



Sex- and trait-specific silver-spoon effects of developmental environments, on ageing

Krish Sanghvi¹ · Felix Zajitschek² · Maider Iglesias-Carrasco¹ · Megan L. Head¹

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Abstract

The environment organisms experience during development can have effects which carry over into their adult lives. These environments not only affect adult traits at a given point in time, but also how these traits change with age. Generally, favorable developmental environments lead to more optimal adult traits while stressful environments are deleterious (“silver-spoon effect”). But whether developmental environments affect how whole-organism performance traits change with age or whether they affect males and females differently lacks evidence. Here, we test whether experiencing favorable developmental environments leads to “silver-spoon effects” on life-history traits and whole-organism flight performance of males and females by manipulating developmental density in *Callosobruchus maculatus*. We further test whether such effects are mediated by an individual’s reproductive status by comparing traits of mated versus virgin females. We show that although developmental crowding has no effect on flight performance of either sex, on male adult lifespan, or on female age-dependent survival, it is detrimental to female lifespan and fecundity, as well as female age-dependent reproduction, suggesting that females are more sensitive to differences in developmental density. Additionally, we show that flight traits change with age and differ not only between males and females, which is reflective of sex-specific life-histories and behavior, but also between virgin and mated females. Our study is important for understanding sex-specific responses to developmental environments in life-history, behavioral, and ecologically important traits which may affect resource allocation, dispersal, and mating strategies, hence fitness.

Keywords Flight · Senescence · Sex-specific · Mating · Silver-spoon effect · *Callosobruchus maculatus*

The first author of this paper is a current graduate student in his first year of PhD.

✉ Krish Sanghvi
krishsangvi2007@gmail.com

Extended author information available on the last page of the article

Introduction

An individual's developmental environment can have long lasting effects on its phenotype, which carry over into its adult life (Lee et al 2013; English et al 2016). For instance, empirical studies often show that individuals which experience stressful environments (e.g. extreme temperatures or poor nutrition) early in life, have poor condition and perform worse as adults compared to those which do not, hence supporting the “silver-spoon” hypothesis (Lummaa and Clutton-Brock 2002; Monaghan 2008; Jonsson and Jonsson 2014). Examples of “silver-spoon effects” come from organisms from across the animal kingdom, in which individuals who develop in stressful environments have shorter lifespans as adults (van de Pol et al 2006), are less fecund (Cam et al 2003), have poorer performance (Fleming et al 1997), and faster deterioration of traits (Nussey et al 2007) than those from optimal developmental environments.

The population density that individuals experience during development is one of the environmental parameters which has received considerable attention in the context of how developmental environments affect adult traits. There is a general consensus that high density during development has negative effects on individual physiological and life-history traits (reviewed in Peters and Barbosa 1977). For instance, animals which develop under crowded environments have a smaller body size (Flockhart et al 2012; Yang et al 2015), lower reproductive output (Prout and McChesney 1985; Scott 1994; Muller et al. 2016), and shorter lifespans (Descamps et al 2008; Fantinou et al 2008) than those from less crowded environments. However, silver-spoon effects are not necessarily observed for all traits which are important in determining fitness. For instance, experiencing higher, hence unfavorable developmental density, has been shown to increase dispersal ability (Appelbaum and Heifetz 1999; Braendle et al 2006), competitiveness (Stockley and Seal 2001), disease resistance (Wilson et al 2002; although see Michel et al 2016, for how genes and environments interact in complex ways across generations to affect immunity), and development rates (Bauerfeind and Fischer 2005) in animals. Indeed, owing to energetic and physiological constraints amongst life-history traits (Partridge and Silby 1991), high quality developmental environments may not always lead to more favourable adult traits, and instead, silver-spoon effects on various traits will be context-dependent. Despite considerable interest in how developmental environments affect adult traits, there is relatively little research on whether effects of developmental environments on age-dependent traits differ between males and females, or between individuals of different mating status.

Age effects may be particularly important for behavioral, physiological, and life-history traits such as reproduction, locomotion, and whole-organism performance, which are labile rather than static (Lailvaux and Husak 2014). This is because early life environments may not only affect these traits at a given point in time, but may also affect how these traits change throughout an individual's lifetime (Balbontin and Moller 2015). For instance, senescence, which is the intrinsic deterioration of fitness components with increasing age, has been shown to accelerate when developmental environments are stressful, hence demonstrating a “silver-spoon effect” (Cooper and Kruuk 2018; see also: Graves and Mueller 1993; Joshi and Mueller 1997, for deleterious effects of density on age-dependent survival). Effects of developmental density have also been shown for age-dependent reproduction (Lints and Lints 1969). Furthermore, males and females may also vary in which life-history traits they prioritize to maximise fitness, leading to sex-specific effects of age and the environment on these traits (Zajitschek et al 2009). Additionally, an individual's mating status may influence

timing of various life-history decisions, such as when to disperse, lay eggs, have offspring, or die, and thus also influence how they senesce (Hassall et al 2015). But whether these effects of mating on status on senescence are mediated by developmental environments remains unclear.

The effects of age on whole-organism performance traits has been shown to be affected by the juvenile environment in some studies (e.g. calling effort in crickets shown by Kasumovic et al 2012a, b), however, more evidence is needed to test the generality of these effects across other species, performance traits, and environments. Studies which test the effects of developmental environments on age-dependent flight traits are particularly important because if whole-organism flight performance declines with age and at different rates in different environments, it could influence the decision of organisms to disperse and the optimum timing of dispersal. Higher developmental densities have also been shown to induce dispersal polymorphisms in insects (Harrison 1980; Denno and Roderick 1992; Applebaum and Heifetz 1999; Han 2020), and studying effects of developmental environments will allow us to understand the different strategies individuals use to avoid crowding and find mates, and help us predict how individuals invade novel environments (Ochocki and Miller 2017). Additionally, if deterioration of flight traits with age differs between males and females, or with their reproductive status, it may have important implications for sex-biased dispersal, mating, and avoidance of inbreeding (Pusey 1987).

