Social modulation of ageing in termites

Lin, Silu

DOI:
10.33612/diss.233551297

Chapter 5

Synthesis

5.1 How and why does sociality change ageing?

Molecular mechanisms underlying the remoulding of reproduction-maintenance trade-off by sociality

Being both long-lived and highly fecund, insect queens seem to confound the classic reproduction-maintenance trade-off that is common in solitary insects, but how this is connected with sociality on a molecular level is not well-understood yet. Recently, molecular networks that depict the reproduction-maintenance trade-off in insects has been proposed to study this phenomenon (Rodrigues & Flatt 2016; Korb *et al* 2021). These networks emphasise the role of the conserved nutrient-sensing IIS/TOR signalling pathways and the endocrine regulations on fecundity and longevity related genes. Hereafter, I refer to them as "trade-off genes". Rodrigues and Flatt (2016) propose that genes along the nutrient-sensing/endocrine/fecundity axis (the IIS-JH-Vg/YP circuit) may have been rewired in social insects. This theory has been used to explain the honey bee *Apis mellifera* queens' long life and high fecundity (Corona *et al.*, 2007), but it has not been tested in termites. In Chapter 2, we used the termite *C. secundus* to test this theory. We discovered that *C. secundus* queens are distinguished by a single module of co-expressed genes that comprises all components from the IIS-JH-Vg/YP circuit. Additionally, it includes many genes that are involved in chemical communications. This suggests that the IIS, JH, and Vg/YP are positively connected to each other in termite queens, just as in solitary insects (**Fig. 5.1**). This idea is further confirmed in another experiment in which lowered JH titres yielded largely negative effects on fecundity-related genes (Chapter 2). These findings imply that the rewiring of the IIS-JH-Vg/YP circuit did not account for the positive correlation between reproduction and maintenance in termites. The IIS-JH-Vg/YP circuit, on the other hand, is positively linked to genes involved in chemical communications (**Fig. 5.1**), providing the first substantial molecular evidence that the longevity-fecundity trade-off in social insects is linked to social communication. These findings provide a unique perspective on how sociality affects ageing on a molecular level.

Another possibility of how sociality might affect molecular mechanisms of ageing is via gene duplication, though this is just speculation at this point. In insect societies, different castes may experience contrasting selection pressures due to their distinct roles (Chau & Goodisman, 2017). For example, in Chapter 4, we show that selection on alleles controlling age-specific survival may be constantly high in reproductives but very low in workers for termites with high sociality (**Fig. S4.7**). Caste-biased gene expression in reaction to their corresponding selection pressures is one way to enable such phenotypic diversity. Gene duplication has been shown to facilitate caste-biased gene expression through sub-functionalisation and/or neo-functionalisation of genes in a termite *Reticulitermes speratus* (Shigenobu *et al.*, 2022), and Apoidean bees (Chau & Goodisman, 2017; Harpur & Smith, 2017). Particularly in termites *Zootermopsis nevadensis* and *Cryptotermes secundus*, vitellogenin, insulin receptor, juvenile hormone biosynthesis genes have expanded (Terrapon *et al*., 2014; Kremer *et al*., 2018; Harrison *et al*., 2018; Jongepier *et al*., 2018; Shigenobu *et al.*, 2022; Chapter 2 in this thesis). In *R. speratus*, genes related to chemical communication are duplicated and exhibit caste-biased expression (Shigenobu *et al.*, 2022). These duplicated genes are known to correlate with ageing (Rodrigues & Flatt 2016; Korb *et al* 2021; Chapter 2 in this thesis). Examining the impact of gene duplication in determining the effect of sociality on ageing might be an interesting direction for future research.

To summarize, sociality has the potential to reshape molecular mechanisms underlying the reproduction-maintenance trade-off by rewiring "trade-off genes", connecting "trade-off genes" to genes related to social communication, and enabling caste-biased gene expressions of the "trade-off genes" via gene duplication.

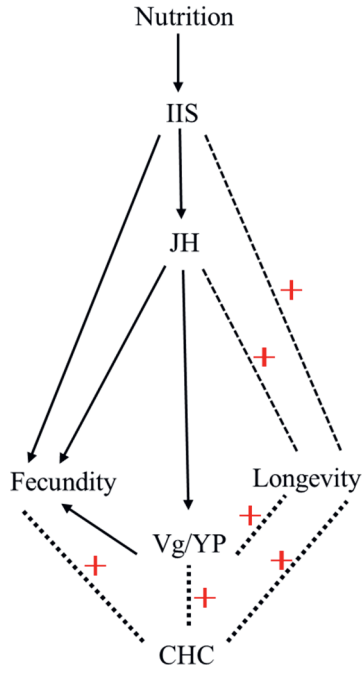

Figure 5.1. The IIS-JH-Vg/YP circuit in *C. secundus* is positively associated with genes that are related to chemical communication (shown by CHC). Solid arrows indicate direct activation. Dashed lines with plus signs above indicate positive correlation.

