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Current Opinion in Insect Science

The male has done his work — the male may go

Jürgen Heinze

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.

Address
LS Zoologie/Evolutionsbiologie, Universität Regensburg,
93040 Regensburg, Germany

Corresponding author: Heinze, Jürgen (juergen.heinze@ur.de)

Current Opinion in Insect Science 2016, **16**:22–27

This review comes from a themed issue on **Social insects**

Edited by **Judith Korb**

http://dx.doi.org/10.1016/j.cois.2016.05.005

2214-5745/Published by Elsevier Inc.

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].

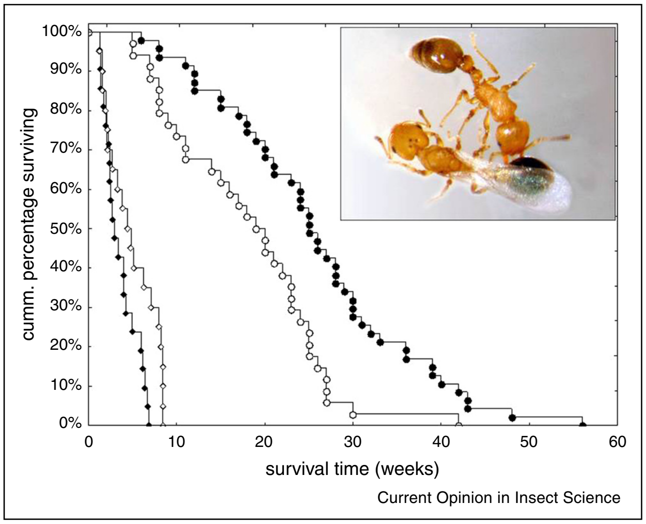
Obtaining data on social insect longevity is difficult, and solid life history data, such as age-specific mortality rates or fecundities of queens are widely lacking. Even less data exists for males. My review aims to compile the little that is known about lifespans and the evolutionary plasticity of 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

[24,46,51], and when fed in the laboratory, male bullet ants, *Paraponera clavata*, lived for almost four months [25]. How sperm depletion affects their residual lifespan is unknown, but males might die earlier when their sperm supply is exhausted.

Intranidal mating and the evolution of tough guys

Sexuals of many social bees and wasps occasionally mate in the vicinity of the nest or on its surface (e.g., [23•]), but mating in the safety of the nest (intranidal mating) is mostly restricted to ants. Males enter alien nests (e.g., [52]) or mate in their natal nest with related female sexuals. In both cases, males can in principle mate with multiple female sexuals over a prolonged period of time except when intranidal mating is suicidal [32,33].

In monogynous species with intranidal mating, local mate competition selects for highly female-biased sex ratios. To inseminate all their sisters, males need an enormous amount of sperm, as exemplified by the pupa-like males of the parasitic ant *Anergates atratulus*, whose abdomens are completely full of sperm [53]. In facultatively polygynous *Hypoponera*, intranidal mating has led to the evolution of male winglessness and particular mate securing tactics, such as mate guarding [54,53,54,55,56,57] and lethal fighting [58,59]. This is accompanied by a prolonged lifespan: wingless males of *Hypoponera opacior* mate with up to eight female sexuals and live for up to 33 days [57]. Despite of the increased and prolonged reproductive activity, histological examinations of males of *Hypoponera* and also other species with intranidal copulation did not give any evidence for sperm replenishment [53].

The only males of social Hymenoptera that have re-evolved continuous spermatogenesis are the wingless males of *Cardiocondyla* [[10]; Figure 1], perhaps as an adaptation to intranidal mating and the year-round availability of female sexuals in tropical environments. They engage in lethal fighting with their rivals, and successful males are capable to monopolize mating with freshly eclosed female sexuals even for months. Individual males can successfully inseminate more than 80 female sexuals [60], a record in mating frequency among males of social Hymenoptera. Surprisingly, the winged males of several *Cardiocondyla* species are also capable of large numbers of copulations, even though their spermatogenesis ceases a few days after adult emergence. Winged males of *Cardiocondyla emeryi* can achieve 40 or more matings probably because they transfer only around 1000 sperm cells during each copulation [60].

