Insectes Sociaux (2026) 73:91–99
https://doi.org/10.1007/s00040-025-01032-2

Insectes Sociaux

RESEARCH ARTICLE

No correlation between mother and daughter life-history traits in *Cardiocondyla obscurior*

L. M. Jaimes-Nino[1,2] · J. Oettler[2]

Received: 28 October 2024 / Revised: 25 February 2025 / Accepted: 17 March 2025 / Published online: 12 May 2025

Abstract
Fitness variation among individuals can be explained by both genetic and non-genetic factors, such as maternal age. Little is known about the genetic and non-genetic factors influencing fitness variation in ant queens. From queens of the ant *Cardiocondyla obscurior* exhibiting either high or low fertility, we set up genetic lines and found no correlation between maternal and daughter queen lifetime fertility or lifespan, indicating low heritability of life-history traits. However, differences in fertility suggest that developmental variation is influenced by the maternal environment or by mate quality. Finally, we found that maternal age, specifically the remaining reproductive output of the mother, had no effect on daughter fitness traits. This is coherent with the hypothesis that senescence in ant queens is selected against until very old ages because of late-life fitness gains.

Keywords Continuusparity · Fertility · Longevity · Social insects · Trait heritability

Introduction

Parents can contribute both genetically and non-genetically to their offspring's fitness. Early theory predicted that traits related to fitness are weakly explained by genetic variation and exhibit low heritability, because alleles conferring highest fitness will be driven quickly to fixation by natural selection in a population in equilibrium (Fisher 1930 in Fisher 1999). Traits less directly associated with fitness should, on the other hand, have a higher genetic variation, e.g., morphological traits compared to lifetime reproductive success and survival, more examples reviewed in (Visscher et al. 2008). However, later studies showed that fitness-related traits often exhibit higher levels of additive genetic variance (i.e., effect due to individual alleles) compared to non-fitness traits (Houle 1992), likely due to a larger number of loci associated with fitness (Merilä and Sheldon 1999). For instance, studies in *Drosophila melanogaster* showed that much of the lifetime fertility in adult female fitness was attributable to genotype (Long et al. 2009; Pischedda and Chippindale 2006). Moreover, in social insects, the existence of supergenes, i.e., non recombinant genomic regions linked to complex traits (e.g., colony founding strategy, queen number, and queen size) of *Solenopsis invicta*, *Formica* spp., and *Pogonomymex californicus*, imply that variation in queen fertility can be genetically explained (De Gasperin et al. 2024; Errbii et al. 2024a; Purcell et al. 2014; Ross 1992; Scarparo et al. 2023; Wang et al. 2013).

Other than genetic contribution, non-genetic developmental factors can explain offspring variation, i.e., effects of the parental phenotype on the offspring phenotype that cannot solely be ascribed to the parental or offspring genome (Uller 2008). Parental effects are predicted to occur if there is a strong correlation between the parent and the offspring environment, or if the offspring environment is a direct consequence of the parental phenotype (Uller 2008). For example, the parental social environment of *D. melanogaster* affects offspring body weight and lipid composition (Morimoto 2022), and the mother's nutritional state affects the offspring's performance under malnutrition leading to plasticity in behavior (Vijendravarma et al. 2012). In ants, the parental social environment can affect body size of worker offspring (Jaimes-Nino et al. 2022), but little is known about the genetic and non-genetic factors influencing fitness variation in ant queens.