Sociality changes the level of selection

Life on earth has evolved from single replicators to multicellular organisms through major evolutionary transitions (Szathmáry & Smith, 1995; Korb & Heinze, 2004). The formation of social insect societies has been identified as one of the major evolutionary transitions that surpasses the level of multicellular organisms (Szathmáry & Smith, 1995; Korb, 2010; Szathmáry, 2015). A common feature of all major evolutionary transitions is cooperation between entities (Szathmáry & Smith, 1995; Korb, 2010).

Social insect societies may undergo different levels of selection as individuals cooperate to varying extents, depending on their degrees of sociality. The idea of superorganism tackles colony-level selection by comparing reproductives to germline and workers to soma (Boomsma & Gawne, 2018). This analogy, however, may be controversial because soma implies sterility of workers, but only a subgroup of social insects meets this criterion (e.g., higher termites, Bernadou et al., 2021). So, how should we understand the colony-level selection in species with non-sterile workers? Understanding this question is important to understanding why the longevity-fecundity trade-off appears to be uncoupled not only in superorganismal insects but also in non-superorganismal species. In Chapter 3, we show that when deprived of food, colonies of a non-superorganismal species, *C. secundus*, exhibit a trade-off between maintenance and reproduction, which is achieved by workers abandoning cooperation and dispersing. These findings suggest that non-superorganismal insects can achieve colony-level fitness through their workers' direct fitness. We compare termites with low social complexity to *Hydra*, a multicellular organism with low biological complexity and no obvious germline-soma separation, using the concept of organismality (Queller & Strassmann, 2009; Korb & Heinze, 2016). This comparison indicated a notable similarity between Hydra and *C. secundus* colonies' potential immortality, namely, a huge number of stem cells and high renewability.

Sociality changes the strength of selection

The strength of age-specific selection hinges on the sensitivity of fitness to survival and reproduction rates at different ages (Roper *et al.*, 2021). According to traditional ageing models, the strength of selection on survival decreases with age. As a result, ageing is unavoidable (Hamilton, 1966; Charlesworth, 2000). This prediction, however, is based on the assumption that a population is purely age-structured (Roper *et al.*, 2021). Social insects violate this assumption because they are also caste-structured. So, how might

this violation reshape the selection strength? In Chapter 4, we developed individual-based models based on termite caste development pathways and investigated how these caste systems influence ageing. We showed that reproductives have a longer life expectancy than workers in all situations with more realistic parameter values (**Fig. 4.3b, 4.3e, 4.3h**). In particular, reproductives exhibit negligible senescence in the intermediate and high sociality scenarios, as evidenced by a consistent high survival rate till the end of life (**Fig. S4.7e, S4.7h**). These findings imply that sociality can alter the strength of selection, resulting in varying rates of ageing for individuals who do different kinds of labour. This could be because caste systems result in different reproductive values for reproductives and workers.

Kin selection effect on ageing

Kin selection theory has been utilized as a framework to understand the evolution of the human post-reproductive lifespan (Lee, 2003; Bourke, 2007) and, more recently, to comprehend cooperative breeders' prolonged longevity (Kreider *et al.*, 2022). In social insects, kin selection effects on ageing have been hypothesised to emerge in two ways. First, workers may begin to age when they begin to gain indirect fitness because the onset of ageing aligns with the timing of gaining fitness (Lucas & Keller, 2020). Or, since their direct fitness is accomplished by producing future queens and males rather than future female workers (Kramer *et al.*, 2022), queens have a delayed onset of ageing. However, these two hypotheses may not be sufficient to describe the kin selection effect in termites for two reasons. First, some termite workers can also gain direct fitness by inheriting the nest. Therefore, the onset of ageing in workers might also be influenced by the timing of them gaining direct fitness. Second, the onset of ageing in termite queens and kings may not only be driven by the timing of producing alates but also by the timing of producing workers with reproductive potential.

In Chapter 4, we explored the effect of the workers' reproductive potential on caste-specific ageing in termites. We present a new perspective on how the

interplay of worker reproductive potential and extrinsic mortality influences the kin selection effect on caste-specific ageing. We show that, regardless of extrinsic mortality, reproductives live only slightly longer than workers when the latter have high reproductive potential. Regardless of extrinsic mortality, reproductives live more than ten times longer than workers when the latter have no reproductive potential. Extrinsic mortality, on the other hand, can alter workers' potential for direct fitness by modifying the chance of inheritance when they have intermediate reproductive potential. These results imply that the reproductive potential of workers and caste-specific extrinsic mortality are the primary drivers of the differences in caste-specific ageing between species with different degrees of sociality. This is because these two factors can modify the kin selection effect on ageing by changing the reproductive values of workers and reproductives.

