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The male has done his work — the male may go

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Perennial social insects are famous for the extraordinary longevity of their queens. While the lifespan of termite kings matches those of queens, males of social Hymenoptera are usually considered to die after one or a few copulations. While this is true in species with highly synchronized nuptial flights, in others males mate over much longer periods. Male longevity is not correlated with the life span of queens but appears to be adapted to mating opportunities. This is demonstrated by the extreme life span of *Cardiocondyla* ant males, which monopolize mating with virgin queens over many months. *Cardiocondyla* offers the opportunity to investigate why male longevity varies even among closely related taxa and how male age affects sperm and offspring quality.

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Introduction

Social insects are ideal models for investigations about why animals age and why they do so at different speeds. The lifespan of female reproductives (queens) of ants, honeybees, and termites is supposedly many times longer than that of solitary insects. Absolute longevities become less exceptional when the duration of larval development is taken into account — then even the ephemeral mayflies may live for three years [1], and periodical cicadas [2] and wood-boring beetles [3] outlive most ant and termite queens. Nevertheless, the reproductive lifespan of queens remains unrivaled [[4], this issue]. In addition, queens live longer than their non-reproductive nestmates, which opens questions about the epigenetic regulation of aging [this issue]. Furthermore, both mating and reproduction positively affect the lifespan of queens, and the fecundity/longevity trade-off typical for multicellular organisms appears to be absent [[5,6•], Figure 1].

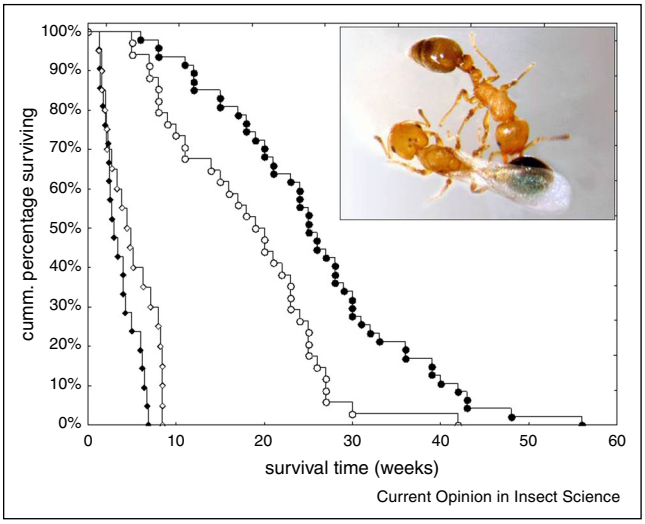
Obtaining data on social insect longevity is difficult, and solid life history data, such as age-specific mortality rates or fecundities of queens are widely lacking. Even less data exists for males. My review aims to compile the little that is known about lifespans and the evolutionary plasticity of aging in males of social insects, with a focus on social Hymenoptera. Furthermore, I intend to show that the lifespan of male ants, bees, and wasps does not simply reflect the longevity of conspecific queens but is adapted to the duration of the time span during which mating partners are available.

Males: unsocial, unobtrusive, and perishable?

In termites, male reproductives (kings) form a stable pair-bond with the queen(s). Because of their lifelong spermatogenesis, kings can continuously transfer sperm to the queen and their lifespans appears to match those of their cohabitant [7••]. This reflects the evolution of termites from roachlike ancestors with biparental care (e.g., [8•]). In contrast, social Hymenoptera evolved from solitary species with exclusively maternal care and no contribution from the male other than sperm (e.g., [8•]. Unlike the promiscuous macho males that feature in textbooks about sexual selection, the males of ants, bees, and wasps appear to be sissies: short-lived, ill-equipped for fighting and sexually not very potent [9••]. With one notable exception (see below; [10]), males of social Hymenoptera start their sexual life with a fixed amount of sperm sufficient for only one or a few inseminations, because their testes degenerate before or shortly after emergence [11,12]. As in similarly sperm-limited, 'prospermatogenic' parasitoid wasps [13], males that cannot replenish their sperm supplies expend it shortly after eclosion and there is no need for much investment in self-maintenance [14•]. In particular the males of ants are often brittle compared to queens or workers: they may have shorter telomeres [15] and a reduced immune function [16,17,18]. It has been suggested that haploid males are more sensitive because of the lack of a heterozygote advantage [19], but comparisons among males with different reproductive life histories did not support a fundamental role for ploidy [20].