✉ L. M. Jaimes-Nino
jaimes.luisa@outlook.com

[1] Institute of Organismic and Molecular Evolution, Johannes Gutenberg University, 55128 Mainz, Germany

[2] Zoologie/Evolutionsbiologie, Universität Regensburg, 93053 Regensburg, Germany

Parental effects can also negatively influence offspring traits, for example parental age, known as the "Lansing effect" (Lansing 1947). Sensu stricto, it refers to the negative effect on offspring survival, and sensu lato, it can comprise negative effects ranging from developmental time, mass at maturity, to fertility (Zehnder et al. 2007). Potential causes are changes in parental care or provisioning (Limmer and Becker 2009), the transmission of epigenetic factors (Plaistow et al. 2015; Schroeder et al. 2015), or variations in the developmental environment (Brown and Shine 2009). The evolutionary implications of the Lansing effect are significant, because early produced offspring may have higher fitness value for parents compared to offspring produced later in life (Smith and Fretwell 1974). Theoretically, a reduction in the value of late-life reproduction leads to steeper age-related declines in the force of natural selection (Barks and Laird 2020). A meta-analysis revealed a tendency for a Lansing Effect in insects (Orthoptera, Hemiptera, Coleoptera), with an estimated effect of maternal age on offspring's lifespan of up to −22% (Ivimey-Cook et al. 2023). To the best of our knowledge, a Lansing Effect has not been studied in a social insect. Given that social insects are highly fertile at old ages (Jaimes-Nino et al. 2022; Korb and Heinze 2021; Kramer et al. 2015), and first build a workforce before the colony invests in sexual reproduction (Oster and Wilson 1978), it is important to determine if late produced offspring is less fit. Further, recent findings showed that ant queens of *Cardiocondyla obscurior* exhibit senescence, i.e., a decrease in reproduction and increase in mortality with age, only shortly before death (Jaimes-Nino et al. 2022). We thus predicted that a Lansing effect is less likely to occur in ant queens given their long healthspan.

Here, we tested for genetic and non-genetic effects on offspring fitness using queens of the ant species *Cardiocondyla obscurior*. Specifically, we ask (1) whether there are differences in the life-history traits fertility and longevity across maternal lineages, (2) whether mother and daughter life-history traits are correlated, and (3) whether daughter fitness is affected by maternal age?

Methods

Model organism and maintenance

Cardiocondyla obscurior (Formicidae: Myrmicinae), the two-colored heart node ant, forms small colonies in trees and shrubs around the tropics and subtropics (Oettler 2021). Queens show high variability in egg productivity and lifespan within the same population; they produce on average 300 (± 198 SD) offspring and live on average 25 weeks (± 8 SD) (Jaimes-Nino et al. 2022). Colonies are polygynous (composed of several queens), workers lack ovaries and are completely sterile. Two male morphs are found in this species, a wingless ergatoid (i.e., worker-like) male equipped with long, sickle-shaped mandibles which they employ in lethal fights with rival males to monopolize reproduction; and winged males that are occasionally found (Heinze 2017; Heinze et al. 2005; Oettler et al. 2010). Colony size ranges from a few workers up to 150 (median = 28.5, SD = 31.4, $n = 62$) in their natural habitat (Jaimes-Nino et al. 2022), but can reach larger numbers in contained laboratory colonies when being given nesting space. The ants used here were collected in 2011 from bark cavities in coral trees (*Erythrina* sp.) in Japan (Errbii et al. 2021; Schrader et al. 2014), transferred to Regensburg, and thereafter propagated in the lab for several years. Experimental colonies were set up from these highly inbred stock colonies. All colonies were kept in a climate-controlled room on a 12 h dark 22 °C/12 h light 26 °C cycle, with 75–80% humidity, and fed ad libitum with honey, cockroaches, and flies three times per week.

Selection of maternal queens

To obtain maternal lines showing natural variation in fitness, we took advantage of a previous study where single queens were monitored for life (Jaimes-Nino et al. 2022, Supplementary File 2). These queens were allowed to mate with a single wingless male from the natal colony, which were then kept in standardized colonies for life (10, 20, or 30 workers; corresponding to natural colony size), and fertility and lifespan were monitored weekly.

After 15 weeks, we selected 9 low and 7 high productive queens based on their egg productivity in the first 15 weeks after mating. Low productive queens were defined as queens producing less than 200 eggs and high productive as queens producing more than 200 eggs [median eggs at 15 weeks = 151, $N = 108$, data in (Jaimes-Nino et al. 2022) and this study].