Here, we test whether unfavorable environments caused by high developmental density can lead to “silver-spoon effects” on an organism’s components of fitness, and whether this varies with age, sex, or the mating status of an individual. To get a full-picture of how age and developmental density interact to affect fitness, we measure both age-dependent life-history traits (i.e. survival and fecundity) and age-dependent whole-organism flight performance in the seed beetle *Callosobruchus maculatus* (J. Fabr. 1775). We then test whether the way in which individuals respond to differences in developmental density is dependent on their sex or mating status, and whether the effects of favorable developmental densities benefit expression of all traits or only a few. We do not expect all measured traits to show a silver-spoon effect due to possible density-mediated trade-offs between life-history and performance traits. For example, low developmental densities in seed beetles may lead to higher fecundity, but shorter lifespans (Vamosi 2005), and higher flight ability (Utida 1972; Messina and Renwick 1985; Appleby and Credland 2001). We hypothesize that traits which influence fitness more directly, such as reproduction, will be more sensitive to developmental stress than other fitness components such as survival (as shown for reproductive versus survival senescence in a meta-analysis by Cooper and Kruuk 2018).

Methods

Material

Our stock population of *C. maculatus* was originally sourced from stock kept at the University of Western Australia since 2005 (Dougherty et al 2017). Prior to the current experiment, this stock was raised in our lab for 9 generations on cowpeas (*Vigna*

unguiculata) under high developmental density conditions (approximately 10–15 eggs laid on each bean by multiple females, and 200 beans per container), at 24–28 °C.

Experimental design

To investigate how developmental density affects adult life-history and whole-organism flight performance traits, and the way these traits change with age, we set up two developmental densities: low and high.

For the low developmental density treatments, 45 females were randomly chosen from our stock population within 3 days of their eclosion, and were individually placed in a petri dish (10 cm diameter), along with two males and 15 cowpeas. Females and males were left overnight in these dishes to mate and lay eggs on the cowpeas. The following morning the cowpeas were checked for eggs, and 200 cowpeas out of the total 675 beans, were randomly chosen from across the 45 dishes. If the bean had more than one egg laid on it, the extra eggs were scraped off prior to being used to ensure that all beans used had only one egg on each of them. Cowpeas were then transferred into five cylindrical containers (2 cm × 4.5 cm) which had holes in the lid for ventilation, with each container holding 40 beans. Although all 45 females contributed towards the eggs used in our experiment, the number of eggs contributed by each female was not known.

For the high developmental density treatment, 150 females and 300 males were randomly chosen from our stock population within 3 days of their eclosion. A total of five female and ten males were placed in each petri dish (10 cm diameter) with 15 cowpeas per dish, and a total of 30 such petri-dish replicates were set up. Females and males were left overnight in these dishes to mate and lay eggs on the cowpeas. The following morning, the cowpeas were checked for eggs and a total of 200 cowpeas, each with at least five eggs laid on them, were randomly sampled from across the 30 petri dishes (200 beans sampled out of 450). Forty cowpeas were transferred into each of five cylindrical containers (2 cm × 4.5 cm), which had holes in the lid for ventilation. In the high density treatment, the number of eggs per container ranged between 216 and 280. For both treatments, all eggs in each container were laid on the same day and were incubated at 27–28 °C, and between 20 and 40% relative humidity.

Development time and survival

We checked the containers daily for emerging beetles. As adults emerged, we recorded their development time (time elapsed between date of laying and date of eclosion) and transferred them to individual Eppendorf tubes with a small hole in the lid for ventilation, with each tube being given an individual label. Because *C. maculatus* adults do not need to feed or drink after eclosion, we did not provide them with food or water. The sex of emerged beetles was identified following Beck and Blumer (2014). Once in individual tubes, we checked adult beetles daily to determine whether they were dead or alive, so that we could calculate their adult lifespan (days elapsed between emergence and death). A total of 501 females and 535 males emerged from the high density treatment, while a total of 85 females and 100 males emerged from the low density treatment, all of which had their lifespans measured.

Female fecundity

To determine the number of eggs laid each day throughout a female's lifetime and her total fecundity, we selected a random subset of females from each density treatment (High density: $N=69$, Low density: $N=49$) on the same day that they eclosed, and transferred them into individual petri dishes with 2 random males from the stock population and 15 cowpeas, which were replaced daily with a new set of 15 cowpeas. After the cowpeas had been laid on, they were stored in small plastic bags in a $-20\text{ }^{\circ}\text{C}$ freezer, so that the eggs could be counted later. We sampled fewer females from the low density treatment because only a total of 86 females emerged from this treatment, and we wanted to balance the number of low-density females across the virgin-flight assay (see below) and fecundity assay.

Measuring flight

We measured flying ability and propensity to fly for 86 virgin females and 162 virgin males from the high-density treatment, and 32 virgin females and 98 virgin males from the low-density treatments, every second day, from the day they eclosed until 18 days after emergence. In addition, we measured the flight traits of all the females which were used in the female fecundity assays (mated females (N): High density = 69, Low density = 49), in the same way as the virgin-flight assay to test the effect of mating on flight. To elicit a flight response, we probed beetles by using the back of a pair of soft forceps to tap on the beetle's body and then observed the beetles for 15 s. We repeated this process and recorded the beetle's flight ability and propensity to fly across the whole 30 s (past assays of flying ability by other studies show low repeatability: see Appendix 2 in supplement for more information).

