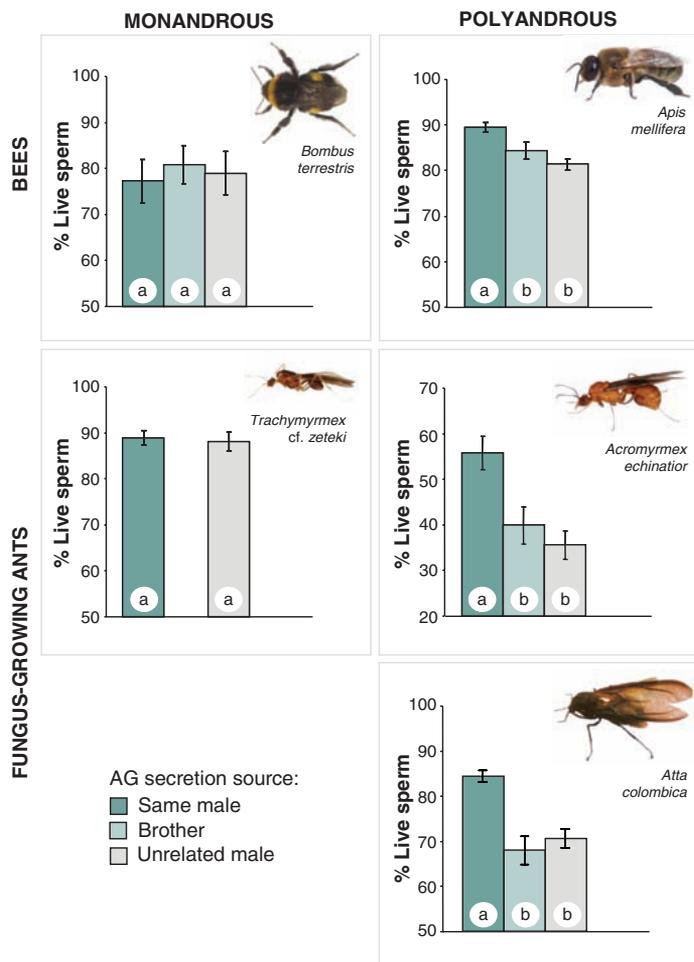


Fig. 2. The effect of own, related (brother), and unrelated male AG secretion on sperm survival (mean \pm SEM) in the monandrous bumble bee *B. terrestris* and fungus-growing ant *Trachymyrmex cf. zeteki*, and the polyandrous honeybee *A. mellifera* and fungus-growing ants *A. echinator* and *A. colombica*. Photos of males are given in the panels. The brother treatment could not be performed for *Trachymyrmex cf. zeteki* (18). Those bars labeled with different letters (a or b) differ significantly (all $P < 0.001$), whereas those with the same label do not (all $P > 0.1$).



AG secretion, a brother or an unrelated male, did not differentially affect sperm survival ($\chi^2 = 2.44$, $df = 1$, $P = 0.118$ for *Apis*; $\chi^2 = 1.16$, $df = 1$, $P = 0.282$ for *Acromyrmex*; and $\chi^2 = 0.25$, $df = 1$, $P = 0.616$ for *Atta*). This suggests that the negative effects on sperm survival are triggered by a self versus nonself recognition process.

These results are consistent with some form of ejaculate competition in polyandrous honeybees and leafcutter ants, and suggest that AG secretions contain both compounds that are favorable for sperm survival (Fig. 1) and substances that may incapacitate sperm of competing males (Fig. 2). To assess the combined effect of these putative forces on sperm survival, we repeated the second experiment for the three polyandrous species (but without the brother treatment), while adding an equal mix of own and alien AG secretion as an additional treatment (18) (Fig. 3). Overall treatment effects were significant in all cases ($\chi^2 = 8.31$, $df = 2$, $P = 0.016$ for *Apis*; $\chi^2 = 7.26$, $df = 2$, $P = 0.027$ for *Acromyrmex*; and $\chi^2 = 10.82$, $df = 2$, $P = 0.005$ for *Atta*). However, own AG secretion does not appear to offset the negative effects of alien AG secretion, as pure alien and mixed AG treatments always resulted in similar but reduced sperm survival compared to the pure own AG treatment (detailed statistics are in the legend to Fig. 3).

After 30 min of exposure to alien AG secretion, sperm survival was reduced by 6.6% in *Apis*, 14.7% in *Atta*, and 18.0% in *Acromyrmex* relative to treatment with own AG secretion (Fig. 2). However, the residence time of inseminated honeybee sperm in the bursa copulatrix and lateral oviducts before being stored or discarded is 40 to 90 hours (21), whereas ejaculates of *A. colombica* are probably transferred to the spermatheca almost immediately

(22). Because rival ejaculates of *Atta* have less time to compete before being stored, there may be more damage per minute of exposure. This is consistent with *A. mellifera* queens expelling some 95% of the sperm provided by 10 to 20 matings (21), whereas *A. colombica* queens store essentially all sperm provided by 2 to 5 matings (22, 23). Typical sperm prestorage time in *A. echinator* is unknown, but is up to 5 hours in *A. versicolor*, where queens appear to store around 10% of inseminated sperm (24).

