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.
Keywords: Ageing, Biodemography, Colony growth, Mortality dynamic, Social insects, Sociality, Super-organism

Article:

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 (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 life-span (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 over-night 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 for-aging 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 re-corded 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 flight-span 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 proportion of foraging records of individual bees involving pollen collection varied between 0 and 1 with a mean and a median of 0.26 and 0, respectively. Approximately 10% of the foragers were only observed collecting pollen and 50% were never observed returning with pollen. Worker lifespan (Table 1) did not significantly differ between the two trials ($\chi^2 = 1.2$, $p = 0.276$; Fig. 1). In both trials, workers in the small hives lived significantly longer than workers in the large hives (trial 1: $\chi^2 = 27.3$, $p <$

0.001; trial 2: $\chi^2 = 95.1$, $p < 0.001$). AFF differed significantly between trials ($\chi^2 = 17.6$, $p < 0.001$), which was mainly due to the small hive workers' earlier AFF in the second trial than in the first (Table 1). In both trials, the small hive had a significantly older AFF than the large hive (trial 1: $\chi^2 = 85.2$, $p < 0.001$; trial 2: $\chi^2 = 88.4$, $p < 0.001$; Fig. 2). Flightspan did not significantly differ between the two trials ($\chi^2 = 1.9$, $p = 0.168$) and followed in all cases an approximate negative exponential distribution function (Fig. 3). The uni-factorial analyses in each separate trial indicated that workers of the large hive had a slightly longer flightspan in the first trial ($\chi^2 = 4.0$, $p = 0.045$) but a shorter flightspan in the second trial ($\chi^2 = 36.7$, $p < 0.001$) (Table 1). Overall, more pollen was gathered in the second than in the first trial ($Z = 4.2$, $n_1 = 965$, $n_2 = 985$, $p < 0.001$) (Fig. 4). In both cases, workers in the small hive collected more pollen, with the difference more pronounced in the second trial (trial 1: $Z=2.1$, $n_{big}=506$, $n_{small}=459$, $p=0.033$; trial 2: $Z=6.4$, $n_{big}=475$, $n_{small} = 510$, $p < 0.001$).

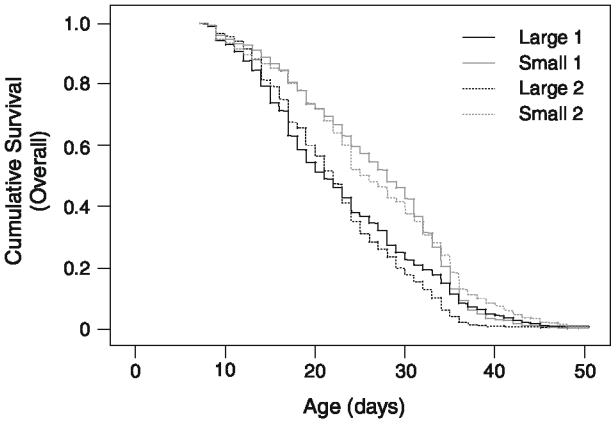

Fig. 1. Overall honey bee worker survival in all four colonies. Mortality dynamics were consistent between hives of the same treatment. The large hives were twice the size of the small hives and showed increased mortality in the focal worker cohort.

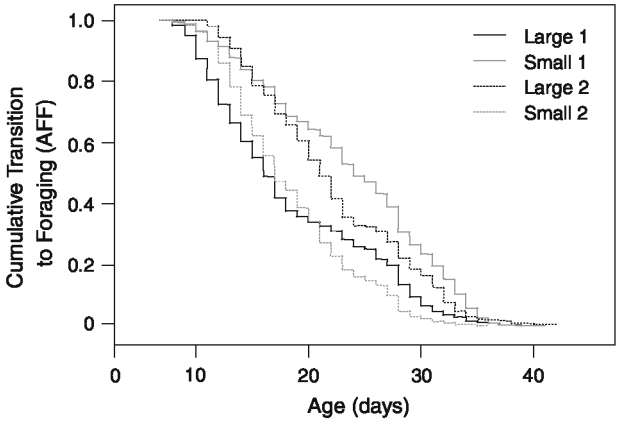

Fig. 2. The time workers spent in the hive before foraging (age at first foraging) was increased in the small hives relative to the large hives.

The multi-factorial Cox-regression analysis of lifespan in the whole data set indicated simultaneous effects of treatment (small hive compared to large hive hazard ratio=0.74 (0.68–0.82), Wald = 36.5, $p < 0.001$), AFF (hazard ratio = 0.93 (0.92–0.94), Wald = 514.2, $p < 0.001$), and pollen collection (hazard ratio = 0.68 (0.58–0.80), Wald = 21.1, $p < 0.001$) but not trial (hazard ratio 0.99 (0.90–1.08), Wald = 0.1, $p = 0.776$).