Flying ability for each individual was scored using an ordinal point system based on the action they performed during the trial. Scores ranged from 1 to 4. Beetles which only crawled and showed no wing movement, received a score of "1". Beetles that opened their wings but did not leave the ground received a score of "2". Beetles that opened their wings and left the ground but did not fully fly received a score of "3". Finally, beetles that opened their wings and flew fully in a vertical direction received a score of "4". We compared our scoring system to that used by Utida (1972) and Appleby and Credland (2001), which drops individuals from a height and gives them a binomial score based on whether they fly or not. We found the method of probing individuals to elicit a flight response to have fewer false negatives and be more repeatable than expected by chance (see appendix 2 in supplementary information), hence used this method for our experiment. A similar method which probes individuals to elicit flight has been previously used effectively by Frazier et al (2008) and Esterhuisen et al. (2014) in Diptera.

For beetles which had a flying ability score of ≥ 2 , we also measured their flying propensity as the number of times they performed the given action. All flight measures were scored blind to the density treatment the beetle came from.

Data analysis

Age-independent effects

To test whether developmental density affected the proportion of beetles that emerged from eggs or the sex ratio of eclosed beetles, we ran two separate logistic regression models using the function *glm* in the package *stats* in R v3.5.2 (R Development Core Team 2011). Both models used a binomial error distribution (family = binomial, “logit” link function), and included developmental density as a fixed effect. To model the effects of density on emergence of beetles, we used the binomial variable, emergence into adulthood (yes/no), as the dependent variable. To model the effect of density on sex ratio, we used the binomial variable, sex of eclosed beetles (male/female), as our dependent variable. We checked both the models for over-dispersion using the package *DHARMA* in R v3.5.2 (Hartig 2020), and they were not over-dispersed ($P > 0.9$ for both). The inclusion of container as a random effect created a singular fit in the model (created using *glmer* in *lme4*), hence we chose to exclude the random effect of container from both logistic regression models. To analyse the effects of developmental density on male and female static traits (i.e. development time, adult lifespan) we used linear mixed models (LMM). In both models, developmental density, beetle sex, as well as their interaction were included as fixed effects while the container of beans that a beetle came from was included as a random effect. To look at the interactive effects of density and sex on adult lifespan, we only modelled data from virgin beetles (i.e. we excluded females used in the fecundity assays) in order to avoid the known effects of female mating on adult traits (Ronn et al. 2006; Jigisha et al 2020). However, to explicitly test for effects of female mating status and its interaction with density on female adult lifespan, we ran a second LMM in which female adult lifespan was the response variable, and female mating status, developmental density, and their interaction were specified as fixed effects. In this model, container was again specified as a random effect.

For our analyses of age-independent effects, we ran a “full” model with interactions wherever present. Non-significant interaction terms were removed to test for main-effects in our models (Engqvist 2005). To further test for robustness of P values for interaction terms, we compared full and main-effects models using log-likelihood ratio test (LRT) with function *anova* in R (the results of the LRT models were similar to those of the “full” model, hence LRT outputs are only reported in supplementary Tables S6, S7, S8). P values for all *lmer* models were calculated using Satterthwaite’s method in the R package ‘lmerTest’ (Kuznetsova et al. 2017). For all models, residuals were checked visually to ensure they met the assumptions of normality and homoscedasticity. When they did not, as was the case for development time, the response variable was power transformed (most suitable transformation determined using the *power.Transform* function in the *car* package of R v3.5.2). Effect sizes wherever reported, were calculated as “Hedge’s *g*” (following Eqs. (1) and (2) in Nakagawa and Cuthill 2007).

We analysed age-independent flying ability of virgin males and females as a binary response (no flight vs. flight). To test binary flight ability, we used a z-test of equality of proportions to compare male and female frequency of flight (function *prop.test* in R package *stats*). We further tested binary flight ability in virgin males (due to very low virgin female flight responses), using a logistic regression with a binomial distribution (function *glmer* in package *lme4*; Bates et al. 2014), with density as a fixed effect, and container as a random effect.

Age-dependent effects

To model age-dependent responses for fecundity, and ability and propensity to fly, we fitted general additive mixed models (function *gam* in package *mgcv*; Wood 2012), with individual identity and container as random effects (using the term *bs* = “re”). We included adult lifespan as a fixed effect in all models to account for selective disappearance (Pol and Verhulst 2006). For each separate response variable, we started with a global model, containing separate curves for each treatment group. In a first step, we determined the best-fitting smooth classes (thin plate splines, cubic regression splines, shrinkage version of cubic regression splines; tested with standard smooth classes, or tension product smooth classes), using the Akaike Information Criterion (AIC) for model comparisons. The best-fitting smooth classes for the global model was then used in further models.

Flying ability was recorded as an ordinal response, with the first three levels signifying increasing ability to fly (level 1: no wing movement, level 2: wing movement but no lift, level 3: wing movement and lift but no flight), and flight as the fourth level. We therefore used the ordered categorical model family (*ocat*) available for *gam* in R. For this, threshold values of an underlying latent variable (following a logistic distribution) at which the response variable changes, are estimated. To evaluate the effects of variables of interest on the location and shape of age-dependent trajectories, curvature can be modelled as group-specific (e.g. sex-specific) or general (across groups), adding group-specific or general smooth terms to models. If the shape of the estimated trajectory is not different between groups, the trajectory could still differ in location along the y-axis (overall lower or higher values of the response variable). This effect can be modelled by adding a group-specific fixed effect (intercept) to the model (following Zajitschek et al 2012). For analysis on age-dependent flight ability and propensity, we tested the global model against models with either sex-specific curvature or sex-specific curvature and intercept (independent of developmental density), with either density-dependent curvature or density-dependent curvature and intercept (independent of sex), with sex-specific intercept (same curvature, independent of density), and with density-dependent intercept (same curvature, independent of sex). We only used data collected on virgin individuals for this analysis.

