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## Q2 Aging- and task-related resilience decline is linked to food responsiveness in highly social honey bees

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## ABSTRACT

Conventional invertebrate models of aging have provided striking examples for the influence of food- and nutrient-sensing on lifespan and stress resilience. On the other hand, studies in highly social insects, such as honey bees, have revealed how social context can shape very plastic life-history traits, for example flexible aging dynamics in the helper caste (workers). It is, however, not understood how food perception and stress resilience are connected in honey bee workers with different social task behaviors and aging dynamics.

To explore this linkage, we tested if starvation resilience, which normally declines with age, depends on food responsiveness in honey bees. We studied two typically non-senesced groups of worker bees with different social task behaviors: mature nurses (caregivers) and mature foragers (food collectors). In addition, we included a group of old foragers for which functional senescence is well-established. Bees were individually scored for their food perception by measuring the gustatory response to different sucrose concentrations. Subsequently, individuals were tested for survival under starvation stress.

We found that starvation stress resilience, but not gustatory responsiveness differed between workers with different social task behaviors (mature nurses vs. mature foragers). In addition starvation stress resilience differed between foragers with different aging progressions (mature foragers vs. old foragers). Control experiments confirmed that differences in starvation resilience between mature nurses and mature foragers were robust against changing experimental conditions, such as water provision and activity. For all worker groups we established that individuals with low gustatory responsiveness were more resilient to starvation stress. Finally, for the group of rapidly aging foragers we found that low food responsiveness was linked to a delayed age-related decline in starvation resilience.

Our study highlights associations between reduced food perception, increased survival capacity and delayed aging in highly social honey bees. We discuss that these associations may involve canonical internal nutrient sensing pathways, which are shared between honey bees and animal models with less plastic aging dynamics.

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## 1. Introduction

Research in model organisms has uncovered a remarkable plasticity in aging and longevity, and has identified regulatory networks that strongly affect the onset and progression of aging (Gems and Partridge, 2013). Such regulatory networks can be governed, for example, by sensory systems that signal food and other environmental cues to molecular pathways, which in turn control longevity. As influences of sensory signals on aging are demonstrated for only a few model systems, it is not yet established if such links are of general significance for aging.

Experimental evidence for the interplay between sensory processing and aging is best established for invertebrate genetic models (Linford et al., 2011). For example, mutations as well as targeted ablation of gustatory and olfactory sensory processing can alter lifespan in *Caenorhabditis elegans* (Apfeld and Kenyon, 1999; Alcedo and Kenyon, 2004) and in *Drosophila melanogaster* (Libert et al., 2007). Further, the smell of food alone is sufficient to reduce starvation stress resistance, and to shorten lifespan during dietary restriction — a widely used laboratory strategy to slow aging (Libert et al., 2007). These influences of food signals suggest a crosstalk between external food sensing and life-extending internal nutrient sensing pathways (Alcedo et al., 2013). The canonical internal nutrient sensing pathways, which signal an individual's energy balance and affect lifespan include the insulin/insulin growth factor signaling (IGF) and the target of rapamycin (TOR) pathway (Gems and Partridge, 2013).

In highly social honey bees, individual physiology and also longevity are affected by a range of social signals that carry information about the

Abbreviations: GRS, gustatory response score; PER, proboscis extension response.

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colony's demographical state. For example, reproductive queens release a mandibular pheromone, which slows the behavioral transition to short-lived worker types, improves starvation resilience and increases abdominal nutrient storage (Fischer and Grozinger, 2008). In contrast, the presence of brood or brood pheromone alone acts as a lifespan-shortening signal, likely by its action on abdominal nutrient storage (Amdam et al., 2009; Smedal et al., 2009; Münch et al., 2013b). While these effects suggest that pheromone-sensing systems can affect resilience and longevity in honey bees, links between external food-sensing systems and aging are not clear. First indications for such a linkage come from studies of the so-called pollen hoarding syndrome, where worker bees bias their food choice to either nectar or pollen, the main sources of carbohydrates or protein and lipids, respectively. These preferences in food collection behaviors are part of a phenotypic syndrome (Sih et al., 2004) that links food (gustatory) perception with other behavioral traits, and also with molecular signaling pathways that influence survival (Page et al., 2012b).

Likely the most prominent contributions of the honey bee model to aging research have been studies that established how changed social task behaviors affect aging progression in the worker caste (Münch and Amdam, 2010; Amdam, 2011). Experimental manipulations of colony demography provide well-established tools to evoke worker task transitions, which in turn can slow, accelerate or reverse behavioral and cellular senescence in worker bees (Seeley, 1995; Baker et al., 2012; Margotta et al., 2012; Münch et al., 2013b). The caste of the non-reproducing workers includes different behavioral castes, for example foragers that collect pollen, nectar and water outside the hive, as well as nest bees that produce a protein rich food jelly and engage in hygienic behaviors. Foragers age most rapidly, while nurse bees, even when having the same chronological age, can remain without detectable symptoms of behavioral senescence (Behrends et al., 2007; Münch and Amdam, 2013). Consequently, aging in honey bee workers is more closely linked to different social tasks than to chronological age (Behrends et al., 2007). Symptoms of behavioral and cellular senescence that are documented for the honey bee model include altered learning, flight and home finding performance (Behrends et al., 2007; Vance et al., 2009; Münch et al., 2010), changed abundance of cellular senescence markers (Williams et al., 2008; Hsieh and Hsu, 2011; Tolfsen et al., 2011; Münch et al., 2013b), changed brain protein levels (Wolschin et al., 2009; Baker et al., 2012) as well as alterations in immune and epigenetic state (Amdam et al., 2005; Herb et al., 2012; Aurori et al., 2013).

