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Editorial overview: Social insects: aging and the re-shaping of the fecundity/longevity trade-off with sociality

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Judith Korb is a professor for Evolution and Ecology at the University of Freiburg, Germany. She is interested in understanding social evolution. Using termites as models, she is studying the causes and consequences of sociality. She is the speaker of the research unit 'Sociality and the reversal of the fecundity/longevity trade-off' recently funded by the German Science Foundation.

Most organisms age, but why and how is still debated. Within insect colonies, individuals vary in longevity despite sharing the same genetic background. Reproductives can live for decades while their non-reproducing counterparts often have a lifespan of a few months or even days only. This variation is even more strikingly given that reproduction in most organisms is associated with decreased lifespans (i.e., there is a fecundity/longevity trade-off). In this section issue, we review all aspects of aging with a focus on social insects. This issue reveals the promises that research on social insects offer to obtain fundamental insights into aging and fecundity. It also outlines current challenges as well as potential future avenues.

What is aging?

One speaks about aging in the context of certain products like wine or spirits. In this case, aging refers to the passing of time, which entails complex chemical reactions that modify the flavor of the respective product. In the context of living beings, aging also involves the passing of time, and it usually entails a progressive decline in motor and cognitive performance, and a loss of physiological functions, including fecundity [1,2]. Medawar [3] proposed a clear distinction between aging and senescence, the former referring only to the passing of time and the latter to the loss of body functions with time. In this section issue, aging and senescence are used interchangeably, implying a decline in body function with age.

Aging and the re-shaping of the fecundity/longevity trade-off with sociality

Most higher organisms age and a trade-off between longevity and fecundity exists. Social insects seem to be a major exception to this rule. Reproducing females (queens) of honeybees, ants and termites are well known for their long reproductive lifespans (e.g., up to 20 years for some ants and termites) [4]. By contrast, their non-reproducing counterparts, the workers and soldiers, live usually only in the magnitude of months or days, despite sharing the same genetic background [5]. While kings of termites have similar lifespans as queens, the males of social Hymenoptera are generally short-lived. However, the review by Heinze shows that male longevity varies substantially inter-specifically as well as intraspecifically and the causes for this are not well understood.

Facultatively social insects at the threshold of sociality provide an excellent opportunity to unravel the causes underlying the re-shaping of the fecundity/longevity trade-off with sociality. Séguret *et al.* review factors favoring sociality in such socially plastic Hymenoptera and summarize first data for underlying mechanisms. Toth *et al.* summarize scattered longevity data for Vespid wasps that differ in degree of sociality. These indicate that the longevity difference between castes increases with sociality.

In order to understand the lifespan changes with sociality two questions must be answered: Why do we age? What causes aging? These two questions reflect two complementary approaches for studying aging. The former tries to explain why senescence evolves (evolutionary, ultimate perspective), whereas the latter aims at uncovering mechanistic, proximate causes of senescence.

Why do we age?

Ultimately, one may expect strong selection against aging as natural selection favors traits that increase fitness. However, aging is omni-present. Evolutionary hypotheses regard senescence as an inevitable consequence of natural selection and constraints [6]. The force of natural selection generally declines with increasing age as fewer individuals remain alive due to the inevitability of extrinsic mortality (i.e., the rate of age-independent mortality due to, for instance, environmental hazards) [7]. Thus, the onset of aging should generally increase, and average intrinsic lifespan should decrease, as random extrinsic mortality (i.e., hazards) increases [8]. But note exceptions when extrinsic mortality is condition-dependent [9].

Based on this reasoning, three major aging theories were developed that are non-mutually exclusive: First, the '*mutation accumulation theory*' states that deleterious mutations with late expression can accumulate within a population [3]. Second, '*theory of antagonistic pleiotropy*' emphasis that pleiotropic alleles whose positive effects at young ages outweigh negative effects later in life are maintained in evolution [10]. Third, the '*disposable soma theory*' [11] regards aging as a consequence of allocation trade-offs between investment into soma versus germline. It suggests that delaying senescence has costs, and that the evolution of mechanisms that prevent or repair damage must balance potential benefits against these costs. Because of trade-offs in resource allocation, somatic cells and tissues should only be maintained to a level that will prevent premature decline (i.e., decline at an age when the organism still has a reasonable chance to reproduce) since more investment will be detrimental to other fitness-enhancing functions.

Kramer *et al.* review these theories and identify major limitations when applying them to social insects. It is still not understood why social insect queens live so long and why the fecundity/longevity trade-off is re-shaped with sociality. More targeted modeling approaches are suggested.

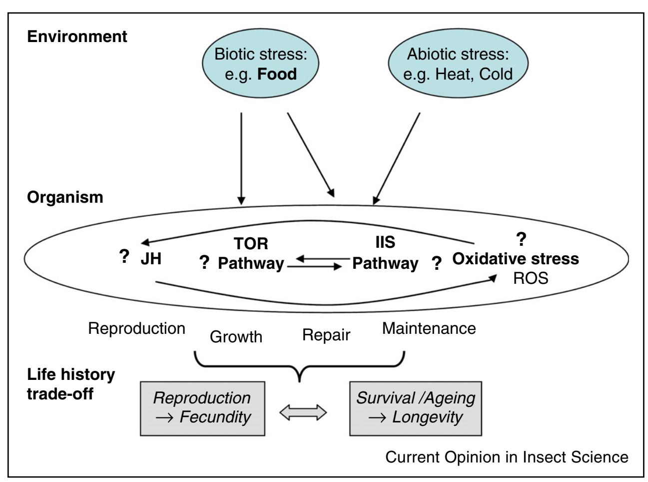
Focussing mainly on ant queens, Negroni *et al.* propose several life history parameters that may affect the fecundity/longevity trade-off. Specifically, two hypotheses are developed to explain why queens in single queen ant societies are longer-lived and have higher fecundities than multi-queen societies.

What causes aging?

Mechanisms underlying aging are intensively studied in model organisms. The interplay between growth, maintenance/repair and reproduction processes determine aging and fecundity. At the level of the organism, aging and fecundity seem to be the outcome of allocation trade-offs often reflected in hardwired molecular pathways (Figure 1).

De Verges and Nehring review evidence for functional decline in social insects with age, with mixed results. They contrast the free radical- with the hyperfunction theory of aging. The former sees aging as a consequence of damage accumulation via reactive oxygen species (ROS), whereas the latter attributes it to an excessive accumulation of biosynthesized molecules, which are produced due to a non stopping developmental program. De Verges and Nehring argue that both processes are not

Figure 1



Proximate mechanisms underlying aging and the fecundity/longevity trade-off. Growth, reproduction, repair and maintenance processes determine the life history traits aging/longevity and reproduction/fecundity. At the level of the organism, they seem to be the outcome of allocation trade-offs and complex mechanistic links between rather hard-wired molecular pathways (e.g., IIS, TOR, oxidative stress/ROS, JH). As direct sensors of environmental conditions the IIS and TOR pathways emerge as central components that interact with JH in regulating aging and the fecundity/longevity trade-off. For further information see text.