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Regulation of life history determines lifespan of worker honey bees (*Apis mellifera* L.)

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Abstract

Life expectancy of honey bees (*Apis mellifera* L.) is of general interest to gerontological research because its variability among different groups of bees is one of the most striking cases of natural plasticity of aging. Worker honey bees spend their first days of adult life working in the nest, then transition to foraging and die between 4 and 8 weeks of age. Foraging is believed to be primarily responsible for the early death of workers. Three large-scale experiments were performed to quantitatively assess the importance of flight activity, chronological age, extrinsic mortality factors and foraging specialization. Forager mortality was higher than in-hive bee mortality. Most importantly however, reducing the external mortality hazards and foraging activity did not lead to the expected strong extension of life. Most of the experimental effects were attributable to an earlier transition from hive tasks to foraging. This transition is accompanied by a significant mortality peak. The age at the onset of foraging is the central variable in worker life-history and behavioral state was found more important than chronological age for honey bee aging. However, mortality risk increased with age and the negative relation between pre-foraging and foraging lifespan indicate some senescence irrespective of behavioral state. Overall, honey bee workers exhibit a logistic mortality dynamic which is mainly caused by the age-dependent transition from a low mortality pre-foraging state to a higher mortality foraging state.
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1. Introduction

The evolutionary theory of aging predicts that a high extrinsic mortality rate in age-structured populations promotes rapid organismal aging and thus increases the intrinsic mortality. This argument is based on the notion that the force of natural selection opposing aging and senescence is directly related to the survivorship to any given age (Rose, 1991; Kirkwood and Austad, 2000). Important empirical support comes from social insects (Keller and Genoud, 1997; Chapuisat and Keller, 2002). Their social group living habits and the construction of sophisticated nests have reduced the external mortality rate for their reproductives and favored exceptionally long lives (Keller and Genoud, 1997). In general, the reproductives live an order of magnitude longer than their sterile helpers, never leave the safety of the nest center, and act simultaneously as stem cells and gonads of their colony "super-organism".

The honey bee (*Apis mellifera* L.) is an emerging model for aging research for multiple reasons (Omholt and Amdam, 2004; Rueppell et al., 2004a). Honey bees have one queen per colony as the sole reproductive. In the queen's presence the thousands of female workers are functionally sterile and perform all non-reproductive tasks in the colony. Worker/queen caste determination is based on nutrition. Queens receive high-quality food, develop in 16 days, and can live several years, producing up to 2000 eggs per day (Page and Peng, 2001). In contrast, the life expectancy of workers varies seasonally from only 3 to 4

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weeks in the summer to over 6 months in the winter (Omholt and Amdam, 2004). Thus, aging in female honey bees is highly variable between and within castes but the proximate factors underlying this plasticity are not clear (Finch, 1990; Corona et al., 2005). This study addresses the proximate causes of worker mortality from a demographic perspective as a first step to understanding the proximate causes for the queen/worker aging plasticity.

The aging rate varies considerably within the honey bee worker caste and this variation is central for understanding the proximate causes of worker mortality (Omholt and Amdam, 2004). Honey bee workers display an unusual type-2 survivorship pattern (Sakagami and Fukuda, 1968) with low mortality rates as young hive bees and high mortality at older ages. The pronounced age-dependent mortality increase is believed to be intimately linked to the workers' behavioral changes throughout life (Page and Peng, 2001). Honey bee workers display a largely age-based division of labor (Winston, 1987; Beshers and Fewell, 2001): Young bees perform in-hive tasks, such as nest maintenance, food processing, and brood care before a relatively sharp transition to foraging outside the hive. Until their death, foragers collect mainly nectar, pollen, water and plant resins, specializing to varying degrees on these resources (Winston, 1987). The significant increase in age-specific mortality has been regarded as evidence for a high mortality caused by foraging activity (Sakagami and Fukuda, 1968; Page and Peng, 2001) and one early report has estimated that up to 98% of workers die outside the hive (Lundie, 1925). However, these reports present data that confound the mortality effects of chronological aging, behavioral and physiological profile, and extrinsic mortality.

Several hypotheses to explain the peculiar worker mortality patterns have been suggested. Down-regulation of the workers' free protein reserves at the onset of foraging is central for the elevated mortality in foragers (Amdam and Omholt, 2002; Omholt and Amdam, 2004). This hypothesis that foragers deplete themselves of protein in face of their high external mortality rate to preserve colony resources (Amdam et al., 2005) focuses on vitellogenin, a major hemolymph protein with immune (Amdam et al., 2005) and anti-oxidant functions (Seehuus et al., 2006). In addition, several other mechanistic hypotheses have been suggested to account for the high mortality rate of foraging workers. First, the external mortality hazards of foraging may be sufficient to explain the high mortality rate of foragers (Sakagami and Fukuda, 1968; Visscher and Dukas, 1997). Possible causes of death include predation, accidents, dehydration, or disorientation. Another influential hypothesis proposes that the limited glycogen reserves in foragers cannot be replenished at older ages, leading to death by exhaustion (Neukirch, 1982). Simple wear-and-tear can lead to the inability to fly and ultimately death (Page and Peng, 2001), or oxidative tissue damage may limit lifespan (Corona et al., 2005). While experimental data show that some of these processes take place, but with the exception of vitellogenin titers (Nelson et al., 2007; Amdam et al., 2007) they have not been linked quantitatively to mortality rates. It is difficult to distinguish between these alternative hypotheses because it is difficult to determine the cause of death for individual worker honey bees.

Demographic techniques cannot directly establish individual causes of death but actuarial analysis of the mortality patterns can test general mortality models and aid in the discrimination of competing hypotheses on major mortality factors (Carey, 2001). We performed three large-scale demographic experiments to analyze worker mortality patterns and better understand aging in honey bees. Specifically, we assessed (1) the importance of extrinsic risk on worker mortality, (2) how foraging is quantitatively related to mortality, (3) how variation in life history between two selected strains correlates with mortality, and (4) how chronological age affects mortality.

The first experiment was designed to eliminate most extrinsic mortality factors by training bees to forage within a flight cage. We predicted the cage-restricted workers to have a significantly lower mortality, particularly as foragers, if extrinsic mortality factors such as predation, disorientation, or other accidents (Visscher and Dukas, 1997) played a major role in limiting honey bee worker lifespan.

The second experiment addressed the quantitative aspect of foraging by varying the amount of foraging within flight cages by restricting access to food. We predicted significantly lower worker mortality, particularly as foragers, in the limited colony if worker mortality is quantitatively related to foraging effort (Neukirch, 1982).

In the third experiment, we compared worker mortality between two honey bee strains (high and low pollen-hoarding strains; Page and Fondrk, 1995) to assess how their life-history differences, including life expectancy (Amdam et al., 2007), relate to age-specific mortality during the in-hive and foraging state. Compared to the low pollen-hoarding strain, the high strain workers specialize more on pollen foraging (Page et al., 1995), initiate foraging earlier (Pankiw and Page, 2001; Rueppell et al., 2004b), and have larger and more active ovaries (Amdam et al., 2006). When young, the high pollen-hoarding bees have higher levels of vitellogenin. However, vitellogenin levels drop faster in adult high pollen-hoarding bees causing an earlier initiation of foraging (Amdam et al., 2007). Thus we predicted that the worker mortality is higher in the high pollen-hoarding strain then in the low strain specifically at intermediate ages when they exhibit lower vitellogenin titers and earlier foraging.

2. Methods

2.1. Experiments

We studied focal cohorts of honey bees (*Apis mellifera* L.) in colonies of a natural age composition. Honey bee queens in the source colonies were induced to lay eggs in