To further test the effect of mating on whole-organism flight performance in females, we used a similar modelling strategy, except that we only used female flight measurements recorded between their day of eclosion and 8 days after emergence, because no mated females survived beyond that age. Adult lifespan was not included in the final analyses for all best-fitting models. The AIC of the best fitting model was at least 2 units smaller than the next best-fitting model.

To test whether there were any sex-specific effects of developmental density on age-dependent survival in adult virgin beetles, we modelled the survival data using the non-parametric log-rank test with the *survdiff* function ($\rho=0$) in the *survival* package in R v3.5.2. We tested the effects of density for each sex separately. Kaplan–Meier curves were used to visualise the data. We chose not to use a Cox proportional-hazards model because our mortality curves violated the assumption that requires the proportional difference in survival between treatments to remain constant over time when checked visually (Hess 1995).

Results (model outputs in supplement)

Age-independent traits

Developmental density had a significant effect on emergence success of beetles with a smaller proportion of beetles emerging from high developmental density than low developmental density containers (Coeff=0.697, $z=2.321$, $P=0.020$, Odds ratio=1: 2.010). Developmental density did not affect sex ratio of eclosed beetles (Coeff=0.078, $z=-0.487$, $P=0.626$). Development time was not affected by an interaction between sex and developmental density (Chisq.=1.272, DF=1, $P=0.259$), or by developmental density (Chisq.=1.052, DF=1, $P=0.304$, Hedge's $g=0.141$). But there was an overall effect of sex (Chisq.=41.918, DF=1, $P<0.001$, Hedge's $g=0.294$), with males (Mean \pm SE=24.691 \pm 0.052) developing faster than females (Mean \pm SE=25.110 \pm 0.065).

Developmental density and sex interacted significantly to affect adult lifespan ($t=-2.505$, DF=1085.474, $P=0.012$) indicating that high developmental density reduced virgin female adult lifespan (Hedge's $g=0.247$) while increasing virgin male adult lifespan (Hedge's $g=-0.272$), compared to low developmental density (Fig. 1). When looking at the effects of mating on female adult lifespan, we found that mated females lived for a shorter duration than virgin females ($t=24.830$, DF=577.877, $P<0.001$, Hedge's $g=2.730$). But female adult lifespan of mated and virgin females was not affected by an interaction between mating status and developmental density ($t=1.152$, DF=572.735, $P=0.250$) or by an independent effect of density ($t=1.081$, DF=53.486, $P=0.284$). Female total fecundity was affected by developmental density (Coeff=12.07, Chisq.=11.255, DF=1, $P<0.001$, Hedge's $g=0.560$), with females from high density treatments

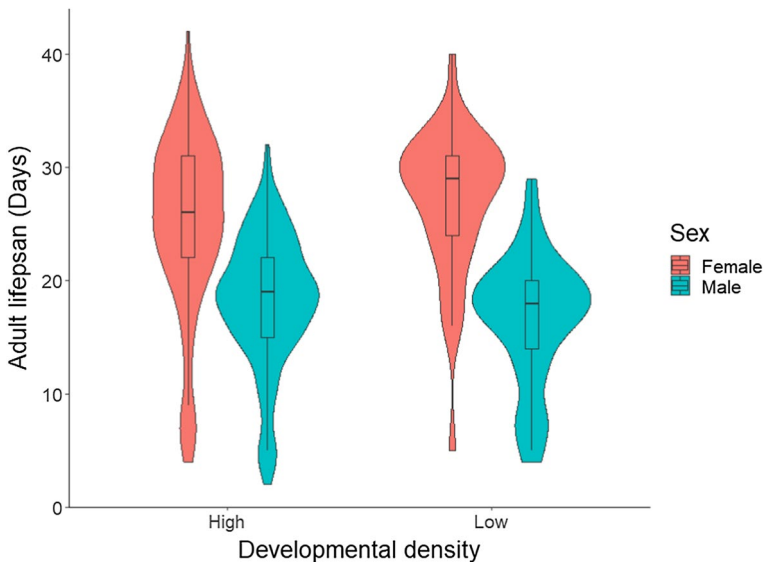


Fig. 1 Effect of sex (red: female, blue: male) and developmental density (high and low) on adult lifespan of virgins. Smoothed probability density of adult lifespan data is represented using violin plots along with medians and inter-quartile ranges

laying significantly fewer eggs than females from low developmental density (mean eggs laid \pm SE: High density = 75.800 ± 1.700 , Low density = 87.900 ± 1.800).

We compared virgin male and virgin female age-independent flying ability by assigning them a binary score (flight vs. no flight). Virgin males were more likely to fly than females (Chisq. = 14.030, DF = 1, $P < 0.001$, Odds ratio = 1: 0.130). Out of 377 measured virgin male ($n = 259$, with 2157 individual measurements) and female ($n = 118$, with 1086 individual measurements) beetles, only 43 males and 3 females flew at least once when physically stimulated. Due to the very low numbers of virgin females exhibiting flight, we only tested whether developmental density had an overall effect on binary flying ability in virgin males. Density had no effect on age-independent binary flying ability in virgin males (GLMM: Coeff = 0.064, SE = 0.234, $z = 0.273$, $P = 0.785$).