Table 1
Average ± SD of lifespan, AFF, and flightspan in all four experimental groups (with 95% confidence intervals).

Group	Worker lifespan	AFF	Flightspan
Large hive 1	22.8 ± 9.4 (22.1–23.5), *n* = 671	18.6 ± 7.5 (17.9–19.2), *n* = 506	7.5 ± 6.6 (6.9–8.1), *n* = 506
Large hive 2	22.3 ± 7.6 (21.7–22.9), *n* = 609	18.4 ± 5.7 (17.9–18.9), *n* = 475	6.5 ± 5.3 (6.0–6.9), *n* = 475
Small hive 1	26.6 ± 8.9 (26.0–27.3), *n* = 680	23.8 ± 7.6 (23.2–24.5), *n* = 459	6.7 ± 6.0 (6.1–7.2), *n* = 459
Small hive 2	26.4 ± 9.7 (25.6–27.1), *n* = 709	22.2 ± 6.9 (21.6–22.8), *n* = 510	8.8 ± 6.9 (8.2–9.4), *n* = 510

The hazard for onset of flight (AFF) was overall decreased by the small hive treatment (small hive versus large hive hazard ratio = 0.57 (0.52–0.62), Wald = 149.2, $p < 0.001$). This effect was very similar between the first trial (hazard ratio = 0.57 (0.50–0.64), Wald = 73.7, $p < 0.001$) and second trial (hazard ratio = 0.56 (0.49–0.64), Wald = 76.6, $p < 0.001$). Cox-regression analysis of flightspan in the whole data set indicated simultaneous effects of treatment (small hive versus large hive hazard ratio = 0.80 (0.73– 0.88), Wald = 22.3, $p < 0.001$), AFF (hazard ratio = 1.04 (1.03– 1.05), Wald = 120.0, $p < 0.001$), and pollen specialization (hazard ratio = 0.67 (0.56–0.79), Wald = 22.7, $p < 0.001$) but not trial ($\chi^2 = 0.2$, $p = 0.621$).

The permutation tests of the effects of trial, treatment and their interaction on lifespan indicated a significant effect of the social environment, colony size, ($p < 0.0001$) but not of trial ($p = 0.500$) or the interaction between the two factors ($p = 0.614$). In contrast, significant effects on AFF were indicated for treatment ($p < 0.0001$), trial ($p = 0.034$) and their interaction ($p = 0.022$). Similarly, flight-span was affected by treatment ($p = 0.0075$), trial ($p = 0.047$), and their interaction ($p < 0.0001$) although the direction of the trial effect was opposite for AFF and flightspan.

A stronger negative relation between the AFF and flightspan in the small hives was reconfirmed by bi-variate regression of flightspan on AFF separately for all four experimental groups (Fig. 5): The regression results for

the small hives were in the first trial b = -0.29 ± 0.03 (SE), r^2 = 0.14, $F_{(1, 457)}$ = 72.2, p < 0.001 and the second trial b = -0.28 ± 0.04, r^2 = 0.08, $F_{(1, 508)}$ = 46.2, p < 0.001. The results for the large hives were b=-0.12±0.04 (SE), r^2=0.02, $F_{(1, 505)}$ = 10.5, p = 0.001 and b = -0.14 ± 0.04, r^2 = 0.02, $F_{(1, 473)}$ = 10.7, p = 0.001, respectively. In both trials, the value of the regression coefficient in the large hive was significantly lower than that in the small hive (first trial: p = 0.001; second trial: p = 0.017).

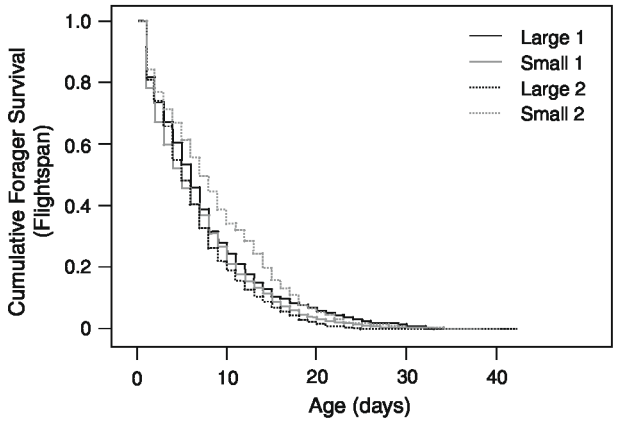

Fig. 3. Lifespan after the transition to foraging is short and the treatment effect less apparent, even though multi-factorial analyses indicate a consistent reduction of flightspan by larger colony size.

