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Honey bee (*Apis mellifera*) workers live longer in small than in large colonies

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ABSTRACT

Social insect colonies are highly integrated units that can be regarded in some respects as super-organisms, with colony size and individuals analogous to body size and cells in unitary organisms. In both, unitary organisms and super-organisms, the relation between body/colony size and lifespan of the constituent units (cells/individuals) is important for understanding systemic aging but remains to be explored. Therefore, this study compared the life-history and longevity of individual honey bee workers between a large and a small colony social environment. We found that individuals in large colonies were consistently shorter lived than individuals in small colonies. This experimental effect occurred in both principal life history phases of honey bee workers, the in-hive and the foraging stage, independently of the age of the workers at their transition between the two. Nevertheless, this age of first foraging was a key determinant of worker longevity, in accordance with previous studies. The large colonies raised more brood, built more comb, and foraged at higher rates. Our results do not comply with the idea that social group size has a positive effect on individual longevity. Instead, our findings suggest that large and small colonies follow different demographic growth trajectories, trading off longevity of individuals for overall colony growth. Similarly, multi-cellular organisms might sacrifice maintenance and repair of their individual constituent cells for enhanced metabolic activity and organismal growth, leading to the widely-observed negative correlation between longevity and body size within species.

1. Introduction

Body size is a biological variable of fundamental importance to most aspects of life. Across animals, large species are longer lived than smaller species, although the potential explanations of this common relationship are diverse (Finch, 1990; Arking, 2006; de Magalhaes et al., 2007). However, within species, smaller individuals live usually longer than large ones (Patronek et al., 1997; Miller et al., 2002). This negative relation may be due to a life-history trade-off between longevity versus growth and reproduction. Although such a trade-off becomes apparent in genetic studies (Miller et al., 2002) and responses to dietary restriction (Phelan and Rose, 2005), its cellular manifestations remain largely unknown. Specifically, it is not known whether cells from short-lived, large individuals differ in their in-vivo life expectancy or aging patterns from cells of longer-lived, smaller individuals of the same species. The cellular level is crucial for understanding aging at the organismal level but individual cells are difficult to study under natural, in-vivo conditions.

In eusocial insects, such as the honey bee (*Apis mellifera* L.), cooperative individuals form colonies that constitute biological units at a higher level of biological integration (Wilson, 1971; Seeley, 1989; Hölldobler and Wilson, 2008). These colonies are in several key aspects analogous to multi-cellular unitary organisms, but their lesser degree of integration makes them more amenable to experimental manipulation and study of their constituent individuals (Rueppell et al., 2004). Colony size of social insects can be analyzed similarly to body size of unitary organisms in an ecological (Kaspari and Vargo, 1995; Kaspari, 2005) and a life-history context (Seeley, 1989; Bourke and Franks, 1995).

Colonies may also be regarded as the social environment for individual workers, allowing the assessment of social factors that influence lifespan. Individual worker longevity is negatively correlated with colony size across different species (Bourke, 1999, 2007). However, comparative studies between species are complicated by a number of confounding variables because various aspects of social insect biology change with colony size, including queen-worker dimorphism, social organization, and complexity (Bourke, 1999). These factors in turn affect individual life expectancy (Bourke, 2007) and the life expectancy of colonies (Kaspari and Vargo, 1995). Within most social insect species however, queen-worker dimorphism and other confounding variables do not change with colony size.

Group size in many social organisms may represent the evolutionary outcome of an individual optimization of fitness

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(Krause and Ruxton, 2002), which is a function of survival and reproduction. Even among the integrated colonies of social insects, considerable variation in group sizes exists within species that may be ontogenetic or not (e.g. Clemencet and Doums, 2007). Large colony size in social insects is usually associated with higher reproductive output, competitiveness, and colony longevity (Wilson, 1971; Hölldobler and Wilson, 1990; Kaspari and Vargo, 1995; Karsai and Wenzel, 1998) but it is not clear how individual longevity relates to colony size at the intra-specific level.

On the one hand, group size is believed to increase individual longevity through social facilitation in animals in general (Krause and Ruxton, 2002). Specifically in social insects, a positive association would be expected if group synergistic effects prolong individual lifespan by more efficient protection, homeostasis, or division of labour that reduces individual workload. On the other hand, a transition from risk-sensitive to risk-prone worker strategies with increasing colony size could be predicted because the loss of single individuals is a less severe hazard for larger colonies (Strassmann, 1985). Additionally, the social dynamic in large colonies could lead to more growth and reproduction versus somatic worker maintenance in the "super-organism", analogous to the possibility of large individuals with short-lived cells in unitary species. This particularly may be true because foraging activity is controlled by a positive feedback loop which leads to more foraging effort in large colonies (Eckert et al., 1994).