Age-dependent traits

Density had a significant effect on age-dependent fecundity trajectories. A model with density-specific curvature provided the best fit compared to models with either one overall curve (same shape and location), or a model that allowed for a different location along the response variable axis (overall lower and higher fecundity), but with identical overall curvature (Δ AIC = 27.5 to the next best fitting model). Low density females laid more eggs in early adult life, compared to high density females, with very similar fecundity being observed in mid- and late-adult life (Fig. 2).

The best model (Δ AIC = 21.8 to the next best fitting model) for age-dependent flying ability (measured as a 4-level response variable) included sex-specific trajectories (Fig. 3a). Males showed overall higher flying ability than females, which was also evidenced by the significant effect of sex when added as a fixed effect in the best-fit model (sex as fixed effect: Coeff = 1.115, SE = 0.328, $z = 3.405$, $P < 0.001$). Density had no such effect on age-dependent flying ability (Coeff = -0.230, SE = 0.328, $z = -0.702$, $P = 0.483$).

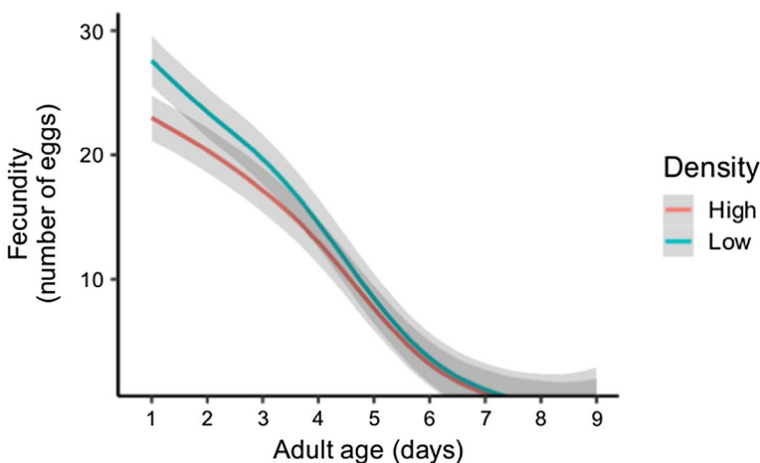


Fig. 2 Effects of age and density on female fecundity for beetles from Low and High density. Grey shaded bands represent 95% confidence intervals

Fig. 3 **a** Effect of age, sex, and density (high or low) on flying ability in virgin males and females. **b** Effect of age and mating status on flying ability in mated and virgin females. **c** Effect of age and sex on flying propensity in virgin males and females. Flying ability is an ordinal response made of four different levels corresponding to an increasing ability to fly. Flight, the highest level, is not shown, as the low numbers of recorded instances of flight did not result in a prediction of flight. Flying propensity is measured as the number of times beetles performed their given flying ability action of ≥ 2 . Shaded bands represent 95% confidence intervals

Mated females had far fewer measurements of flight taken during their shorter lives (mean \pm SE of 3.530 ± 0.070 days, maximum of 5 measurements before death), compared to virgin females (mean \pm SE of 9.200 ± 0.180 days, maximum of 10 measurements before death). For this reason, we only used the first 5 flight measurements of virgin and mated females to test for treatment effects on flying ability. The model with two separate terms for virgin and mated females but not for density, was the best fitting model (Δ AIC = 2.3 compared to the next best-fitting model). Mated females showed a clear ageing pattern, with a peak in flying ability seen at two days of age followed by a decline over the next three days, with no such pattern in virgin females (Fig. 3b).

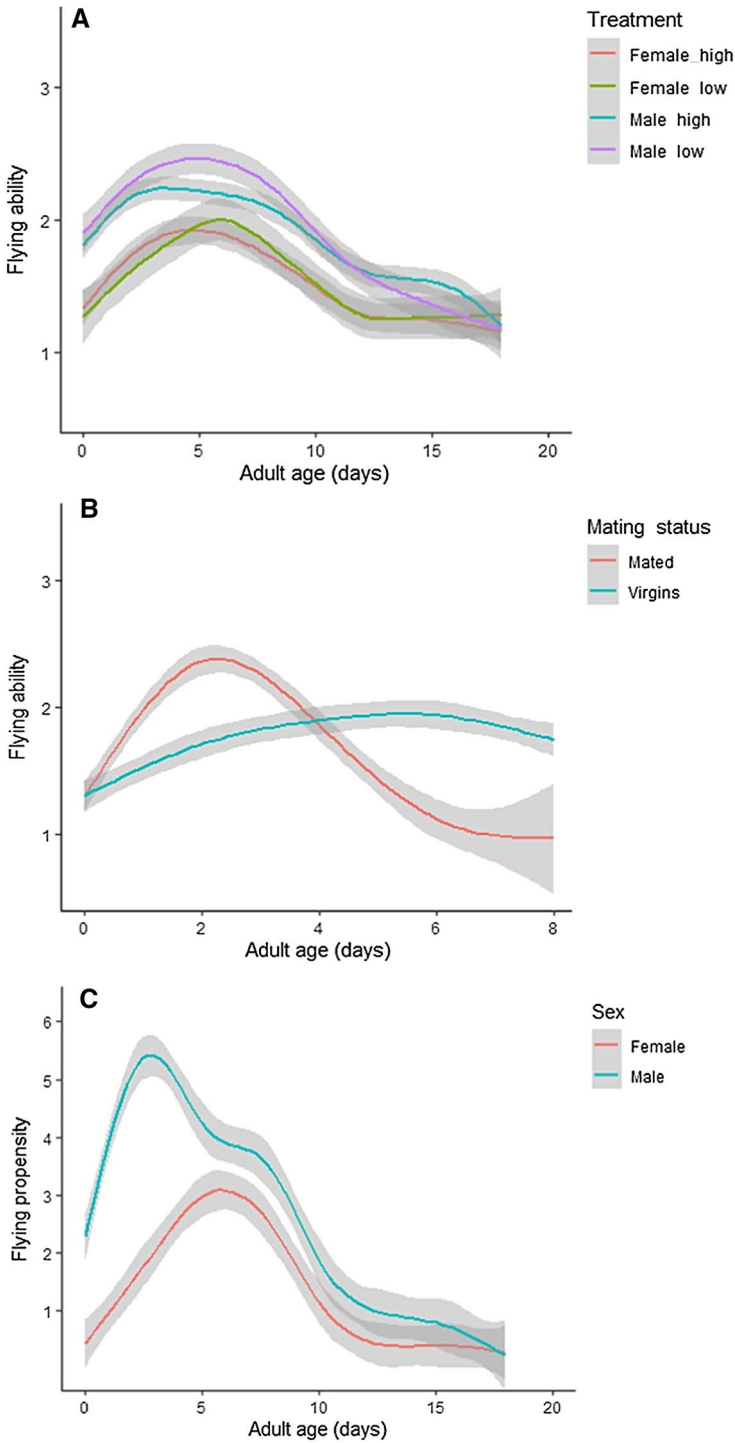
The best model for age-dependent propensity to fly (Δ AIC = 118 compared to the next best fitting model) and earliest age of peak in propensity to fly (Δ AIC = 1 compared to the next best fitting model), included sex-specific effects. Virgin females showed a later and lower peak than virgin males (Fig. 3c). The first age at which maximum propensity to fly was reached was on average 2.300 ± 0.340 SE days earlier in males compared to females. Density had no effect.