The maternal age at the eclosure of the daughter queens was recorded (median = 31, range: 25–43 weeks), and the point of oviposition was estimated to be 5 weeks prior to eclosure, approximately the developmental time from egg to adult. The largest range in age from a single mother from which we obtained daughter queens was 10 weeks (Queen A30_10, maternal-age range: 28–38 weeks). The maternal age at death was recorded for 10 of the 16 mother queens. The remaining six had been sacrificed for RNAseq after egg laying ceased at an old age (in Jaimes-Nino et al. 2022), meaning that most of the maternal egg production was censored.

Daughter queens' productivity

In this species, queens typically mate once in the natal nest with a related wingless ergatoid male (Heinze 2017; Heinze et al. 2005; Oettler et al. 2010). Daughter queens and males were collected at the pupal stage and transferred to a new

nest with ten workers from the stock colony of the maternal queen. Males were left in the nest until they died. Colony size was standardized to 10 workers monthly, starting from the tenth week after the daughter queen had enclosed. The productivity of the daughter queens (egg, workers, and pupae production) was recorded monthly. Newly produced sexuals were counted and removed weekly. A total of 56 daughter queens successfully mated, 1–6 per maternal queen. The lifespan of 54 daughter queens was monitored. The precise date of death of two daughter queens is unknown but estimated ± 2 weeks. Colonies were monitored until the last eggs had developed into a pupa, ca. 4 weeks after the queen's death.

Statistical analyses

Differences across maternal lineages

To test for a lineage effect on the daughters' fertility, we implemented a model as follows:

Daughter_egg_production ~ Maternal_ID
+ (1 | Recorded_dead)

using a negative binomial distribution (nbinom2 in glmmTMB, v. 1.1.2.3; Pinheiro et al. 2011). All models were checked for correct distribution (KS test), dispersion and outliers using the function *simulateResiduals* (DHARMA package version 0.4.6, Hartig 2020). We detected overall residual deviations from the expected distribution by checking graphically the residuals and the qq-plot (DHARMA package). We used the Anova test to report the X^2 of the model (car package, v.3.1-3), and we used the *glht* function (multcomp R package, v.1.4-20) as a post hoc test to compare multiple means. Similar models were implemented exchanging egg production for queen pupa production (nbinom2 distribution) and caste ratio (Gaussian distribution).

The survival probabilities of the daughter queens among maternal queens were modeled using the *coxme* function (coxme R package v. 2.2-16)

coxme(Surv(Week, Death) ~ (Maternal_ID)+(1|Recorded_dead)

and tested with a likelihood ratio tests (anova function, stats package v. 4.4.1) compared to a model without the Maternal_ID fixed term.

Fertility

We tested whether daughter productivity correlates with maternal productivity (eggs, worker pupae, and queen pupae). We also investigated whether a known effect of the maternal colony size on worker body size in this species (Jaimes-Nino et al. 2022), which also influenced daughter queen productivity, by including the variable maternal colony size into the model as

Daughter_egg_production ~ Maternal_egg_production
+ Maternal_colony_size + (1|Maternal_ID),

using a nbinom2 model distribution with a zero-inflation component (zi = ~1). The zero-inflation component was used in the model to account for excess zeros given that it showed a significant effect (Estimate = −4.179, SE = 1.207, $z = -3.462$, $p < 0.001$). The DHARMa residual diagnostics also confirmed that the ZINB model improved residual dispersion and accounted for the observed zero excess. We included a random effect of the maternal nest, given that we found a significant effect of maternal lineage in the previous section. Similar models were implemented exchanging egg production for queen pupa production and caste ratio, without the need of a zero-inflation component.

