



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.

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