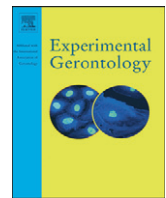




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Worker lifespan is an adaptive trait during colony establishment in the long-lived ant *Lasius niger*

Boris H. Kramer^{a,*}, Ralf Schaible^b, Alexander Scheuerlein^{b,**}^a Groningen Institute for Evolutionary Life Sciences, University of Groningen, Nijenborgh 7, 9747, AG, Groningen, The Netherlands^b Max Planck Institute for Demographic Research, Rostock, Germany

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ABSTRACT

Eusociality has been recognized as a strong driver of lifespan evolution. While queens show extraordinary lifespans of 20 years and more, worker lifespan is short and variable. A recent comparative study found that in eusocial species with larger average colony sizes the disparities in the lifespans of the queen and the worker are also greater, which suggests that lifespan might be an evolved trait. Here, we tested whether the same pattern holds during colony establishment: as colonies grow larger, worker lifespan should decrease. We studied the mortality of lab-reared *Lasius niger* workers from colonies at two different developmental stages (small and intermediate-sized) in a common garden experiment. Workers were kept in artificial cohorts that differed only with respect to the stage of the colony they were born in. We found that the stage of the birth colony affected the body size and the survival probability of the workers. The workers that had emerged from early stage colonies were smaller and had lower mortality during the first 400 days of their life than the workers born in colonies at a later stage. Our results suggest that early stage colonies produce small workers with an increased survival probability. These workers are gradually augmented by larger workers with a decreased survival probability that serve as a redundant workforce with easily replaceable individuals. We doubt that the observed differences in lifespan are driven by differences in body size. Rather, we suspect that physiological mechanisms are the basis for the observed differences in lifespan.

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1. Introduction

Social insects offer researchers a unique opportunity to study the evolution of lifespan and aging due to the extreme lifespans of queens, and the striking differences between the lifespans of queens and workers. While most researchers agree that the worker-queen lifespan differential evolved as a response to differences in the extrinsic mortality risk faced by queens and workers, the mechanism how extrinsic mortality molded the evolution of aging phenotypes is still being debated (Keller and Genoud, 1997; Heinze and Schrempf, 2008; Parker, 2011; Kramer and Schaible, 2013a). Moreover, the differences in the survival rates among polymorphic worker castes have been linked to different levels of extrinsic mortality risk that emerged as a consequence of the division of labor (Keller and Genoud, 1997; Heinze and Schrempf, 2008; Jemielity et al., 2005; Calabi and Porter, 1989; Chapuisat and Keller, 2002; Kramer and Schaible, 2013b).

Even in species with only one worker caste lifespan was found to be highly plastic. In most eusocial species, workers switch from performing safe tasks within the colony early in life to performing risky tasks like foraging later in life. The transition to taking on risky tasks is accompanied by physiological changes and increased mortality, which indicates that maintenance costs and intrinsic mortality risk can be regulated over the lifespan of an individual (O'Donnell and Jeanne, 1992; O'Donnell and Jeanne, 1995a; O'Donnell and Jeanne, 1995b; Tofilski, 2002; Camargo et al., 2007; Rueppell et al., 2007). Other factors, such as worker body size and the division of labor, also influence worker lifespan. In *Solenopsis invicta*, larger workers with a low metabolic rate live longer than smaller workers with a high metabolic rate (Calabi and Porter, 1989). Note, however, that the direction of the body size-lifespan correlation may be reversed, as shown in *Oecophylla smaragdina* and *Acromyrmex subterraneus* (Camargo et al., 2007; Chapuisat and Keller, 2002).

Worker lifespan may also depend on colony size, which in turn affects social complexity (Bourke, 1999) and the social environment (Parker, 2011), and determines the temporal division of labor (Ribbands, 1952; Fukuda and Sekiguchi, 1966; Robinson, 1992; Huang and Robinson, 1996; Amdam and Omholt, 2002; Rueppell et al., 2007; Münch et al., 2008; Woyciechowski and Moron, 2009). In a comparative

* Corresponding author.

** Correspondence to: A. Scheuerlein, Max-Planck Institute for Demographic Research, Konrad-Zuse-Straße 1, D-18057, Rostock, Germany.

E-mail addresses: b.h.kramer@rug.nl (B.H. Kramer), scheuerlein@demogr.mpg.de (A. Scheuerlein).

study across several eusocial species of hymenoptera, Kramer and Schaible (2013b) found that the lifespan differential between the queen and the workers increased with average colony size, but that there was no general trend in species-specific worker or queen lifespans when they were compared independently (with the exception of closely related species). This failure to find a clear trend was probably due to a variety of ecological differences between the compared species (Kramer and Schaible, 2013b). Larger colonies are socially more complex, and consist of highly specialized workers to maximize colony efficiency. This complexity may ultimately lead to reduced investment in individual workers in species with large colonies (Kramer and Schaible, 2013a).

A similar trend is seen among different sized colonies within species. Workers from large honey bee colonies lived shorter lives than workers from small colonies (Rueppell et al., 2009), and the winter survival of *Formica neorufibarbis* workers was reduced in larger colonies.

These differences in demographic rates among workers affect not only colony fitness, but also colony growth rate, colony size, and colony lifespan (Hölldobler and Wilson, 1990; O'Donnell and Jeanne, 1995a; Billick, 2003). The high degree of diversity of worker lifespans in established colonies raises the question of whether colony growth affects the lifespans of workers; and, ultimately, the queen-worker lifespan differential (Kramer and Schaible, 2013b). We expect to find that during the establishment of a colony worker survival is reduced as colonies grow larger, such that colony size during hatching determines a worker's mortality risk.