Longevity and Lansing effect sensu stricto

We tested if there was a correlation between maternal and the daughter lifespan using the *coxme* function. The daughter fertility was included in the model as covariate. Further, the maternal colony ID and whether or not the censoring was completed (six mothers were sacrificed for RNAseq after egg laying ceased) were included as random effects. Additionally, we tested for a Lansing effect, specifically whether the maternal age had a negative effect on the daughter's lifespan. Because aging is a non-linear process in *C. obscurior* (Jaimes-Nino et al. 2022), we tested the maternal age using as a proxy the proportion of reproductive output remaining, with the following model:

coxme(Surv(Week, Death) ~ Maternal_Lifespan
+ Proportion_maternal_offspring_output
+ Daugther_Fertility + (1|Maternal_ID)
+(1|Recorded_dead).

We removed one data point that was highlighted as outlier given the martingale residual deviation far from 0 (< −3) using the function *residuals* (stats package v. 4.4.1.). For visualization purposes, we additionally categorized the senescence status of the mother as whether or not the mother showed reproductive senescence (i.e., a decrease in egg production, Jaimes-Nino et al. 2022, and this study) at the point of ovipositing the daughter. We tested whether senescent or not senescent mothers differed in the proportion of the reproductive output remaining using the model

Proportion_maternal_output ~ Senescent_category
+ (1|Recorded_dead).

Lansing effect sensu lato

To test if senescent mothers produced daughters with lower fitness, i.e., whether the proportion of reproductive output remaining of the mother correlates to the daughter fertility, we implemented the following model:

$$\log(\text{Daughter\_egg\_production} + 1) \sim \text{Proportion\_maternal\_output} + (1|\text{Maternal\_ID}),$$

using a Gaussian distribution, with a log transformation on the response variable. Similar models were implemented to explain the worker and queen pupae production.

Results

Maternal life-history traits

A batch of 108 single-queen colonies from a previous experiment (Jaimes-Nino et al., 2022) was used to select 9 and 7 maternal queens exhibiting low and high productivity, respectively, at 15 weeks of age (Fig. 1B). 15 weeks is a good predictor for lifetime productivity (Pearson's $r = 0.74$, df = 96, $p < 0.001$, Fig. 1A), and correlates with total female sexual productivity (Pearson's $r = 0.37$, df = 96, $p < 0.001$). Highly productive queens produced on average 344.7 (SE ± 82.4) more eggs during their whole life than the low-productive queens (lm, T-value = −4.18, $p < 0.001$, Fig. 1C), but did not differed in lifespan (Kaplan–Meier log-rank test, $X^2_1 = 0.3$, $p = 0.6$), even though total productivity and lifespan were positively correlated in the batch of 108 queens (Fig. 1C). Of the 108 maternal queens, 66 produced less than 10 males in total (61% of all queens, Supplementary Fig. 1A), and approximately 50% of all their males were laid during the lapse of a week (Supplementary Fig. 1B).

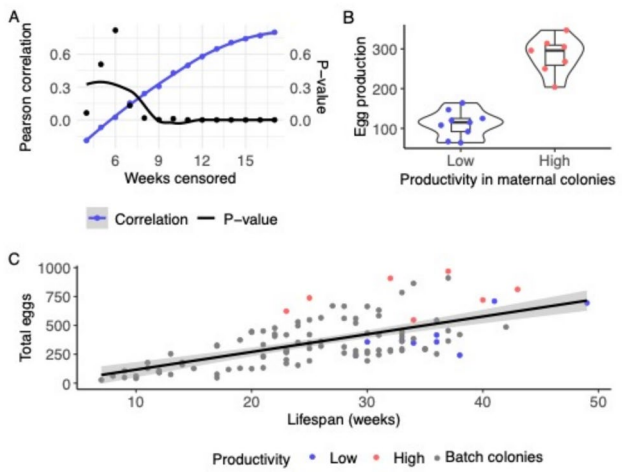

Fig. 1 Productivity of maternal single-queen colonies. **A** Estimate of total queen productivity based on the censored cumulative number of eggs laid from weeks 4 to 17 from (Jaimes-Nino et al. 2022). The blue line represents the Pearson correlation and the orange line the p value of the correlation. The graph uses a loess smoothing method and a confidence interval of 95% for the Pearson correlation. **B** Egg productivity of the 16 maternal queens at week 15 after eclosure classified as low and high productive. **C** Relation between lifespan and total fertility of the batch of 108 queens from which the 16 maternal queens were selected, indicated in blue and red as low and high productive, respectively