Furthermore, the result that high extrinsic mortality can reduce workers' chance of inheriting the nest in the intermediate sociality stage may be in line with the fact that the switch of lifestyles from wood-dwelling (i.e., workers face low extrinsic mortality) to foraging (i.e., workers face high extrinsic mortality) underlies the transitional stage of social evolution of termites (Korb, 2008a, 2008b). These findings help us understand how social evolution reshapes ageing.

5.2 Examining social effects on ageing

There are remarkable taxonomic and species-specific idiosyncrasies in how social organisms age (Korb & Heinze, 2021). To understand the causes and consequences of these idiosyncrasies, we need to consider different facets of the social effect on ageing. Here, I summarise the contents of this thesis into a conceptual framework that captures both the factors, mechanisms, and evolutionary processes that underpin the social effect on ageing (**Fig. 5.2**). A framework like this might be helpful to guide future research and resolve differences between studies on various species.

For example, to understand how a social act might affect the ageing of the helper (i.e., the individual who provides help) and the receiver (i.e., the individual who receives help) differently, we need to examine the direct and indirect fitness gains of the helper. And the helper's fitness gains are influenced by the degree of sociality, extrinsic mortality, and resource availability. In extreme cases, when the helper can only gain indirect fitness (i.e., strong selection at group level), we expect the helper to be short-lived because it has zero reproductive value, while we expect the opposite for the receiver. In less extreme cases, when the helper can gain both direct and indirect fitness, the lifespan difference between the helper and the receiver should depend on their differences in terms of reproductive values. The larger the difference in reproductive values, the more pronounced the differences in their lifespans will be.

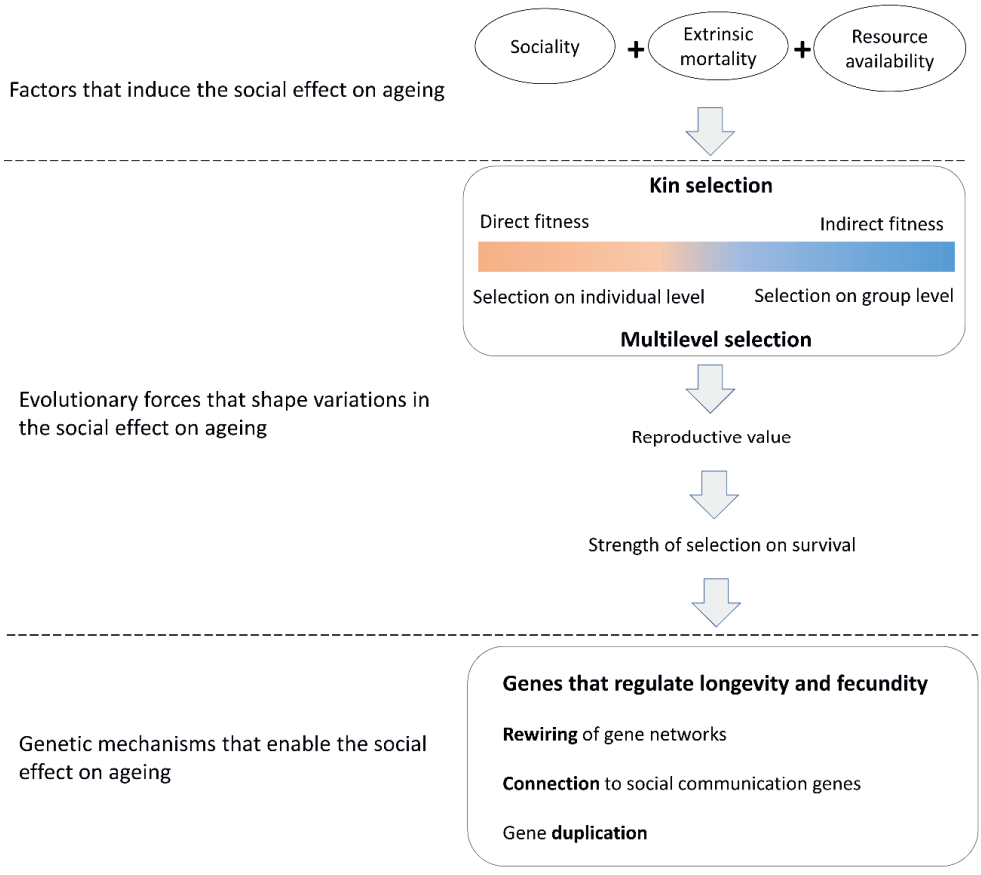

Figure 5.2. A conceptual framework for examining the social effect on ageing. Sociality, extrinsic mortality, and resource availability are the environmental factors that induce the social effect on ageing. Variations in these factors can shape variations in helpers' direct and indirect fitness gains, resulting in a hierarchy of selection levels. Variations in the fitness of individuals and selection levels can change individuals' reproductive values, resulting in differential selection pressure on individuals' survival. The differential strength of selection on survival is manifested in changes in genes that regulate longevity and fecundity in three ways: the rewiring of genes, the links to social communication genes, and gene duplications.