We suggest that worker lifespan may have evolved as an adaptive trait, which is regulated according to the demands of the colony. Using artificial colonies of the ant *Lasius niger*, we expect to find that the average survival of workers from small one-year-old colonies is greater than the average survival of workers from larger two-year-old colonies.

2. Methods

2.1. *Lasius niger* as a model organism

Queens of the ant species *L. niger* have the longest lifespan reported in eusocial insects, with a maximum lifespan of 28 years. The average worker lifespan in this species is, however, much shorter, at one to two years (Kutter and Stumper, 1969). As queens have a long lifespan with a high level of reproductive output, we assume that we would find no age-specific changes in egg quality and production in queens between eight and 20 months old. Typically, queens in species such as *L. niger* with claustral independent nest foundation (Keller and Passera, 1989) do not forage themselves, but raise the first workers solely on resources from their body reserves, apparently trading off worker size against worker number (Tschinkel, 1988). These first workers, often called "minims" or "nanitic workers," have been shown to be more efficient at brood rearing than later-born, larger workers (Porter and Tschinkel, 1986). In *L. niger* the switch from the production of small workers in small colonies to the production of regular sized workers in larger colonies is accompanied by a shift to cooperative foraging at a threshold colony size of 75 individuals (Mailleux et al., 2003).

2.2. Ant collection

Seventeen dealate (wings are shed after the mating flight) *L. niger* queens were collected on July 13, 2009, after a mating flight in Rostock, Germany (Lat = +54° 5' 35.86", Lon = +12° 6' 40.50"), and were transferred to the laboratory in order to set up the source colonies that would be used for the experiment. No permission was needed to collect the *L. niger* queens, as the species is considered neither protected nor endangered under German law, and the collection was conducted on the campus. After collection, the queens were housed in test tubes containing water tanks in a climate chamber under constant temperatures (22 °C) without light. After the first brood emerged, the test

tubes were opened and placed in plastic boxes (12 × 17 × 4 cm). Food (honey-water and boiled, chopped house crickets, *Acheta domestica*) was provided and replaced weekly, with the water tanks being renewed as needed. Throughout the winter (15.10.–15.3.) the plastic boxes containing the source colonies were housed in a box and placed in a dark room at ambient temperatures in Rostock, northern Germany. The queens went into hibernation and ceased laying eggs while all of the brood changed into larvae.

2.3. Experimental setup

To create artificial colonies of same-aged individuals without marking individuals (which may have affected the behavior of other workers), we checked the colonies weekly, and removed the newly hatched callow workers (with a maximum age difference of 3–4 days due to the time needed for cuticular hardening) from all our source colonies throughout June and July of 2010 and 2011 (see Fig. 1). Callow workers were produced at the same rate across all of the source colonies. The extracted workers were then merged into artificial colonies, each of which consisted of workers from all of the source colonies. We will henceforth refer to these artificial colonies as cohorts. We are aware that this procedure may have introduced additional heterogeneity within the ES and the IS cohorts due to source colony effects. Still, the sampled workers from both the IS and ES groups originated from the same source colonies and heterogeneity levels were similar. Eggs and larvae from the source colonies were provided in similar numbers for all of the cohorts so that the workers could engage in natural colony tasks, but no queen was provided. Throughout the entire experiment, the cohorts were kept in constant laboratory conditions at 22 °C without hibernation. Due to the fact that individually distinct cuticular hydrocarbons develop after emergence (Vander Meer et al., 1989), we did not observe either the aggregation of workers originating from the same source colony or aggressive interactions between workers from different source colonies.

In addition to following a weekly feeding regime, we checked for dead workers, supplied the cohorts with eggs (~1 per worker) from the natal colonies, and removed pupae to prevent the hatching of new workers in our cohorts.

To analyze changes in worker survival rates during colony establishment, we extracted workers at two stages. The early stage workers were collected after first hibernation, when the source colonies were ~8 months old and contained on average 18 ± 8 workers (see scheme in Fig. 1). We established six cohorts with a total of 217 workers (mean cohort size: 36 ± 7) by collecting one cohort per week between June and July 2010. We will refer to these cohorts as ES, since they are derived from colonies in an early stage in colony establishment (see Fig. 1).

One year later (June and July 2011), after the second hibernation, the source colonies were 20 months old and contained on average 250 ± 79 workers (range: 122–392); well above the threshold for cooperative foraging and the production of regularly sized workers (Mailleux et al., 2003). At this stage we were able to establish three cohorts with a mean cohort size of 58 ± 18 workers from the source colonies, and called them intermediate stage (IS) colonies (see Fig. 1). In order to test solely for the effect of the stage the colony workers were derived from, and not for the effect of the size of the colony they lived in, we made an effort to establish experimental cohort sizes of similar sizes. The cohort sizes did not differ significantly between the ES and the IS treatments (*t*-test: $p = 0.190$, $df = 2.23$, $t = -1.86$), and all of the cohorts were smaller than the critical size of 75 individuals that has been shown to induce changes in foraging behavior (Mailleux et al., 2003). The deceased workers from each experimental group (ES and IS) were collected and pooled for head width measurement.

All of the workers had died by May 2014, when the experiment ended.