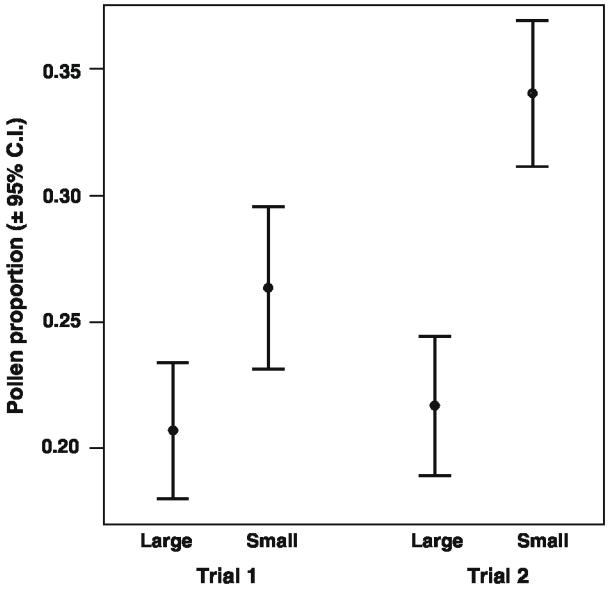

Fig. 4. The proportion of foraging records involving pollen collection averaged over all workers was consistently higher in the small hives than in the large hives.

Brood area was estimated in the first and second small hive as 1935 cm^2 and 1160 cm^2, respectively, and 2450 cm^2 and 2355 cm^2 in the corresponding large hives. In addition, the large colonies showed higher building activities, constructing cells on the empty foundation considerably faster. Workers in the large hives also exhibited higher foraging rates than workers in the small hives (Z = 3.1, n_1 = 969, n_2 = 981, p = 0.002), as measured by the number of foraging records (days) during their foraging lifespan (flightspan): foragers of large hives were observed 61% of the days foraging and foragers of small hives 57%.

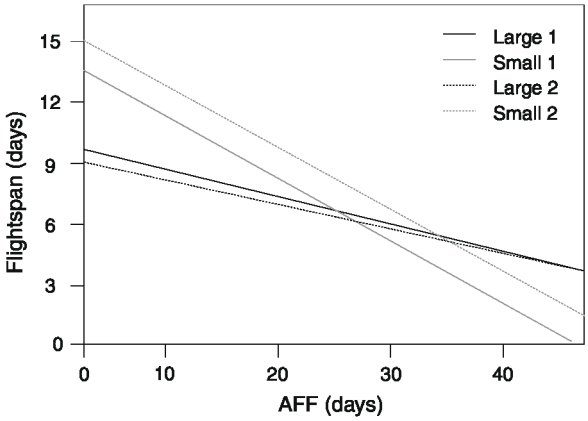

Fig. 5. Relationship between the pre-foraging and foraging lifespan. The negative trade-off between the two life-history stages suggests that aging occurs before the initiation of foraging, albeit at a slower rate than in foragers.

4. Discussion

Our results clearly demonstrate that workers introduced to our large colony environments lived shorter than workers introduced into a smaller colony environment. Both principal life history stages were shortened concurrently: With other factors statistically accounted for, workers in a large colony environment initiated foraging earlier and died after a shorter foraging lifespan. This experimental effect was strong and consistent in spite of the generally negative relationship between the pre-foraging and for-aging stages, as observed within our experimental groups and in previous studies (Rueppell et al., 2007, 2008). Thus, a larger colony size

shortened both life history phases independently, which could be caused by a consistently higher work load throughout life. The large colonies constructed more comb, reared more brood, and foraged at higher rates. This suggests that individual worker lifespan may have been traded off for overall colony growth. To the extent that the super-organism analogy (Wilson, 1971; Seeley, 1989; Hölldobler and Wilson, 2008) holds in this context, our findings imply that cells in large, unitary individuals could also be shorter lived. Due to the tight integration of unitary organisms this could lead to the observed intra-specific negative association between body size and lifespan (Miller et al., 2002; Phelan and Rose, 2005), while in social insects large colonies usually live longer because workers can be readily replaced (Kaspari and Vargo, 1995; Karsai and Wenzel, 1998; Bourke, 1999).