Within virgin males, there was a significant effect of density on age-dependent survival probability (Chisq. = 8.1, DF = 1, $P = 0.004$), with males developing in low density showing a steeper decline in age-dependent survival than males from high density. This deleterious effect of low density on age-dependent survival probability was not observed in virgin females (Chisq. = 0.5, DF = 1, $P = 0.472$) (Fig. 4).

Discussion

The effects of environmental stress experienced during development can have long lasting consequences for fitness and ecologically relevant traits (Monaghan et al. 2012). Developmental environments can not only affect individuals at a given point in time, but throughout their lives, hence influencing how these traits senesce (Cooper and Kruuk 2018). Here, we test whether favorable developmental environments are beneficial to life-history and whole-organism performance traits (“silver-spoon effects”), including how these traits age, as well as whether males and females respond differently to changes in developmental environments. To do this, we experimentally manipulated the developmental densities of male and female *C. maculatus*, by subjecting them to either developmental crowding or not. We then measured their resultant developmental (development time, egg to adult viability) and adult traits (eggs laid, lifespan) throughout their adult lives. We further tested whether developmental environments affected whole-organism performance traits of flight ability and propensity to fly in a sex-specific way.

Development time was not affected by density or by a density by sex interaction. It has been shown that early life stress, including developmental crowding can decrease development time (Ireland and Turner 2006; Ludewig et al 2017). The decrease in development time with higher densities is usually predicted to occur because it allows organisms to



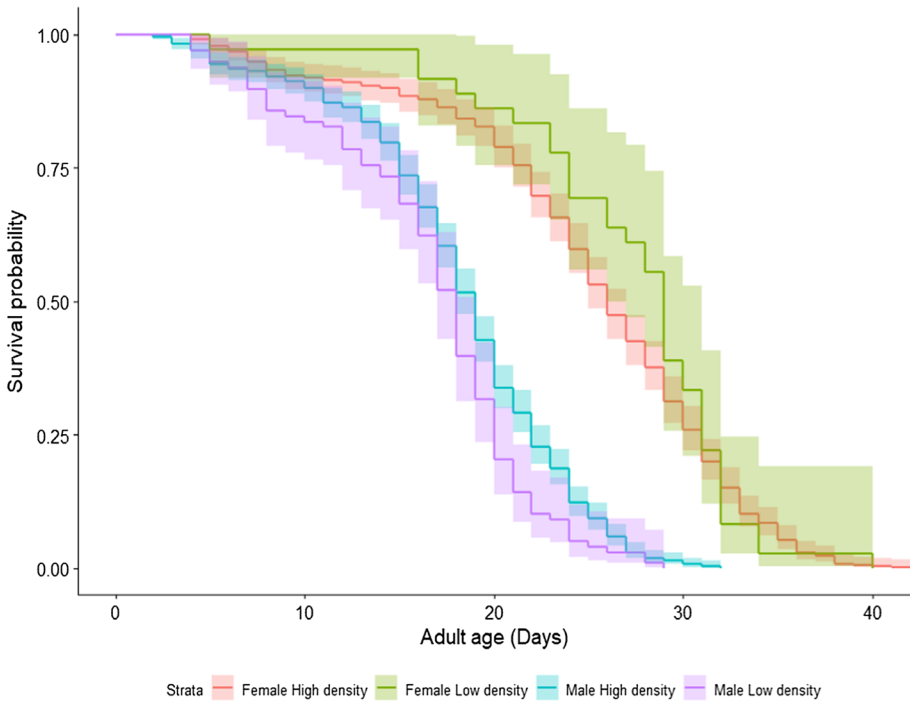


Fig. 4 The survival probability of virgin males and virgin females from high and low developmental densities with increasing adult age, using Kaplan–Meier curves. Shaded error bars represent 95% confidence intervals. (purple: males from low density; blue: males from high density; red: females from high density; green: females from low density)

emerge sooner to acquire resources and mates earlier than their competitors (Bauerfeind and Fischer 2005). However, *C. maculatus* is facultatively phytophagous and does not need to feed after emergence in order to survive and reproduce (Credland et al 1986) which may explain why we did not see high developmental density accelerate development. We did however find that males develop quicker than females, a pattern which has been found previously by Harano and Miyatake (2011), and could be driven by the need for males to compete for access to females. The fact that this pattern is not affected by developmental density or by its interaction with sex, but is affected by sex suggests that it could be sexual selection rather than resource competition which controls seed beetle developmental rate.