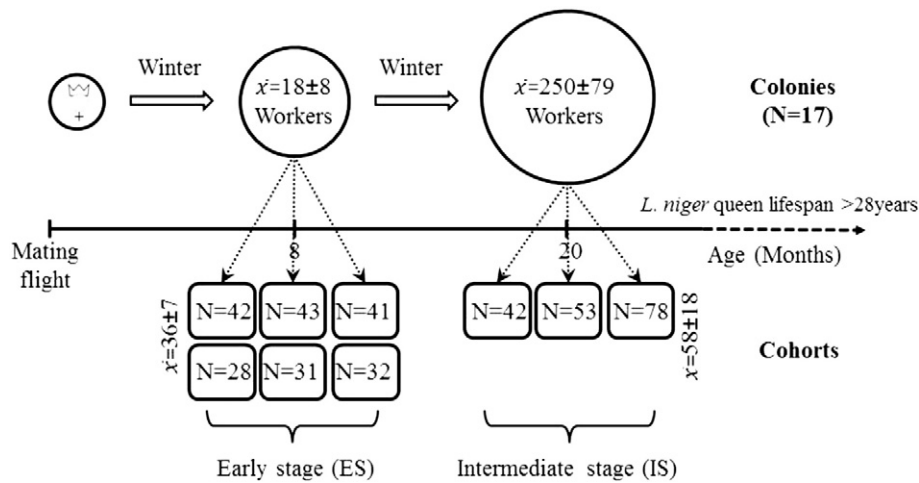


Fig. 1. Experimental setup. Queens were collected after the mating flight from the field and transferred to the laboratory, where they produced the first nanitic workers. After the first winter at ambient temperatures, callow workers were collected from the source colonies at an early stage (ES) in colony establishment to create six cohorts. After the second overwintering at ambient temperatures, we collected callow workers from the colonies at an intermediate stage (IS) of colony establishment to create three cohorts.

2.4. Head width measurement

The dead workers were pooled by cohort, and their head width was measured with a ruler in 15-fold magnified pictures of individuals using a binocular microscope (Zeiss™). The differences between the experimental groups were analyzed using a *t*-test.

2.5. Survival analysis

We calculated each individual's age at death in days, using the date the callow was collected from its natal colony as the birthdate (maximum error: four days for cuticular hardening). Individuals that died due to accidents were treated as right-censored. We used Cox proportional hazard regression analysis to analyze differences in survival between the cohorts within each experiment, and to compare the two treatments. To test whether early and late life mortality differed between the treatments, we compared subsets using the first, second, third, and last quartiles of individual deaths between treatments with Cox proportional hazard regression. We repeated this procedure by building subsets that used only the first middle and the last 50% of the deaths per experiment.

To compare hazard rates, we fitted several mortality models (exponential, Gompertz, Gompertz-Makeham, Weibull; see Pletcher, 1999 for details) to the age-at-death data of the pooled experiments. Model selection using the AICc criterion (Burnham and Anderson, 1998) revealed that the Gompertz models had the lowest AICc relative to the other models in both experimental treatments (ES: AICc = 1974; IS: AICc = 1581).

As actually experienced colony size is a major factor in honey bee worker lifespan (Rueppell et al., 2009), we tested whether worker survival was affected by shrinking cohort size. We modeled the current colony size as a time-varying covariate on worker survival using Cox proportional hazard regressions. The experimental treatment (ES, IS) and the cohort were also entered into the model. We started with a maximal model containing all parameters, and eliminated the non-significant terms step by step until a minimum adequate model was reached using ANOVA's (Crawley, 2002).

All of the statistical analyses were performed using R-statistical software (R Core Development Team, 2010) and the packages *survival* (Therneau and Lumley, 2011) & *MaxLik* (Toomet and Henningsen, 2010).

3. Results

3.1. Head width

The workers from the early stage (ES) colonies had a mean head width of 1.08 ± 0.07 mm ($N = 57$). The workers raised from the intermediate stage (IS) colonies (head width: 1.15 ± 0.06 mm, $N = 50$) were significantly larger than the workers from the ES colonies (*t*-test: $p < 0.001$, $df = 105$, $t = -5.35$) (Fig. 2). The density distribution shows considerable overlap in head width, and it seems that the late IS cohort consisted of a fairly large share of small workers.

3.2. Survival

The IS workers had significantly shorter lives than the ES workers ($n = 310$, events = 260, coefficient = -1.07 , $p < 0.001$). The survival curves of the treatments as well as of the cohorts within the treatments

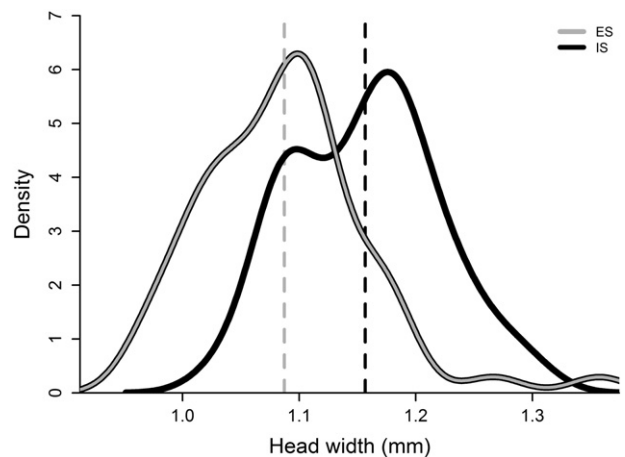


Fig. 2. Density plot showing the head width of the different experimental groups. The head widths of cohorts derived from early stage colonies (ES, $N = 57$) (gray) and of cohorts derived from two-year-old intermediate stage colonies (IS, $N = 50$) (black) were different (*t*-test: $p < 0.001$, $df = 105$, $t = -5.35$). The dashed lines indicate mean head width.