Differences across maternal lineages

We tested for differences in fertility and longevity across maternal lineages from which we obtained more than two daughter queens. This corresponded to a subset of 48 daughters originating from 11 maternal queens (6 low and 5 high productive). Some maternal lines were significantly more productive than others (eggs, $X^2_{10} = 22.50$, $p = 0.01$, Fig. 2A), and produced consistently more queens ($X^2_{10} = 34.73$, $p < 0.001$, Fig. 2B), but did not differ in caste ratio ($X^2_{10} = 6.32$, $p = 0.79$, Supplementary Fig. 2). On average, the maternal line E20_16 had 11.5 (SE ± 1.88) times more eggs and 16 (SE ± 2.3) times more queens than the least productive line C10_30. Adding a fixed term of the maternal lineage did not significantly improve the model fit ($X^2_{10} = 8.99$, $p = 0.53$) when explaining the longevity of the daughters.

Fertility

There was no correlation between maternal and daughter productivity (glmmTMB, eggs: z value = 0.50, $p = 0.62$, worker pupae: z value = 0.54, $p = 0.60$, queen pupae: z value = 0.52, $p = 0.60$, caste ratio: z value = −0.33, $p = 0.74$, Supplementary Fig. 3). The size of the maternal colony had no effect on the daughter's productivity (eggs: z value = 0.11, $p = 0.91$, worker pupae: z value = 0.19, $p = 0.85$, queen pupae production: z value = 0.10, $p = 0.92$), or caste ratio (z value = −0.22, $p = 0.83$).

Longevity and Lansing effect sensu stricto

Maternal and daughter lifespan were not correlated (coxme, z value = −0.24, $p = 0.81$). Additionally, in the same model, we assessed a Lansing effect by testing whether the remaining proportion of the mothers' reproductive output affected the daughter's lifespan. For visualization purposes, we classified reproductive senescence, depending on whether queens show a decrease in egg production at the point of producing