Our results showed that sex and developmental density interacted to affect adult lifespan of virgins, with virgin female adult lifespan being more negatively affected by high developmental density than virgin male adult lifespan. This suggests a “silver-spoon effect” of density on virgin female adult lifespan but not on virgin male adult lifespan. One reason for this could be that females of *C. maculatus* are larger than males, hence would require more space and resources inside the bean when developing, than males. Consequently, this would mean that the effects of developmental competition would be more severe for female fitness than male fitness as has also been seen in a butterfly (Fantinou et al 2008). In further support of our results, previous research on *C. maculatus* by Iglesias-Carrasco et al (2020) has shown that males were generally less affected by larval competition than females. However, our results contrast with studies on other species which have shown that

developmental crowding (Descamps et al 2008) and early life stress (Lee et al 2013) reduce overall adult lifespan in both males and females in a similar way, as well as other studies which show no effect of early-life stress on female lifespan but a significant effect on male lifespan (Wilkin and Sheldon 2009). We did not find such effects which could be due to the different physiologies of the species being studied. Although we observed a difference in emergence rates of beetles between high and low developmental density treatments, there was no difference in sex ratios of emerged beetles between treatments. Hence, it is unlikely that the lack of effect of density on male adult lifespan is due to selective disappearance of males at the developmental stage.

As predicted, female lifetime fecundity, which is more closely related to net fitness than survival or flight performance, showed a silver spoon effect (Monaghan 2008; Cooper and Kruuk 2018). Specifically, females from high density treatments had a lower total lifetime fecundity than females from low density treatments. This detrimental effect of high density on fecundity has been shown previously in animals such as leaf beetles (Muller et al. 2016), *Drosophila* (Prout and McChesney 1985), salamanders (Scott 1994), and in *C. maculatus* (Credland et al 1986; Vamosi 2005). There is also strong evidence which suggests that in general, stressful developmental environments should affect reproductive traits negatively (van de Pol et al 2006; Hayward et al 2013).

In addition, we found a clear effect of density on age-dependent declines in female fecundity. Females from low density environments showed a higher number of eggs laid during early-adult life than females from high density, showing higher early-adult life investment in reproduction. Such higher investment in early-adult life reproduction has been shown to cause a faster rate of reproductive senescence (Bowhuis et al. 2010; Hammers et al 2013) possibly caused by hypothesized trade-offs between early-life reproduction, and late-life reproduction and survival, although surprisingly we did not observe this. A possible reason for this could be that females developing in low densities are in better condition than females from high densities due to a “silver-spoon effect” of favorable developmental environments. This could allow females from low developmental densities to not only reproduce more, but also live longer (Reznick et al 2000) without experiencing accelerated deterioration in reproduction with age that is caused by a lifespan-reproduction trade-off. Future studies could test whether these effects of age, sex, and environment on traits are due to differences in body mass.

In virgin males, developmental density affected age-dependent survival, with males from low density treatments showing steeper decline in survival with increasing age than males from high density treatments. One reason for this could be that low density males invest more in reproductive traits such as sperm production, leading to trade-offs between reproduction and age-dependant survival (Hammers et al 2013). This is something future studies could investigate. No such deleterious effect of low developmental density was observed on age-dependent survival in virgin females. This reinforces our previously stated finding of a “silver-spoon effect” in females, who do not bear a cost on survival despite having higher early-life fecundity. This could be due to females from low densities being of a superior condition than those from high densities. Such sex-specific effects of the environment on age-dependent survival have also been shown by Zajitschek et al (2009) in crickets (who manipulated the adult nutritional environment), and point towards different life-history strategies of males and females.

Our study showed a difference in age-dependent trajectories in whole-organism flight ability between mated and unmated females, with mated females showing a higher ability to fly as well as a steeper decline in flying ability with age. Additionally, mated females also had a reduced lifespan compared to virgin females. This suggests that silver-spoon

effect of favourable developmental environments are mediated by an individual's reproductive status and relative investment in various fitness components such as reproduction, survival, and performance (Roff 1984; Ghalambor et al 2003). The difference in flight between virgins and mated females may arise because females try to avoid male harassment and mating costs after having mated once, due to additional mating with the same male providing no benefit to females (Okada et al 2019). It could also be because females want to disperse after having mated, in search of beans to lay their eggs on. These results are consistent with costs of mating and male-harassment associated with other female traits such as adult lifespan and fitness (Ronn et al. 2006; den Hollander and Gwynn 2009; Gay et al 2009). Such effects of mating status on ageing of whole-organism performance traits have been shown to occur previously in crickets as a result of terminal investment in performance traits when survival prospects decline with increasing age (Lailvaux et al 2011), which could also be true for our study.