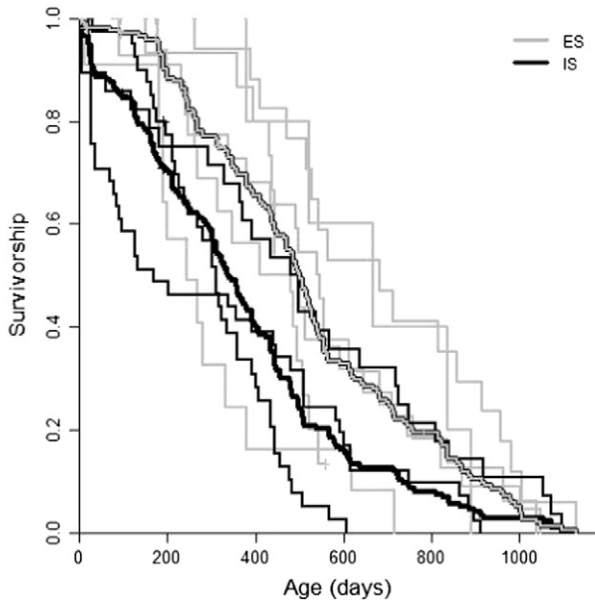


Fig. 3. Survivorship of workers hatched in colonies at different developmental stages. The fat gray line represents workers from the pooled cohorts derived from the early stage colonies (ES), while the thin gray lines represent the survival of the six individual cohorts. The bold black line represents the workers from the pooled cohorts derived from the intermediate stage colonies (IS), and the thin lines represent the three individual cohorts. The IS cohorts had significantly shorter lives (Cox-ph: $n = 3104$, events = 260, coefficient = -1.07 , $p < 0.001$).

are shown in Fig. 3. For the ES colonies the mean lifespan was 434.35 ± 43.58 days (95% CI), and the maximum lifespan was 1129 days. In contrast, the mean lifespan for the IS colonies was lower, at 309.23 ± 36.24 days (95% CI); and the maximum lifespan was shorter, at only 1094 days.

Further insights can be gained by looking at the plots of the Gompertz hazard fits and the 95% confidence intervals in Fig. 4. The ES cohorts had lower age-dependent mortality rates until about 400 days

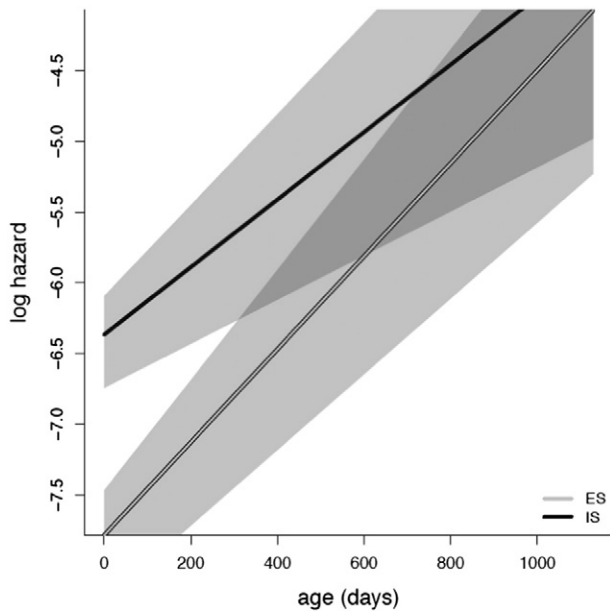


Fig. 4. Log hazard rates and 95% confidence intervals of a Gompertz model fitted to the data presented in Fig. 3. The gray line refers to a Gompertz hazard for the cohorts derived from early stage colonies (ES; $h(\text{Age}) = 0.000416 + \exp(0.003287 * t)$); the black line refers to the Gompertz hazard for the cohorts derived from intermediate stage colonies (IS; $h(\text{Age}) = 0.001719 + \exp(0.002387 * t)$). Confidence intervals for each of the fits are shown as shaded polygons.

of age, after which the mortality rates of the cohorts were indistinguishable.

This finding is confirmed by CoxPH regression analysis of the quartiles of individual deaths: the first 50% of deaths (first and second quartiles, see Table 1) occurred earlier in the IS cohort. After half of the individuals of each cohort had died, the cohorts were indistinguishable with respect to mortality risk.

Diminishing experimental cohort size over time modeled as a time-varying covariate in a CoxPH regression model was not a significant determinant of mortality. The only covariates in the minimum model were cohort size (coefficient = -0.009 , $p = 0.102$), which turned out to be non-significant; and experimental treatment (coefficient = 0.28 , $p < 0.001$).

4. Discussion

Information on worker lifespan in ants is generally scarce, and this is the first study on the lifespan of a monomorphic ant worker caste during establishment in the life course of a colony. Our results indicate that worker size and lifespan are determined by the stage of the colony workers hatched in: early stage (ES) colonies produced smaller workers that lived longer than workers from intermediate stage (IS) colonies, even when the workers that hatched in colonies at different stages were kept in a similar social environment. The tendency for worker body size to increase throughout colony development has been described before (Mailleux et al., 2003).

Furthermore, we show that the differences in the mean lifespans of the ES and the IS workers were attributable to different rates of age-dependent mortality before the workers were 400 days old. After they reached an age of around 400 days, the rates of aging among the workers in both groups were high, and indistinguishable (Fig. 4). With conditions for the experimental cohorts being identical, these differences in mortality risk must have been established during larval development in the source colony.