Empirical data on the intra-specific relationship between colony size and individual lifespan suggest an overall positive association in wasps (O'Donnell and Jeanne, 1992) but evidence in honey bees is equivocal (Fukuda and Sekiguchi, 1966; Winston, 1979; Harbo, 1986). This inconsistency in the honey bee literature could be due to methodological problems, including lifespan estimates without following individually marked bees. However, it could also be due to a non-linear phase transition at different colony growth stages or sizes (Oster and Wilson, 1978). Increasing colony size may increase worker life expectancy in a certain range of colony sizes due to improved colony homeostasis or decreased workload but decrease life expectancy in a different colony size range due to increased brood rearing activity and an increased workload (Eckert et al., 1994).

Therefore, we set up an experiment to compare individual worker life-histories and lifespan between two differently-sized colonies as social environment. We used large cohorts of individually marked worker honey bees and monitored their foraging activity in addition to survival because the transition from in-hive duties to foraging is a major determinant of honey bee worker lifespan (Rueppell et al., 2007, 2008; Amdam et al., 2007, 2009).

2. Materials and methods

The experiment was conducted in Tempe, Arizona, during May–July 2007 with commercial, European honey bees *Apis mellifera* (*ligustica*). Two pairs (experimental trials) of one small and one large hive were made up from respectively one and two pounds (one pound approximates 4500 individuals) of worker bees. The bees were shaken from a mixture of European source hives and then randomly divided into the experimental treatment groups. These groups were then installed in five-frame nucleus hives with queens that had mated naturally.

One week later, twelve frames of brood comb with ready-to-emerge worker brood were collected from the same European source hives kept in the experimental apiary. Bees emerged overnight in a temperature (34 °C) and humidity (50%) controlled incubator. They were individually marked by gluing numbered plastic tags on their dorsal thorax and 796 were introduced into each observation hive. Just prior to that, 400 and 800 untagged new workers were introduced to the small and large hive, respectively, to facilitate the introduction process for the tagged, focal individuals. One day later, colonies were transferred into glass-walled observation hives that each contained one frame of honey, one fully drawn, empty frame, and two frames of foundation. One day after this transfer, daily survival and foraging observations began. In addition, we observed the comb building and estimated the total brood area (in cm^2) at the end of the experimental period to evaluate the productivity of the hives.

Worker survival was monitored daily after sunset by systematically recording all marked individuals present in the colony. Since worker bees return daily to their hive as long as they are alive, death was inferred for one day after the last recording of a bee. All bees returning from foraging trips were recorded daily for 2 h during the peak of foraging activity to determine the age of foraging initiation. Workers returning with pollen on their legs were classified as pollen foragers, all others were classified non-pollen foragers. From the foraging records, we calculated the number of foraging days and the pollen foraging bias as the proportion of foraging observations for each worker that included pollen collection. From the combined data records, lifespan (days from eclosion to last recorded sighting), the age of first foraging (AFF, equal to the lifespan as in-hive worker), and flightspan (days from AFF to last recorded sighting) were calculated. Only workers that were recorded at least on two occasions were included in the analysis.

AFF was estimated from all workers that were observed foraging. A second estimate for overall AFF was obtained by considering all unobserved individuals as censused data points with unobservable AFF because the workers died before the onset of foraging. Since this corrected AFF did not change the outcome of subsequent analyses, only the results from the original AFF are reported.

Trials were compared with a Mantel–Cox log-rank test, using trial as factor and small vs. large as different strata. Within each trial the treatment effect on lifespan, AFF, and foraging span was assessed by log-rank tests. Pollen specialization and foraging rates did not contain censored data and could not be transformed to approximate a normal distribution, therefore, non-parametric Mann–Whitney *U*-tests were performed. To assess the simultaneous effects of treatment, trial, pollen specialization, and AFF on lifespan and flightspan, a stepwise Cox regression was performed with treatment and trial as categorical variables in the first block and pollen specialization and AFF as continuous variables in the second block. The same analysis was performed separately for each trial omitting the variable "trial" from the model. As an additional significance test, we permuted all worker lifespan, AFF, and flightspan data among the four colonies and calculated the *F*-values for trial and treatment effects (10,000 times) to empirically determine the significance of the actual values.

3. Results

After the initial five days before the observations were started, 671 (84.3% of the original 796) workers remained in the first large hive, 609 (76.5%) in the second large hive, 680 (85.4%) in the first small hive, and 709 (89.1%) in the second small hive. The observations were terminated after 47 days, which led to less than 1% of the lifespan data in each group being censored. Minimum and maximum recorded lifespan among all workers in our experiment was 7 and 50 days, respectively, with a mean of 24.6 and a median of 24 days. Over all foragers, the AFF ranged from 8 to 42 days with a mean and a median of 20.7 and 20 days, respectively. Incorporation of workers that were not observed foraging as censused data points increased the estimate of mean and median AFF to 22.5 and 22 days, respectively. The flightspan ranged from 1 to 42 days with a mean and a median of 7.4 and 6 days, respectively. The pro-