Taken together, comparing slowly aging nurse bees with rapidly aging foragers provides an opportunity to study how resilience decline and food perception may be linked to different social task behaviors. In honey bees, food perception or more precisely gustatory responsiveness, can be individually assessed by using an innate reflex to sucrose – the proboscis (tongue) extension response (PER) (Page et al., 1998). When different sucrose concentrations are applied to their antennae, highly responsive bees show a proboscis extension response to all concentrations and even to water. In contrast, less responsive bees respond only to higher sucrose concentrations. Gustatory responsiveness correlates with other sensory modalities (Scheiner, 2004; Erber et al., 2006) as well as with learning performance (Scheiner et al., 2001a, 2001b). Yet, while learning decline is a robust measure of aging in honey bees, data on age- and task-related changes in gustatory responsiveness are inconclusive (Behrends et al., 2007; Rueppell et al., 2007; Amdam and Page, 2010; Münch et al., 2013b), perhaps due to different experimental conditions. Also, in contrast to other aging models it is not known how food sensing may modulate age-related functional decline.

Here we study possible associations of gustatory perception with declining stress resistance by using an established test of resilience: survival under starvation. We first asked if worker groups with different social tasks and with different aging progressions also differ in starvation resistance. Then we tested the hypotheses that an individual's gustatory perception is linked to different survival capacities and aging

progressions. Finally, we conducted control experiments to identify, if correlations between worker task groups and starvation resilience might have been biased by experimental conditions, including locomotor activity and water availability during starvation.

## 2. Material and methods

### 2.1. Animals and phenotype identification

Experiments were conducted with honey bees (*Apis mellifera carnica* Pollmann) collected from sister-queen colonies at our apiaries at the Norwegian University of Life Science (Aas, Norway). Honey bees were either sampled from outdoor colonies (Results Sections 1, 2) or from colonies housed in an indoor flight room (controls described in Results Section 3). The flight room could accommodate two colonies with worker types that express typical summer behaviors – brood rearing, foraging – during winter months from October to May. Each sister-queen colony replicate was housed in a  $4.6 \times 2.0 \times 2.0$  m<sup>3</sup> compartment with a day–night cycle of 12 h and temperatures set to 25 °C, respectively 17 °C (Münch et al., 2013b).

To assess effects of social task, we contrasted two typically non-senesced groups of mature nurses and mature foragers with a matching chronological age range between 26 and 43 days. To assess effects of aging, we included a group of old foragers, in which diverse symptoms of functional and cellular senescence emerge as a function of extended foraging duration ('foraging age') but not of chronological age. The identification of honey bee worker and aging types was essentially carried out as described previously (Münch et al., 2013a). To obtain mature nurses and mature foragers with a similar chronological age range, brood frames were removed from the replicate colonies and transferred into an incubator (34 °C). Once emerged, individuals received a paint mark on the thorax that specified the date they have emerged. Age-tagged bees were re-introduced into their native colonies, and were allowed to mature into nurse bees and foragers. All mature foragers had received a second paint mark, when returning from their first foraging flight, i.e. they carried one paint mark specifying their chronological age and another paint mark specifying the time they had spent foraging (foraging age  $\geq 6$  days). To this end, hives were observed on a daily basis during the period of main foraging activity. After onset of foraging in a significant number of pre-marked bees (2–3 weeks after introducing marked newborn bees), returning foragers were re-marked daily. To avoid false-identification of foragers, paint marking of returning bees was discontinued during daily periods of readily identifiable orientation flights, i.e. when pre-foraging bees depart from or enter the hives (Münch et al., 2013a). Foragers were, in addition, identified either by their distended abdomen (indicating nectar load) or by filled pollen baskets. During marking, the hive entrance was narrowed to a small opening. Foragers used for experiments conducted in the flight room (see Results Section 3) were marked directly at the pollen and nectar feeders.

As before, the group of old forager bees was identified by a paint mark that confirmed extended foraging with a minimum foraging duration of 18 days (Wolschin et al., 2009).

For each round of experiments, the different worker types were tested together at the same day. For each experiment we included similar numbers of individuals from at least two sister-queen colonies. Honey bees were collected into cages, with approximately 20 bees per cage. Cages were kept overnight in an incubator (HERAcCell 150, Thermo Scientific) at 32 °C and 70% relative humidity. Water and a sucrose solution (30% in dH<sub>2</sub>O) were provided ad lib until the start of the test protocol.

### 2.2. Assessing gustatory responsiveness

Bees were chilled on ice until motionless, and mounted individually in plastic holders. Care was taken to restrain the bees in a way that largely prevented leg and abdominal movements. To normalize for

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