Our finding that there were differences in worker survival confirms our hypothesis that larger colonies produce shorter lived workers, and is in line with the results of a comparative study across several species of social insects with different average colony sizes (Kramer and Schaible, 2013b). It appears that during the growth phase individual colonies follow a specific pattern that mimics a general pattern found across species: i.e., as colonies grow larger, workers live shorter lives. This was also found to be the case in honey bee workers that were transferred into differently sized colonies (Rueppell et al., 2009).

Worker lifespan thus appears to be a plastic trait that is shaped by both proximate and ultimate factors. Currently, however, these factors are little understood (Kramer et al., 2016; Negroni et al., 2016). Here, we focus on two factors only: differences in the developmental stage of the natal colonies and differences in body size. Lifespan was shorter in the larger (IS) workers. This may be indicative of lifespan costs associated with larger body size that are caused by faster growth or a prolonged growth period, as has been shown in some mammals (Patronek et al., 1997; Miller et al., 2002; Rollo, 2002). An asymptotic

Table 1

Comparisons of the truncated survival curve between workers from early/small (ES) and two-year-old/large colonies (IS) (CoxPH). First 25% (50%): only the first 25% (50%) of individuals that died in each treatment entered the analysis. Last 25% (50%): only the last 25% (50%) of the individuals that died entered the analysis.

Subset	N	Events	Coefficient	P
First 25%	96	53	-1.479	<0.001
Second 25%	99	96	-0.616	0.006
Third 25%	97	93	0.161	0.469
Last 25%	98	96	-0.427	0.755
First 50%	195	149	-1.088	<0.001
Middle 50%	200	193	-0.928	<0.001
Last 50%	197	191	-0.446	0.921

body size and growth rate during larval development are regulated by the natal colony, and presumably affect the demographic properties of the individuals. But the link between worker body size and lifespan in social insects remains unclear, as body size and lifespan may be positively or negatively associated (Calabi and Porter, 1989; Camargo et al., 2007; Chapuisat and Keller, 2002).

An alternative explanation for this relationship has been offered by studies on worker lifespan of *O. smaragdina* and *A. subterranea* (Camargo et al., 2007; Chapuisat and Keller, 2002). Workers in these species with polymorphic worker castes exhibit much larger morphological differences than *L. niger* workers, and show a negative association of body size and lifespan that may be linked to task specialization and corresponding mortality (Chapuisat and Keller, 2002). Thus, the extended lifespan of workers produced in small *L. niger* colonies may have evolved as a response to reduced extrinsic risk, instead of being a physiological constraint of reduced growth. In fact, small workers produced in newly formed colonies of *L. niger* have been shown to be more efficient in brood-rearing than larger workers, which are more efficient at foraging. Moreover, it has been shown that workers in larger colonies (>75 individuals) of *L. niger* tend to forage cooperatively, whereas workers in small colonies are more likely to engage in individual foraging (Mailleux et al., 2003). This pattern may suggest that there is a tendency toward task specialization across the different worker cohorts, and that each role carries its own extrinsic mortality risk. This specialization may have in turn led to the evolution of different aging phenotypes (Porter and Tschinkel, 1986; Mailleux et al., 2003; Hölldobler and Wilson, 1990).

Apart from a proximate trade-off between body size and lifespan, the observed differences between size and the rate of aging among the ES and the IS workers may have evolved as a response to demands at the colony level. During independent and claustral colony foundation, resources from the queen's body can be either invested in the production of a higher number of smaller workers, or in fewer workers with a larger body size. It has been shown in *L. niger* that the size of the colony positively affects the colony's survival during these early weeks (Oster and Wilson, 1978). Selection acting on increased colony survival would favor more numerous and smaller workers with longer lifespans (Mailleux et al., 2003). Once a critical colony size is reached and the risk of colony extinction due to low worker numbers is minimal, larger workers with a higher capacity for resource acquisition are produced. These larger workers also tend to engage in riskier behavior, and are therefore more likely to die from extrinsic causes (Mailleux et al., 2003). However, the loss of an individual worker is less detrimental in larger colonies, as there are more individuals to replace the dead workers (Strassmann, 1985; Rueppell et al., 2009).

Social complexity, including the degree of caste differentiation and of task specialization, increases with colony size. In general, large colonies can only be maintained by species with polymorphic worker castes, as social complexity makes the increasing specialization (e.g., morphological and behavioral specialization) of workers a necessity. (Alexander et al., 1991; Bourke, 1999; Changizi et al., 2002; Hölldobler and Wilson, 1990). This pattern can also be seen in species with a monomorphic worker caste, in which the workers develop morphological differences as the colony grows in size (Wilson, 1976). These morphological differences among the workers may indicate that they perform different tasks, and thus have different levels of mortality risk. It is tempting to speculate that the IS cohort in our case did not consist of larger workers only. Rather, as the little peak to the left of the main peak in the size distribution (Fig. 2) shows, small workers were still present in the intermediate IS cohort. The hazard curves in Fig. 4 confirm this observation. The slope of the hazard in the IS group is lower than the slope of the hazard in the ES group. It is possible that the large workers with a high mortality risk died earlier, while the small workers in the IS group with a low mortality risk remained in the cohort for a longer period of time. This may have led to a reduction in the slope of the hazard; an effect that is known to occur when there is

heterogeneity in mortality risk among the individuals of a cohort (Vaupel and Yashin, 1985). As a result, the two hazard lines converge at higher ages (see Fig. 4), when presumably only small workers are left in both ES and the IS cohorts. It is therefore possible that in a species with a seemingly monomorphic worker caste, differences between the individual workers accrue as the colony increases in size (Seligmann, 1999; Thomas and Elgar, 2003; Holbrook et al., 2011).