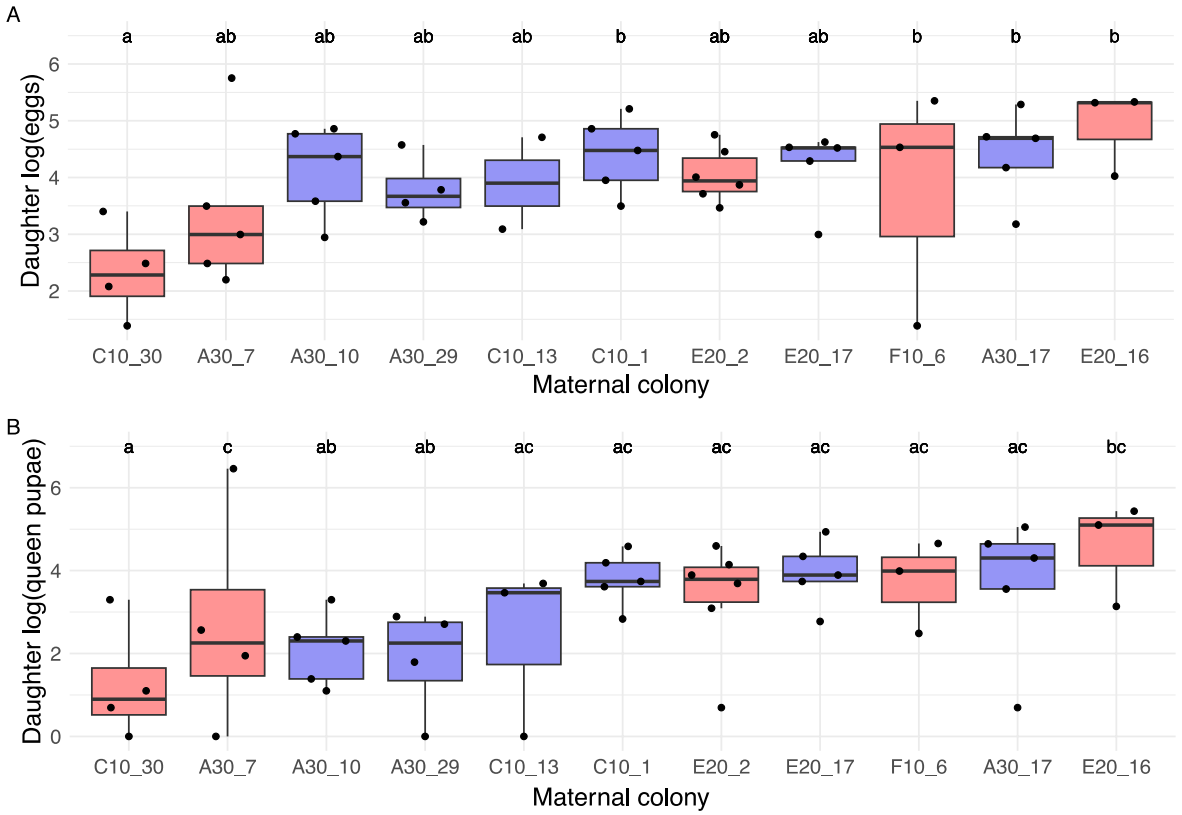

Fig. 2 Productivity of daughter colonies per maternal line. **A** Total eggs, and **B** total queen pupae produced in log scale. Different letters indicate significantly different mean estimates at p value < 0.05. Maternal queens were labeled with a letter followed by the number of workers present in the maternal colony, and an identification number. Blue and red boxes indicate mother queens classified as low and high productive, respectively

the daughter. This proportion can be used as a proxy of senescence status, as "senescent" and "not senescent" mothers differed significantly in the proportion of reproductive output accomplished (glmmTMB, z value = 6.83, $p < 0.001$, Fig. 3A). This proxy had no effect on the daughter's lifespan (coxme, z value = 0.97, $p = 0.33$, Fig. 3B) or the fertility of the mother (high vs. low, z value = 0.28, $p = 0.78$). Similarly, maternal age at oviposition and daughter lifespan were not correlated (coxme, z value = 1.37, $p = 0.17$).

Lansing effect sensu lato

The proportion of the maternal remaining reproductive output did not affect the daughters' fertility (glmmTMB, eggs: z value = −0.18, $p = 0.85$; worker pupae: z value = −0.58, $p = 0.56$; queen pupae: z value = −0.78, $p = 0.43$, Fig. 3C).

Discussion

Queens of the ant *Cardiocondyla obscurior* show a positive correlation between fertility (egg and sexual production) and lifespan (Jaimes-Nino et al. 2022; Kramer et al. 2015), but the causes of such variation are unknown. A genetic influence on worker and queen mass, caste, and sex ratio in the ant *Temnothorax curvispinosus* was suggested (Linksvayer 2006), but the study did not examine the effect past one generation and did not distinguish between genetic variation and maternal effects (Schwander et al. 2010). In *F. selysi,* the monogyne-associated genotype correlated with higher survival and larger colony sizes after 1 year of colony establishment (De Gasperin et al. 2024), but the genetic influence on the total life fertility has not been studied. Here, we selected high- and low-productive maternal queens of *C. obscurior* and monitored their daughters' life productivity.