The negative association of individual lifespan and colony size has several potential explanations. It could be explained by workers changing from a risk-averse life-history tactic in a smaller colony to a risk-prone tactic in a larger colony. At the ultimate level, this could be due to the fact that the individual has a relatively lower value in larger colonies. Nectar foragers were reported to maximize net energy efficiency due to mortality risks associated with foraging but only one hive of unreported size was used (Schmid-Hempel et al., 1985). A later study showed that nectar foragers work harder in larger colonies but this study did not measure mortality consequences (Eckert et al., 1994). Our data corroborate the positive relation between colony size and work load on foragers by demonstrating an earlier AFF and higher foraging intensity in the larger hives, although we overall chose smaller colonies than previous studies and gathered individual, lifetime foraging data. Furthermore, our experiments tie adult survival to the AFF, reconfirming earlier studies (Rueppell et al., 2007, 2008). One of our earlier studies also suggested a colony size effect on individual worker longevity (Rueppell et al., 2008). It is important to note, however, that our treatment of colony size manipulation had a consistent effect on individual workers that was independent of AFF. It seems rather that the treatment affect was associated with the positive effect of pollen collection on lifespan. Workers in small colonies collected more pollen and lived longer. The effect of the tendency to collect pollen on lifespan was ambiguous in earlier studies, probably dependent on environmental conditions (Rueppell et al., 2007, 2008). Therefore, we conclude that the experimental treatment effect in this study was the primary effect with simultaneous consequences on foraging choice, overall work load, and the rate of aging of worker honey bees.

Another ultimate reason for the experimental results could be that our large hive treatment set the hives on a reproductive trajectory. Honey bee colonies reproduce by splitting the colony after attaining a critical size. In temperate areas, the timing of this growth is critical to allow successful reproduction (Winston, 1987). To achieve reproductive size, more comb construction, resource collection, and brood rearing are essential. Thus, the large hives may have invested more into growth while the small hives may have been on a colony survival trajectory, maximizing energy efficiency and prolonging their workers' lives (Houston et al., 1988). The trade-off between growth and reproduction versus longevity (via somatic maintenance and repair) occurs also in multi-cellular, unitary species (Arking, 2006). The regulatory mechanisms of colony growth in relation to season and reproductive opportunity have not been experimentally addressed but it is generally assumed that colony growth is a function of colony size and in the ergonomic phase growth and size may be linked by positive feedback (Oster and Wilson, 1978).

Finally, there might not be an ultimate explanation of our results. The experiment was designed not to overpopulate our observation hive to avoid negative density effects and we ensured sufficient food resources for all colonies through the experiment. However, it is impossible to exclude these factors completely. The amount of brood affects the work load of nurse bees and pollen foragers (Eckert et al., 1994). Since we only recorded the longevity of the experimental cohorts and did not monitor the development of the total hive populations, it is not possible to calculate the per-capita brood rearing loads in the different treatment groups. However, the negative dependency of foraging span on AFF was weaker in the large hives than in the small hives, indicating that workers may have aged less as nurse bees in the large hives before initiating foraging (Guzmán-Novoa et al., 1994; Rueppell et al., 2007). The shortened lifespan of workers in larger hives might have also been a consequence of increased/earlier recruitment to foraging because larger hives have more successfully returning foragers, providing more recruitment to foraging.

In general, our results agreed well with previous studies in terms of the average duration of honey bee worker lifespan and its components, AFF and flightspan (Sakagami and Fukuda, 1968; Neukirch, 1982; Page and Peng, 2001; Rueppell et al., 2007, 2008). In addition, the transition from in-hive to foraging tasks proved again to be the strongest predictor of worker lifespan, consistently reducing the remaining lifespan after the transition but increasing overall lifespan (Guzmán-Novoa et al., 1994; Rueppell et al., 2007, 2008). In the small hives, workers "traded" one day of foraging tenure for every three days of in-hive life, but in the large hives, the trade-off was about one day of foraging per seven days of in-hive life. This trade-off depends on the stochasticity of the mortality of foragers and on hive- and external environmental conditions. The variability of this trade-off presumably prevents a narrow optimization of the AFF as the central life history parameters for honey bee workers, which could explain the behavioural plasticity and genotypic variability in honey bee workers for this trait (Rueppell et al., 2007).

In conclusion, this study supports the claim that individual life-span of workers is strongly dependent on the social colony environment (Karsai and Wenzel, 1998; Rueppell et al., 2008). Increased colony size shortened individual worker lifespan, in accordance with inter-specific trends (Bourke, 1999, 2007). Our results suggest that honey bee colonies may trade off longevity of their individual workers for overall colony growth. The super-organism is a useful concept at the interface of social demography and aging research to highlight differences and similarities between different levels of biological organization. Studying resource allocation and transfers in insect colonies may thus reveal general principles of the evolutionary mechanisms underlying plastic aging rates. Our results should stimulate the question whether the negative effect of body size on longevity within unitary species (Patronek et al., 1997; Miller et al., 2002) is due to shorter-lived cells, analogous to the reduced worker lifespan in our study.

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