Another line of argumentation for why colonies would increasingly invest in larger, costlier workers as they grow in size is that ergonomic optimization during colony ontogeny might result in shifting optimal worker body sizes. This is especially likely to occur in species with monomorphic worker castes (Oster and Wilson, 1978; Schmid-Hempel, 1992; Tschinkel, 1993). Following Jeanne (1986), there are two ways to optimize the net energy a worker can contribute to the colony. First, the production costs of a worker can change. As the production of larger workers is more costly, the potential resource loss is greater if a larger worker dies by predation than if a smaller worker is lost (Calabi and Porter, 1989). Second, the production costs of each larger worker can be counterbalanced by the reduction in maintenance costs (Calabi and Porter, 1989). Compared to their smaller counterparts, larger *L. niger* workers are more efficient foragers, and have lower mass-specific metabolic costs. Thus, the net gain of resources obtained with each foraging trip increases (Mailleux et al., 2003). Ergonomic selection could, therefore, ultimately lead to an increase in the net energy contributed by each worker, depending on the state of the colony (Oster and Wilson, 1978; Jeanne, 1986; Kramer and Schaible, 2013a).

We conclude that the differences in rates of aging of the ES and the IS cohorts are attributable to the source colonies the workers hatched in, and not from the social environment in the experimental setup, which was similar for all cohorts. Given that the maximum lifespan of *L. niger* queens is 28 years, and that *L. niger* queens are unlikely to show reproductive senescence over their lifespan (Hölldobler and Wilson, 1990; Heinze et al., 2013), especially during the first two years of life, it is unlikely that age rather than colony size would trigger life history decisions leading to shorter lived workers. Although we cannot disentangle the issue of whether body size is the sole driver of the survival differences, or whether larger colonies produce workers of lower quality than small colonies, it is clear that both body size and lifespan are parameters under the control of the colony the workers are born into.

5. Conclusions

Our study provides further evidence of a pattern that is commonly found in social insects: as colonies grow, workers live shorter lives. This shortening of the lifespan in large colonies is associated with a morphological change; worker size becomes more variable, with most workers attaining larger body sizes. As the colony switches to cooperative foraging, which coincides with the production of larger workers, the quality of the worker, measured in terms of mortality risk, changes. These changes are due to the higher levels of extrinsic risk faced by the worker in a more complex environment. At the same time, larger colonies have higher survival probabilities, and the loss of an individual worker is less detrimental to the colony. Due to the increased redundancy of the workforce, a shorter worker lifespan may be beneficial for the colony, as reduced costs can alter the cost-benefit ratio of individual workers.