Differences across maternal lineages

We found that the selected maternal lines differed in productivity but not in longevity. As we used long-term laboratory

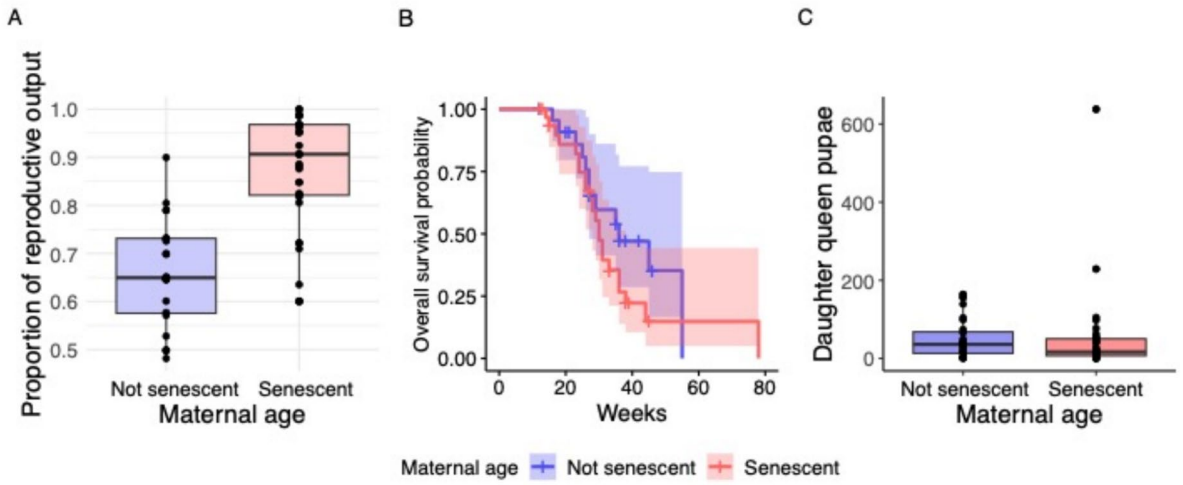

Fig. 3 No effect of maternal age on daughter's longevity and fertility. **A** The not senescent maternal's age corresponded to a median egg production of 65% of the total fertility, and the senescent to a median of 97% of the total fertility (not senescent: min = 48%, max = 90%, senescent: min = 59%, max = 100%, $n = 56$), **B** No effect of the mother's senescence status was observed on the survival probability of daughters, and **C** no effect on queen pupae production of daughter queens

colonies of this tramp ant, collected in 2011 from a population that had experienced a genetic bottleneck, we expected them to be highly inbred without much genetic variation. However, maternal lines could differ due to variations in the developing environment. For example, colony size correlates positively with the size of workers produced (Jaimes-Nino et al. 2022), suggesting that the nursing behavior by workers is decisive for adult body size. Workers in the maternal nest may similarly affect the development of queens, and could have influenced their size and associated fecundity, assuming that they are correlated. However, there was no correlation of colony size with differences between maternal lines. The next step would be a cross-fostering design where daughter queens develop in different independent nests, to disentangle the genetic component from the environmental effects.

Additionally, the observed variation in offspring fertility may be linked to the interaction between maternal and paternal genotypes and phenotypes. Studies in the Argentine ant *Linepithema humile* have shown that the maternal lineage can influence the total offspring production, and the paternal lineage the total female caste ratio, nursing, and foraging traits (Libbrecht et al. 2011; Libbrecht and Keller 2013). In *C. obscurior*, queens mate once inside the nest and wingless males generally mate with multiple females. In our experiment, males mated only once. To further understand the differences between maternal lines, one should compare replicate lines from the same male, to disentangle the maternal and the paternal genotype influence on the queen fertility. Specifically, sperm traits might affect queen fertility (Fuessl et al. 2018; Schrempf and Heinze 2008), and gene expression (Wyschetzki et al. 2015), and are known to be highly variable between wingless males, even across ejaculates of the same male (Metzler et al. 2018).