Because every sperm cell provides a potential fitness benefit after the sperm storage process is complete (14, 15), we expected queens to either prevent hostile AG secretion from being stored, or to neutralize antagonistic interactions between ejaculates shortly after they enter the spermatheca. We tested this by collecting virgin *A. colombica* queens and artificially inseminating them with Hayes solution to obtain spermathecal fluid suspensions (18). Exposure of freshly dissected sperm from male accessory testes to mixtures of spermathecal fluid and seminal fluid of another male showed that spermathecal fluid maintains sperm survival at normal levels (Fig. 4). Thus, we conclude that spermathecal fluid has the potential to prevent the negative effects of AG secretion on alien sperm.

These results reveal consistent postmating sexual selection and sexual conflict in eusocial insects. They complement work elucidating why multiple queen-mating evolved (9, 25–27) and show that ants and bees are suitable models for testing sperm competition theory. This is because males have no influence on the fate of ejaculates after mating, and sperm storage has two distinct phases: a provisional one, varying across species from seconds to a few days, during which sperm competition may serve

female interests; and a much longer permanent phase during which queens are expected to maximize the survival of all sperm. It therefore seems reasonable to expect that selection on male traits that enhance ejaculate competition is proportional to the duration of prestorage ejaculate interaction and to the ratio of inseminated versus long-term-stored sperm.

Antagonistic effects similar to those reported here may have arisen in other eusocial Hymenoptera that have evolved from single to multiple queen-mating (6, 25–27), and spermathecal fluids that neutralize aggressive male AG compounds (compare to Fig. 4) may also be found in dwarf honeybees where sperm is directly transferred to the spermatheca (28), as in *Atta* (22). However, although phenotypic expressions of these sexual conflicts might be similar, their independent evolutionary origins suggest that the genes and pathways involved are different (7). Clarifying such molecular mechanisms is now feasible, as recent studies have shown that honeybee spermathecal proteomes differ appreciably from male AG proteomes (17, 29, 30), consistent with functional differences connected with operating when sperm is in a state of long-term dormancy or metabolically active.

Fig. 3. Own AG secretion does not counteract the negative effects on sperm survival (mean \pm SEM) of the AG secretion of other males in polyandrous ants and bees: *A. mellifera*, *A. echinator*, and *A. colombica*. Overall treatment effects were significant in all three cases (see text). Specific contrasts were not significant for pure alien AG secretion versus a mixture of own and alien AG secretion ($\chi^2 = 0.00$, $df = 1$, $P = 0.964$ for *Apis*; $\chi^2 = 0.05$, $df = 1$, $P = 0.823$ for *Acromyrmex*; and $\chi^2 = 0.40$, $df = 1$, $P = 0.529$ for *Atta*). However, contrasts were significant for pure own versus pure alien AG secretion ($\chi^2 = 4.86$, $df = 1$, $P = 0.028$ for *Apis*; $\chi^2 = 6.75$, $df = 1$, $P = 0.009$ for *Acromyrmex*; and $\chi^2 = 9.25$, $df = 1$, $P = 0.002$ for *Atta*), and for pure own versus a mixture of own and alien AG secretion ($\chi^2 = 6.58$, $df = 1$, $P = 0.010$ for *Apis*; $\chi^2 = 4.62$, $df = 1$, $P = 0.032$ for *Acromyrmex*; and $\chi^2 = 9.89$, $df = 1$, $P = 0.002$ for *Atta*).

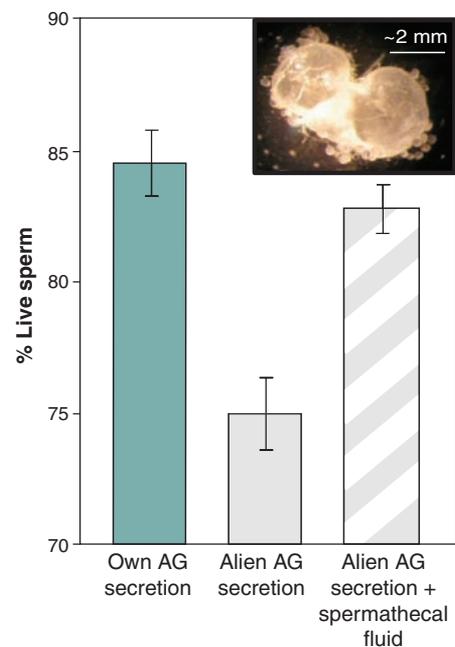
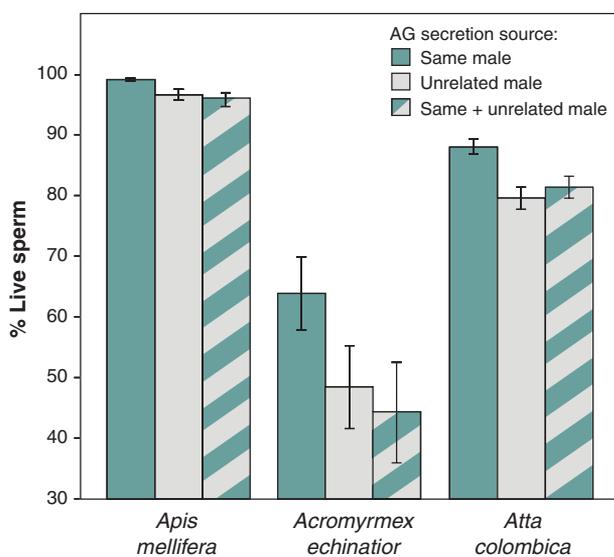