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References

- Alexander, R.D., Noonan, K.M., Crespi, B.J., 1991. The evolution of eusociality. In: Sherman, P.W., Jarvis, J.U.M., Alexander, R.D. (Eds.), *The Biology of the Naked Mole-Rat*. Xvi + 518p. Princeton University Press, Princeton, New Jersey, USA. Illus. Maps.
- Amdam, G.V., Omholt, S.W., 2002. The regulatory anatomy of honeybee lifespan. *J. Theor. Biol.* 216 (2), 209–228.
- Billick, I., 2003. Worker demography in the ant *Formica neorufibarbis*. *Ecol. Entomol.* 28 (2), 139–144. <http://dx.doi.org/10.1046/j.1365-2311.2003.00503.x>.
- Bourke, A.F.G., 1999. Colony size, social complexity and reproductive conflict in social insects. *J. Evol. Biol.* 12 (2), 245–257. <http://dx.doi.org/10.1046/j.1420-9101.1999.00028.x>.
- Burnham, K., Anderson, D., 1998. *Model Selection and Inferences*. Springer Verlag, New York.
- Calabi, P., Porter, S.D., 1989. Worker longevity in the fire ant *Solenopsis invicta*: ergonomic considerations of correlations between temperature, size and metabolic rates. *J. Insect Physiol.* 35 (8), 643–649. [http://dx.doi.org/10.1016/0022-1910\(89\)90127-3](http://dx.doi.org/10.1016/0022-1910(89)90127-3).
- Camargo, R.S., Forti, L.C., Lopes, J.F.S., Andrade, A.P.P., Ottati, A.L.T., 2007. Age polyethism in the leaf-cutting ant *Acromyrmex subterraneus brunneus* Forel, 1911 (Hym., Formicidae). *J. Appl. Entomol.* 131 (2), 139–145. <http://dx.doi.org/10.1111/j.1439-0418.2006.01129.x>.
- Changizi, M., McDannald, M., Widders, D., 2002. Scaling of differentiation in networks: nervous systems, organisms, ant colonies, ecosystems, businesses, universities, cities, electronic circuits, and legos. *J. Theor. Biol.* 218 (2), 215–237. <http://dx.doi.org/10.1006/jtbi.2002.3070>.
- Chapuisat, M., Keller, L., 2002. Division of labour influences the rate of ageing in weaver ant workers. *Proc. R. Soc. B* 269 (1494), 909–913. <http://dx.doi.org/10.1098/rspb.2002.1962>.
- Core Development Team, R., 2010. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Austria, Vienna.
- Crawley, M.J., 2002. *Statistical Computing: An Introduction to Data Analysis Using S-Plus*. Wiley.
- Fukuda, H., Sekiguchi, K., 1966. Seasonal change of the honeybee worker longevity in Sapporo, North Japan, with notes on some factors affecting the life-span. *Jpn. J. Ecol.* 16 (5), 206–212.
- Heinze, J., Schrempf, A., 2008. Aging and reproduction in social insects – a mini-review. *Gerontology* 54 (3), 160–167. <http://dx.doi.org/10.1159/000122472>.
- Heinze, J., Frohschammer, S., Bernadou, A., 2013. Queen life-span and total reproductive success are positively associated in the ant *Cardiocondyla cf. kagutsuchi*. *Behav. Ecol. Sociobiol.* 67 (10), 1555–1562. <http://dx.doi.org/10.1007/s00265-013-1567-9>.
- Holbrook, C.T., Barden, P.M., Fewell, J.H., 2011. Division of labor increases with colony size in the harvester ant *Pogonomyrmex californicus*. *Behav. Ecol.* 22 (5), 960–966. <http://dx.doi.org/10.1093/beheco/arr075>.
- Hölldobler, B., Wilson, E.O., 1990. *The Ants*. In: Hölldobler, B., Wilson, E.O. (Eds.), *The Ants*. Xiii + 732p. Harvard University Press, Cambridge, Massachusetts, USA (Illus. Maps: XIII + 732P).
- Huang, Z.-Y., Robinson, G.E., 1996. Regulation of honey bee division of labor by colony age demography. *Behav. Ecol. Sociobiol.* 39 (3), 147–158. <http://dx.doi.org/10.1007/s002650050276>.
- Jeanne, R.L., 1986. The evolution of the organization of work in social insects. *Monit. Zool. Ital* 20 (2), 119–133.
- Jemielni, S., Chapuisat, M., Parker, J.D., Keller, L., 2005. Long live the queen: studying aging in social insects. *Age* 27 (3), 241–248. <http://dx.doi.org/10.1007/s11357-005-2916-z>.
- Keller, L., Genoud, M., 1997. Extraordinary lifespans in ants: a test of evolutionary theories of ageing. *Nature* 389 (6654), 958–960. <http://dx.doi.org/10.1038/40130>.
- Keller, L., Passera, L., 1989. Size and fat content of gynes in relation to the mode of colony founding in ants (Hymenoptera; Formicidae). *Oecologia* 80 (2), 236–240. <http://dx.doi.org/10.1007/bf00380157>.
- Kramer, B.H., Schaible, R., 2013a. Life span evolution in eusocial workers—a theoretical approach to understanding the effects of extrinsic mortality in a hierarchical system. *PLoS One* 8 (4), e61813. <http://dx.doi.org/10.1371/journal.pone.0061813>.
- Kramer, B.H., Schaible, R., 2013b. Colony size explains the life span differences between queens and workers in eusocial Hymenoptera. *Biol. J. Linn. Soc.* 109, 710–724. <http://dx.doi.org/10.1111/bij.12072>.
- Kramer, B.H., Sander van Doorn, G., Weissing, F.J., Pen, I., 2016. Lifespan divergence between social insect castes: challenges and opportunities for evolutionary theories of aging. *Curr. Opin. Insect Sci.* 16, 76–80. <http://dx.doi.org/10.1016/j.cois.2016.05.012>.
- Kutter, H., Stumper, R., 1969. Sixth International Congress of the International Union for the Study of Social Insects, September 15–20, Bern, Switzerland.
- Mailleux, A.-C., Deneubourg, J.-L., Detrain, C., 2003. How does colony growth influence communication in ants? *Insect. Soc.* 50 (1), 24–31. <http://dx.doi.org/10.1007/s00400300004>.
- Miller, R.A., Harper, J.M., Galecki, A., Burke, D.T., 2002. Big mice die young: early life body weight predicts longevity in genetically heterogeneous mice. *Aging Cell* 1 (1), 22–29.