Developmental density did not influence age-independent whole-organism flight performance of virgins of either sex. We suggest that future studies should manipulate adult density to test if it affects dispersal, as has been shown in *Tribolium* beetles (Endriss et al 2019). We found significant effects of sex on age-independent flight traits showing that males generally flew more than females. One reason for males being more willing to fly could be due to sex biased dispersal (Pusey 1987). Sex-biased dispersal arises due to different costs (energetic, predation) and benefits (novel environment, mating opportunity, inbreeding avoidance, reduced competition) of dispersal to each sex (Baines et al 2017; Li and Kokko 2019). Although most evidence for male sex-biased dispersal comes from mammals and birds (review: Li and Kokko 2019), laboratory studies such as Downey et al (2015) and Mishra et al (2020), which measured dispersal as crawling distance, show male-biased dispersal in insects like *Callosobruchus* and *Drosophila* respectively. A recent study also showed male biased dispersal in butterflies during the early breeding season, but female biased dispersal during the late season (Plazio et al 2020), suggesting that these differences were due to different reproductive strategies of males and females, which could also be the case in *C. maculatus*.

For virgins, flight performance changed with age in addition to being affected by sex, but was not affected by density. Flying ability and propensity to fly increased in early-adult life and then deteriorated in late-adult life for both sexes, but males showed an earlier peak and onset of deterioration in flight than females. This pattern of initial increase followed by deterioration with age, in flight performance, follows a classic senescence curve (Jones et al 2014), and has been reported by Ahman and Karlsson (2009) in the flight of butterflies. Such age-related changes could be attributed to changes in flight muscles with age, as shown in *Drosophila* (Miller et al 2008), or an accumulation of free radicals with age due to the metabolic costs associated with flying (Lane et al 2014). We thus suggest that whole-organism performance traits, which affect processes such as mate finding and dispersal, but are not direct measures of fitness, can also change and deteriorate with age. These should thus be considered as fitness components as suggested by the ecomorphological paradigm (Ghalambor et al. 2003). Maklakov et al (2009) also report such age and sex-specific senescence in whole-organism performance for sexual signalling in crickets. Incorporating sex-specific age-dependent measures of whole-organism performance traits such as flight is important to help us understand ecological patterns and processes such as age-structure in, and gene flow between populations. It will also help us understand how individuals choose to allocate resources towards different life-history traits as they age (reviewed in Lailvaux and Husak 2014).

Our results do not support the presence of density-dependent dispersal morphs in *C. maculatus*. Density-dependent development of dispersal morphs has been predicted to arise when individuals need to disperse from crowded conditions to avoid competition and has

been shown in grasshoppers, water striders, and aphids (Harrison 1980; Denno and Roderick 1992; Applebaum and Heifetz 1999; Han 2020). Our experiment, which unlike previous studies on *Callosobruchus* (Utida 1972; Messina and Renwick 1985; Appleby and Credland 2001), measures flying ability throughout an individual's life and on both sexes using a repeatable method, did not find that crowded developmental conditions induced higher flight performance.

Conclusion

Although our study substantiates previous findings of “silver-spoon effects”, it shows that these effects of more favorable developmental environments leading to optimized life-history traits are sex- and trait-specific. Specifically, we do not find such “silver-spoon effects” of developmental environments on whole-organism flight performance traits, even when measured throughout an organism's life. Instead, we show strong sex-specific differences in male and female age-dependent flight. Overall, our results can be summarised as two findings. First, there is a “silver-spoon” effect of favorable developmental environments on female fitness traits of fecundity, reproductive senescence, and lifespan, without any trade-offs with age-dependent survival, with no such effects being observed in males. This suggests that females from favorable environments are of significantly better condition than females from less favorable environments, while male condition is not as sensitive to environmental changes. Second, the differences in male and female age-dependent flight reflect differences in male and female behavior, physiology, and life-history strategies. We suggest that males have evolved to prioritise dispersal and outbreeding, which they do by flying more and earlier than females. We also suggest that females have evolved to prioritise mating, and once mated, to avoid additional costs of mating on lifespan by flying away to search for beans to lay eggs on. To get a holistic picture of silver-spoon effects on fitness, future studies should measure both life-history traits such as reproduction and lifespan, and performance traits, which are all important components of fitness. Additionally measuring how these traits change with age will give us a clearer understanding of how selection pressures on organisms may change with time, and whether there are possible-trade-offs between traits.

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Author contributions KS, MH, MI-C conceived the idea and designed the experiment. KS, MH collected the data. KS, MH, FZ, MI-C analysed the data. KS wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data availability Data will be made available on DRYAD upon acceptance of this manuscript. This manuscript is accompanied with videos that demonstrate the various flight ability ordinal scores which we have assigned to the beetles in our method. This is available on Open Science Framework under an anonymous folder. (https://osf.io/2dp8r/?view_only=0e428ce25c284db195972c4b01e53057). Under this same OSF

folder, we have also uploaded an excel file of our data for reviewers to view. An earlier version of this MS has been uploaded on BioRxiv, <https://doi.org/10.1101/2020.08.24.265736>

Declarations

Ethics statement We did not need any ethics approval for working with seed beetles, but we ensure that our experimental procedures meet the ethics standards as specific by ABS/ASAB guidelines.

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Authors and Affiliations

Krish Sanghvi¹  · Felix Zajitschek²  · Maider Iglesias-Carrasco¹  · Megan L. Head¹ 

Felix Zajitschek
felix@zajitschek.net

Maider Iglesias-Carrasco
Miglesias15@gmail.com

Megan L. Head
Megan.head@anu.edu.au

¹ Research School of Biology, Australian National University, Acton, ACT 2601, Australia

² Evolution and Ecology Research Centre, School of BEES, University of New South Wales, Sydney 2052, Australia