While the pre-reproductive lifespan of males may span more than one year in boreal and subboreal *Camponotus* ants, where adult sexuals hibernate before mating [21], adult males of many ants and honeybees live only for a few days and die during or soon after copulation. They are 'flying sperm-bearing missiles constructed only for the instant of contact and ejaculation' [22] — as epitomized by the title of this review, freely adapted from Friedrich Schiller's drama *Fiesco*. This, however, is not true for all Hymenoptera: males of some species live for several

Figure 1



Survival rates of males (diamonds) and queens (circles) of the ant *Cardiocondyla obscurior*. The color of the symbols indicates previous mating activity: black circles (●) indicate queens that had mated once, open circles (○) virgin queens (data from [5]); black diamonds (◆) indicate males that had access to ten female sexuals, and open diamonds (◇) males that had access to only three or female sexuals (data from A. Schrempf, M. Adam, and S. Lempa). The insert shows a winged female sexual and a wingless fighter male (photo by A. Schrempf).

weeks (e.g., [23•,24,25]) even though they rarely reach the lifespan of female reproductives.

Though data on the lifespan of both sexes are available for only a few taxa, a quick comparison across the Hymenoptera suggests that male lifespan does not simply mirror variation in queen lifespan. For example, the average longevities of female reproductives and males of the paper wasp *Polistes lanio* were 7 months and 10 days, respectively [26]. Queens and males of *Ectatomma ruidum* ants lived on average for 8.8 years and 7 days, those of *Atta* leaf cutter ants for more than 10 years and 3 days [25,27], and those of Southeast Asian *Cardiocondyla* ants both reached maximal lifespans of many months [28]. Instead it appears that male longevity depends on the duration of the time span during which female sexuals are available.

One-shot drones: suicidal mating and male aggregations

In honey bees [29], several stingless bees [30,31], and a few species of queenless ants (*Diacamma* [32], *Dinoponera* [33]), male mating is suicidal: the genital appendages of males remain stuck in the female genital opening. It has been debated whether this might be a strategy of males to prevent queens from re-mating, but at least in honey bees, the attached genitals do not impair multiple mating [34]. Before their single mating, honeybee males may live in the hive for several weeks or months. In stingless bees, they leave the nest about 2–3 weeks after eclosion and congregate for a few additional days or weeks in front of nests with female sexuals, waiting for their chance to mate and die [35].

In the highly synchronized nuptial flights (male aggregation syndrome) of some ants and stingless bees, competition for access to female sexuals may be intense. Large body size may be advantageous during scramble competition [36], but the huge number of competitors and the short duration of the mating period make it difficult to monopolize female sexuals. Overt male–male aggression is therefore not favored by selection. Like in species with suicidal mating, males in such species often die after a few days of hectic sexual activity. In the field, males may survive for several days and wait for additional mating opportunities [37••,38], but most quickly fall victim to predation (e.g., [39,40]), starvation, or desiccation.

The lifespan and reproductive performance of both suicidally mating and one-shot drones presumably reflect the low probability of males having a second chance to mate when female sexuals are available only during a very short period of time and operational sex ratios are highly male-biased [9••].

Territory defenders and patrollers

In many ants, wasps, and bumblebees, receptive female sexuals are available over a longer period of time and scattered over a larger space. In consequence, males are selected to have longer reproductive lifespans than when mating occurs synchronously during one or a few days. Female sexuals may be present year-round in tropical ants [41,42] and over several weeks in many temperate Hymenoptera [43]. Individual males may leave their natal nest to search for and copulate with mating partners for several days or even weeks [25,37••]. Though still finite, their sperm stores often suffice for multiple copulations — the record for ants other than *Cardiocondyla* (see below) is 10 in *Harpagoxenus sublaevis* [44].

Multiple mating over a prolonged period appears to be common in bumble bees and wasps [9••,45,46]. Males of the polistine wasp *Mischocyttarus mastigophorus* search for female sexuals for several weeks during the day, but stay overnight in their natal nests, where they feed on nectar and insect prey provided by workers [47]. In other species, males are not allowed to return after they have left their colony (e.g., [9••,35]). They defend sites that likely are visited by females or patrol their flight routes [24,48,49] and appear capable of feeding and successfully avoiding predation. Interestingly, in *Polistes lanio* [50] and the ant *Neoponera inversa* (own observations), males that were captured by hand bent their abdomen like stinging females — this might effectively discourage naïve predators. Male paper wasps and bumble bees may survive for several weeks without support from their workers