Moreover, males produced by mated queens are 90% of the wingless morph (Jaimes-Nino et al. 2022). Here we showed that most queens do not produce more than ten males during their lifetime, but instead of producing them in regular intervals of time, most of the males are laid during the lapse of a week. Wingless males are known to engage in lethal fights with other wingless morphs, ignoring other winged males (Heinze and Hölldobler 1993). This could correspond to a mechanism for selecting the fittest males, analogous to sperm competition. Afterward, wingless males mate intranidally, live up to 3 months, and generally do not disperse to other nests (Metzler et al. 2016). In our experiment, the males were selected from the pupal stage, before they had any opportunity to fight against their male nestmates, and possibly preventing an important step of sexual selection. Future studies should investigate the impact of the effect of sexual selection on the highly variable fitness of queens.

Correlation between mother and daughter life-history traits

There was no correlation between mother and daughter fertility or longevity. While traits that are strongly associated with fitness are expected to exhibit low heritability (Fisher 1999; Jones 1987), studies have shown genetic variance underlying traits such as lifetime reproductive success (Long et al. 2009; Pischedda and Chippindale 2006). We cannot rule out that the negative results are caused using inbred stock colonies with low genetic diversity. Nevertheless, high

recombination rates (Errbii et al. 2024b) and transposable element activity (Errbii et al. 2021) result in genetic variation in this species. Further, ten generations of complete sib-mating are needed to observe signs of inbreeding depression such as higher brood mortality (Schrempf et al. 2006), but several generations of sib-mating rarely occurs in laboratory conditions due to colonies being polygynous.

Another possibility for these negative results could be conflict over caste and sex allocation between workers and queens affecting fertility. However, *C. obscurior* workers rear both castes to pupation with similar success, and queens seem to have control over sex and caste allocation of the offspring (Schultner et al. 2023), and thus, the effect of workers should be minimal in biasing total queen fertility. Still, we cannot rule out that raising daughters and their mates/brothers in the same maternal environment might have biased the results. In the future, a cross-fostering design would be important to assess parental and sibsocial effects, i.e., social environment effects by the workers/sisters.

Lansing effect

We evaluated maternal ages ranging from 25 to 43 weeks, older than the median lifespan of 25 weeks (Jaimes-Nino et al. 2022; Oettler and Schrempf 2016), and did not find an effect of maternal age on the daughters' longevity and fertility. The weakening of selection in older individuals against reproductive and actuarial senescence is known as the selection shadow (Haldane 1941; Hamilton 1966). It has an onset at maturation in iteroparous species, sometimes with a transgenerational negative effect (Ivimey-Cook and Moorad 2020; Ivimey-Cook et al. 2023). *C. obscurior* exhibit an increase in mortality long after reproduction started, and a very short senescent period (Jaimes-Nino et al. 2022). The results here support our "Continuusparity" hypothesis, namely that selection against senescence is maintained in ant queens until late in life when the maximum investment into the production of sexual occurs (Jaimes-Nino et al. 2022). We conclude that queens produce equally fit sexual daughters at old ages, the period of life in which fitness returns are maximized. This has evolutionary implications, because if maternal age has no consequences for fitness, queens could, in principle, delay reproduction until environmental conditions are optimal for the colony growth.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00040-025-01032-2.

Acknowledgements The authors would like to thank Thomas Anthony Keaney, Thomas Flatt, and two anonymous reviewers for the helpful comments. The authors would like to thank Judith Weber for her help in obtaining data from the heritability experiment. The authors would also like to thank Federico Olivera-Rodriguez, Benjamin Dofka, Melanie Schlossberger, Leonard Mecka, and Maike Fallböhmer for helping maintain the colonies. Finally, we want to thank the DFG Research Unit FOR2281.

Funding Open Access funding enabled and organized by Projekt DEAL. This research was supported by a grant from the FAS-G (Finanzielles Anreizsystem zur Förderung der Gleichstellung) of the University of Regensburg to LMJN, and grants of the Deutsche Forschungsgemeinschaft to JO and LMJN (OE549/2-2, 3, JA3614/1-1). No funding sources were involved in study design, data collection and interpretation, or the decision to submit the work for publication.

Data accessibility All data sets to reproduce the figures and results are available as supplementary material.

Declarations

Conflict of interest The authors declare no competing interests.

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