Wingless males of most *Cardiocondyla* species have reproductive lives of about a month (Figure 1) with one exceptional male being sexually active until its death at the methuselahic age of 194 days [61]. Matching their varying degree of sperm limitation, winged males live typically shorter than wingless males (Wilcoxon matched pairs test with published medians or means from six species with male polyphenism, median wingless 27, median winged 19.5 days, $W = 15$, $P = 0.062$), even though a few reached lifespans of more than 50 days [60]. With a mean longevity of 210 days and extreme lifespans of more than one year, the wingless males of an undescribed Southeast Asian *Cardiocondyla* have the longest reproductive lifespan known in social Hymenoptera [28]. Their longevity comes close to that of the species' queens, which, as is typical for tropical *Cardiocondyla*, also is about one year. Unlike termite kings [7••], long-lived *Cardiocondyla* males do not repeatedly copulate with the queen but rather inseminate all her daughters, though in several species males can inseminate their virgin mother and thus help her to found a new colony [62]. The proximate factors underlying the extended spermatogenesis and lifespan of wingless males are presently not known, but transcriptome comparisons of larvae indicate that the ontogeny of wingless males is fundamentally different from that of winged males and the female castes [63•]. Furthermore, the large variation in average lifespans among different species suggests that environmental factors, in particular seasonality and the robustness of nest sites, may drive the evolution of male longevity.

The fecundity/longevity tradeoff in male Hymenoptera: live hard, die young?

While the almost fundamental life history trade-off of fecundity versus longevity is relaxed, absent, or even reversed in the queens of social insects [this issue], there is little evidence that this may also be the case in males. Many hymenopteran males follow a strategy of 'live hard, die young' [20,46]. In species with suicidal mating, early mating invariably reduces the lifespan of a male, but whether mating and sperm depletion also shorten the lifespan of males that are capable of multiple copulations is not known. Males of solitary parasitoid wasps have been observed to survive for several weeks after having exhausted their sperm supplies [64]. Such sperm-depleted males may continue to copulate with their mating partners and in this way decrease the females' capability of storing sperm from other males [65]. Whether males of social Hymenoptera might similarly benefit from survival after having exhausted their limited sperm supplies remains unknown.

Male lifespan and mating frequency were positively associated in wingless males of *Hypoponera opacior*, probably because longer-lived males had more mating opportunities and could eliminate pupal rivals. Excluding males that never mated removed the significance of this positive association [57]. In *C. obscurior*, wingless males that had access to no or few female sexuals reached higher maximal lifespans than males with access to many female sexuals, indicating a trade-off between reproduction and longevity (S. Lempa, M. Fuessl, and A. Schrempf, unpublished; Figure 1).

The optimal age of a hymenopteran father

Sperm quality may vary with male age [66••], and this has consequences for male and sperm competitiveness and offspring viability (e.g., [67]). In Hymenoptera with sperm-limited, but repeatedly mating males, females should avoid copulation with old males, because their exhausted sperm stores might lead to male-biased sex ratios among the offspring (e.g., [68]) and prevent successful colony founding. Concerning sperm quality and viability one might argue that the time between spermiogenesis and copulation is negligible compared to that between insemination and fertilization. Nevertheless, male age affects the speed and duration of copulations in bumblebees [51] and the total number of sperm cells and sperm viability [69,70,71,72]. In species with life-long sperm production, male age and the time since the last copulation might similarly affect sperm quality: at least sperm length appears to vary with age in *Cardiocondyla* males, but the consequences of this variation for sperm competition or fertilizing capability have not been studied. In choice experiments in *Cardiocondyla venustula*, queens appeared to be indifferent to male age (S. Jacobs, unpublished observation).

Conclusions

The different life expectancies of males of social insects exemplify that aging is not a mere consequence of the accumulation of damage but a trait that evolves. Male longevity is adapted to the duration of the time for which mating partners are available, and though hymenopteran males never reach the lifespan of termite males, they may occasionally survive for months. Our understanding of sexual selection in social insects [73••] is still far from complete. The diversity of male life histories suggests that there is more to discover about this 'neglected gender' [74]. The large lifespan variation in particular among closely related species of *Cardiocondyla* ants to explore the proximate and ultimate causes of the different paces of aging.

Acknowledgements

I thank J. Korb for inviting me to write a contribution about male Hymenoptera and DFG for support (He1623/38).

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