Fig. 4. Spermathecal fluid eliminates the negative effects of other males' AG secretions on sperm survival in *A. colombica* (mean \pm SEM). The inset shows a dissected spermatheca 1 hour after having been artificially inseminated with Hayes saline. The first two bars differ significantly ($\chi^2 = 15.04$, $df = 1$, $P < 0.001$), as do the second and third bar ($\chi^2 = 13.59$, $df = 1$, $P < 0.001$), but the bar on the right does not differ significantly from the bar toward the left ($\chi^2 = 2.38$, $df = 1$, $P = 0.123$).

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Supporting Online Material

www.sciencemag.org/cgi/content/full/327/5972/1506/DC1

Materials and Methods

References

16 November 2009; accepted 17 February 2010

10.1126/science.1184709

Patterns of Diversity in Marine Phytoplankton

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Spatial diversity gradients are a pervasive feature of life on Earth. We examined a global ocean circulation, biogeochemistry, and ecosystem model that indicated a decrease in phytoplankton diversity with increasing latitude, consistent with observations of many marine and terrestrial taxa. In the modeled subpolar oceans, seasonal variability of the environment led to competitive exclusion of phytoplankton with slower growth rates and lower diversity. The relatively weak seasonality of the stable subtropical and tropical oceans in the global model enabled long exclusion time scales and prolonged coexistence of multiple phytoplankton with comparable fitness. Superimposed on the decline in diversity seen from equator to pole were “hot spots” of enhanced diversity in some regions of energetic ocean circulation, which reflected lateral dispersal.

In both marine and terrestrial environments, many taxa exhibit a decline in species diversity with increasing latitude (1, 2), and this pattern has important implications for ecosystem structure and function (3). The extent to which and why marine phytoplankton may follow such patterns is not yet clear, although it has been argued that the biogeography of microbes is governed by a similar set of processes as for macroorganisms (4). There is some evidence of latitudinal diversity gradients among certain taxa of marine microbes, including bacterioplankton (5, 6) and coccolithophorids (7, 8), although the generality

of these patterns, particularly in the open ocean, is, as yet, equivocal (9, 10).

In a recent study, a three-dimensional and time-varying global ocean circulation, biogeochemistry, and ecosystem model was initialized with a relatively large number (78) of virtual phytoplankton types whose traits were assigned stochastically from plausible ranges of possibilities (10–12). The modeled phytoplankton communities “self assembled” according to the relative fitness of the phytoplankton types in the regionally and seasonally varying resource and predatory environment. The emergent phytoplankton populations captured the observed large-scale oceanic patterns in the distribution of phytoplankton biomass and community structure, including the observed niche differentiation among ecotypes of the cyanobacterium *Prochlorococcus* in the Atlantic Ocean (11).

Here, we have studied an ensemble of 10 integrations of the global model, each member having a different, stochastically seeded selection of phytoplankton types, to examine and interpret

the emergent patterns of phytoplankton diversity. In each of the solutions, after a decade of integration, a dozen or so phytoplankton types account for more than 99% of the total global phytoplankton biomass. Others persist at low abundance or with limited geographic distribution, and some decline toward virtual extinction. Fast-growing “opportunistic” phytoplankton tend to dominate the biomass of the variable high latitudes, whereas “gleaners” (those best able to survive on minimal resources) dominate the stable, low-latitude seas (12, 13). There is also a degree of local coexistence among phytoplankton types. On an annual, vertically averaged basis, the phytoplankton diversity in the euphotic zone (here assumed to be 0- to 260-m depth) is lower in the polar and subpolar oceans and higher in tropical and subtropical latitudes (Fig. 1A). This meridional gradient is clearly seen in the zonally averaged view (Fig. 1B) and is consistent with numerous observations of marine and terrestrial ecosystems (1, 2), including the sparse observations of marine microbial diversity (5–8). Superimposed on the model’s meridional gradient are “hot spots” of highest diversity, which are generally associated with regions of energetic circulation such as the western boundary currents. The Atlantic Ocean hot spots appear to be consistent with observations of increased diatom diversity near the North African and South American coasts (8).

The mechanisms for maintaining the diversity of life on Earth have long interested ecologists (14, 15), and the explanations for the meridional diversity gradient have been classified as historical, evolutionary, or ecological in nature (6, 16). Historical explanations invoke events and changes in Earth history, such as Milankovitch cycles, in setting current species diversity. Evolutionary explanations examine the rates of speciation and extinction and their balance through time (17, 18). These processes are not resolved in

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