- Münch, D., Amdam, G.V., Wolschin, F., 2008. Ageing in a eusocial insect: molecular and physiological characteristics of life span plasticity in the honey bee. *Funct. Ecol.* 22 (3), 407–421. <http://dx.doi.org/10.1111/j.1365-2435.2008.01419.x>.
- Negrone, M.A., Jongepier, E., Feldmeyer, B., Kramer, B.H., Foitzik, S., 2016. Life history evolution in social insects: a female perspective. *Curr. Opin. Insect Sci.* 16, 51–57. <http://dx.doi.org/10.1016/j.cois.2016.05.008>.
- O'Donnell, S., Jeanne, R.L., 1992. Lifelong patterns of forager behaviour in a tropical swarm-founding wasp: effects of specialization and activity level on longevity. *Anim. Behav.* 44 (6), 1021–1027. [http://dx.doi.org/10.1016/s0003-3472\(05\)80314-8](http://dx.doi.org/10.1016/s0003-3472(05)80314-8).
- O'Donnell, S., Jeanne, R.L., 1995a. Implications of senescence patterns for the evolution of age polyethism in eusocial insects. *Behav. Ecol.* 6 (3), 269–273. <http://dx.doi.org/10.1093/beheco/6.3.269>.
- O'Donnell, S., Jeanne, R.L., 1995b. Worker lipid stores decrease with outside-nest task-performance in wasps – implications for the evolution of age polyethism. *Experientia* 51 (7), 749–752. <http://dx.doi.org/10.1007/bf01941274>.
- Oster, S.D., Wilson, E.O., 1978. *Caste and ecology in the social insects*. In: May, R.M. (Ed.), *Monographs in Population Biology*. vol. 12 (352pp).
- Parker, J.D., 2011. What are social insects telling us about aging? *Myrmecol. News* 13, 103–110.
- Patronek, G.J., Waters, D.J., Glickman, L.T., 1997. Comparative longevity of pet dogs and humans: implications for gerontology research. *J. Gerontol. Sci. Med. Sci.* 52 (3), B171–B178. <http://dx.doi.org/10.1093/gerona/52a.3.b171>.
- Pletcher, S.D., 1999. Model fitting and hypothesis testing for age-specific mortality data. *J. Evol. Biol.* 12 (3), 430–439. <http://dx.doi.org/10.1046/j.1420-9101.1999.00058.x>.
- Porter, S.D., Tschinkel, W.R., 1986. Adaptive value of nanitic worker in newly founded red imported fire ant colonies (*Hymenoptera formicidae*). *Ann. Entomol. Soc. Am.* 79 (4), 723–726. <http://dx.doi.org/10.1093/aesa/79.4.723>.
- Ribbands, C.R., 1952. Division of labour in the honeybee community. *Proc. R. Soc. B* 140, 32–43. <http://dx.doi.org/10.1098/rspb.1952.0041>.
- Robinson, G.E., 1992. Regulation of division-of-labor in insect societies. *Annu. Rev. Entomol.* 37, 637–665. <http://dx.doi.org/10.1146/annurev.ento.37.1.637>.
- Rollo, C.D., 2002. Growth negatively impacts the life span of mammals. *Evol. Dev.* 4 (1), 55–61. <http://dx.doi.org/10.1046/j.1525-142x.2002.01053.x>.
- Rueppell, O., Bachelier, C., Fondrk, M.K., Page, R.E., 2007. Regulation of life history determines lifespan of worker honey bees (*Apis mellifera* L.). *Exp. Gerontol.* 42 (10), 1020–1032. <http://dx.doi.org/10.1016/j.jexger.2007.06.002>.
- Rueppell, O., Kaftanoglou, O., Page, R.E., 2009. Honey bee (*Apis mellifera*) workers live longer in small than in large colonies. *Exp. Gerontol.* 44 (6–7), 447–452. <http://dx.doi.org/10.1016/j.jexger.2009.04.003>.
- Schmid-Hempel, P., 1992. Worker castes and adaptive demography. *J. Evol. Biol.* 5 (1), 1–12. <http://dx.doi.org/10.1046/j.1420-9101.1992.5010001.x>.
- Seligmann, H., 1999. Resource partition history and evolutionary specialization of subunits in complex systems. *Biosystems* 51 (1), 31–39. [http://dx.doi.org/10.1016/s0303-2647\(99\)00011-8](http://dx.doi.org/10.1016/s0303-2647(99)00011-8).
- Strassmann, J.E., 1985. Worker mortality and the evolution of castes in the social wasp *Polistes exclamans*. *Insect. Soc.* 32 (3), 275–285. <http://dx.doi.org/10.1007/bf02224916>.
- Therneau, T., Lumley, T., 2011. *Survival: Survival Analysis, Including Penalised Likelihood*. R Package Version 2 (36-5).
- Thomas, M., Elgar, M., 2003. Colony size affects division of labour in the ponerine ant *Rhytidoponera metallica*. *Naturwissenschaften* 90 (2), 88–92. [http://dx.doi.org/10.1016/0020-1790\(81\)90008-1](http://dx.doi.org/10.1016/0020-1790(81)90008-1).
- Tofilski, A., 2002. Influence of age polyethism on longevity of workers in social insects. *Behav. Ecol. Sociobiol.* 51 (3), 234–237. <http://dx.doi.org/10.1007/s00265-001-0429-z>.
- Toomet, O., Henningsen, A., 2010. maxLik: Maximum Likelihood Estimation. With Contributions from Spencer Graves. R package version 0.7-2. URL <http://CRAN.R-project.org/package=maxLik>.
- Tschinkel, W.R., 1988. Colony growth and the ontogeny of worker polymorphism in the fire ant, *Solenopsis invicta*. *Behav. Ecol. Sociobiol.* 22 (2), 103–115. <http://dx.doi.org/10.1007/bf00303545>.
- Tschinkel, W.R., 1993. Sociometry and sociogenesis of colonies of the fire ant *Solenopsis invicta* during one annual cycle. *Ecol. Monogr.* 63 (4), 425–457. <http://dx.doi.org/10.2307/2937154>.
- Vander Meer, R.K., Saliwanchik, D., Lavine, B., 1989. Temporal changes in colony cuticular hydrocarbon patterns of *Solenopsis invicta*: implications for nestmate recognition. *J. Chem. Ecol.* 15 (7), 2115–2125. <http://dx.doi.org/10.1007/bf01207442>.
- Vaupel, J.W., Yashin, A., 1985. Heterogeneity's ruses: some surprising effects of selection on population dynamics. *Am. Stat.* 39 (3), 176–185. <http://dx.doi.org/10.2307/2683925>.
- Wilson, E.O., 1976. Behavioral discretization and number of castes in an ant species. *Behav. Ecol. Sociobiol.* 1 (2), 141–154. <http://dx.doi.org/10.1007/BF00299195>.
- Woyciechowski, M., Moron, D., 2009. Life expectancy and onset of foraging in the honeybee (*Apis mellifera*). *Insect. Soc.* 56 (2), 193–201. <http://dx.doi.org/10.1007/s00040-009-0012-6>.